

Habitat overlap/niche segregation in two *Umbilicaria* lichens: a possible mechanism

D.W. Larson

Department of Botany, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Summary. *Umbilicaria muhlenbergii* and *Umbilicaria papulosa* are two similar lichens which show extensive habitat overlap. Current theory predicts that for those resources that are limited, and of critical importance to both species, segregation is demand for or use of those resources ought to be present. Controlled experiments showed that the upper and lower cortical surfaces of the two species functioned in very different ways so that *U. muhlenbergii* is wetted most rapidly by runoff and mist-like precipitation whereas *U. papulosa* is wetted most rapidly by large raindrops. An analysis of the meteorological conditions in the natural habitat for the two lichens shows that the four months providing significant productivity in *U. papulosa* are the same months with a very high frequency of thunderstorms (which produce large drops). Conversely, the months which produce the greatest production in *U. muhlenbergii* are spread out over most of the year. When water is supplied after periods of dryness, the two species absorb it at different times and from different sources. This difference supports current ideas about niche segregation in plants but represents the first time it has been demonstrated for lichens.

Introduction

Current ecological theory shows that habitat overlap (coexistence) between two species must be accompanied by niche segregation for those resources which are critical to the survival of the organisms involved and which are also limited in supply. Studies such as Grace and Wetzel (1982) clearly show that many aspects of a plant's morphology or physiology can provide the necessary levels of segregation to permit coexistence. While in the past there may have been a tendency to infer that niche segregating mechanisms were present rather than to directly measure them (Werner 1979), the more recent use of coexisting members of the same or similar genera (Solbrig 1971; Turkington and Harper 1979; Grubb 1976; Werner 1977) has provided much more information concerning the mechanisms by which coexistence is established and maintained in the field. Even in these studies, however, competition as the force producing the observed pattern cannot be easily measured because of the difficulty in knowing exactly what the range of resources are for the plant at each life cycle stage, as well as knowing what amounts of crucial resources can be considered "limiting". Nowhere has the study of com-

petitive interactions in plants been more difficult than in the lichens. Their inherent slow growth and sensitivity to laboratory conditions have made it virtually impossible to directly measure resource use, niche segregation or competition in nature (Topham 1977; Lawrey 1981). It has thus been necessary to use distribution patterns alone, as a measure of competitive interactions.

In a field study reported earlier (Larson 1979) patterns of species distribution and abundance in an *Umbilicaria* dominated community were described. In that paper two species, *Umbilicaria papulosa* (Ach.) Tuck. (= *Lasallia papulosa* (Ach.) Llano) and *Umbilicaria muhlenbergii* (Ach.) Tuck., (= *Actinogyra muhlenbergii* (Ach.) Schol.) which Llano (1950) had already shown to co-occur extensively in North America were found to have the same distribution pattern on a local scale. In a later study (Larson 1981), some preliminary evidence of a mechanism allowing for this coexistence was uncovered. This work showed that under mist-like wetting conditions the upper cortex of *U. muhlenbergii* played little role in inhibition, while in *U. papulosa* the upper cortex was equally important to wetting as the lower cortex. It was thought that *U. papulosa* and *U. muhlenbergii* were able to coexist because of differential demand for an essential and limited resource: direct precipitation allocated preferentially to *U. papulosa*, and runoff allocated preferentially to *U. muhlenbergii*.

The current study was designed to test this idea more directly by dealing with four specific questions: first, can the differences in absorptive characteristics between the two species be confirmed without the use of artificial blocking agents? Second, does the form of the precipitation influence water uptake? Third, can the differences in wetting be explained by examining cortical topography, anatomy, or elemental composition? Fourth, is the frequency of precipitation in the field sufficiently limiting to account for the observed pattern of coexistence?

Methods

The first two questions presented above required the execution of experiments under controlled conditions in the laboratory. The third question was dealt with through the use of scanning electron microscopy and energy dispersive x-ray analysis, and the fourth question required the analysis of previously published literature and Environment Canada meteorological records.

Water uptake

The topography of the natural rock surfaces upon which *U. muhlenbergii* and *U. papulosa* grew in the field, was too complex to allow precipitation or runoff to be regulated in a repeatable fashion (see Larson 1979 for details of the collecting site and field environment). Thus all wetting experiments were run indoors under simulated field conditions. For this purpose a cement slab (of dimensions 70 cm L, 40 cm W, 5 cm thick) was cast, and erected on a wooden support at a angle of 45° (the mean slope for sites occupied by both species). The surface of the slab was flat, but showed a surface roughness essentially equivalent to that of the natural substrate. At the top of the slab, a rectangular trough 2 cm deep was cast along the length of which small indentations were made into the surface, to encourage an even flooding of the entire rock surface during the runoff experiments. In all cases, the lichens were held to the rock by an arched piece of stiff wire pressing on the umbilicus of thalli used. This type of contact gives as good an approximation as possible of the type of contact between lichen and substrate in the field, while still allowing repeated weighing of the thalli.

