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THE ECOPHYSIOLOGY OF SURFACE CRYPTOGAMS FROM ALPINE TUNDRA AND SEMI-ARID GRASSLAND OF SOUTHWESTERN ALBERTA

By

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ABSTRACT

The seasonal response patterns of net photosynthesis and respiration (and nitrogenase activity in Nostoc) are described within a multivariate framework of temperature, moisture and light for the alpine and grassland crustaceous lichens Rhizocarpon superficiale and Caloplaca trachyphylla respectively and for the grassland surface cyanophyte Nostoc commune. These physiological responses are discussed in context of each species' boundary layer environment, with particular emphasis placed on interactions between environmental constancy and adoption of acclimation strategies.

For R.superficiale the high frequency of thermal fluctuations experienced by hydrated thalli, sometimes on an hourly basis, precluded any strategy of seasonal acclimation. Instead, photosynthetic rates exhibited a broad temperature response, remaining near 1 mg CO_2 h^{-1} g^{-1} from 1 up to 21 °C, with no changes evident between seasonal responses. In marked contrast C.trachyphylla shows a distinct winter/summer pattern of photosynthetic acclimation. In winter months rates are optimal near 7 °C, while in summer the temperature optima of net photosynthesis shift to 21 °C. These changes correlate well with predictable seasonal microclimate events, particularly those associated with winter Chinook snowmelt periods. A third pattern of response was seen in N.commune, where no seasonal changes in response patterns were evident and both nitrogenase activity and net photosynthesis were maximal near 35 °C. This response pattern allows maximum carbon gain and nitrogen fixation

during spring and summer periods following precipitation events, while its more sheltered aspect reduces the importance of winter snowmelt periods.

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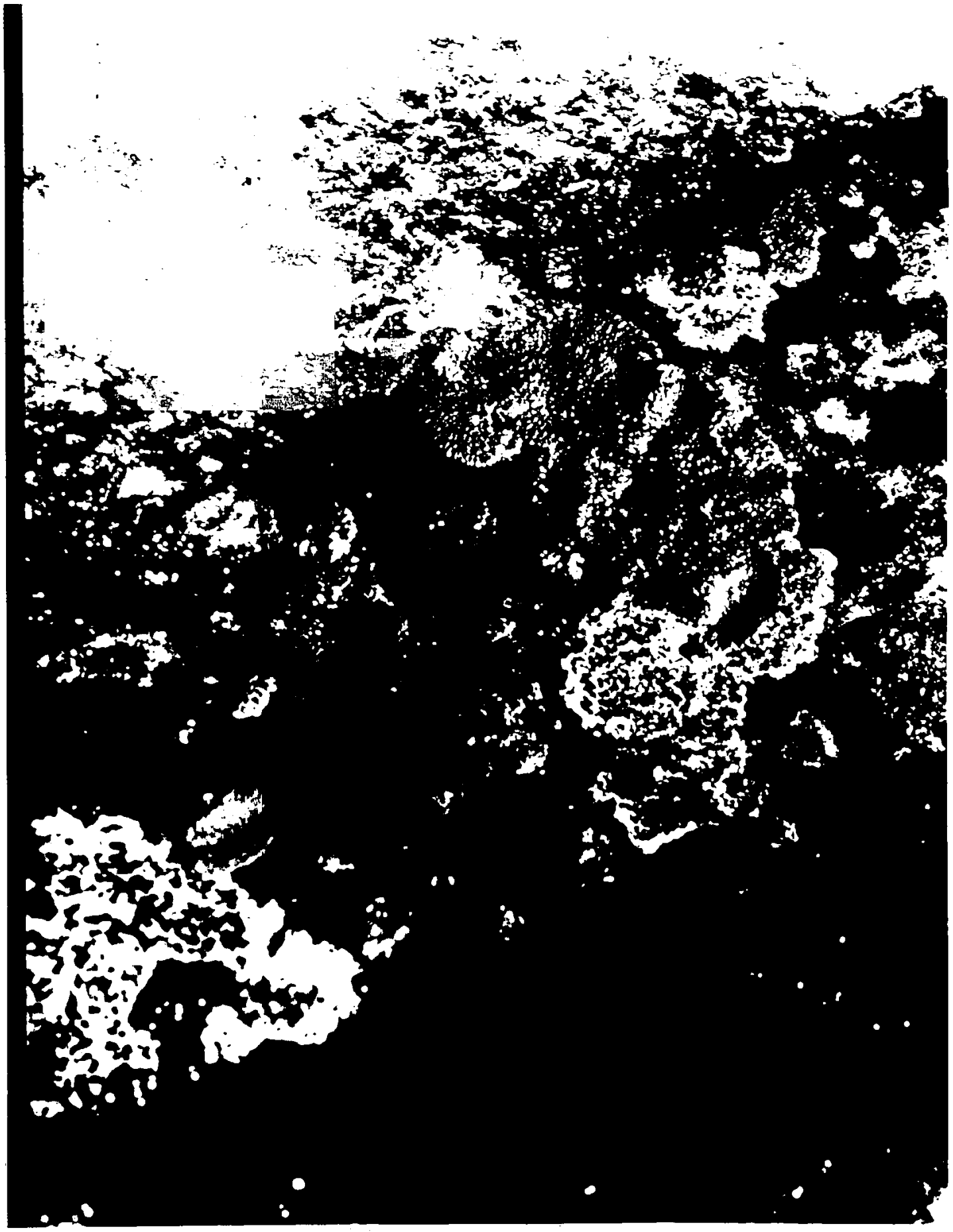
Plate 1

Thalli of the crustaceous lichen *Caloplaca trachyphylla* under midwinter snowmelt conditions.



Section 1.

INTRODUCTION

(1.1) The Operating Environment

The study of interactions between plants and their environment is central to the field of plant ecology. Early investigators considered assemblages of plant species as holistic entities, which like organisms were born, grow, reproduce, and die (Clements 1916, 1928). Change in vegetation with time (succession) was compared to developmental stages of organisms, having a characteristic sequence and tending towards a fixed endpoint or climax type. Tansley (1920) pointed out the rigidity of this approach to the study of vegetation, noting that while some species were indeed always found in the company of certain others (ie. an organismic approach), many exceptions existed. These inconsistencies led Gleason (1926) to propose a more individualistic concept of plant community development. Gleason suggested that plant communities were merely fortuituous assemblages of species, the existence of each being determined by individual interactions with environmental parameters. The absence of discrete boundaries between plant communities was cited in support of this concept, each species responding to environmental gradients independently in time and space. This individualistic concept of physiological-environmental interactions subsequently led to a much

greater emphasis on documentation of actual physical parameters experienced by plant species. As a means of coping with the increasing flood of information Mason and Langenheim (1957) proposed that the term operating environment be used to denote those physical attributes of the plants environment which are actually interacting with physiological processes. These interactions could either be direct, as in the case of temperature dependent biochemical reactions, or indirect, as in the case of seasonal cues triggering subsequent physiological events. This definition was based on the presumption that considered physical phenomena were actually experienced (by the organism) on the same spatial and temporal scales as that measured by the researcher. While this may seem a redundant statement of fact, the critical examination of spacial gradients under field conditions has only recently become widespread practice. The review of boundary layer microclimate concepts by Geiger (1965) in particular, was especially instrumental to this increased awareness.

