Experimental strain analysis of Clarens Sandstone colonised by endolithic lichens

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Endolithic lichens occur commonly on Clarens Sandstone in South Africa, where they significantly contribute to the weathering of sandstone by means of mechanical and chemical weathering processes. This preliminary investigation reports on the successful use of strain gauges in detecting strain differences between sandstone without epilithic lichens and sandstone colonised by the euendolithic lichen *Lecidea* aff. *sarcogynoides* Körb. Mechanical weathering, expressed as strain changes, in Clarens Sandstone was studied during the transition from relatively dry winter to wet summer conditions. Daily weathering of sandstone due to thermal expansion and contraction of colonised and uncolonised sandstone could be shown. Our results show that liquid water in sandstone enhances the mechanical weathering of uncolonised Clarens Sandstone while water in the gaseous phase enhances mechanical weathering of sandstone by euendolithic lichens.

Key words: strain gauge, endolithic, sandstone, weathering, microclimate, lichen.

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Introduction

Endolithic lichens occur universally in a diversity of rock types and exhibit a variety of growth forms classified by Golubic *et al.* (1981). In harsh environments like the hot (Danin & Garty 1983; Friedmann 1972; Friedmann 1980) and cold (Friedmann *et al.* 1981; Friedmann 1982) deserts of the world, endolithic lichens are successfully exploiting a microhabitat unavailable to phanerogams. Existing knowledge on endolithic lichens was reviewed by Friedmann & Ocampo-Friedmann (1984), Lawrey (1984) and Nienow & Friedmann (1993). Piervittori *et al.* (1994) compiled a bibliographic review of literature on lichens and biodeterioration.

Weathering of substrates in which endolithic lichens grow has been ascribed to chemical and mechanical processes (Nienow & Friedmann 1993; Syers & Iskandar 1973). Conflicting evidence as to the relevance of lichens to weathering and soil formation has been highlighted by Syers & Iskandar (1973). The significance of endolithic lichens to soil formation in the eastern Orange Free State was discussed by Wessels & Schoeman (1988) and Wessels & Wessels (1991). Using Scanning Electron Microscope studies, Wessels & Schoeman (1988) have shown the effect of chemical weathering by the euendolithic lichen *Lecidea* aff. *sarcogynoides* Körb. on Clarens Sandstone. Based on the average diameters of the largest thalli on a datable Clarens Sandstone substrate Wessels & Wessels (1995) determined that annual radial growth proceeds at a rate of 2.1 mm per year. Vertical penetration of the sandstone theoretically occurs at a rate of 0.1 mm per year. The photosynthetic performance of

Lecidea aff. *sarcogynoides* and other endolithic lichen species was investigated by Wessels & Kappen (1993; 1994) in different sandstone and climatic types of South Africa. Little is known about the exact rates and mechanisms by means of which endolithic lichen communities weather rocks in other parts of the world.

Mechanical weathering of sandstone by endolithic lichens within sandstone has never been quantified or studied in detail and only speculative information about the mechanical weathering of rocks by colonising endolithic lichens exists (Lawrey 1984; Nienow & Friedmann 1993; Wessels & Schoeman 1988). The principal aim of this pilot study was to decide whether strain gauges can be used to measure strain differences in colonised and uncolonised sandstone. Strain gauges are important tools for the electrical measurement of mechanical quantities (Hoffmann 1973). Such gauges measure both tensile and compressive strain; continuous variations of strains eventually cause fragmentation of substrates such as sandstone. In addition we also aimed at investigating the relationship between micro-climatic and strain changes in sandstone. We consequently measured several micro-climatological parameters at the lichen colonised Clarens Sandstone outcrop. In addition, we chose to set up the experiment during the change over from relatively dry winter to rainy summer conditions.

Study site

Golden Gate (28°31'S; 28°37'E) lies in the Bethlehem district of the Orange Free State Province, South Africa. The park lies in the Rooiberg Mountain Range, between 1 892 and 2 837 m a.s.l. Grass species cover large parts of the park with its severely undulating topography. The park is characterised by impressive sandstone outcrops belonging to different geological formations (Groenewald 1986). Endolithic lichens form the dominant cryptogamic component of exposed sandstone outcrops in the park. The study concentrated on a north-facing Clarens Sandstone outcrop, called the Les-site (Wessels & Wessels 1995), 3.6 km from the Glen Reenen Rest Camp along the Ribbok-loop road.

Material

A thallus of the euendolithic lichen species *Lecidea* aff. *sarcogynoides* Körb. was used in the study. Specimens of the experimental material are deposited in the National Herbarium, Pretoria. The thallus grows slanted at 6° toward the north and 9° toward the east, had an average diameter of 450 mm and fronts directly north.

Methods

Microclimatic measurements

Air and sandstone temperatures were measured by means of copper constantan thermocouples (1.0 mm wire diameter). The air temperature was measured at the centre of the measuring site within a radiation screen (Control Instruments, Johannesburg), 400 mm above the sandstone surface. Relative humidity (RH) of the air was measured within the same radiation screen with a Vaisala humidity probe, Model HMP35A (Vaisala, Helsinki, Finland). Rainfall was recorded with a tipping bucket rain gauge, Model P501-I (WeatherMeasure, Sacramento) at the centre of the measuring site. The rim of the rain gauge was 489 mm above the sandstone surface.

Relative humidity of sandstone air spaces was determined with a second Vaisala probe at the centre of the measuring site. The probe was inserted into a tight fitting hole 35 mm below the sandstone surface and sealed at the surface with "Prestik" (Bostik Ltd, England). Sandstone temperature was measured by a thermocouple placed on the surface of the sandstone and sealed off with SG 250 protective coating (Hottinger Baldwin Messtechnik GMBH, Darmstadt).