Runoff experiments. In order to examine the process of water uptake in the two species when only the lower cortex was involved, experiments were run in which only runoff was supplied. Thirty replicates of each species were selected from the Muskoka site on the basis of uniformity in weight and diameter. Only intact, healthy specimens were used. The air-dry weight (10% r.h. at 20° C) of each specimen was recorded. Runoff runs were executed by supplying water to the trough at a rate of 300 ml min⁻¹ (this amounts to 7.5 ml min⁻¹ cm⁻² of horizontal rock face, a value arbitrarily selected because it neither flooded over the top of test samples, nor did it allow the runoff to become sparse or intermittent) then measuring at one minute intervals the weight change in individual thalli until saturation was evident. To roughly separate surface water from intra-thallus water, two weight measurements were taken at each time interval: one before, and another following light blotting. The results for all thirty replicates were then plotted as thallus water content (g·H₂O·g⁻¹ thallus dry weight over time).

Direct precipitation experiments. In order to examine the process of water uptake when the upper cortical surfaces were involved, a series of experiments were run involving direct precipitation and no runoff. In these runs, the same thirty replicates were used as above. Thalli were mounted on a parafin block (1 cm on a side), so that runoff could not be absorbed and an atomized spray (with mean droplet diameter of 10 µm) was then directed to the material from a distance of about 50 cm. The water flow rate into the nozzle was 30 ml min⁻¹ and was broadcast onto about 400 cm² of the rock slab's surface. Weight change over time was measured as above.

Drop absorption experiments. Neither of the above experiments was designed to examine the process of water uptake as effected by the dimensions of the precipitation particle. Thus, experiments were set up in which the four cortical surfaces were exposed to a droplet size gradient. The work involved the measurement of the rate at which single drops of liquid water were absorbed into the upper/lower cortical

surfaces of the two species. Ten thalli were used per treatment; one test spot per drop size per thallus per species. Three drop sizes were used: 25 µl, 1 µl and 0.1 µl. Two parameters were measured under each treatment. 1. the time required (in seconds) for the liquid water to totally disappear from the cortical surface being observed, 2. the maximum diameter (in mm) of the wetted zone of thallus. A Zeiss dissecting microscope at 20× magnification was used in all determinations.

Scanning electron microscopy of the cortical surfaces

The third question above, required little more than a direct examination of the cortical surfaces involved using a JSM-35C scanning electron microscope. Accelerating voltage was set at 25 KV. Specimens were air-dried, coated with gold/palladium then viewed. Since it was possible that the wetting characteristics were influenced by accumulations of minerals (eg. silicon) in the cortical surfaces, relative abundance of detectable elements was determined by using energy dispersive X-ray analysis. For these experiments, thalli were imbedded in 3-hydroxybutanemethacrylate (3-HBMA) so that background x-ray emission from chlorine, silicon or sulphur, contained in other commonly used resins would be minimized (Protz pers. comm.). After embedding, sections were cut on a diamond saw, then surface polished (up to 1000 grit) in order to minimize errors in x-ray detection due to topographical interference. Polished sections were then carbon coated and sampled at five positions within each zone of interest for a 100 second time interval.

Precipitation in the field

The objective in this section of the project was to determine the nature of the size distribution of precipitation in the field, because rate of wetting appeared to be so strongly influenced by drop size. An extensive literature on the subject of cloud microphysics and the mechanics of precipitation provided all the necessary information regarding the nature of drop-size distributions in different types of precipitation events. Environment-Canada weather records for the Muskoka airport site (lat. 44 58N, long 79 14W), covering the period 1941–1970 provided all the additional information regarding the frequency and type of precipitation events in the field.

Results

Wetting runs. Figure 1 shows the time course of wetting due to runoff in *U. papulosa* thalli. The mean weight of these thalli was 0.37 g, the mean diameter was 37 mm. Unblotted thalli have thallus moisture contents which rise slowly over a period until saturation occurs at twenty minutes. Blotted thalli show the same trend although the magnitude of the final wet weight is 50% smaller. The time required to achieve 50% of the final wet weight (T_{50}) is around three minutes for the blotted thalli and two and one half minutes for the unblotted material.

Figure 1 also shows the result for *U. muhlenbergii* (mean wt. 0.61 g, mean diameter 41 mm) under the same conditions. For this species, the maximum moisture content of 240% occurs at four minutes, and the T_{50} is only one minute. Blotted thalli show only slight reductions in weight but are otherwise similar to the unblotted material.

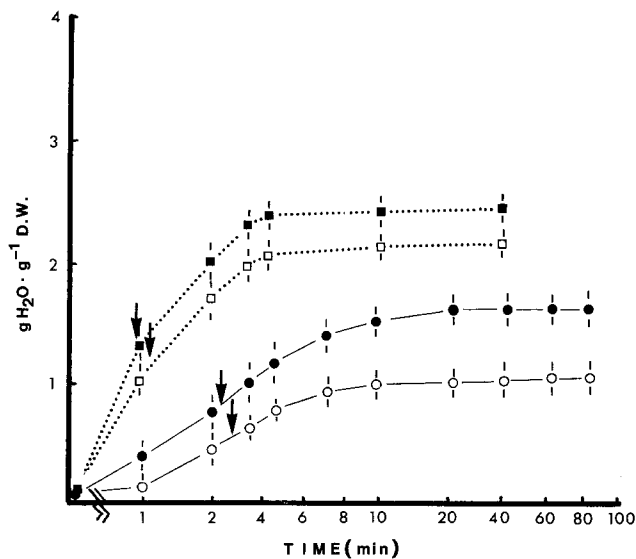


Fig. 1. Change in thallus water content ($\text{g} \cdot \text{H}_2\text{O} \cdot \text{g}^{-1}$ thallus dry wt.) with time, when material exposed to RUNOFF ONLY. Symbols: ■ *U. muhlenbergii* not blotted; □ *U. muhlenbergii* blotted; ● *U. papulosa* not blotted; ○ *U. papulosa* blotted. Arrows indicate time to reach 50% of maximum water content (T_{50}). Each point shows the mean of 30 replicates \pm standard error of the mean