The two habitats studied in the present work, alpine tundra and semi-arid grassland, are each characterized by a predominance of plant species whose primary ecophysiological strategy is one of stress tolerance (Grime, 1979). Competitive interactions in these habitats should thus be minimal, while adaptations of physiology to environmental extremes commonplace (Grime, 1979). Emphasis was therefore placed on examining the magnitude and nature of environmental extremes faced by surface cryptogams of alpine and grassland habitats, and their physiological reactions to these extremes. This is not to say that no

other parameters are interacting with their physiology (for instance ionic status), merely that microclimatic parameters, because of their overiding importance in controlling the rate of of physiological processes, are a particularly important area of investigation.

Due to the complexities introduced in work with higher plants by stomatal, root, and specialized reproductive structures, many workers have adopted poikilohydrous cryptogams as experimental organisms for definition of operating environments (Kappen, 1973; Kershaw, 1984). The current research program also utilized surface cryptogams as experimental organisms. More specifically, the responses of net photosynthesis, respiration, and for one species nitrogenase activity, were examined within the framework of temperature, moisture and light conditions established under in-situ field conditions. The resulting synthesis of physiological and microclimatic data were used to determine the operating environment of each species.

(1.1.1) The Alpine - Grassland Contrast

The physiological response of surface cryptogams to their environment was followed in two contrasting habitats: alpine tundra and semi-arid grassland.

In alpine areas the lichen genus Rhizocarpon is a particularly widespread surface cryptogam, characteristically growing closely adpressed to exposed rock surfaces (Flock, 1978). It is a genus which is widely used for lichenometric dating (Porter, 1981), yet little is known

of its habitat or metabolic adaptations. This lack of information on the ecology of Rhizocarpon reflects a general absence of work on crustaceous species until very recently (See Kappen et al., 1981; Pentecost, 1980; Roux, 1979), largely due to the difficulties inherent in working with material adhering to a rock surface. Because of the importance of Rhizocarpon in alpine areas it was felt that a member of this genus would be ideal for studying the responses of alpine surface cryptogams. Accordingly the seasonal rates of net photosynthesis and respiration were determined for a population of R.superficiale (Schaer.) Vain., concurrent with an examination of its boundary layer environment. The choice of the study area was largely dictated by substrate requirements as removal of intact crustaceous lichen colonies for laboratory examination required thinly bedded rock formations from which small sheets (with lichens intact on their upper surface) could be removed. The widespread Precambrian sedimentary rock of the Lewis overthrust fault in the Southwestern Alberta Rockies proved ideal in this respect, with abundant R.superficiale colonies widespread on higher elevation crestal ridges (2100 m).

This study area also proved amenable to the dual interest in both alpine and desert surface cryptogams, as the topography breaks abruptly to cool-steppe grassland only kilometers from the chosen alpine study site. Unfortunately there was no one species common to both habitats in sufficient number for comparitive ecophysiological investigation. However, the crustaceous lichen Caloplaca trachyphyla (Tuck.) A.Zahlbr. was quite abundant at the grassland site, where it is typically found on

sedimentary rock slabs, either exposed glacial erratics, or on eroded bedrock formations. Its highly exposed habitat was reminiscent of that of R.superficiale, both species predominating on slightly elevated rocky ridges surrounded by low sedge and grass communities. C.trachyphylla was thus chosen as the second main species for examination of ecophysiological responses. Again, easy access and substrate requirements played a role in chosing the specific study areas (See Fig. 1).

At the grassland site surface colonies of terrestial blue-green algae (Cyanobacteria) were very common on open soil surfaces. While the role of of diazotrophic blue-green algae and lichens symbionts in the fixation of atmospheric nitrogen is well known (Paul, et al., 1971; Clark, 1977; Reuss and Innis, 1977; Woodmansee, 1978), critical examination of this physiological activity in context of microclimatic parameters was largely lacking for Canadian grasslands. The development of the acetylene reduction assay for nitrogenase activity (Dilworth, 1966; Crittenden and Kershaw, 1979) provides an ideal method for experimental studies, which in combination with CO_2 gas exchange measurements allows an even more comprehensive documentation of physiological strategies. Terrestrial colonies of N.commune Vaucher were thus chosen as the third study organism of the thesis research. Again boundary layer effects were followed over seasonal periods under field conditions. Recent work by Sheriden (1983) allows a comparison of physiological strategies between alpine and grassland cyanophytes, while field microclimate work with R.superficiale allows an appreciation of

boundary layer effects in the alpine environment.

(1.1.2) The Physical Environment

In both laboratory and field studies particular emphasis was placed on thermal parameters, controlling as they do the rate of many physiological processes, both directly and through secondary interactions with water status. Standard meteorological data are usually measured under well ventilated, diffuse radiation conditions, at approximately 1 meter above the ground. These measurements often have little relevance to the actual temperature experienced by surface cryptogams of open habitats, although they may reflect the thallus temperatures of finely pendulous arboreal lichens (Coxson et al., 1983). To appreciate the thermal environment of a surface cryptogam, it is instructive to examine the energy exchange processes at the soil surface. By day, temperatures over a vertical profile are often highest at the soil surface, with net radiant absorption leading to energy accumulation. By contrast, at night the soil surface may experience the lowest temperatures, with net radiant emission leading to energy depletion. The amplitude of the diurnal temperature changes is thus greatest at the soil-air interface, often resulting in very steep vertical temperature profiles during high radiant emission periods. Energy transfer from the soil surface is impeded by the presence of a thin layer of air, the laminar boundary layer, which adheres to the soil air interface and in which only laminar flow is possible. This allows only radiative and non-convective molecular

diffusion transfers of energy from the surface plane, a factor of extreme importance to many crustaceous and even some foliose and fruticose cryptogams which grow largely within the laminar boundary layer. Under still air conditions surface temperatures will be higher than under windy conditions, but surface albedo, the magnitude of incoming radiation and latent/sensible energy balance will all modify the actual boundary layer temperatures achieved in a given situation. A crustaceous surface cryptogam may thus exhibit little specialized adaptation to mean air temperatures at two meters, particularly in arctic and alpine habitats. Gates and Janke (1966), for example, found temperature extremes of up to 57 °C on open alpine tundra soils, while Rouse (1976) documented temperatures approaching 60 °C on open subarctic soil surfaces. Present research thus incorporated extensive documentation of the thermal environments of surface cryptogams over a range of hydration and light conditions.

(1.1.3) Physiological Responses

Physiological responses of poikilohydrous surface cryptogams to environmental parameters can be broadly divided into two general catagories. First, during periods of dehydration, even though no physiological activity may be detectable (ie. gas exchange), some surface cryptogams respond to ambient environmental conditions, as reflected by patterns of metabolic activity on subsequent rehydration. In particular, high tissue temperatures while dessicated, in some surface cryptogams can

result in a severe decline of subsequent photosynthetic activity. In addition, photosynthetic temperature optima (on rehydration) in some species of surface cryptogams reflect mean tissue temperatures experienced during previous dessication periods. The second broad category of responses is that of surface cryptogams during periods of thallus hydration, ie while metabolically active. Again, the process of photosynthetic acclimation provides a major potential avenue of interaction. Other possible responses of hydrated surface cryptogams include various changes in photosynthetic quantum efficiency, as well as changes in rates of respiratory and nitrogenase activity.