The presence of liquid water within the sandstone was qualitatively determined by recording the interaction between the electrical conductivity of sandstone and its moisture regime. Such a sensor consists of two copper electrodes (3.2 mm in diameter) driven into holes 3 mm in diameter, 20 mm deep and 10 mm apart. One member of the pair was connected to a 5-V reference signal and the other to a 12.0 kOhm fixed resistor connected to ground. The voltage drop across the fixed resistor was then recorded. One such sensor was placed in the uncolonised sandstone, next to the experimental thallus.

A supply voltage of 5 V was applied to the strain gauges and electrodes of the liquid water sensors. To prevent oxidation of the electrodes, the supply voltage was applied to the electrodes only during logging times that lasted for five seconds every 10 minutes.

Strain measurements

Strain changes in the uncolonised sandstone and lichen thallus were measured with multiple-grid strain gauges, Model XY91 3/120 (Hottinger Baldwin Messtechnik GMBH, Darmstadt). One strain gauge was attached to the surface of the lichen, at its growing edge. A second strain gauge was placed directly opposite the first (grids facing the same directions) on the rim of uncolonised sandstone (called rim). The rim (slanted 6° toward the north and 2° toward the east) surrounds the lichen thallus and protrudes *ca.* 4.0 mm above the surface of the sunken lichen. Care was taken to select flat surfaces at both measuring positions.

Both strain gauges were cemented onto cleaned substrates with X60 cold hardening adhesive (Hottinger Baldwin Messtechnik GMBH, Darmstadt). They were sealed against external effects such as humidity and mechanical disturbance with protective coating SG250 (Hottinger Baldwin Messtechnik GMBH, Darmstadt). To increase the sensitivity of the strain gauges, we connected the individual elements of the multiple grid strain gauges to opposite arms of the Wheatstone bridges (Hoffmann 1986). With this configuration we could not differentiate between radial and tangential strains at the measuring points. During the experiment we could only measure the change in strain with reference to the state of strain present at the beginning of the investigation. Our results, therefore, represent strain changes associated with a changeover from relatively dry winter to wet summer conditions.

Temperature compensation was achieved through two inactive strain gauges, completing the four elements of the Wheatstone bridge. Two single element strain gauges Model LY11 6/120 (Hottinger Baldwin Messtechnik GMBH, Darmstadt), were used as inactive strain gauges. These strain gauges were not attached to the substrate but the flexible wires connected to the strain gauges were glued to the sandstone. The two inactive sets of strain gauges were sealed from the natural elements by covering both with the bottom of a Petri dish (90 mm in diameter) which was tightly sealed with "Prestik". During the day, the Petri dish was covered with reflective aluminium foil to prevent overheating of the inactive strain gauges. All the strain gauges were connected to thin, flexible wire, by means of soldering terminals—Model LS7 (Hottinger Baldwin Messtechnik GMBH, Darmstadt). A four-wire connecting system was used.

Outputs from all the sensors were connected to a personal computer, modified as a data logger (PC-logger). The PC-logger consists of a 286-motherboard fitted with a PC74 analog to digital converter board (Eagle Technology, Cape Town). Power to the PC-logger was supplied by two 115AH 12V, charged at the site with a 40 W solar panel. Power rectification and stabilisation to the PC-logger motherboard was through a DC-DC converter, Series DC 100 (Eagle Technology, Cape Town). Logging of the data was done every ten minutes and started at 21:00 on 25 October 1994 and ended at 16:00 on 1 November 1994. Time is given as South African standard time (30 °E). The logged data was serially transferred from the PC-logger to a laptop computer on a daily basis.

Results

Macroclimate of the study area

Golden Gate falls within the summer rainfall region of South Africa and receives an average rainfall of 837 mm per annum. On average 103 rainfall incidences occur per year, frequently as thunder storms. Most of the rainfall incidences occur during October to April. The winters are cold and the summers mild; the average monthly minimum temperatures for January and July are 13.2 °C and 0.3 °C, respectively. Average monthly maximum temperatures for the

