187

Influence of Exogenous Factors on the Ethylene Production by Lichens. I. Influence of Water Content and Water Status Conditions on Ethylene Production*

S. OTT and P. SCHIELEIT

Botanisches Institut, Heinrich-Heine-Universität, Universitätsstr. 1, D-40225, Düsseldorf, Germany

Tel. 49 (211) 311 3537, Fax 49 (211) 311 2881

Abstract

The influence of liquid water and water vapour on ethylene production has been examined in lichen species belonging to different genera (*Cetraria*, *Peltigera*), containing different photobionts (green algae, cyanobacteria) and colonizing distinct environments. *Cetraria islandica*, characterized by a broad ecological amplitude, was represented by two ecotypes. The results clearly show a correlation between ethylene production and water content but there are intergeneric as well as intrageneric differences. The results obtained in this investigation are an interesting parallel to the observations on photosynthesis in lichens with green algae and cyanobacteria in connection with water vapour and liquid water. There are indications that the photobionts in lichens are involved in ethylene production of the thallus.

Keywords: ethylene production, *Peltigera aphthosa*, *P. canina*, *P. rufescens*, *Cetraria islandica*, liquid water, water vapour, water relations, thallus anatomy

1. Introduction

The postulated high phylogenetic age of lichens can be seen as evidence for the optimal function of a system of interaction in which two originally separate

---

organisms, one a heterotrophic mycobiont and the other a photoautotrophic photobiont, are forming a complex union which functionally can be interpreted as a single organism. Different aspects of the symbiotic interdependence of the two partners have been studied in great detail, such as enzyme patterns in lichen thalli which are correlated with reproduction and ecology (Fahselt, 1988, 1992; Hageman and Fahselt, 1990) and partner-recognition (Bubrick et al., 1985; Galun and Kardish, 1993). In particular, photosynthesis has been investigated comprehensively especially in connection with exogenous factors like water and temperature (Lange et al., 1985, 1990a, b; Kappen, 1989; Schroeter, 1991; Schroeter et al., 1991). Morphological research has described complicated processes of growth, differentiation and morphogenetical influences (Honegger, 1988; Jahns, 1984, 1988; Ott, 1988). Complex interactions between the bionts of the lichen symbiosis obviously require a regulative system.

In higher plants, metabolic and morphogenetical processes are controlled by growth substances, one of which is ethylene. Ethylene plays an important role and influences growth, differentiation, senescence and other processes. Ethylene is considered to be a phytohormone which, even in very small amounts, can react synergistically or antagonistically with other phytohormones (Lieberman, 1979). The biosynthesis of ethylene can be influenced endogenously as well as exogenously. Endogenous regulation processes can induce the biosynthesis of ethylene during maturity, senescence or germination. Physical, chemical and biological factors can cause stress which promote the biosynthesis exogenously (Yang and Hoffman, 1984).

Ott and Zwoch (1992) investigated ethylene production of lichens belonging to different systematic groups containing different types of photobionts (cyanobacteria, green algae) and living in different ecological habitats. All these lichens produced ethylene, the amount of which varied depending on age, physiological conditions and thallus structure. An increase of ethylene production in lichens from air-polluted environments was shown by Lurie and Garty (1991). The results obtained by Lurie and Garty as well as by Ott and Zwoch suggest biosynthesis of ethylene which is, just as in higher plants, considerably influenced by endogenous as well as exogenous factors.

It is known from higher plants that ethylene synthesis depends on temperature and water status (Abeles, 1973; Abeles et al., 1992). Exogenous influences are of particular importance to lichens as these poikilohydrous organisms are very sensitive to them, especially to changes in water relations. Water content influences photosynthesis, respiration and other physiological activities because all these processes depend on the hydration of reaction spaces. The complexity of water relations is illustrated by the observation

(Lange and Matthes, 1981; Lange and Tenhunen, 1981; Lange et al., 1986, 1989) that the importance of wetting of the thallus with water vapour or liquid water differs in lichens with cyanobacteria or green algae as photobionts.

Even if lichens are not able to regulate their water content to the same degree as higher plants, the water distribution inside the lichen thallus is not uniform, a fact that indirectly also influences gaseous exchange. Water in lichens is mostly stored in the apoplast, usually in the hyphal walls and in the gelatineous sheath of the cyanobacteria (Blum, 1973) and only rarely in the interhyphal cavities (Honegger, 1991). Even in saturated thalli, the central parts of the medulla are not filled with water, these open spaces facilitating transport and storage of gases. Gaseous exchange between inner parts of the thallus and the surrounding air can be impeded by the cortex, especially in saturated conditions when capillary spaces have been closed by the swelling of cortical cell walls. Because of the importance of measuring gaseous ethylene, this aspect has to be discussed with respect to thallus anatomy and ethylene measuring.