The first of these factors, the response of surface cryptogams to environmental extremes while dry, has been regarded for many years as unimportant. Many authors have expressed the view that dry surface cryptogams are immune to extremes of temperature based on the evidence presented by Lange (1953). Using the temperature at which respiration rates decreased by half in air dry stressed lichen thalli as an index of heat resistance, Lange found values ranging from 70 °C in Alectoria sarmentosa to 101 °C in Cladonia pyxidata. More recent studies however (Lange et al., 1970, 1975), using net photosynthesis as a more sensitive indicator of heat stress, have established that for the desert lichen Ramalina maciformis even short exposures to temperatures above 65 °C can be deleterious. MacFarlane and Kershaw (1978, 1980) have re-examined the sensitivity of lichens in an air-dry state to heat stress and for a number of northern boreal species have found extreme sensitivity to temperatures as low as 25 °C. They also reported that differential

levels of thermal tolerance between species correlated closely with extremes of heat stress normally encountered in respective habitats.

In addition to the changed concepts of thermal stress sensitivity in surface cryptogams, multifactorial experiments have shown that seasonal acclimation of net photsynthesis can be an important strategy for maximizing yearly carbon gain (Kershaw, 1977a, b; Larson and Kershaw, 1975a, d). Prosser (1955) (see also Larson, 1980) refers to acclimation as a process by which homeostasis of photosynthetic capacity is maintained at maximal rate despite seasonal or other environmental changes. Acclimation in this sense has been reported for the arctic species Alectoria ochroleuca, Cetraria nivalis and Bryoria nitidula (Larson and Kershaw, 1975a, d) and for the temperate species Peltigera canina and P.polydactyla (Kershaw, 1977a). However recent work with Cladonia rangiferina, Parmelia disjuncta (Tegler and Kershaw, 1980; Kershaw and Watson, 1983) and several Umbilicaria species (Larson, 1980), shows no evidence of seasonal acclimation, but rather points to a range of alternate strategies adopted in various habitats.

(1.2) The Factorial Framework

A critical element in the determination of ecophysiological strategies is the documentation of gas exchange parameters within a full factorial framework of temperature, moisture, and light. For example, the correlation of latitude with photosynthetic temperature optimum stems largely from work of Lange (1965), whose results were based on net

photosynthetic rates measured at full thallus saturation only, rather than over the integral of the drying curve. As gas exchange at saturation is dominated, in many species, by respiratory responses, interpretation of net photosynthetic results is confounded by the temperature dependence of respiration. Thus the use of net photosynthetic rates measured only at saturation can impart marked bias on subsequent data interpretation.

A further example of incomplete experimental design is seen in studies of Turk (1981), who attempted to follow seasonal changes in photosynthetic temperature optima of subalpine lichens. However, most of his seasonal CO_2 exchange assays were below light saturating intensities (at 260 uE m^{-2} s^{-1} PAR). Kershaw et al. (1983), MacFarlane et al. (1983), Prezelin (1981) and Badger et al. (1982) all emphasize that photosynthetic temperature acclimation can only be fully documented above light saturation (See Section 4.2). Thus the capacity changes found by Turk cannnot be clearly interpreted, despite multifactorial documentation in other dimensions. These criticisms apply equally to much of the earlier work on surface cryptogams examining seasonal acclimation patterns (Larson and Kershaw, 1975a, d; Kershaw 1977a, b).

Full definition of temperature limits is also crucial to multivariate analysis. In this respect Lechowicz (1982) used as an example the study of Lechowicz and Adams (1973), where net photosynthesis was followed only at 22 °C in experiments examining sun/shade population differences. Subsequent work (Lechowicz and Adams, 1974) showed this temperature range was inappropriate for examination of optimal

temperature responses. Care must also be taken that cuvette temperatures are carefully monitered, preferably with thermocouples inserted within plant tissue. The study of Jones (1981) for instance, found a marked depression of gas exchange (C_2H_2 reduction) at midday in field incubations under full solar insolation. However, no measures were taken to prevent cuvette overheating, nor was this monitored. Although Jones interpreted the midday depression of gas exchange as physiological, it probably stemmed from overheating within the experimental cuvettes. In current work in-situ field cuvette temperatures showed marked elevation under full radiation conditions unless submerged in a water bath.

Repeated sampling on a time scale corresponding to the environmental parameter under consideration is also frequently overlooked in environmental studies. Larson (1981), for example discussed at length the seasonal acclimatory pattern Umbilicaria species, yet his data contains only a single winter-summer comparison. Kershaw and Webber (1983) documented almost weekly changes in photosynthetic response curves for the lichen Peltigera praetextata, while MacFarlane et al. (1983) and Kershaw et al. (1983) both showed clear monthly changes in Cladonia rangiferina and C.stellaris respectively. Data interpretation from only limited seasonal sampling can be quite misleading, particularly in habitats with marked intra-seasonal changes.

A final factor, often overlooked after other criteria of the multifactorial protocol are satisfied, is the provision of adequate pretreatment and storage conditions. Lechowicz (1978) for instance, fully documented the photosynthetic response of Cladonia lichens over

dimensions of temperature, moisture and light. Yet his experimental replicates were stored air dry at 0 °C in the dark "until used in experiments". MacFarlane et al. (1983) and Kershaw et al. (1983) have shown that storage temperature regime and photoperiod conditions play a critical role in inducing seasonal capacity changes in these same Cladonia lichens. The storage conditions used by Lechowicz would probably have caused a marked decline in photosynthetic capacity with time, a factor for which no controls were established. The physiological lability of surface cryptogams while in an air dry state has recently been emphasized by several authors, some even suggesting that photosynthetic temperature optima can track ambient conditions while thalli are dehydrated (Kershaw, 1977a, b; Kershaw and Webber, 1983; Larson, 1980; Kershaw and MacFarlane, 1980). Clearly, interpretation of physiological strategies adopted by surface cryptogams in the context of their physical environment requires not only strict control and simultaneous examination of temperature, moisture and light conditions, but also an appreciation of temporal variation, both under field and laboratory conditions.

Figure 1

The location of the study site in Southwestern Alberta; A) Table Mountain Alpine Collection Site (2160 m; 49 degrees, 22 minutes N; 114 degrees, 16 minutes W); B) Prairie Bluff Alpine Field Microclimate Site (2133m; 49 degrees, 18 minutes N; 114 degrees, 12 minutes W); C) Pearce Grassland Site (945 m; 49 degrees, 47 minutes N; 113 degrees, 16 minutes W). The approximate position of the 3000 ft (1044 m), 4000 ft (1392 m) and 6000 ft (2088 m) contours is indicated on map, although local topography may differ considerably from these general trends.