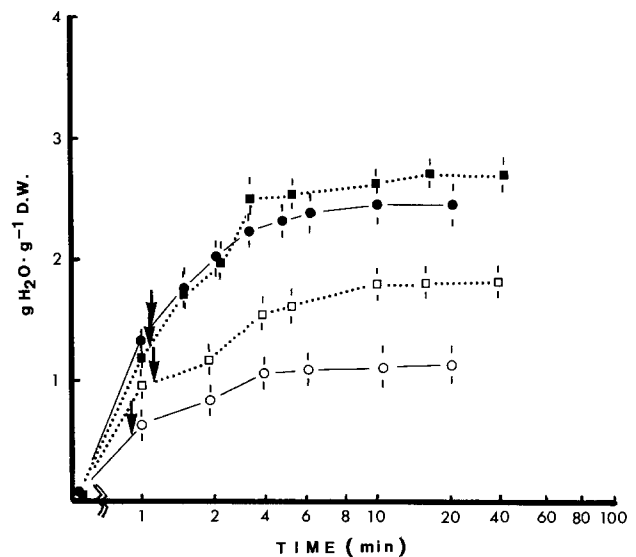


Fig. 2. Change in thallus water content ($\text{g} \cdot \text{H}_2\text{O} \cdot \text{g}^{-1}$ thallus dry wt.) with time when material exposed to DIRECT PRECIPITATION ONLY. Symbols same as Fig. 1

Table 1. Comparison of the rate of disappearance of water droplets from the surface of lichen thalli. Mean values \pm 1.S.D. are shown, ($n=10$)

Zone	Drop size	<i>U. papulosa</i>	<i>U. muhlenbergii</i>
Upper cortex	25 μl		
	time to imbibe (sec)	23.4 \pm 10.41	* 3360 \pm 1608
	diameter of zone (mm)	28.4 \pm 3.80	* 3.4 \pm 0.47
	1 μl		
	time to imbibe (sec)	4.6 \pm 1.4	* 1788 \pm 996
	diameter of zone (mm)	8.4 \pm 1.2	* 1.0 \pm 0.6
	0.1 μl		
	time to imbibe (sec)	1.5 \pm 0.27	* 25.2 \pm 13.0
	diameter of zone (mm)	—	—
Lower cortex	25 μl		
	time to imbibe (sec)	93.8 \pm 54.6	* 9.0 \pm 7.6
	diameter of zone (mm)	12.4 \pm 2.3	N.S. 14.0 \pm 2.2
	1 μl		
	time to imbibe (sec)	57.1 \pm 23.3	* 1.6 \pm 0.85
	diameter of zone (mm)	5.2 \pm 1.3	N.S. 4.0 \pm 0.77
	0.1 μl		
	time to imbibe (sec)	1.55 \pm 0.44	N.S. 0.98 \pm 0.49
	diameter of zone (mm)	—	—

* Indicates significant difference with $p < 0.01$ using Student's t-test

Figure 2 shows the pattern of weight increase when the thalli are exposed to direct precipitation alone. In these experiments, all treatments have the same T_{50} , and show saturation at about ten min. The only difference between the species is that blotting *U. papulosa* thalli removes more weight than in *U. muhlenbergii*.

Drop absorption

Table 1 provides a comparison of the two species in terms of the rate of absorption of drops into the upper/lower cortical surfaces. For the upper cortex, *U. papulosa*, shows

a very rapid rate of absorption, even for the largest volumes used. As drop size decreases, rate of absorption increases, though not in a direct proportion. A remarkable feature of the upper cortex of this species is the large area that the absorbed water is distributed to. The diameter of the area wetted by the 25 μl drop (3 mm in diameter to start with) is 28.4 mm (615 mm^2). Soon after the water is distributed to this area, the white granular appearance of the upper cortex returns, giving the impression that the water is transferred to the algal layer and medulla soon after being absorbed and distributed by the upper surface.

In striking contrast to the situation above, the upper

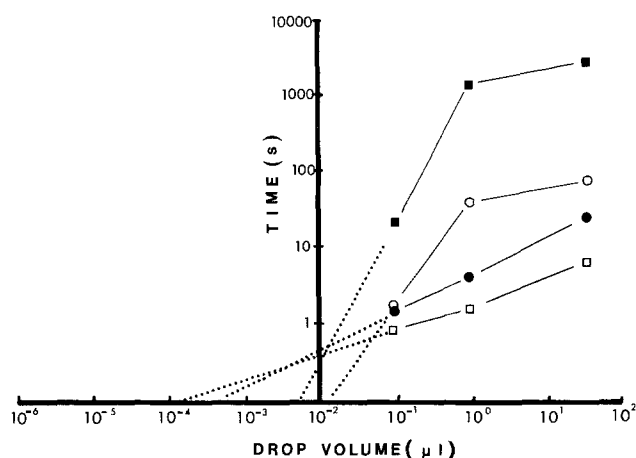


Fig. 3. The relationship between volume of drops applied and the time required for complete absorption of the drop. Symbols: ■ *U. muhlenbergii* upper cortex; □ *U. muhlenbergii* lower cortex; ● *U. papulosa* upper cortex; ○ *U. papulosa* lower cortex. Extrapolation and zone of convergence shown with dotted lines