The water relations of lichens and physiological activities such as photosynthesis and respiration depend on the nature of the different photobionts. Therefore ethylene production in relation to water content should be studied in lichen species with cyanobacteria as well as those with green algae. We chose *Peltigera canina* and *Peltigera rufescens* with cyanobacteria and *Peltigera aphthosa* and *Cetraria islandica* with green algae. *P. aphthosa* actually contains two photobionts, as there are cyanobacteria in cephalodia. Like the physiological work of Lange et al. (1986, 1989) the study of ethylene production was carried out on thalli wetted with both liquid water and water vapour.

Investigations on the interactions between water content and ethylene production have to be carried out with fresh material. Specimens in one stand show variable responses. *P. canina* and *P. aphthosa* mostly occur in wet, cool and shadowy habitats while *P. rufescens* prefers a dry and warm environment. *C. islandica* has a broad ecological amplitude and two ecotypes were examined: dark brown specimens from sunny habitats and light coloured material from shaded environments.

The investigations addressed six questions:

1. Is there a correlation between water content and ethylene production?
2. Does wetting with liquid water rather than water vapour influence ethylene production?
3. Are there differences between responses of lichens with cyanobacteria and green algae as photobiont?

4. Do anatomical differences between the species affect the measurable ethylene production?

5. Is ethylene production different in sunny and shady habitats?

6. Are there differences in the reactions of ecotypes of the same species?

2. Materials and Methods

Plant material

The investigation was made with lichen material sampled at the natural habitat in the following places:

Cetraria islandica: South Sweden, Västergötland, at two localities in a forest area near Mullsjö (Brännasen).

Peltigera aphthosa: Switzerland, Muotal, Bödmerenwald, Eigeliswald

Peltigera canina and *Peltigera rufescens*: Germany, Eifel, Wöllersberg near Gerolstein.

Air-dried lichens were transported to the laboratory as soon as possible (1 day) and stored in a growth chamber under constant conditions for no longer than 7 weeks at a day/night cycle of 14 hr light (66 W/m²), 13° C, c. 60% r.h. and 10 hr dark 10° C, c. 60% r.h. Every day the lichens were wetted with deionized water to maintain their photosynthetic vitality.

Ethylene determination

The lichen material was cleaned with foreceps of soil and organic material. Subsequently, whole undamaged single thalli of different sizes, which had been wetted with liquid water or water vapour, were transferred to gas-tight vials and incubated in darkness for 24 hr at 25° C. The vials differed in their volume depending on the size of the thallus (70 ml, 20 ml, 5 ml, 2.5 ml). All these factors were included in the calculations (nl g^{-1} h^{-1}). All data of ethylene production are related to dry weight of the lichen thalli. After the incubation period, 1 ml head-space samples from the vials were analysed immediately for ethylene with a gas chromatograph. Dry matter determinations and measuring of water content were carried out after GC analysis. Each series of measurements contained ca. 30 replicates.

GC analysis

One-millilitre head-space samples were analysed for ethylene with a GC equipped with a flame ionization detector and a column (1.5 m long, 3 mm diameter) packed with Porapak S (80–100 mesh) operating at a pressure of

75 kPa H_2, 110 kPa synthetic air and 120 kPa He. Temperatures were adjusted to 30, 150 and 250°C at the column, injector and detector, respectively. Calibration was performed with standard gases (Messer Griesheim, Germany).

Statistical analysis

Statistically significant differences were identified by the Wilcoxon test ($P \leq 0.05$). This test was used because of heterogeneity of the lichen material.

Water content

The water content of the thalli was adjusted in three alternative ways:

1. Oversaturation — the lichen thalli were sprayed with deionized water until their surface was covered with a continuous water film. Large drops of water were removed by shaking and not by blotting.

2. Saturation — the thalli were sprayed and surface water was blotted off.

3. Wetted by water vapour — air-dried thalli were placed in humid air (97% r.h. over salt solution) for 4 hr and transferred into the vials as quickly as possible.