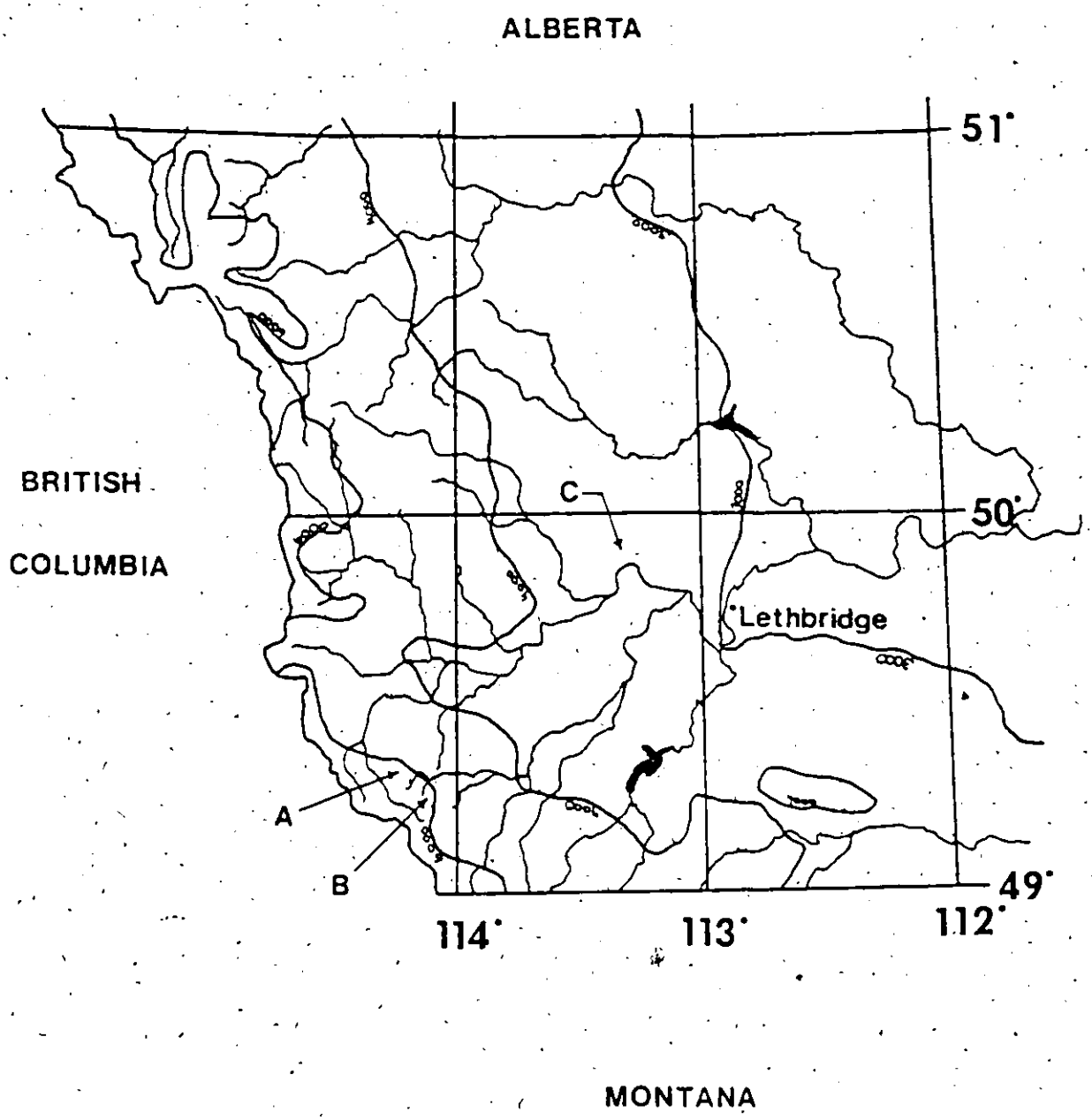
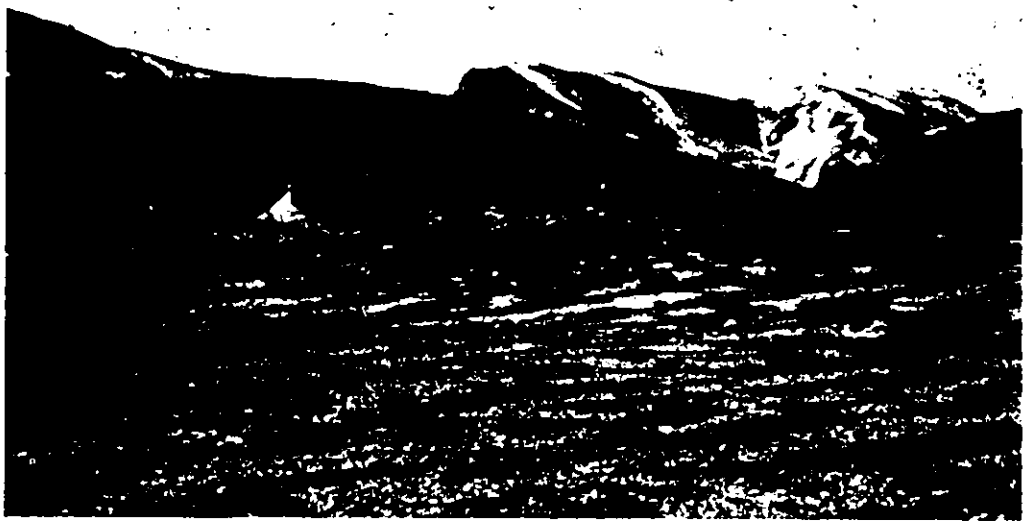

ALBERTA
51°
BRITISH
COLUMBIA
C
50°
Lethbridge
A
B
49°
114°
113°
112°
MONTANA

Figure 2

A) Top: View east across the Table Mountain Collection Site, December 27, 1980; B) Bottom: View south across Prairie Bluff Field Site, July 8, 1980.



Section 2.

METHODS

(2.1) The Study Sites

(2.1.1) The Alpine Environment

In the frontal ranges of Southwestern Alberta surficial relief is dominated by numerous glacial carved features, dating from the last major Wisconsin glaciation. Hanging valleys, steep walled cirques and sharp ridges all contribute to form very steep topographic relief. Older rock formations are usually encountered with increasing elevation in the frontal ranges due to the Lewis overthrust fault, a dominant geological feature of the region. Basically older Precambrian rocks have been thrust eastward over younger Mesozoic formations along the low angled Lewis fault, followed by uplift of the region and subsequent erosion and alpine glaciation (Dept. Mines and Res. Canada, 1943). This unique relief was ideally suited for the purposes of the present study, as these older Precambrian rock formations at elevation largely consist of finely bedded marine sedimentary deposits, typically reddish argilites, physical properties of which are very near to those of fine slates. Surface colonies of R.superficiale could thus be removed intact on discrete rock sheets for subsequent laboratory examination. Two sites with abundant

R.superficiale populations were chosen for study (See Figs. 1 and 2). The first site on Table Mtn. (2160m), an extensive ridge crest area of alpine tundra, was the main collection area for laboratory replicates, while a second site on Prairie Bluff (2133m) was the focus of field access. The R.superficiale populations in both sites are restricted to the exposed ridge crests, where wind exposure is maximal and which are usually blown clear of snow in winter months (See Fig. 2a).

The nearest meteorological station with complete long term records is at Beaver Mines (1282 m), some 6 km north of Table Mtn. while the nearest station at similar elevation is 60 km north at Livingston Lookout (2128 m), however, only summer records are kept here. Long term data from these two sites are given in Table 1.