cortex of *U. muhlenbergii* neither absorbs water quickly, nor laterally disperses water to other tissues in the thallus. 25 μ l drops required on average some 3360 s to disappear. An inevitable error in such long time intervals is the evaporation that would be occurring from the drop surface during the run. Such evaporation would mean that the 3360 s time is a very conservative estimate of the low absorptive capacity of the upper cortex of this species. The maximum size of the wetted zone remains as the size of the drop initially applied. As drop size decreases, absorption times increase at a much faster rate than for *U. papulosa*, so that a 0.1 μ l drop is absorbed in 25 s. Thus while *U. papulosa* absorbs large drops 146 times faster than *U. muhlenbergii*, the smallest drops are absorbed only 22 times faster.

A reversal of species characteristics is apparent when the lower cortical surfaces are examined. For *U. papulosa*, 25 μ l drops are absorbed relatively slowly, and are not dispersed over as large an area as above. As drop size decreases, the rate of absorption increases at the same rate as for the upper cortex of *U. muhlenbergii*. In contrast, the lower cortex of *U. muhlenbergii* absorbs even the largest drops used, at an extremely rapid rate. The mean time to disappearance was only 9 s, and this value drops as low as 0.98 s for the 0.1 μ l drops used. Lateral distribution of imbibed water is considerable, though not as great as it was for the upper cortex of *U. papulosa*.

Figure 3 shows a plot of "time to disappearance" against drop volume (and diameter) for the four surfaces studied. It shows three important things not immediately evident in Table 1. Firstly, the order of the curves for each surface shows that the absorptive capacities of the two species are reversed. *U. muhlenbergii* has an upper cortex which is very resistant to absorption, whereas in *U. papulosa*, it is the lower cortex which shows this tendency. Conversely, the lower surface is extremely absorptive in *U. muhlenbergii* and the upper cortex has this feature in *U. papulosa*. Second, the shape of the curve for *U. muhlenbergii* (upper cortex) is similar to that for *U. papulosa* (lower cortex) and similarly, the upper cortical response of *U. muhlenbergii* is the same as that for the lower cortex of *U. papulosa*. Third, all the differences between the treatments decline as drop size decreases. If one extrapolates from the existing

data points, it would appear that for drops of volume 0.01 l or less (diameter 0.20 mm or less) the differences amongst the four surfaces approach zero. This result is significant in view of the 5.23×10^{-1} pl drop volume (10 m diameter) used in the direct precipitation experiments described above.

Scanning electron microscopy

An oblique view of *U. papulosa* at relatively low power ($\times 200$), and perpendicular views of both cortical surfaces at higher power ($\times 500$) are shown in Fig. 4a, b, c). It is evident from these micrographs that the upper cortex of this species is between 20 and 30 μ m thick (Fig. 4a), but that above this zone, an irregularly granular necrotic zone is found, somewhere between 10 and 15 μ m in thickness. This upper surface layer of the cortex is a translucent grey colour under the light microscope, and it is precisely this layer that seems to be responsible for absorbing and redistributing the available water. The average "grain size" is about 10 μ m in diameter and from Fig. 4(b) seems to be composed of the cell walls and extracellular matrix of perhaps 5 to 10 cells. The exposed parts of the lower cortex in *U. papulosa* also have a granular appearance (Fig. 4(c)), but the "grain size" is more like 30 μ m, and there is no translucent nature to these cells. The lower cortex is about 30 μ m in thickness.

The results for *U. muhlenbergii* are given in 4d, e, f. The oblique view (Fig. 4d) at $200\times$ shows a much thicker thallus but a very different set of dimensions for the two cortical surfaces. The upper cortex appears to be just a single cell in thickness (about 8 μ m) while the lower cortex is fully half the thickness of the entire thallus (about 60 μ m). The upper cortex as shown in Fig. 4e is extremely smooth, with no details indicating the growth pattern or development of the underlying cortical cells. In contrast the lower cortex has a very pronounced grain (with mean size of 30–40 μ m) imposed by the downward growth of lamellae from this surface (Fig. 4f).

Table 2 shows that the order of absorptive characteristics from most to least does not correlate exactly with either a measure of surface roughness, cortical zone thickness or area to which the water is distributed. This suggests that some other factor in addition to topography and anatomy controls water absorption in these plants.

Energy dispersive x-ray analysis

Only eight elements showed accumulated detections far exceeding the baseline: they included Na, Al, Si, P, S, Cl, K, Ca, and Fe. There was no trend in these data, however, showing a correlation between rate of wetting and any of the elements samples. This result suggested that any biochemical feature of these four surfaces which controls water uptake, was not based on large differences in key minerals such as silicon.