Directly after GC analysis the moisture content of every single thallus was determined by weighing on an analytical balance (Mettler PM 100). After air drying of thalli (24 hr), dry matter of each thallus was determined by weighing once more. The difference in weight between dry and wet thalli is a measure for actual water content.

3. Results
Morphology and anatomy of the lichens

The surface of some lichens exhibits a cortex that forms a barrier against the entry of water and gases into the thallus. At the same time it probably prevents the diffusion of ethylene and other gases from the interior. All three *Peltigera*-species examined are corticated on their upper side, with a rather thick cortex in *P. rufescens* (Fig. 1) and a relatively thinner layer in *P. aphthosa* where the cortex also bears cephalodia (Fig. 2). The thallus of *C. islandica* is corticated on both sides, but in some places the cortex is pierced by pseudocyphellae where pores serve for gas exchange (Fig. 3).
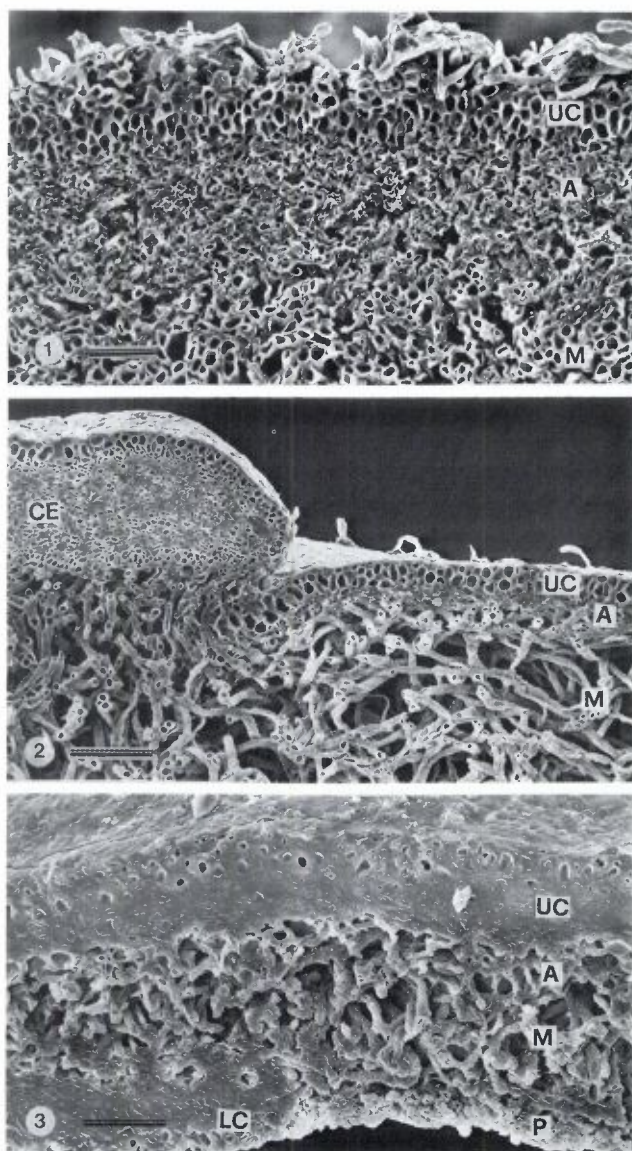
Figure 1–3. Cross sections of thalli.

(1) *Peltigera rufescens* with a well-developed upper cortex (UC), the algal layer (A) and the medulla (M) (bar = 100 μm); (2) the typical anatomical structure of *Peltigera aphthosa* with a relatively thin upper cortex (UC), a very thin algal layer (A), the well-developed medulla (M) and a cephalodium (CE) (bar = 200 μm); (3) *Cetraria islandica* with an upper (UC) and lower cortex (LC), the algal layer (A), the medulla (M) and a pseudocyphelle (P) (bar = 100 μm).

The influence of moisture on ethylene production

The measurements made on ethylene production of different species in correlation to the three degrees of water content (oversaturation, saturation, water vapour) include a number of ethylene rates below the sensitivity of the integrator of the GC. Some ethylene was released, but small peaks seen on the chromatogram could not be integrated (Table 1).