In the frontal ranges of southwestern Alberta snowmelt periods occur frequently in the winter months. Characteristically the Chinook wind occurs as a strong westerly flow of Maritime air subsiding east of the frontal mountain ranges. This air is cooled adiabatically at the saturated lapse rate as it rises over the mountains and in its descent to the plains is warmed diabatically at the dry lapse rate, which is twice the cooling rate during the ascent (Shaw, 1976). Meteorological data from Beaver Mines (Table 1) reflects the influence of alternating periods in cold continental and warmer Pacific airmasses, with temperature extremes for December ranging from +21 to -44 °C. Longley (1967) notes that on average temperatures above 4 °C are recorded on over 28 days over the period from December through February (at Waterton Lakes Townsite ca. 25 km southeast of Prairie Bluff). Collections of R.superficiale at Table

Mtn. in December 1979, January, February and April 1980 were all made under Chinook conditions. Snowmelt was evident at midday during these collections, although because of inversion conditions the valley floor remained cold. Snowfall periods are frequent well into June at both alpine sites and infrequently occur during July and August. Major summer precipitation periods usually result from easterly circulation of conditionally unstable air and orographic uplift with subsequent heavy precipitation on the eastern slopes of the Rockies (Reinelt, 1967). During fair weather periods thundershower activity often sweeps over the alpine study sites, having developed along the continental divide 15 km westward.

Table 1. Temperature (°C) and precipitation (cm) data for Beaver Mines (49° 29' N - 114° 10' W, 1285 m) and Livingston Lookout (49° 54' N - 114° 21' W., 2133 m) Alberta. (Environment Canada, 1971)

Beaver Mines	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean daily temp.	-8.5	-5.2	-3.0	3.0	8.4	11.8	15.3	14.4	10.3	5.9	-0.9	-5.1	3.9
Mean daily max.temp.	-3.2	0.3	2.5	8.8	15.0	18.4	23.7	22.4	17.5	11.9	4.2	-0.2	10.1
Mean daily min.temp.	-13.8	-10.8	-8.6	-2.8	1.7	5.2	6.9	6.3	3.1	-.1	-6.1	-9.9	-2.4
Extreme max. temp.	13.3	15.6	19.4	30.6	30.0	32.2	35.6	33.9	35.0	28.3	23.9	21.1	35.6
No. years of record	35	36	36	36	36	36	36	36	36	36	35	36	
Extreme min. temp.	-45.6	-43.3	-39.4	-27.8	-20.6	-3.9	-1.1	-6.7	-11.7	-29.4	-38.3	-44.4	-45.6
No. years of record	36	35	36	36	36	36	36	36	36	36	36	36	
No. days with frost	29	26	28	22	11	2	*	1	8	16	23	28	194
Mean rainfall	0.2	0.3	0.2	0.8	6.2	10.7	3.5	4.9	4.1	1.3	0.6	0.3	33.0
Mean snowfall	47.0	38.6	42.2	51.8	12.4	3.3	0.0	0.0	13.0	24.6	35.6	39.1	307.6
Mean total precip.	4.9	4.1	4.4	6.0	7.4	11.0	3.5	4.9	5.5	3.7	4.1	4.2	63.8
Greatest rain in 24 hours	5.1	1.7	0.8	3.8	9.4	11.2	5.9	5.7	4.4	3.8	2.1	2.2	
No. years of record	58	57	58	53	53	53	51	54	52	57	57	57	
greatest snow in "	78.7	76.2	53.3	50.8	35.6	40.6	0.0	10.2	61.0	61.0	78.7	55.9	
No. years of record	55	56	53	51	54	58	56	57	51	53	52	51	
Livingstone Lookout													
Mean daily temp.						6.7	11.4	10.4	5.4				
Mean daily max. temp						12.2	18.0	16.7	11.1				
Mean daily min. temp						1.2	4.7	4.2	-0.5				
Extreme Max. Temp.				17.2	22.2	25.6	25.0	28.3	24.4	21.1			
No. years of record				1	4	8	7	7	7	5			
Extreme. Min. Temp.						-7.8	-3.9	-6.1	-12.8	-12.8			
No. years of record						7	7	7	8	1			
No. days with frost						10	2	3	11	28			

Table 2. Temperature (°C) and precipitation (cm) data for Lethbridge, Alberta. (Environment Canada, 1971).

49° 38' N - 112° 48' W, 920 m

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean daily temp.	-9.4	-5.5	-2.4	5.2	10.9	14.9	18.8	12.6	12.6	7.6	-0.6	-5.1	5.3
Mean daily max. temp.	-3.7	0.2	3.3	11.6	17.5	21.2	26.4	25.1	19.5	14.1	5.0	0.1	11.7
Mean daily min. temp.	-15.1	-11.3	-8.2	-1.1	4.2	8.6	11.1	10.0	5.6	1.0	-6.3	-11.1	-1.0
Extreme max. temp.	16.6	18.8	23.3	21.1	32.7	38.3	38.8	38.3	36.6	31.6	22.7	18.3	38.8
No. years of record	33	33	33	33	33	33	33	33	33	33	33	33	
Extreme min. temp.	-42.7	-42.7	-37.7	-25.5	-11.6	-1.6	2.7	0	-6.1	-21.6	-33.8	-42.7	-42.7
No. years of record	33	33	33	33	33	33	33	33	33	33	33	33	
No. days with frost	28	26	27	19	6	*	0	*	4	13	24	28	175
Mean rainfall	0.0	0.0	0.2	1.3	4.4	8.8	4.4	3.9	2.6	0.8	0.1	0.0	26.9
Mean snowfall	24.8	23.6	25.6	24.1	6.6	1.4	0.0	0.0	1.9	14.7	23.6	23.8	180.5
Mean total precip.	2.2	0.3	2.56	3.6	5.1	8.9	4.4	3.9	3.7	2.2	2.3	2.1	43.6
Greatest rain in 24 hours	0.3	0.6	0.7	5.3	4.8	7.2	4.7	5.4	1.9	3.6	0.5	0.9	7.1
No. years of record	33	33	33	33	33	33	33	33	33	33	33		
Greatest snow in 24 hours	18.7	24.4	26.6	52.8	32.5	10.9	T	3.8	55.1	35.8	37.8	21.5	55.1
No. years of record	33	33	33	33	33	33	33	33	33	33	33	33	

(2.1.2) The Grassland Environment

The grassland study site was located in an area of Stipa comata-Bouteloa gracilis dominated grassland near Lethbridge, Alberta (Fig.1). General topographic relief is minimal, 1 to 2 meters, with deep deposits of glacial till from late Wisconson glaciation overlaid by wind deposited silts (Dept. Mines and Technical Surveys Canada, 1962). The study site is at the edge the Oldman river where erosional features have exposed large areas of Cretaceous sandstones, on which populations of C.trachyphylla are common. When wet, the thalli of C.trachyphylla can be scraped off the sandstone by carefull insertion of a blade under the margins, leaving only a monolayer of sand grains attached to the thalli undersurfaces. This contrasts with the alpine populations of R.superficiale, which fragmented severely on attempted removal. Soils at this grassland site were almost completely covered by a mosaic of cryptogamic species, including lichens, mosses and terrestial algae. Only discrete colonies of N.commune free on the soil surface were used for physiological research. Other crusts in intimate contact with the soil column and surface lichens were not used in current work.

The climate at this site is semi-arid, yearly precipitation totals ranging from ca. 25 to 50 cm. About a third of the total precipitation falls as snow between October and April, while the heaviest monthly rainfall occurs in May and June. Monthly mean temperatures range

from over 18 °C in July, to below -15 °C in January (Environment Canada, 1971). Long term climatic data from the nearest meteorological station is given in Table 2. The Chinook snowmelt phenomena described above for the alpine environment is equally marked at the grassland site. It is most striking when it follows the passage of arctic frontal systems through the area, with skies clearing abruptly and temperatures rising as much as 30 °C in a 24 hour period (Shaw, 1976). Recorded temperature extremes at Lethbridge, Alberta in January reflect the magnitude of these potential changes, covering the range of -43 to +21 °C (Environment Canada, 1971). In an average winter alternating predominance of arctic continental and Pacific maritime air masses provide Chinook snowmelt sequences ca. every 14 days, typically accompanied by strong dry westerly winds (Beaty, 1972). In summer months rainfall periods are infrequent, being largely sporadic evening thundershower activity, with occasional major precipitation periods.