Precipitation in the field

The above results made it necessary to know the drop-size distributions to be typically found in natural precipitation events. While the ecological literature contained essentially no information on this subject, there was an abundance of available data relating to the topic in the area of cloud

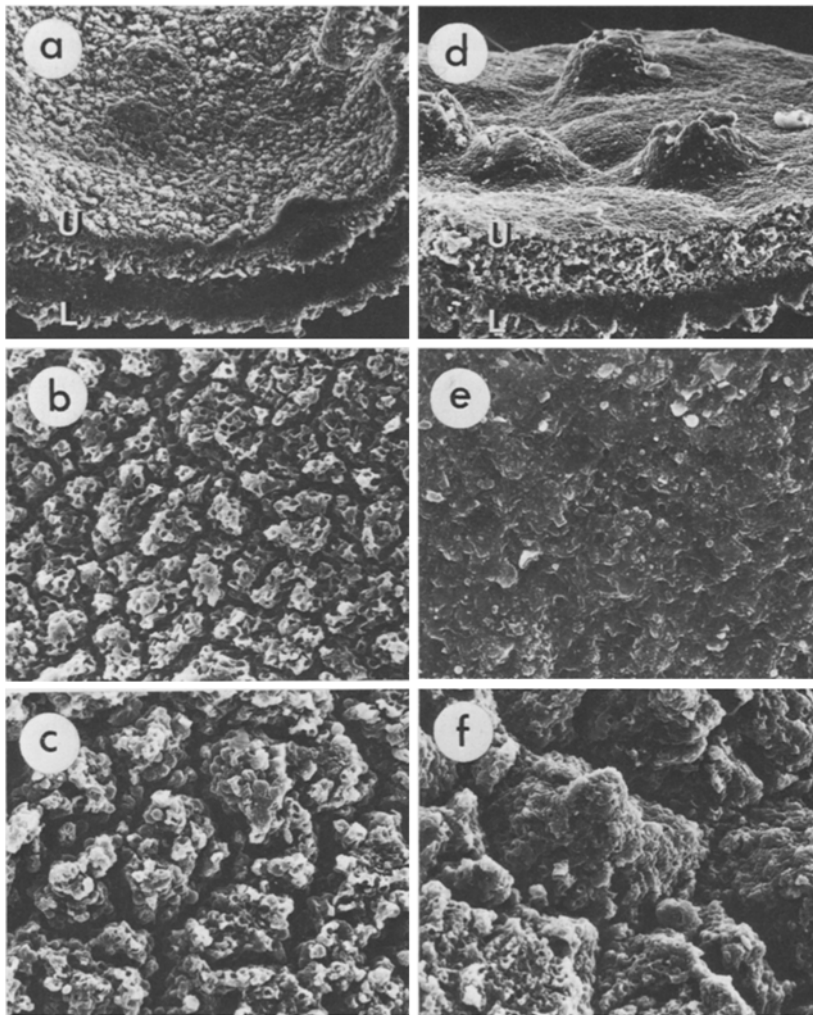


Fig. 4a–f. Scanning electron micrographs of *U. papulosa* and *U. muhlenbergii*.

a Oblique view of *U. papulosa* at $\times 200$.

Symbols *U* upper cortex. *L* lower cortex.

b Perpendicular view of *U. papulosa* at $\times 500$ showing granular upper cortex.

c Perpendicular view of *U. papulosa* of lower cortex at $\times 500$.

d Oblique view of *U. muhlenbergii* at $\times 200$.

Symbols: *U* upper cortex, *L* lower cortex.

e Perpendicular view of *U. muhlenbergii* of upper cortex at $\times 500$.

f Perpendicular view of *U. muhlenbergii* of lower cortex at $\times 500$

Table 2. The relationships between absorptive characteristics of the four surfaces studied and cortical surface thickness and topography

Order of Absorbance (25 μ l drop)

U. muhlenbergii (l.c.) > *U. papulosa* (u.c.) > *U. papulosa* (l.c.)
> *U. muhlenbergii* (u.c.)

Order of Areas to which water is distributed (25 μ l drop)

U. papulosa (u.c.) > *U. muhlenbergii* (l.c.) > *U. papulosa* (l.c.)
> *U. muhlenbergii* (u.c.)

Order of surface roughness

U. muhlenbergii (l.c.) > *U. papulosa* (l.c.) > *U. papulosa* (u.c.)
> *U. muhlenbergii* (u.c.)

Order of cortical thickness

U. muhlenbergii (l.c.) > *U. papulosa* (l.c.) > *U. papulosa* (u.c.)
> *U. muhlenbergii* (u.c.)

microphysics and the artificial stimulation of rain. The information relevant to the current investigation is summarized in Fig. 5. Figure 5(a) for example shows that there is a direct relationship between drop size distribution and the type and timing of the precipitation event. Early in thunderstorms, the number of drops per square meter per second, is skewed in such a way that a much higher propor-

tion of large drops impact the ground. Continuous heavy rain has far fewer large particles; the explanation most commonly involved is that the terminal velocity of large drops is higher, thus leading to their earlier appearance in the precipitation event. Light, discontinuous rain has particle sizes skewed in such a way that a high frequency of small droplets is present. Figure 5(b) shows the frequency distribution of drops (number per cubic meter per mm of the size class distribution) for similar types of events differing only in intensity. Again, it is clear that the frequency of large particles increases as the intensity of the event increases. Figure 5(c) shows the range of particle sizes found for precipitation of differing form: an important point to reiterate here is that three drop sizes tested above (25 μ l, 1 μ l, 0.1 μ l) fall directly into the category of “rain”, while the atomized spray whose mean diameter was about 10 μ m (less than 1 pl) was more properly a form of “fog” or “mist”.