Of the species examined, *P. aphthosa* and *P. canina*, both from shadowy habitats, showed the highest rates of ethylene release when saturated and oversaturated. The production rates of both ecotypes of *C. islandica* obviously were much lower. *P. rufescens*, a species from sunny habitats, showed values between *C. islandica* and the two other species of *Peltigera*. The mean of ethylene production in relation to the different levels of water content are shown in Table 1. The significance of the differences between the mean values

Table 1. Ethylene production and water content after treatment with liquid water and water vapour

Water status	Water content in % (mean value)*	SD	Ethylene production in nl/g/h (mean value)*	SD	Percentage of samples with unquantifiable amounts (traces of) ethylene
Cetraria islandica (Shade population)					
Oversaturation	143.5	21.6	0.21	0.17	16.70
Saturation	91.3	8.1	0.17	0.15	30.90
Water vapour	56.6	30.5	0.31	0.16	10.00
Cetraria islandica (Sun population)					
Oversaturation	183.1	40.6	0.09	0.11	54.80
Saturation	95.1	6.9	0.07	0.09	61.90
Water vapour	38.2	7.4	0.37	0.14	3.30
Peltigera aphthosa					
Oversaturation	381.6	68.6	1.62	0.48	0.00
Saturation	263.6	52.5	1.12	0.31	0.00
Water vapour	44.8	8.4	0.05	0.09	77.40
Peltigera canina					
Oversaturation	438.9	62.8	1.27	0.75	7.30
Saturation	256.9	29.8	1.07	0.55	3.60
Water vapour	44.6	9.5	nt	nt	100.00
Peltigera rufescens					
Oversaturation	394.2	78.8	0.39	0.23	16.70
Saturation	213.5	31.1	0.41	0.18	12.50
Water vapour	47.6	4.00	nt	nt	100.00

* Data represent means of 30 replicates
  nt: unquantifiable amounts

Table 2. Interspecific differences in ethylene production by lichen thalli which have been wetted to differing degrees. Significance level p< 0.05 according to Wilcoxon-test (+).

Oversaturation / Saturation	C. islandica (Shade population)	C. islandica (Sun population)	P. aphthosa	P. canina	P. rufescens
C. islandica (Shade population)		+	+	+	+
C. islandica (Sun population)	+		+	+	+
P. aphthosa	+	+		+	+
P. canina	+	+	+		+
P. rufescens	+	+	+	+	
Water vapour uptake					
C. islandica (Sun population)	+				
P. aphthosa	+	+			
P. canina	+	+	+		
P. rufescens	+	+	+	–	

can be seen in Tables 2 and 3. Table 2 compares the interspecific differences between the species and Table 3 the intraspecific differences between levels of water content.

Table 1 shows that there are species-specific rates of ethylene production in relation to different water content. For evaluation of ecological influences, no intergeneric comparison of the different genera investigated is permitted. The lichen species growing in shady habitats showed higher rates of ethylene production than those growing in sunny habitats dependent of the genus. This observation is true for both saturated and oversaturated conditions.

The distinction between saturation and oversaturation is sufficient for a general picture but for a more exact evaluation, the correlation of ethylene production and release, respectively, with the actual water content must be examined. The correlation was examined by linear regression and the correlation co-efficients (r) for all lichen species and ecotypes are shown in Fig. 4. It is obvious that in the three species of *Peltigera*, ethylene production increases with higher water content while in the two ecotypes of *Cetraria*, the correlation is negative.

The influence of different types of wetting on ethylene production

It has already been pointed out that ethylene production of lichens from shady habitats is higher than in species or ecotypes from an exposed environment. This is true for both the *Peltigera* species and for the ecotypes of *C. islandica*. The results in Table 1 also show an increasing production of ethylene from saturation to oversaturation in *P. aphthosa* and *P. canina* while
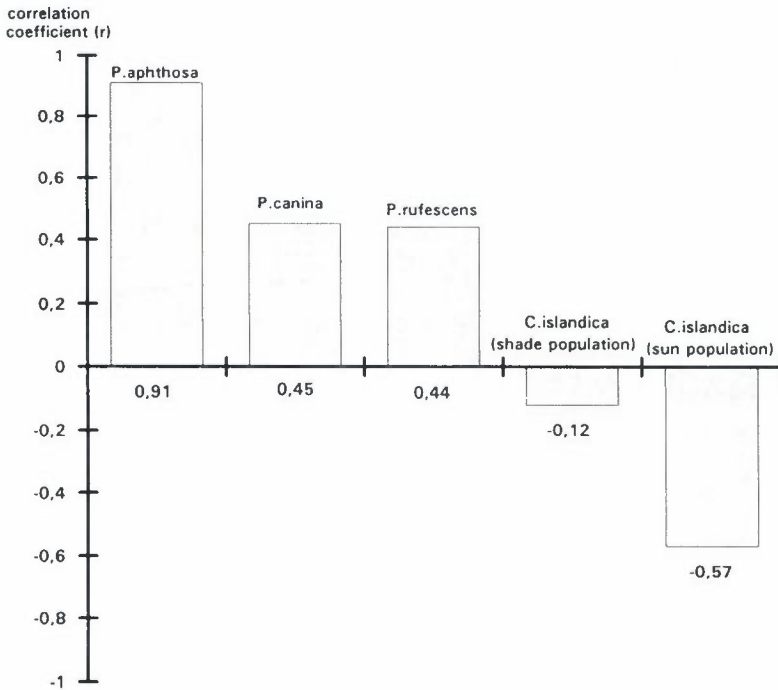
Figure 4. The correlation coefficient shows the degree of correlation between ethylene production and water content of every lichen species examined.