(2.2) CO_2 Gas Exchange

(2.2.1) Measurement and Control

Net photosynthesis and respiration were monitored using a Beckman Model 865 Infra-Red Gas Analysis (IRGA) system modified to allow the simultaneous handling of up to 25 experimental gas exchange cuvettes, following the "discrete" sampling system of Larson and Kershaw (1975c). An open-flow IRGA system was used, where the experimental curvette,

normally on-line with the gas stream, is replaced with a injection port. Samples of air from replicate "discrete" incubation cuvettes held under controlled conditions can then be injected into the IRGA air stream for determination of CO_2 content. Calibration is readily achieved by injection of known standards into the air stream. These "discrete" incubations are analagous to the closed-loop IRGA system, but instead of a continuous record of cuvette CO_2 concentration, only spot measurements at regular time intervals are used. This approach has the advantage that large numbers of replicates can be handled on a continuous basis, allowing good experimental control and critical examination of photosynthetic changes on a seasonal basis.

There are two potential problems involved in the use of closed incubation dishes; the absence of any gas mixing within cuvettes and declining levels of CO_2 over the course of experimental incubations. Jarvis (1971) has stressed the importance of well ventilated cuvettes to minimize boundary layer CO_2 resistance (r_a), ie. the finite resistance to the diffusion of gas under still air conditions.

Green and Snelgar (1981a, b) have examined the problem in detail and have concluded that boundary layer resistance (r_a) represents only a small proportion of the unusually high total diffusive resistance (r) reported for lichens. Thus Snelgar et al. (1981a) report a value for r of 50 to 300 s cm^{-1} and Collins and Farrar (1978) 136 s cm^{-1}. Green and Snelgar (1981a) suggest a value of r_a for still air conditions of 7.0 s cm^{-1}, corresponding to a boundary layer depth of 1.03 cm. However their values of r_a were derived for a lichen of 5 cm diameter, a size much

larger than that of current species. Usually experimental replicates are considerably smaller and the estimates of r_a given by Green and Snelgar should be considered as extreme values. Accordingly, the boundary layer resistance to carbon dioxide diffusion becomes a small proportion of the internal diffusive term and the lack of ventilation in closed dishes is rarely a concern.

The restriction of net photosynthesis by low ambient levels of CO_2 presents a much more serious problem. Larson and Kershaw (1975c) show that in Alectoria ochroleuca, Cetraria nivalis and Parmelia caperata, gas exchange rates determined with the "discrete" sampling technique are constant down to CO_2 concentrations of between 200 and 250 ppm. Although their results can not be interpreted as a direct measure of photosynthetic CO_2 dependence due to the potentially large drop in their cuvettes CO_2 levels (from 350 ppm down to final CO_2 measure) between gas sampling, it does provide a confirmation of the validity of their technique for those particular species, a point reaffirmed recently by Link, et al. (1983). Larson and Kershaw (1975c) emphasized that the response patterns found could not be assumed present in all species and that each species studied required separate consideration. Thus the effects of low partial pressures of CO_2 were examined for each of the three species under consideration, both at full thallus saturation and near the optimal level of thallus moisture content for net photosynthesis.

The CO_2 dependency of net photosynthesis in C.trachyphylla at 7 °C and optimal thallus moisture content was further plotted against uM

CO_2 concentration for experimental temperature and pressure conditions. The kinetic constants for ribulose 1, 5-biphosphate (RuBP) carboxylase were then determined by construction of a double reciprocal plot, with $1/mg\ CO_2\ h^{-1}\ g^{-1}$ as the ordinate, and $1/(uM\ CO_2)-r$ (where r equals the CO_2 compensation point) as the abscissa. A first order regression was then used to calculate the kinetic parameters K_c and V_{max} (following Monson et al, 1982). This treatment assumes low physical transport resistance to CO_2, minimal respiratory effects, and that RuBP carboxylase is both rate limiting at low CO_2 concentrations and follows Michaelis-Menten kinetics. While these limitations are unlikely to be significant under present conditions used, they preclude analysis of CO_2 dependency curves at both higher temperatures and at saturating moisture contents.

The critical examination of photosynthetic CO_2 dependency poses particular problems in those surface cryptogams where the response of net photosynthesis is maximal at intermediate water contents, as are those of R.superficiale and C.trachyphylla. Maintaining thalli at these optimal moisture values was difficult, as even slight condensation of thallus moisture on cuvette walls drastically biases the results. Experimental series examining CO_2 dependencies were thus started by allowing thalli to slowly dry down to their optimal moisture content as determined by repeated sequential "discrete" incubations, between which thalli were exposed to a low humidity air stream. Upon reaching their optimal moisture content, wet filter paper discs were put in the cuvettes, which were then kept sealed. Under these conditions of saturating water vapour pressure in the cuvettes, no further changes in thallus moisture content

occurred. The control of cuvette CO_2 levels can then be achieved by repeated small injections of 2% CO_2 (for upward adjustment), or by allowing continued photosynthetic uptake (for downward adjustment) of CO_2 within the sealed cuvettes. Small samples of air removed from the cuvettes at 1 to 5 minute intervals (after a 15 ppm CO_2 change within the cuvette) allowed determination of photosynthetic-CO_2 interactions. This experimental system allows maintenance of near constant thallus moisture context for several hours, after which the repeated injections/withdrawals for CO_2 measurement will usually allow some evaporative flux from thalli. While not an instantaneous measure of CO_2 uptake (d CO_2/dt), the same errors are also inherent in open flow systems (Lange, et al., 1970), where a larger air volume has a finite mixing response.

(2.2.2) The Seasonal Response of CO_2 Gas Exchange to Light, Moisture and Temperature

R.superficiale was collected monthly from the summit of Table Mountain and shipped immediately (usually within 24 hours) to McMaster University where it was stored under growth chamber conditions of daylength, temperature and light approximating to seasonal normals. As outlined above, the crustaceous morphology of R.superficiale required collections on large slabs of argillitic substrate, which on return to laboratory conditions could be chiselled into small chips of ca. 2 cm

diameter, amenable to incubation in discrete 200 cc. IRGA cuvettes. As total control over fracture planes in the argillite substrate was not possible, some rock chips varied in their proportion of younger to older thalli portions, a factor previously implicated in differential rates of photosynthetic activity in other surface cryptogams (Kershaw, 1977a; Nash, et al., 1980) and which is occasionally evident in the response matrix (Fig. 9).

The seasonal gas exchange response matrix in R.superficiale was established for December, April, May and July collections at 1, 7, 14, 21, 28 and 35 °C and over 0, 300, 600, 900 and 1200 uE m^{-2} s^{-1} Photosynthetically Active Radiation (PAR) over the 400 to 700 nm wavelengths for all levels of thallus saturation. Methods for thallus moisture content determination are outlined further in Section 2.2.3 . Prior to assay of net photosynthesis or respiration, replicates were misted with distilled water for 12 hours under seasonal storage conditions to eliminate resaturation effects, except for winter collections which were rehydrated at +1 °C. Temperature control was achieved in reach-in growth chambers, while thallus temperature was monitored with 46 um Cu-Cn thermopiles embedded within the tissue. Light levels were measured with a Li-Cor quantum sensor.