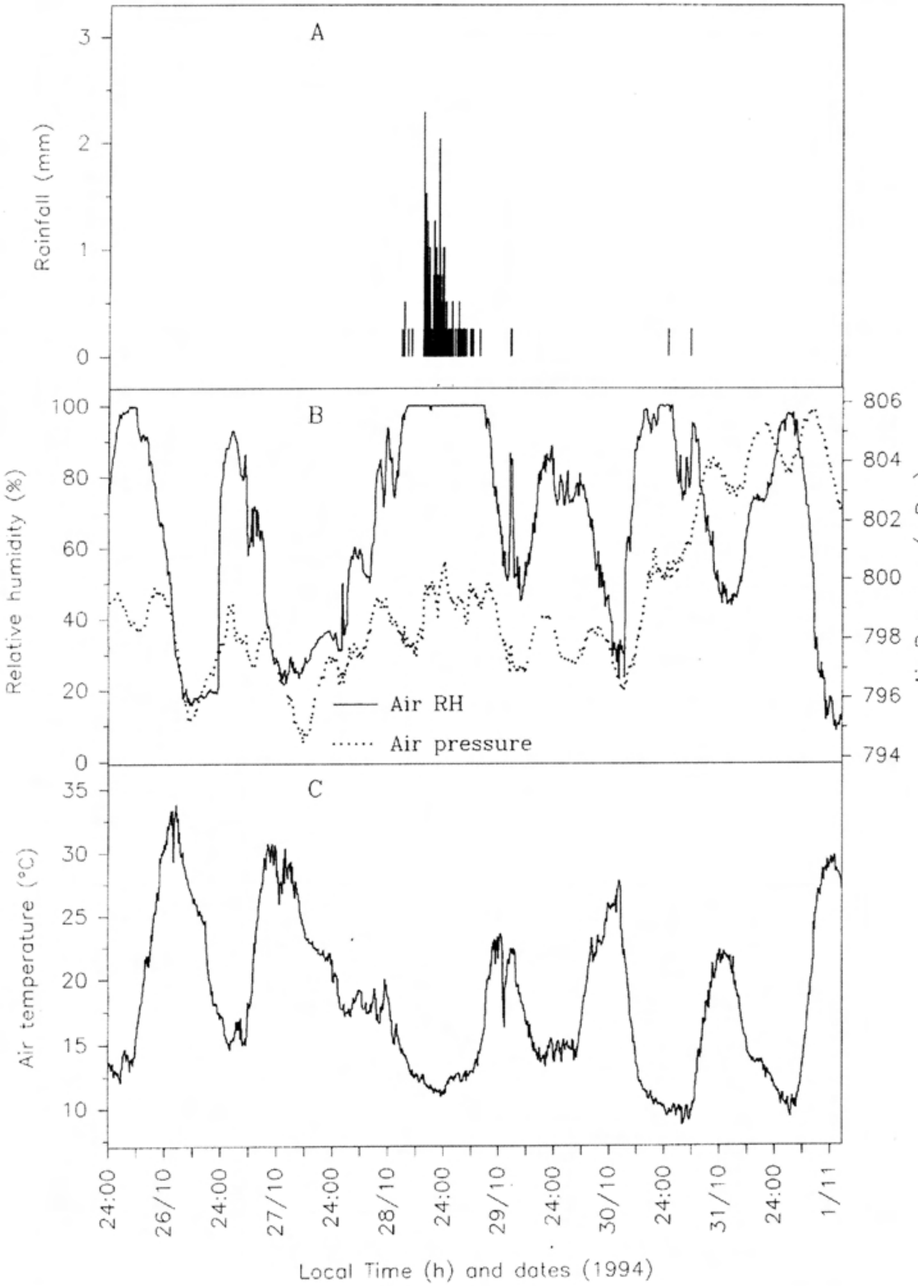

Fig. 1. Diurnal microclimate of a Clarens Sandstone outcrop in the Golden Gate Highlands National Park, South Africa. A: Rainfall incidences and amount of precipitation every 10 minutes. B: Relative humidity of the air and air pressure, measured 400 mm above the sandstone surface. C: Air temperature measured 400 mm above the sandstone surface.

same months are 25.8 °C and 15.2 °C. Infrequent snow falls occur during winter, frost is a regular occurrence during winter nights and dew occurs regularly throughout the year.

Microclimate of the study site

Cloudless conditions prevailed during the morning and early afternoon of 26 October 1994 and most of the day of 1 November 1994. All the other days were cloudy to varying degrees; heavy clouds prevailed on 28 October 1994. Prior to the rainfall incidences (Fig. 1A), the maximum afternoon temperature rose to a high of 33.8 °C (Fig. 1C) and the lowest recorded was 12.5 °C. Days immediately after the first summer rains saw maximum afternoon air temperatures below 30 °C and a minimum as low as 8.6 °C. During the entire measuring period, air temperature showed a range of 25.2 °C.

Air pressures below 800 mb were recorded during the first part of the study period. Unstable air pressures (Fig. 1B), accompanied by moisture-laden easterly winds resulted in 35.3 mm of rainfall, mainly during the night of 28 October and early morning of 29 October (Fig. 1A). Similar short-term changes resulted in two additional rainfall incidences with small amounts of rain falling during the early hours of 31 October (Figs. 1A & 1B). The total amount of precipitation recorded during the survey was 36.3 mm. After the last rainfall incidence on 31 October, air pressure rose sharply and no further rainfall incidences occurred.

The average RH of the air was 66.4%, but showed a considerable range of 91.1%, as RH of the air had dropped to only 8.6% on 1 November 1994 (Fig. 1B). Contrary to changes in air RH, the RH of sandstone air spaces showed little change (Figs. 2A & 3A). Prior to the rainfall incidence, the RH of sandstone air spaces fluctuated between a minimum of 65.2, and a maximum of 85.5%; with an average of 81.6%. Except for short periods of time, the RH of sandstone air spaces after the rain remained at 100% (Fig. 3A). The average RH of sandstone air spaces during the whole measuring period was 91.1%, with a range of only 34.8%.

Daily strain changes within the sandstone and thallus—prior to the rainfall incidence

Diurnal strain changes at the lichen's growing edge and rim as influenced by temperature changes are shown in Fig. 2C. This is evident from the strain gauge tracing on 27 October where oscillating sandstone temperatures resulted in corresponding oscillations in strain at the rim and thallus. During the cloudy morning of 28 October, a gradual increase in sandstone temperature resulted in an equally gradual increase in strain (Fig. 2C). The sensitivity of strain changes in both the lichen thallus and rim to small-scale temperature changes, are highlighted by corresponding sets of arrows in Figs. 2A and 2C.

High nightly air humidities (maxima above 90%) were recorded during the period 26 to 28 October (Fig. 2A). During this period, uptake of water vapour from the air by mycobiont hyphae and photobiont cells resulted in their swelling. Ensuing expansion of the lichen thallus resulted in changes in the sizes of lichen colonised inter crystal spaces and rearrangement of quartz crystals. This resulted in elevated strain values (Fig. 2C) recorded at the growing edge of the lichen, compared to strain differences during the mornings. The effect of high air humidities in combination with high sandstone airspace humidities on thallus strain is particularly evident during the night (Fig. 2C). During periods of high air humidities, strain disparities between the rim and thallus are at their largest.