in *P. rufescens*, no change is apparent. The latter, from dry habitats, seems to reach its maximal ethylene production at the lower water level. Similar to *P. rufescens*, the ecotypes of *C. islandica* do not differ significantly in the ethylene produced in saturated and oversaturated thalli. Perhaps this is an ecological adaptation that is masked by thallus anatomy.

Differences in ethylene production can be observed between experiments with liquid water and water vapour. The results seem to be species-specific (Table 1). This representation includes the mean values of ethylene production, the mean values of water content and the manner of wetting of the thalli. Although all lichen thalli investigated attain nearly the same water content (50%), *P. canina* and *P. rufescens* with cyanobacteria as photobiont produce no ethylene after exposure to water vapour. *C. islandica* with green algae shows higher moisture content after exposure to vapour than after wetting with liquid water. *P. aphthosa* with both kinds of photobionts, green algae as well as cyanobacteria, produces small but measurable amounts of ethylene when exposed to water vapour (Table 1).

Table 3. Intraspecific differences in ethylene production by lichen thalli which have been wetted to differing degrees. Significance level $p < 0.05$ according to Wilcoxon-test (+)

	Oversaturation	Saturation
Cetraria islandica (Shade population)		
Saturation	−	
Water vapour	+	+
Cetraria islandica (Sun population)		
Saturation	−	
Water vapour	+	+
Peltigera aphthosa		
Saturation	+	
Water vapour	+	+
Peltigera canina		
Saturation	+	
Water vapour	+	+
Peltigera rufescens		
Saturation	−	
Water vapour	+	+

4. Discussion

There is a correlation between ethylene production and water content. An exact analysis of the results is difficult since in the lichen interactions between two organisms with different physiology occur. The data presented do not indicate whether both bionts participate in ethylene production. According to Lange et al. (1986) and Bertsch (1966) lichens with green algae and with cyanobacteria can extract about the same amount of water from moist air. But in lichens with green algae photosynthesis is only possible after uptake of water vapour, while lichens with cyanobacteria require liquid water (Lange et al., 1989). The phenomenon can be explained by the high diffusion resistance of the wall of cyanobacteria against water vapour. Büdel and Lange (1991) observed a low turgescence of the cyanobacteria in *P. rufescens* under these conditions. Therefore it seems probable that the cyanobacteria, when water content is insufficient for photosynthesis and respiration, will also be unable to synthesize ethylene. In our experiments the lichens were exposed to moist air for 4 hr. During this time the lichens with cyanobacteria in contrast to those with green algae, according to the results of Lange et al., probably could not show photosynthetic activity. If the mycobiont alone was responsible for ethylene production then the species of *Peltigera* would release measurable amounts after wetting with water vapour but this was not the case. On

the other hand, the results do not indicate that the photobionts alone are responsible for ethylene production. Huang and Chow (1984) pointed out that glucose and methionine are important substrates for ethylene production of fungi and both substances are synthesized by cyanobacteria and released to the mycobiont. The physiological inactivity of the cyanobacterial photobiont in *Peltigera* can, therefore, indirectly stop the production of ethylene by the mycobiont, provided that the mycobiont contains insufficient reserves of these substances. Such an indirect influence seems probable as several ascomycetes are able to produce ethylene (Fergus, 1954; Spalding and Lieberman, 1965; Chalutz et al., 1977; Thomas and Spencer, 1977). Green algae in lichens are physiologically active after wetting with water vapour and can either produce ethylene directly (Driesche et al., 1988) or can stimulate production by the mycobiont. This may explain the response of *C. islandica*. Obviously the photobiont has considerable direct or indirect influence on ethylene production of lichens.