Meteorological conditions at the muskoka research site

Table 3 shows, for a thirty year period from 1941–1970, the monthly variation in rainfall (a), days with rain (b), days without rain (c), rainfall per day with rain (d), days with thunderstorms (e), percentage of rain coming as thunderstorms (f) and mean daily screen height temperatures

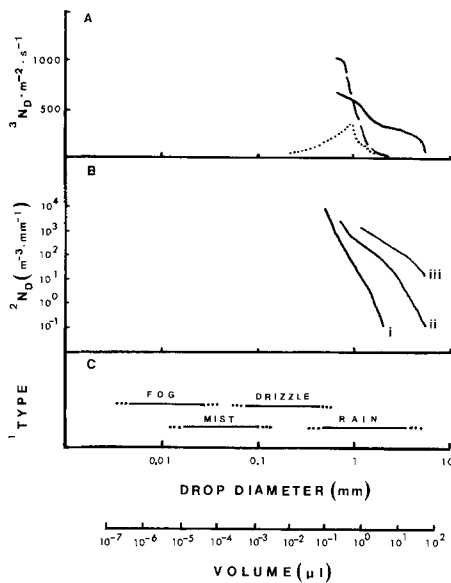


Fig. 5a-c. Composite figure showing **a** the relationship between impact rate ($\cdot m^{-2} \cdot s^{-1}$) for drops of different sizes (N_D) and drop diameter for different types of precipitation events: (—) early in a thunderstorm ($22 \text{ mm} \cdot \text{h}^{-1}$); (---) continuous heavy rain ($15 \text{ mm} \cdot \text{h}^{-1}$); (····) light, discontinuous rain ($3.4 \text{ mm} \cdot \text{h}^{-1}$)⁽³⁾ adapted from Wiesner (1970) and Pruppacher and Klett (1978). **b** The relationship between the number of drops of different sizes N_D and drop size for rain of differing intensity. Symbols: (1) $1 \text{ mm} \cdot \text{h}^{-1}$; (ii) $25 \text{ mm} \cdot \text{h}^{-1}$; (iii) $100 \text{ mm} \cdot \text{h}^{-1}$.⁽²⁾ Adapted from Pruppacher and Klett (1978) and Hitschfeld (1957). **c** Classification of different types of precipitation. ⁽¹⁾ Adapted from Weickmann (1957) and East (1957)

(g). The monthly variation in rainfall covaries exactly with the number of days with rain, leading to a surprisingly constant amount of rainfall per day with rain. It is quite clear, however, from row (c) that water is exceedingly limiting at this site. Not only are the plants continuously dry on the days without rain, but also they are dry a good part of the time on days when rain occurs. While morning dews could occasionally occur, they do not play a very significant role in the water relations and physiology of these *Umbilicaria* lichens. When the rain does occur, the months from June to October have values exceeding seven mm per day, whereas January and February both have values less than five. In contrast with this evenness, the

number of days with thunderstorms (e) is insignificant until April, then rises sharply during May and peaks through June, July and August. Values fall abruptly from September through to the end of the year. Row (f) shows that when one calculates the number of days with thunderstorms as a percentage of the total number of days with rain, the values are again insignificant from November through to March, they rise in April and May, and have a larger value during June, July, August and September. These same months show mean daily temperatures at or slightly above 14°C (row g), the optimum thallus temperature for maximum CO_2 exchange in *U. papulosa* (Larson 1980). Row (h) expresses the percentage of the optimum net photosynthetic rate for *U. papulosa* which is produced by the mean daily temperatures found under row (g). Row (i) shows the same results for *U. muhlenbergii*. The data indicate that the same months (June, July, August and September) which include the highest frequency of thunderstorms, are the same months in which the production and hence growth in *U. papulosa* are at a maximum. Conversely, the highest levels of production and growth in *U. muhlenbergii* are spread across a much wider range of temperatures from $+4.4^\circ \text{C}$ in April to $+1.1^\circ \text{C}$ in November. In other words, only three months where temperatures drop far below 0°C produce a marked reduction in production in *U. muhlenbergii*.

Discussion

Wetting runs and drop absorption

Wetting runs in which runoff alone was supplied clearly show the more rapid rate of water uptake in *U. muhlenbergii* than *U. papulosa*. They also demonstrate that imbibed water is held more tightly within the *U. muhlenbergii* thallus than in *U. papulosa*. In contrast, the impact of direct simulated precipitation on these plants, in the absence of any runoff, produces rates of wetting that are equal for both species.

While at first this result was puzzling, the drop absorption experiments which followed resolved the problem. Table 1 and Fig. 3 show that as drop sizes decrease, there is a reduction in differences amongst the surfaces sampled so that convergence appears at drop sizes less than 0.20 mm ($0.01 \mu l$). Since the droplets produced by the atomiser in the wetting runs were $10 \mu m$ in diameter, it should have

Table 3. Mean Monthly Meteorological Conditions at the Muskoka Airport Weather Station