A decrease in air humidity during the mornings (Fig. 2A) and an increase in thallus temperature (Fig. 2A) resulted in

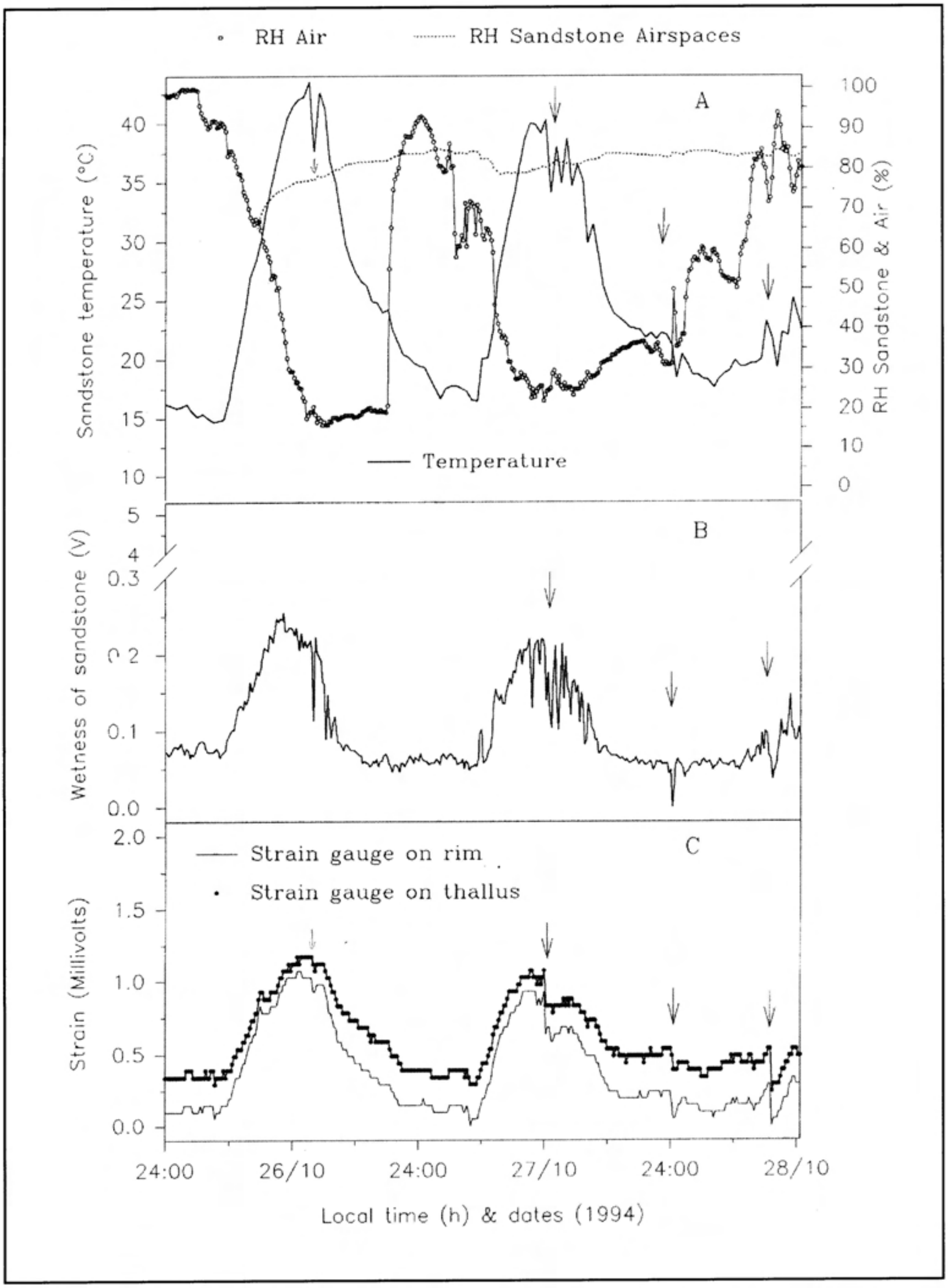

Fig. 2. Diurnal microclimatic conditions and strain changes in lichen-colonised sandstone and surrounding sandstone rim in a Clarens Sandstone outcrop in the Golden Gate Highlands National Park, before a rain shower. A: Sandstone temperature, humidity of the air and humidity of air spaces within the sandstone. B: Wetness trace of the uncolonised sandstone. C: Strain changes in uncolonised sandstone (rim) and an euendolithic lichen colonising the sandstone.

drying out of the thallus due to evaporation. This presumably resulted in the shrinkage of lichen tissue and rearrangement of quartz crystals, giving rise to a slight decrease in thallus strain. Increased RH of sandstone airspaces during the day (Fig. 2A) and simultaneous uptake of available capillary water (Fig. 2B) during the morning will mask the effect of evaporative moisture loss from the thallus on thallus strain. Thermal expansion of the sandstone will furthermore mask the effect of moisture loss from the thallus.

An increase in sandstone temperature during the morning and simultaneous capillary movement of water within the sandstone resulted in slight increases in the water content of the first 20 mm of sandstone (Figs. 2A & 2B). Both factors contributed to an increase in strain at the rim. This resulted in the gradual reduction of strain differences between the thallus growing edge and rim (Fig. 2C). Drying out (Fig. 2B) and cooling of the rim during the afternoon resulted in decreased strain (Fig. 2C). Poorer retention of water by the rim resulted in increased discrepancies between thallus strain and rim strain (Fig. 2C).

Daily strain changes within the sandstone and thallus—after the rainfall incidence

Cooling of the sandstone and thallus prior to the rain shower (Fig. 1A) resulted in a reduction in thallus and rim strain (Fig. 3C). Soon after the rain shower, strain in the wet sandstone rim (compare Figs. 3B & 3C) exceeded that of the lichen thallus (Fig. 3C, ↓a) and continued until the morning of 30 October (Fig. 3C, ←b), a reversal of trends recorded before the rainfall incident (Fig. 2C). This reversal was due to a marked increase in liquid water in the sandstone (compare Figs. 2B & 3B), together with additional strain exerted by lichen hyphae extending into the rim.