It is well known that water relations of the thallus are influenced by its anatomy (Ried, 1960; Lange et al., 1986; Palmer and Friedman, 1990; Schroeter et al., 1991). As we have seen that ethylene production is correlated with water content, it can be postulated that thallus anatomy is of indirect importance for ethylene release.

Probably the structure of the thallus not only influences ethylene production, but also ethylene release from the thallus. Hydration of the surface tissues reduces diffusion of gases (Ried, 1960), an effect which is responsible for the decrease of photosynthetic activity in lichens with thick continuous cortex after saturation with liquid water (Büdel and Lange, 1991; Lange and Tenhunen, 1981; Lange et al., 1985; Coxson et al., 1983). Such an effect was not observed in *Peltigera* by Stocker (1927) and Stalfeld (1939) but others (Lange and Matthes, 1981) discovered a pronounced depression of net photosynthetic CO_2 exchange at supersaturation with water. The reason for this depression in *Peltigera* cannot be a reduction of gaseous exchange through the lower surface but must be due to other causes. In *Peltigera*, ethylene production is stimulated by higher water content and as the diffusion of ethylene through the open medulla (Figs. 1, 2) is possible even in oversaturated thalli, the positive correlation between ethylene release and water content can be postulated.

In *C. islandica* both surfaces are corticated. The cortex is pierced by pseudocyphellae (Fig. 3), but diffusion of gases is certainly slow. Especially in saturated lichens the minute spaces between the cortical hyphae are closed by swelling of the cell walls and also the opening of the pseudocyphellae becomes smaller by swelling of the loose hyphae filling these openings. Even if the ethylene production inside the thallus is stimulated by higher water content,

the restricted diffusion will reduce ethylene release from the lichen. The low values for ethylene release measured after saturation and oversaturation with water could be explained in this way. They do not prove that ethylene production is low but only that ethylene release is reduced. This explanation is hypothetical, as under those water-content conditions which allow high rates of net photosynthesis, i.e. high rates of CO_2 diffusion, the diffusion resistance should also permit ethylene release. Additional information will be necessary in order to solve this question.

After wetting of *C. islandica* with water vapour the pores of the pseudocyphellae remain open, in contrast to pores in thalli exposed to liquid water (Scheidegger, pers. comm.). At the same time the physiological activity of lichens with green algae as photobiont is already high under these conditions and the ethylene release is also on a high level. In *P. aphthosa* with green algae, a high production and release of ethylene could also be expected after wetting with water vapour, but the values were relatively low. Ethylene production was higher than in *P. canina* and *P. rufescens* with cyanobacteria where no activity could be observed, but lower than in *Cetraria*. It must be remembered that the photobionts of *Cetraria* (*Trebouxia*) and *Peltigera aphthosa* (*Coccomyxa*) are not closely related. The permeability of the cell walls of the photobionts and the manner of contact between mycobiont and photobiont (Honegger, 1991) are certainly of importance but must be examined in more detail.

The experiments show lower ethylene production in species or ecotypes from sunny habitats than in those from shady environments. In contrast to *P. canina* and *P. aphthosa*, the thalli of *P. rufescens* growing in exposed habitats show no increase in ethylene production when water content is saturated as opposed to oversatured. Presumably the maximal production of ethylene is already achieved at lower water content, but the nature of this phenomenon has to be further elucidated.

There exists a connection between CO_2 concentration and ethylene release as CO_2 may displace ethylene from its endogenous binding sites (Sisler et al., 1988). Moreover, CO_2 may directly stimulate ethylene synthesis (Aharoni et al., 1979) and, therefore, CO_2 concentration in the thallus is important. Certain conditions, such as darkness and addition of liquid water, increase release of CO_2 of lichen thalli (Lange et al., 1993). On the whole, ethylene synthesis can be inhibited, promoted or even unaffected by CO_2 (Yang and Hoffman, 1984; Philosoph-Hadas et al., 1986; Ullmann et al., 1986; Tan and Thimann, 1989). The actual influence of CO_2 on ethylene production is difficult to estimate as the amount of free CO_2 inside the lichen thallus is unknown. Highest internal CO_2 concentration will exist during darkness. Since the experiments conducted in the present study involved incubation taking

place in darkness at relatively high temperatures, relatively high CO_2 levels within the lichens are to be expected. But without concrete knowledge of CO_2 concentration inside the lichen thallus these problems can not be solved (Ott, 1993).