Month	J	F	M	A	M	J	J	A	S	O	N	D
(a) rainfall (mm)	12.7	12.7	30.5	58.4	76.2	76.2	86.2	76.2	99.0	87.8	63.5	27.9
(b) days with rain	3	3	5	9	12	10	10	10	12	12	10	5
(c) days without rain	28	25	26	21	19	20	21	21	18	19	20	26
(d) rainfall per day with rain	4.2	4.2	6.1	6.4	6.4	7.8	8.6	7.6	8.3	7.3	6.3	5.5
(e) days with thunderstorms	0.1	0.1	0.1	1.4	2.5	4.1	4.9	4.2	2.7	1.6	0.3	0.1
(f) d/b $\times 100\%$	3	3	4	26	21	41	49	42	39	13	3	2
(g) mean daily $^\circ \text{C}$	-10	-8.8	-3.8	4.4	11	16	18	17.7	13.3	8.3	1.1	-6.7
(h) % ^a of max. photosynthetic activity provided by (f), for <i>U. papulosa</i>	0	1	1.5	25	37	91	97	98	92	45	25	1.0
(i) % ^a of max. net P provided by (f) for <i>U. muhlenbergii</i>	0	15	50	81	90	97	95	97	100	87	69	32

^a From Larson (1980) and unpublished data

been expected that rates of wetting would be equivalent for the two species when direct precipitation was applied.

These two sets of experiments, then, produce a very clear result. Direct precipitation leads to a more rapid wetting in *U. papulosa* only when its drop size distribution is skewed in favour of large drops. Conversely, small droplets wet both species equally and runoff is preferentially absorbed and held by *U. muhlenbergii*. The scanning electron micrographs and the energy dispersive x-ray analysis suggest that the combination of cortical surface geometry and the presence of some unknown compound in the cortical extracellular matrix is responsible for these differences in drop absorption. Differences in elemental distribution are clearly *not* present are therefore *not* involved in producing the above effects.

Drop size distribution in nature "Rain" is typically composed of those droplets having large enough volumes (1–200 μ l) so that they fall due to the force of gravity; smaller droplets tend to be resuspended by atmospheric turbulence or fall with extremely low terminal velocities (Twomey 1977; Joss et al. 1968). Other condensed forms of water vapour (fog, mist and drizzle) do not really fall, so much as simply impact solid surfaces that the airmass flows over.

Even within the general category of "rain" a relation exists between drop size distribution and rate of fall. Figure 5 (adapted from Wiesner 1970; Proppacher and Klett 1978; Hirschfeld 1957; Weickmann 1957; East 1957) shows that at the start of precipitation events, when water is most limiting to lichens, the drop-size distribution favours large drops. This is because of the higher terminal velocities they show during fall. Such a pattern is especially true for thunderstorms (Proppacher and Klett 1978) but applies equally well to other kinds of events. If this information is integrated with the earlier wetting results, it would appear that *U. papulosa* is always wetted much more rapidly than *U. muhlenbergii* when precipitation events first start, and especially when thunderstorm activity is present; for it is precisely these conditions that have large drops, and at least initially, no runoff!

Rainfall at the muskoka site

The most important remaining question is "do conditions which result in large interspecific differences in rates of wetting occur frequently enough to be meaningful biologically?" The results in Table 3 provide as clear an answer to this as possible at this time. Days with thunderstorms account for nearly half of the precipitation that occurs in the Muskoka research site in the months from June to September, but the surrounding months have *much* lower percentages. These four months, as it turns out, are also those with mean daily air temperatures that produce over 90% of the maximum net production in *U. papulosa*. The surrounding months also have much lower temperatures which sharply reduce production in this species. Accordingly, *U. papulosa* appears to be specialized in its water relations and productivity to the summer months. Both water and temperature are therefore cofactors limiting productivity in *U. papulosa* for most of the year. The same story is not at all found for *U. muhlenbergii*. This species achieves high levels of production in all months but December, January, and February. In other words, even though *U. muhlen-*

bergii has as high relative production as *U. papulosa* in the summer when thunderstorms are frequent, it shows a *higher* level than *U. papulosa* throughout the rest of the year when thunderstorms are infrequent. Therefore, its production is spread over a much longer time period, and in this sense, is generalized on a temporal basis.

Most other studies of competition and resource use by lichens focus on exploitation of space alone (Pentecost 1980) rather than particular nutrients, water or light. In addition, the usual approach to describing the interactions is to observe the points of contact of one clonal thallus with another, and to describe them in terms of how the margin is formed. This is clearly not a very satisfactory way of examining competitive interactions since it does not give the investigator the ability to observe a change in the plant's response (physiological or otherwise) to the competition. This study represents the first time that direct experimental evidence of partitioning of resources has been found in two potentially competing lichens. This study also represents the first time that different anatomical and morphological characteristics of lichens have been implicated in competitive interactions and it immediately suggests that patterns of habitat overlap described elsewhere (Lawrey 1981; Hawksworth and Chater 1979; Bates 1975, 1978; Hofman et al. 1974; Yarranton and Green 1966) may be controlled by the same sort of partitioning or segregation of resources found for the two *Umbilicaria* lichens dealt with here. It is essential that future research into lichen distribution patterns and physiological ecology take this into consideration.