A reduction in sandstone temperature and drying out of the sandstone (Fig. 3B, ↓c) during the night of 29 October resulted in decreased strain at both measuring points (Fig. 3C, ↓d). After sunrise on 30 October, increased sandstone temperatures (Fig. 3A) resulted in a rapid increase in the water content (Fig. 3B, ↑e) of the first 20 mm of sandstone. High levels of liquid water in the sandstone (Fig. 3B, ↑e) resulted in strain levels at the rim remaining higher than at the growing edge of the thallus ((Fig. 3C, ↓f). Rapid drying out of the sandstone rim on 30 October (Fig. 3B, ←g), resulted in an equally rapid decline in strain at the rim (Fig. 3C, ←b), in spite of the continued increase in sandstone temperature (Fig. 3C, ↓h). Rewetting of the sandstone by light rain showers before sunrise on 31 October resulted in a decline instead of an immediate increase in strain at both measuring points. This phenomenon can be ascribed to the continued decline in sandstone temperature (Fig. 3A, ←i) after the last rain shower had occurred (compare Figs. 1A & 3A). Rising sandstone temperatures after sunrise, together with an increase in water (Fig. 3B), resulted in smaller strain differences between the rim and thallus than the following morning (Fig. 3). Continued drying of the sandstone (Fig. 3B), resulted in a continued decline of strain in the rim—compared with strain at the growing edge of the thallus.

A combination of high air humidities, saturation of sandstone air spaces with water vapour (Fig. 3A) and increased amounts of liquid water in the sandstone resulted in continuous turgidity of the lichen thallus. This resulted in strain at the growing edge of the lichen remaining much higher than strain at the rim (Fig. 3C). Sandstone air spaces saturated with water vapour and equally high levels of water vapour in the air during the night resulted in large strain differences between the two measuring points.

Discussion

Lichens are poikilohydric organisms without specific organs for water

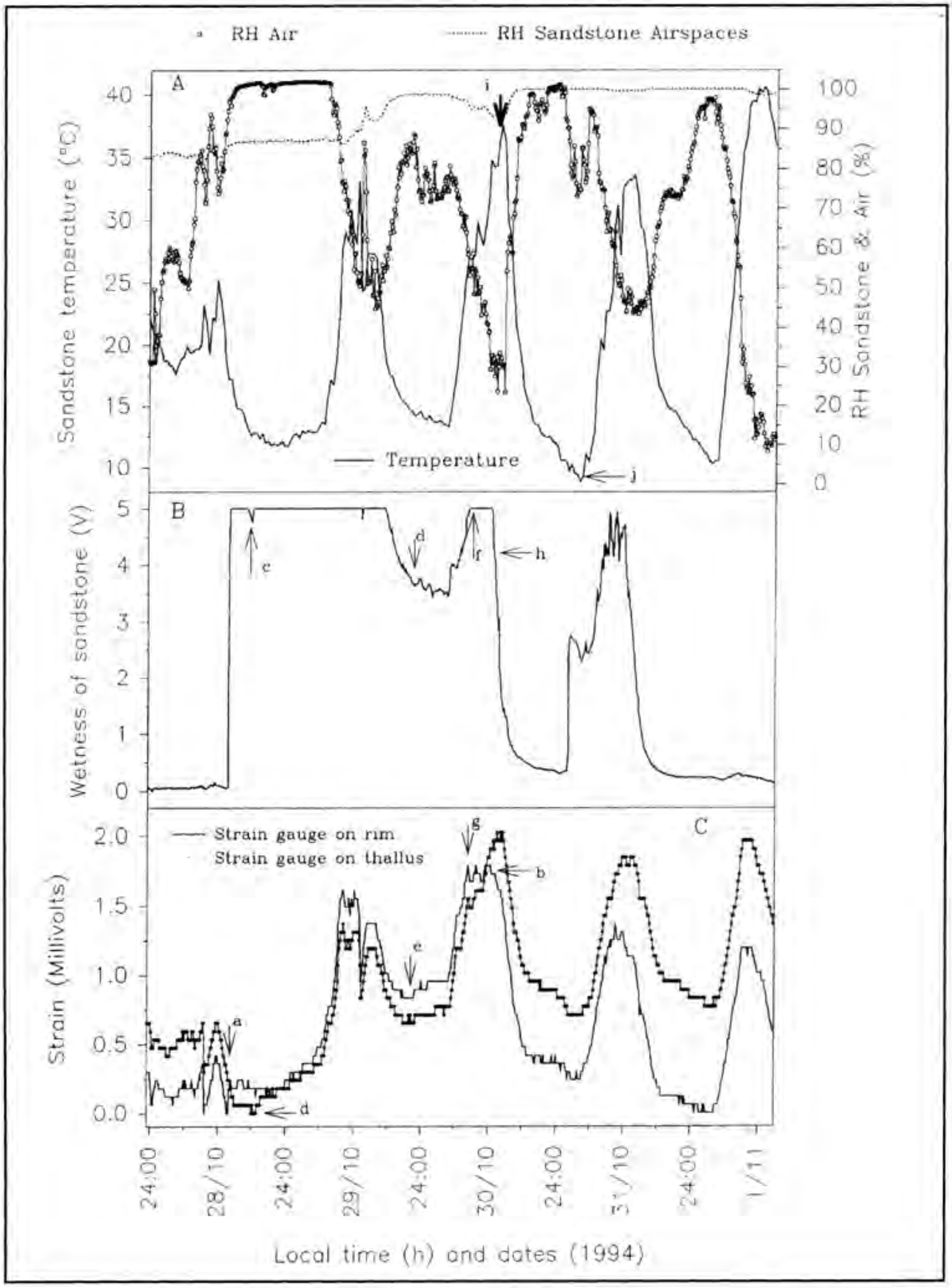

Fig. 3. Diurnal microclimatic conditions and strain changes in colonised sandstone and surrounding sandstone rim in a Clarens Sandstone outcrop in the Golden Gate Highlands National Park, South Africa after a rain shower. A: Sandstone temperature, humidity of the air and humidity of air spaces within the sandstone. B: Wetness trace of the uncolonised sandstone. C: Strain changes in uncolonised sandstone and in an euendolithic lichen colonising the sandstone.