REFERENCES

Abeles, F.B. 1973. *Ethylene in Plant Biology.* Academic Press, New York.

Abeles, F.B., Morgan, P.W., and Saltveit, Jr. M.E. 1992. *Ethylene in Plant Biology.* 2d ed. Academic Press, New York.

Aharoni, N., Lieberman, M., and Sisler, H.D. 1979. Patterns of ethylene production in senescing leaves. *Plant Physiol.* **64:** 796–800.

Bertsch, A. 1966. Über den CO_2-Gaswechsel einiger Flechten nach Wasser-dampfaufnahme. *Planta* **68:** 157–166.

Blum, O.B. 1973. Water relations. In: *The Lichens.* V. Ahmadjian and M. Hale, eds. Academic Press, New York, pp. 381–398.

Bubrick, P., Frensdorff, A., and Galun, M. 1985. Proteins from the lichen *Xanthoria parietina* (L.) Th.Fr. which bind to phycobiont cell walls. Isolation and partial purification of an algal-binding protein. *Symbiosis* **1:** 85–95.

Büdel, B. and Lange, O.L. 1991. Water status of green and blue-green phycobionts in lichen thalli after hydration by water vapour uptake: Does it become turgid? *Bot. Acta* **104:** 361–366.

Chalutz, E., Lieberman, M., and Sisler, H.D. 1977. Methionine-induced ethylene production by *Penicillium digitatum. Plant Physiol.* **60:** 402–406.

Coxson, D.S., Brown, D., and Kershaw, K.A. 1983. The interactions between CO_2 diffusion and the degree of thallus hydration in lichens: some further comments. *New Phytol.* **93:** 247–260.

Driesche, van den, C., Kevers, C., and Collet, M. 1988. *Acetabularia mediterranea* and ethylene: Production in relation with development, circadian rhythms in emission and response to external application. *J. Plant Physiol.* **133:** 635–639.

Fahselt, D. 1988. Measurement of interpopulational variation in five species of epiphytic lichens. *Lichenologist* **20:** 377–384.

Fahselt, D. 1992. Geothermal effects on multiple enzyme form in the lichen *Cladonia mitis. Lichenologist* **24:** 181–192.

Fergus, C.L. 1954. The production of ethylene of *Penicillium digitatum. Mycologica* **46:** 543–555.

Galun, M. and Kardish, N. 1993. Lectins as determinants of symbiotic specificity in lichens. *Cryptogamic Botany* (in press).

Hageman, C. and Fahselt, D. 1990. Multiple enzyme forms as indicators of functional sexuality in the lichen *Umbilicaria vellea. Bryologist* **93:** 389–394.

Honegger, R. 1988. The functional morphology of cell-to-cell interactions in lichens. *Cell to Cell Signals in Plant, Animal and Microbial Symbiosis.* S. Scannerini et al., eds. Springer-Verlag, Berlin, pp. 39–53.

Honegger, R. 1991. Functional aspects of the lichen symbiosis. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **42:** 553–578.

Huang, T.C. and Chow, T.J. 1984. Ethylene production by blue-green algae. *Bot. Bull. Acad. Sinica* **25:** 81–86.

Jahns, H.M. 1984. Morphology, reproduction and water relations – a system of morphogenetic interactions in *Parmelia saxatilis*. In: *Beiträge zur Lichenologie-Festschrift.* H. Hertel and F. Oberwinkler, eds. *Beiheft Nova Hedwigia* **79:** 715–737.

Jahns, H.M. 1988. The establishment, individuality and growth of lichen thalli. *Bot. J. Linnean Soc.* **96:** 21–29.

Kappen, L. 1989. Field measurement of carbon dioxide exchange of the Antarctic lichen *Usnea spacelata* in a frozen state. *Antarctic Science* **1:** 31–34.

Lange, O.L. and Tenhunen, J.D. 1981. Moisture content and CO_2-exchange of lichens. II. Depression of net photosynthesis in *Ramalina maciformis* at high water content is caused by increased thallus carbon dioxide diffusion resistance. *Oecologica* **51:** 426–429.

Lange, O.L. and Matthes, U. 1981. Moisture-dependent CO_2 exchange of lichens. *Photosynthetica* **15:** 555–574.