Each cell of the response matrix for R.superficiale was derived from between 3 to 5 different replicates for each seasonal collections and gas exchange rates are expressed as the mean values for each 20% relative moisture class (See also Section 2.2.3). Standard errors of these within experimental mean values were less than 0.08 mg CO_2 h^{-1} g^{-1}.

C.trachyphylla was also collected on a monthly basis and stored under growth chamber conditions approximating seasonal normals (See Table 1). This response matrix of CO_2 gas exchange was defined for January, March, July and October, over 7, 14, 21, 28 and 35 °C and and 0, 300, 600, 900 and 1200 uE m^{-2} s^{-1} PAR. Pretreatment of material was as for R.superficiale.

In addition, March collected material of C.trachyphylla was stored under both winter and summer conditions (See Table 4) to determine if photosynthetic capacity changes observed seasonally could be induced by experimental manipulation. Gas exchange in these experiments was followed at 7 and 21 °C and 0 and 600 uE m^{-2} s^{-1} PAR across the full moisture response curve. Summer conditions were defined as 30/20 °C day/night respectively and 300 uE m^{-2} s^{-1} PAR under a 14 hour photoperiod, while winter storage conditions were 5/1 °C day/night and 300 uE m^{-2} s^{-1} PAR under a 8 hour photoperiod. Photosynthetic response was assayed after storage of dry thalli under defined winter or summer conditions for one week, with a rehydration period of 12 hours at 5 or 20 °C preceeding IRGA measurements for respective winter and summer stored material. These storage manipulation experiments were repeated a third time in January (1983), with CO_2 exchange again followed at 7 and 21 °C, but over 0, 25, 50, 75, 100, 150, 200, 300, 400, 500, 600, 700, 1000, 1200 and 1400 uE m^{-2} s^{-1} PAR. The magnitude of gas exchange in these replicates was plotted both in mg CO_2 h^{-1} g^{-1} and in mg CO_2 h^{-1} mg Chl a^{-1} following procedures outlined in Kershaw et al. (1983).

The seasonal responses of net photosynthesis and respiration in

N.commune were measured in January, March, July and October, storage and pretreatment again following that outlined above for R.superficiale. Due to the constancy of the moisture response curve in N.commune, most of these assays were conducted at thallus saturation . CO_2 exchange was followed at 7, 14, 21, 28 and 35 °C and at 0, 300, 600, 900 and 1200 uE m^{-2} s^{-1} PAR. Rehydration responses in N.commune were followed at 7, 14 and 21 °C at 0 and 600 uE m^{-2} s^{-1} PAR. In addition, the rehydration response of N.commune at 21 °C was followed for material previously dried under CO_2 free air to determine the nature of intially released CO_2.

The potential activation of photosynthesis and respiration by exposure to high humidities was followed in N.commune by holding thalli over salt solutions of known molarity for 12 hours (following Brock, 1975), after which time assays of CO_2 gas exchange and C_2H_2 reduction were conducted without opening the sealed cuvettes. As only small samples of gas were exchanged for IRGA determinations, the moisture equilibrium established in the curvettes remained undisturbed for several sequential incubations.

(2.2.3) Determination of Thallus Water Content during IRGA Experimental Incubations

Net photosynthesis and respiration data for each cell of the responses matrices were measured through a full drying cycle for each experimental replicate. In both C.trachyphylla and N.commune this simply

entailed gravimetric weighing of thallus replicates between experimental incubations. However, in R.superficiale, the gas exchange rates were measured with thalli intact on small rock chips, each ca. 3 cm diameter by 1 cm thick. The weights obtained during experiments thus included both lichen thalli and rock substrate and were not immediately interpretable as to thallus moisture content. To overcome this problem a regression equation was developed which allowed actual thallus moisture content to be predicted from total moisture content of experimental replicates, ie. R.superficiale thalli and rock weight. Replicate rock chips with lichen intact on their upper surface were dried under controlled laminar flow wind tunnel conditions (Larson, 1979), with weight determinations being taken every 5 minutes. After determination of their oven dry weights the lichen thalli were removed from upper replicate surfaces and a second drying curve under the same conditions was carried out. This allowed the weight differences between rock chips with and without thalli attached to be accurately determined at the same point of relative moisture loss (ie. at the same time from start of drying curve). These two drying curves are shown in Figs. 3a and 3b. The results of Fig. 4, showing the thallus drying curve, are thus derived from the differences between Figs. 3a and 3b. When the data pairs of replicate weight, with and without thalli on their upper surface, were compiled, the regression equation allowing calculation of thallus saturation (y) from total replicate percent moisture content (x) could be calculated for any point of an IRGA run. The regression equation $y=66.3x-7.4$ ($r=0.98, n=20$) was thus obtained (Fig. 3d). Equally the

relation of thallus to substrate moisture content could be derived (Fig. 3c). The changes in thallus moisture content seen in Fig. 3a parallel the results of Pentecost (1980) for lichen-covered rhyolite surfaces.

This equation expressing thallus saturation against total replicate saturation was used subsequently for all experimental runs with R.superficiale. Destructive sampling of some replicates confirmed the basic relationship, however there still remained some small scatter between the moisture response curves of replicate thalli (Fig. 5c). This stems from minor variations in drying rates shown by each uniquely shaped rock chip. Accordingly the thallus moisture content for R.superficiale was expressed on a relative basis, which allowed a reasonable estimate of net photsynthetic or respiratory rates within specific moisture classes. The absolute and relative moisture response curves shown for four R.superficiale replicates in Fig. 5d illustrates this transformation.

(2.2.4) Examination of CO_2 Gas Exchange in Relation to Thermal Stress

Heat tolerance was examined for R.superficiale collected in December and July. Control replicates were stored air dry at 5 °C, while experimental replicates were exposed to a 3 hour midday temperature maximum of either 35 or 45 °C. Temperature was incremented at 30 minute intervals from the night time storage temperature of 5 °C up to midday extremes. Net photosynthetic and respiratory responses to continued heat

exposure of air dry thalli were examined after 1, 2, 7, 14 and 21 days treatment. CO_2 gas exchange was followed at 14 °C, 0 and 600 uE m^{-2} s^{-1} PAR after rehydration pretreatment of 12 hours at 5 °C.

The response of C.trachyphylla and N.commune to heat stress treatments was also examined over a 21 day period. Air dry thalli were held at 60 °C for five hours each midday, changing from a 25 degree C night temperature by 10 °C per hour. Control replicates were held at 25 °C and both groups were assayed for CO_2 gas exchange after 1, 7, 14 and 21 days treatment. CO_2 fluxes were measured at 21 °C and 600 uE m^{-2} s^{-1} PAR after a 6 hour rehydration period under these same conditions.

Figure 3

Changes in the water content of ca. 30 g argillitic rock chips with: A) R.superficiale thalli intact on upper surface (upper left); B) R.superficiale thalli removed from upper surface (lower left). The moisture content for (A) thus includes that held in R.superficiale thalli. Drying conditions in the wind tunnel were 3 m s^{-1} wind speed at 22 °C and 30% relative humidity. Standard error for 10 replicates indicated for each data point. Above data is also transformed to express R.superficiale percent thallus moisture content against: C) total rock saturation only (upper right), ie. only that moisture held within the argillitic substrate and; D) total replicate saturation (lower right), ie. including both lichen and rock held moisture. The least squares 1st order regression equation for (D) is given in Section 2.2.3.