conservation and control over moisture content like phanerogams (Blum 1973). The moisture content of epilithic thalli is thus strongly coupled to environmentally available water and lichen water relations have generated considerable ecophysiological interest (Kershaw 1985; Palmer & Friedmann 1990; Rundel 1988). Little is known about the physiological state of endolithic lichens and associated morphological changes. Such studies have been done on epilithic lichens in the dry state (Ascaso *et al.* 1985; Brown *et al.* 1987) and after water uptake from the air (Büdel & Lange 1991; Scheidegger 1994). The last mentioned researchers found that rising air humidities resulted in increasing turgidity and resultant swelling of lichen thalli. Their findings corroborate our results (Figs. 2 & 3) which show increased strain in a thallus of *L.* aff. *sarcogynoides* at high air humidities. It is shown in Figs. 2 & 3 that the thallus reacted more rapidly and to a larger degree than the rim to changes in the water content of the air. This is especially evident during the morning of 28 October when a combination of high sandstone airspace humidity (Fig. 2A) and increased air humidity resulted in sustained high strain values at the growing edge of the lichen thallus, compared to strain recorded at the rim (Fig. 2C).

Utilisation of the endolithic habitat by lichens requires an anatomical transformation from the formation of plectenchymateous tissue to filamentous growth. Colonisation of the endolithic habitat furthermore entails removal of cementing material which is replaced by more voluminous fungal hyphae and algal cells (Wessels & Schoeman 1988). This leads to an increase in inter crystal space that causes a lateral and vertical expansion of the sandstone-lichen area. Colonisation additionally results in reduced cohesion of quartz grains in the lichen's medullary and cortical layers. Scheidegger (1994) found that thick walled medullary hyphae of *Cetraria islandica* did not collapse at low water content (80% RH). Thick walled medullary hyphae of *L.* aff. *sarcogynoides* may similarly be partly responsible for sustained high levels of thallus strain. The above attributes of a sandstone-lichen-thallus result in a long-term major rearrangement of quartz crystals that relates to increased strain and mechanical weathering.

From the above it is evident that a combination of endolithic lichen thallus morphology and reaction of such a thallus to sustained high air humidities within Clarens Sandstone (Wessels & Wessels 1995) combined with short-term increases in air humidity, ensures constant weathering of the sandstone even during rainless periods. Our results (Figs. 2 & 3) show the amplification effect an increase in moisture (Figs. 3A & 3B) has on the mechanical weathering of sandstone by dramatically increasing the strain (Fig. 3C). It is doubtful whether other rock types colonised by endolithic lichens, but with low air space humidities will be weathered to the same degree as Clarens Sandstone.

The rapid, considerable uptake of water after the rain shower (Fig. 3B) resulted in an obvious rearrangement of the rim's quartz crystals, due to the swift increase in strain at the rim that even exceeded thallus strain (Fig. 3C). Sustained high water content of the sandstone, combined with the effect of colonising turgid thalli, resulted in rim strain exceeding thallus strain for 46 hours after the rain shower (Fig. 3C). Contrary to strain values recorded at the growing edge of the lichen, rim strain values continued to decrease as the water content of the sandstone declined (Figs. 3B & 3C).

Our results (Fig. 3C) indirectly show that after the rain shower the endolithic lichen remained turgid for several days, resulting in sustained high strain values. This was due to the high RH of sandstone air spaces (Fig. 3A)—a characteristic of Clarens Sandstone that indirectly prolongs the weathering effect of rain showers. It is shown in Figs. 2C & 3C that after the rain shower, maximum daily strain values recorded at both measuring