Lange, O.L., Tenhunen, J.D., Harley, P., and Walz, H. 1985. Method for field measurements of CO_2-exchange. The diurnal changes in net photosynthesis and photosynthetic capacity of lichens under Mediterranean climatic conditions. In: *Lichen Physiology and Cell Biology.* D.H. Brown, ed. Plenum, New York, pp. 23–29.

Lange, O.L., Kilian, E., and Ziegler, H. 1986. Water vapour uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologica* **71:** 104–110.

Lange, O.L., Bilger, W., Rimke, S., and Schreiber, U. 1989. Chlorophyll fluorescence of lichen containing green and blue-green algae during hydration by water vapour uptake and by addition of liquid water. *Bot. Acta* **102:** 306–313.

Lange, O.L., Meyer, A., Zellner, H., Ullmann, J., and Wessels, D.C. 1990a. Eight days in the life of a desert lichen: water relations and photsynthesis of *Teloschistes capensis* in the coastal fog zone of Namib Desert. *Madoqua* **17:** 17–30.

Lange, O.L., Pfanz, H., Kilian, E., and Meyer, A. 1990b. Effect of low water potential on photosynthesis in intact lichens and their liberated algal components. *Planta* **182:** 467–472.

Lange, O.L., Büdel, B., Meyer, A., and Kilian, E. 1993. Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* **25:** 175–189.

Lieberman, M. 1979. Biosynthesis and action of ethylene. *Ann. Rev. Plant Physiol.* **30:** 533–591.

Lurie, S. and Garty, J. 1991. Ethylene production by the lichen *Ramalina duriaei*. *Ann. Bot.* **68:** 317–319.

Ott, S. 1988. Photosymbiodemes and their development in *Peltigera venosa*. *Lichenologist* **20:** 361–368.

Ott, S. and Zwoch, I. 1992. Ethylene production by lichens. *Lichenologist* **24:** 73–80.

Ott, S. 1993. The influence of light on the ethylene production by lichens. In: *Beiträge zur Lichenologie-Festschrift S. Huneck.* B.G. Feige und H.T. Lumbsch, eds. *Bibliotheca Lichenologica* **53:** 185–190.

Philosoph-Hadas, S., Aharoni, N., and Yang, S.F. 1986. Carbon dioxide enhances the development of the ethylene forming enzyme in tobacco leaf discs. *Plant Physiol.* **82:** 925–929.

Ried, A. 1960. Thallusbau und Assimilationshaushalt von Laub- und Krustenflechten. *Biologisches Zentralblatt* **79:** 129–151.

Schroeter, B., Jacobson, P., and Kappen, L. 1991. Thallus moisture and microclimate control of CO_2 exchange of *Peltigera aphthosa* on Disco Island. *Symbiosis* **11:** 131–146.

Schroeter, B. 1991. Untersuchungen zur Primärproduktion und Wasserhaushalt von Flechten der maritimen Antarktis unter besonderer Berücksichtigung von *Usnea antarctica* Du Rietz. *Dissertation Universität Kiel* 1–148.

Sisler, E.C. and Wood, C. 1988. Interaction of ethylene and CO_2. *Physiol. Plant.* **73:** 440–444.

Spalding, D.H. and Lieberman, M. 1965. Factors effecting the production of ethylene by *Penicillium digitatum*. *Plant Physiol.* **40:** 645–647.

Ståfeld, M.D. 1939. Der Gasaustausch der Flechten. *Planta* **29:** 11–31.

Stocker, O. 1927. Physiologische und ökologische Untersuchungen an Laub- und Strauchflechten. *Flora* **121:** 334–411.

Tan, Z-Y and Thimann, K.V. 1989. The roles of carbon dioxide and abscisic acid in the production of ethylene. *Physiol. Plant.* **75:** 13–19.

Thomas, K.C. and Spencer, M. 1977. L-Methionine as an ethylene precursor in *Saccharomyces cerevisiae*. *Can. J. Microbiol.* **23:** 1669–1674.

Ullmann, J., Prikryl, Z., Machockova, I., and Krekule, J. 1986. Ethylene production in seedlings of *Chenopodium rubrum*, as influenced by seedlings age, light, and CO_2 concentration. *Biochem. Physiol. Pflanzen.* **181:** 391–396.

Yang, S.F. and Hoffman, N.E. 1984. Ethylene biosynthesis and its regulation in higher plants. *Ann. Rev. Plant Physiol.* **35:** 155–189.