Conclusions

Water is an essential, and an obviously limited resource for poikilohydric plants like lichens. While the amount of time the plants are desiccated varies a great deal, the onset of precipitation releases this limitation and photosynthetic production starts (provided environmental temperatures and other conditions are appropriate). Under these conditions *U. papulosa* gets hydrated more rapidly than *U. muhlenbergii* whose thin, flat upper cortex does not imbibe water very rapidly for the types of drops impacting the thallus, and whose lower cortex has not yet been exposed to runoff. Rain dominated by large drops occurs at least half the time in the summer months, and from physiological data collected earlier, it is quite clear that it is in these months that *U. papulosa* shows the highest net production. Once the precipitation event is in progress, runoff *and* a higher proportion of small droplets appear, leading to a complete wetting of both species. The tighter binding of water in *U. muhlenbergii* and a higher evaporative resistance in it as well (Larson 1979) lead to an extended period of time that *U. muhlenbergii* is wet. In fact, the runoff often occurs after all direct precipitation has stopped and *U. papulosa* has started to dry out. The ability of *U. muhlenbergii* to respond to smaller droplets and runoff combined with a much wider range of environmental temperatures which produce significant net production, adds to the impression of niche segregation between the two species. While the above results in no way suggest that these differences in water relations have necessarily developed in a coevolutionary fashion, they do at least suggest that the extensive habitat overlap here is made more probable by the type of segregation in the demand for water that the two species show.

Acknowledgements. I thank Dr. R. Protz for providing the 3 HBMA for embedding the lichen material and Dr. R. Reader for making comments on an earlier version of the manuscript. This research was supported by the Natural Sciences and Engineering Research Council of Canada.

References

- Bates JW (1975) A quantitative investigation of the saxicolous bryophyte and lichen vegetation of Cape Clear Island, County Cork. *J Ecol* 63:14–162
- Bates JW (1978) The influence of metal availability on the bryophyte and macrolichen vegetation of four rock types on Skye and Rhum. *J Ecol* 66:457–482
- Blanchard DL (1957) Discussion of Raindrop distributions made during “project shower.” Hawaii, 1954. In: Weickmann H, Smith W (eds) *Artificial Stimulation of Rain*. Pergamon Press, Newark, pp 213–223
- East TWR (1957) Precipitation of convective water clouds. In: Weickmann H, Smith W (eds) *Artificial stimulation of rain*. Pergamon Press, Newark, pp 192–201
- Grace JB, Wetzel RG (1982) Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Can J Bot* 60:46–57
- Grubb PJ (1976) A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biol Cons* 10:53–76
- Hitschfeld W (1957) Size distribution generated by a random process. In: Weickmann H, Smith W (eds) *Artificial stimulation of rain*. Pergamon Press, Newark, pp 224–228
- Hofmann F, Nowak R, Winkler S (1974) Substrate dependence of calcareous and silicate rock inhabiting lichens of the Island CIOVO, Yugoslavia. *J Hattori Bot Lab* 38:313–325
- Joss J, Thams JC, Waldvogel A (1968) The variation of raindrop size distribution at Locarno. *Proc Intl Conf on Cloud Physics*. Toronto
- Larson DW (1979) Lichen water relations under drying conditions. *New Phytol* 82:713–731
- Larson DW (1980a) Patterns of species distribution in an *Umbilicaria* dominated community. *Can J Bot* 58:1269–1279
- Larson DW (1980b) Seasonal change in the pattern of net CO₂ exchange in *Umbilicaria* lichens. *New Phytol* 84:349–369
- Larson DW (1981) Differential wetting in some lichens and mosses: the role of morphology. *The Bryologist* 84:1–15
- Lawrey JD (1981) Evidence for competitive release in simplified saxicolous lichen communities. *Am J Bot* 68:1066–1073
- Llano GA (1950) A monograph of the lichen family *Umbilicariaceae* in the Western Hemisphere. Office of Naval Research. Washington, D.C. Navexus P-831
- Marshall JS, Palmer W Mck (1948) The distribution of raindrops with size. *J Meteor* 5:165–166
- Pentecost A (1980) Aspects of competition in saxicolous lichen communities. *Lichenologist* 12:135–144
- Pruppacher HR, Klett JD (1978) *Microphysics of clouds and precipitation*. D Reidel Pub Co, Boston
- Smart HJ, Gee JH (1979) Coexistence and resource partitioning in two species of darters (Percidae) *Etheostoma nigrum* and *Percina maculata*. *Can J Zool* 57:2061–2071
- Solbrig OT (1971) The population biology of dandelions. *Amer Sci* 59:686–94
- Topham PB (1977) Colonization, Growth, Succession and competition. Ch. 3, In: Seaward MRD (ed) *Lichen Ecology*. Academic Press, New York, pp 31–68
- Turkington RA, Harper HL (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture IV. Fine-scale biotic differentiation. *J Ecol* 67:245–254
- Twomey S (1977) *Atmospheric Aerosols*. Elsevier Pub. Co. N.Y.
- Weickmann H (1957) A nomogram for the calculation of collision efficiencies. In: Weickmann H, Smith W (eds) *Artificial stimulation of rain*. Pergamon Press, Newark, pp 161–166
- Werner PA (1977) Colonization success of a “biennial” plant species: experimental field studies in species colonization and replacements. *Ecology* 58:840–49
- Werner PA (1979) Competition and Coexistence of similar species. Ch. 12. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) *Topics in plant population biology*. Columbia University press. New York, pp 287–312
- Wiesner CJ (1970) *Hydrometeorology*. Chapman and Hall
- Yarranton GA, Green WGE (1966) The distribution patterns of crustose lichens on limestone cliffs at Rattlesnake Point, Ontario. *Bryologist* 69:450–461

Received October 8, 1983