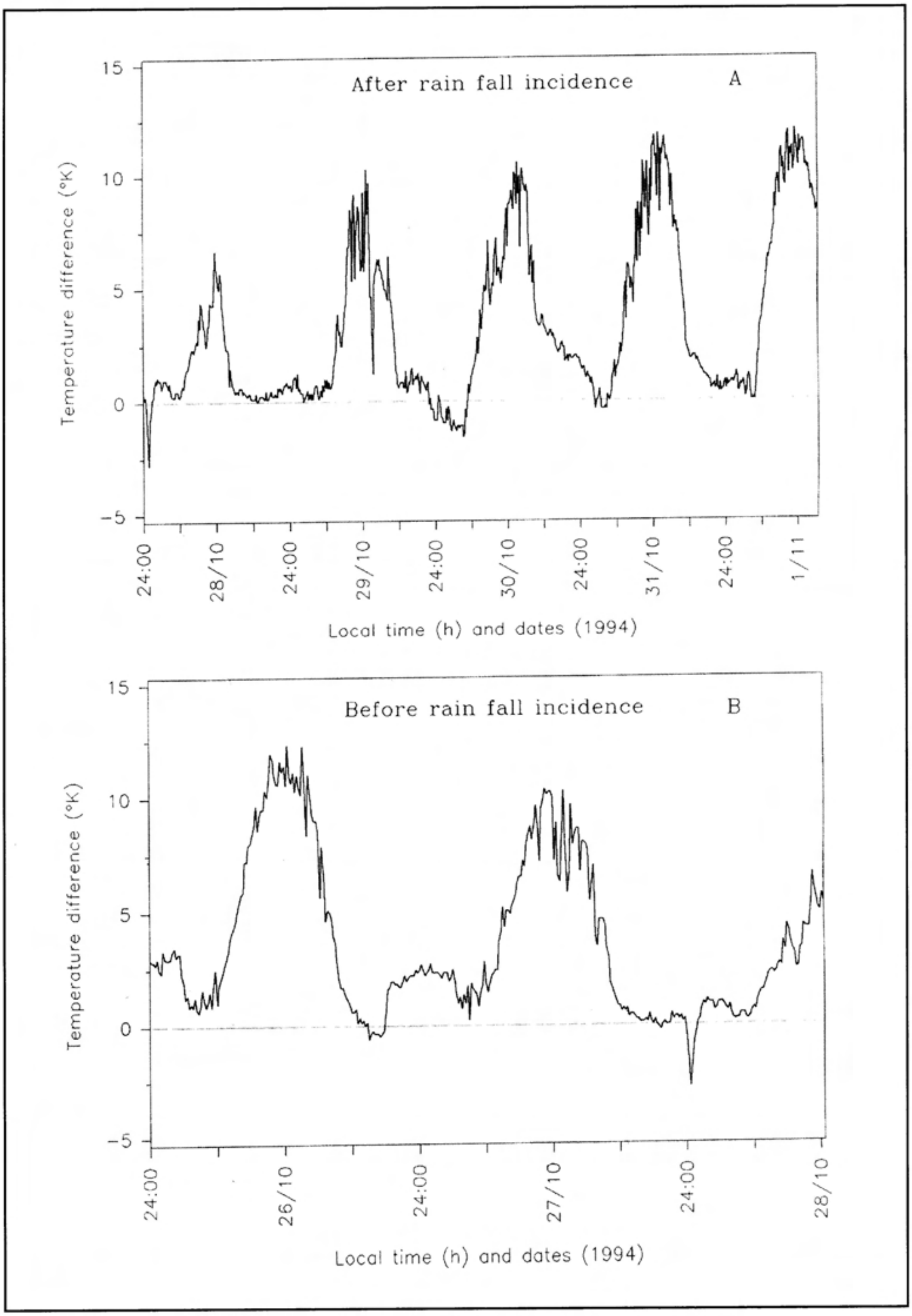

Fig. 4. Daily temperature differences between sandstone surface temperature and air temperature measured in a radiation screen, 400 mm above the sandstone surface.

points were considerably higher than during the rainless period. These results emphasise the catalytic effect sandstone wetness has on its mechanical weathering.

Temperature is an important component of the endolithic environment, regulating the physiological activities of lichens (Kappen 1973; Kershaw 1985; Wessels & Kappen 1993, 1994). As temperature change is significant to the physiology of lichens, it is to the weathering of colonised and uncolonised Clarens Sandstone (Figs. 2 & 3). It is shown in Figs. 4A & 4B that maximum sandstone temperatures during the afternoon exceeded air temperatures by more than 12 °K (Fig. 4). Minimum sandstone temperatures during the early mornings regularly fell below air temperature (Fig. 4), a phenomenon that increases the chances of dew formation on the sandstone. Such dew fall events will have an enhancing effect on the mechanical weathering of sandstone. Wessels & Wessels (1995) reported similar temperature differences for different seasons of the year and showed the regular occurrence of dew on the sandstone outcrop. They also discussed the physiological significance of such temperature patterns to endolithic lichens. From the results shown in Fig. 4 it is evident that mesoclimatic air temperature measurements do not reflect sandstone temperatures at strain gauge measuring points. This characteristic should be considered in studies done under natural conditions. Annual and daily temperature changes result in sustained thermal expansion and contraction (strain changes) in both colonised and uncolonised sandstone (Figs. 2 & 3). This ceaseless mechanical weathering will, in combination with other weathering mechanisms, result in a gradual weakening of the sandstone over time and eventual fragmentation of the sandstone rim

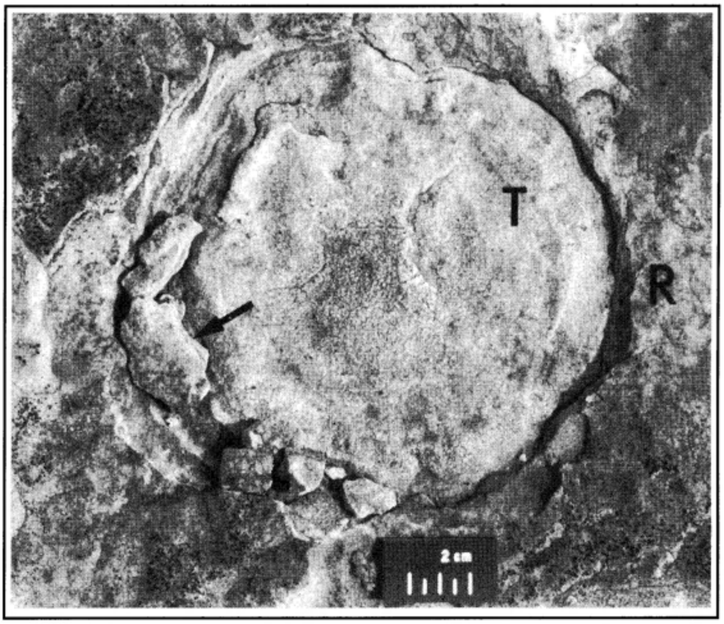

Fig. 5. Continued mechanical and chemical weathering of sandstone surrounding the thallus (T) of the euendolithic lichen *Lecidea.* aff. *sarcogynoides*, eventually results in fragmentation (arrow) of the sandstone rim (R).

(Fig. 5). Small-scale temperature changes on the other hand enhance the weathering effect of diurnal temperature changes (Fig. 2).

From the results presented in Figs. 2 & 3 it is evident that strain gauges can be fruitfully used in explaining the mechanical weathering of rocky substrates colonised by endolithic lichens. Our results highlight the efficient way in which water in a gas form is utilised by endolithic lichens and its enhancing effect on mechanical weathering. Changes in liquid water concentrations in the sandstone are in perfect phase with strain changes in the sandstone. Drastic increases in liquid water have a catalytic effect on the mechanical weathering of uncolonised sandstone. The results also highlight certain physiological aspects of *L.* aff. *sarcogynoides*. Further refinement of the technique and long-term studies will be beneficial in fully understanding the ecophysiology and weathering action of endolithic lichens.

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References

ASCASO, C., D.H. BROWN AND S. RAPSCH. 1985. Ultrastructural studies of desiccated lichens. Pp. 259-274. *In*: BROWN, D.H. (ed.). *Lichen physiology and cell biology.* New York:Plenum Press.

BLUM, O.B. 1973. Water relations. Pp. 381-400. *In*: AHMADJIAN, V. AND M.E. HALE (eds.). *The Lichens*. New York and London:Academic Press.

BROWN, D.H., S. RAPSCH, A. BECKETT AND C. ASCASO. 1987. The effect of desiccation on cell shape in the lichen *Parmelia sulcata* Taylor. *New Phytologist* 105: 295-299.

BÜDEL, B. AND O.L. LANGE. 1991. Water status of green and blue-green phycobionts in lichen thalli after hydration by water vapour uptake: do they become turgid? *Acta Botanica* 104: 361-366.

DANIN, A. AND J. GARTY. 1983. Distribution of cyanobacteria and lichens on hillsides of the Negev Highlands and their impact on biogenic weathering. *Zeitschrift für Geomorphologie* 27: 423-444.

FRIEDMANN, E.I. 1972. Ecology of lithophytic algal habitats in Middle Eastern and North American deserts. Pp. 182-185. In: RODIN, L.E. (ed.). *Ecophysiological Foundation of Ecosystem Productivity in Arid Zones*. Leningrad: Nauka. U.S.S.R. Academy of Sciences.

FRIEDMANN, E.I. 1980. Endolithic microbial life in hot and cold deserts. *Origins Life* 10: 223-235.

FRIEDMANN, E.I. 1982. Endolithic microorganisms in the Antarctic cold deserts. *Science* 215: 1045-1052.

FRIEDMANN, E.I. AND R.I. OCAMPO-FRIEDMANN. 1984. Endolithic microorganisms in extreme dry environments: Analysis of a lithobiontic microbial habitat. Pp. 177-185. *In*: KLUG, M.J. AND REDDY, C.A. (eds.). *Current Perspectives in Microbial Ecology.* Proceedings of the Third International Symposium on Microbial Ecology. Washington, D.C: American Society for Microbiology.

FRIEDMANN, E.I., O.R. FRIEDMANN AND C.P. MCKAY. 1981. Adaptations of cryptoendolithic lichens in the Antarctic desert. *Colloque sur les Ecosystèmes Subantarctiques. 1981, Paimpont, C.N.F.R.A.* 51: 65-69.

GOLUBIC S., E.I. FRIEDMANN AND J. SCHNEIDER. 1981. The lithobiontic ecological niche, with special reference to microorganisms. *Journal of Sedimentary Petrology* 51: 475-478.

GROENEWALD, G.H. 1986. Geology of the Golden Gate Highlands National Park. *Koedoe* 29: 165-181.

HOFFMANN, K. 1973. *Fundamentals of the strain gauge technique: The strain gauge, a universal tool of the experimental stress analysis.* Publication VD73004e. Darmstadt: Hottinger Baldwin Messtechnik GMBH.

HOFFMANN, K. 1986. *Electrical measurement of mechanical quantities: Applying the Wheatstone bridge circuit.* Publication VD72001e. Darmstadt: Hottinger Baldwin Messtechnik GMBH.

KAPPEN, L. 1973. Response to extreme environments. Pp. 311-380. *In*: V. AHMADJIAN AND M.E. HALE, (eds.). *The Lichens*. New York: Academic Press.

KERSHAW, K.A. 1985. *Physiological ecology of lichens*. Cambridge : Cambridge University Press.

LAWREY, J.D. 1984. *Biology of lichenized fungi*. New York: Praeger.

NIENOW, J.A. AND E.I. FRIEDMANN. 1993. Terrestrial lithophytic (rock) communities. Pp. 343-412. FRIEDMAN, E.I. (ed.). *Antarctic Microbiology*. New York:Wiley-Liss, Inc.

PALMER, R.J. AND E.I. FRIEDMANN. 1990. Water relations, thallus structure and photosynthesis in Negev Desert lichens. *New Phytologist* 116: 597-603.

PIERVITTORI, R., O. SALVADORI AND A. LACCISAGLIA. 1994. Literature on lichens and biodeterioration of stonework. I. *Lichenologist* 26: 171-192.

RUNDEL, P.W. 1988. Water relations. Pp. 17-36. *In*: GALUN, M. (ed.). *CRC Handbook of Lichenology*. Boca Raton: CRC Press.

SCHIEDEGGER, C. 1994. Low-temperature scanning electron microscopy: the localization of free and perturbed water and its role in the morphology of the lichen symbionts. *Cryptogamic Botany* 4: 290-299.

SYERS, J.K. AND I.K. ISKANDAR. 1973. Pedogenetic significance of lichens. Pp. 225-248. *In*: AHMADJIAN, V. AND M.E. HALE (eds.). *The Lichens*. New York: Academic Press.

WESSELS, D. AND L. KAPPEN. 1993. Photosynthetic performance of rock-colonising lichens in the Mountain Zebra National Park, South Africa. *Koedoe* 36: 27-48.

WESSELS, D.C.J. AND L. KAPPEN. 1994. Aspect, microclimate and photosynthetic activity of lichens in the northern Transvaal and Karoo. *Cryptogamic Botany* 4: 242-253.

WESSELS, D.C.J. AND P. SCHOEMAN. 1988. Mechanisms and rate of weathering of Clarens Sandstone by an endolithic lichen. *South African Journal of Science* 84: 274-277.

WESSELS, D.C.J. AND L.-A. WESSELS. 1991. Erosion of biogenically weathered Clarens Sandstone by lichenophageous bagworm larvae (Lepidoptera; Psychidae). *Lichenologist* 23: 283-291.

WESSELS, D.C.J. AND L.-A. WESSELS. 1995 (*in press*). Biogenic weathering and microclimate of Clarens Sandstone in South Africa. *Cryptogamic Botany* 5.