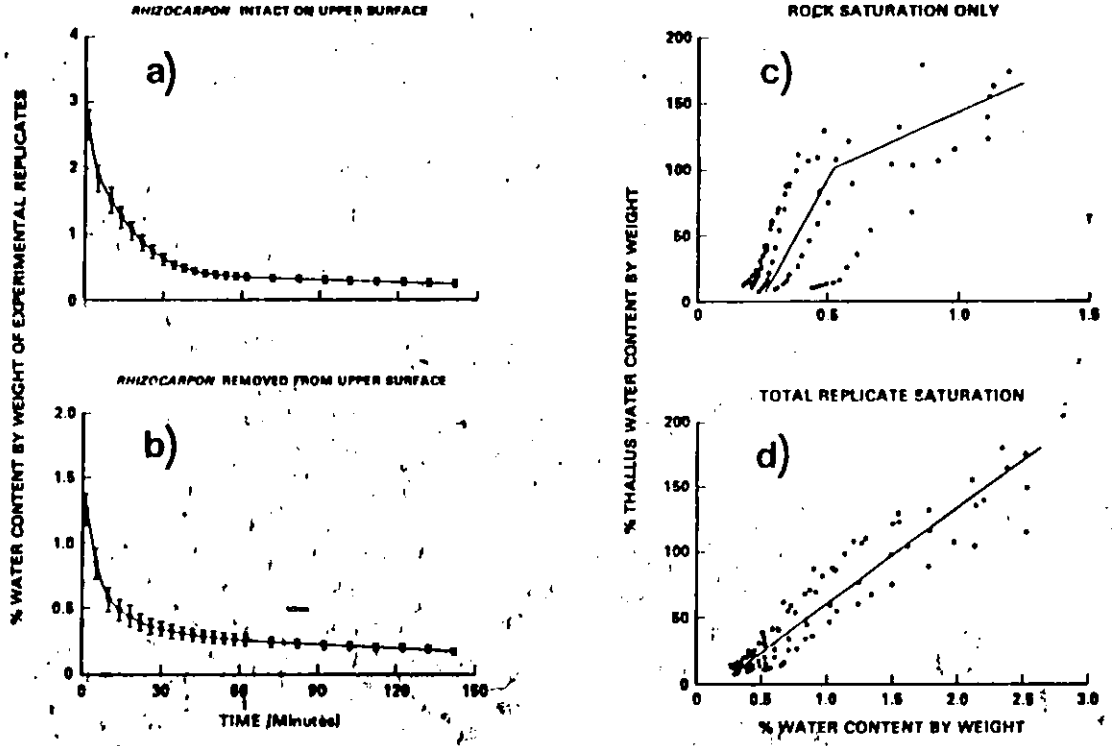

RHIZOCARPON INTACT ON UPPER SURFACE
a)
RHIZOCARPON REMOVED FROM UPPER SURFACE
b)
% WATER CONTENT BY WEIGHT OF EXPERIMENTAL REPLICATES
TIME (Minutes)
ROCK SATURATION ONLY
c)
TOTAL REPLICATE SATURATION
d)
% THALLUS WATER CONTENT BY WEIGHT
% WATER CONTENT BY WEIGHT

Figure 4

Changes in thallus moisture content by weight for R.superficiale thalli held under wind tunnel conditions outlined in Fig. 3. The mean value and associatted SE is presented for 10 replicate incubations.

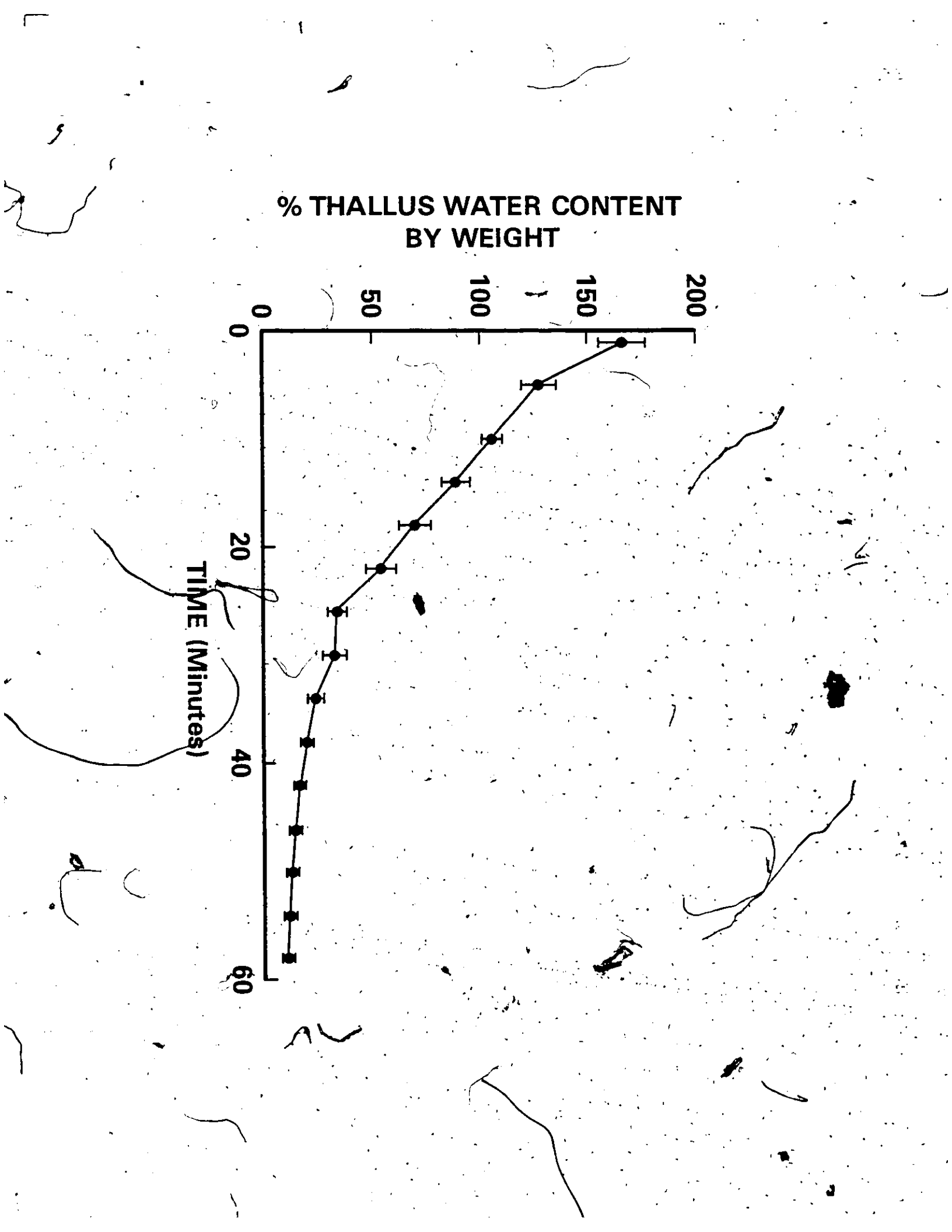
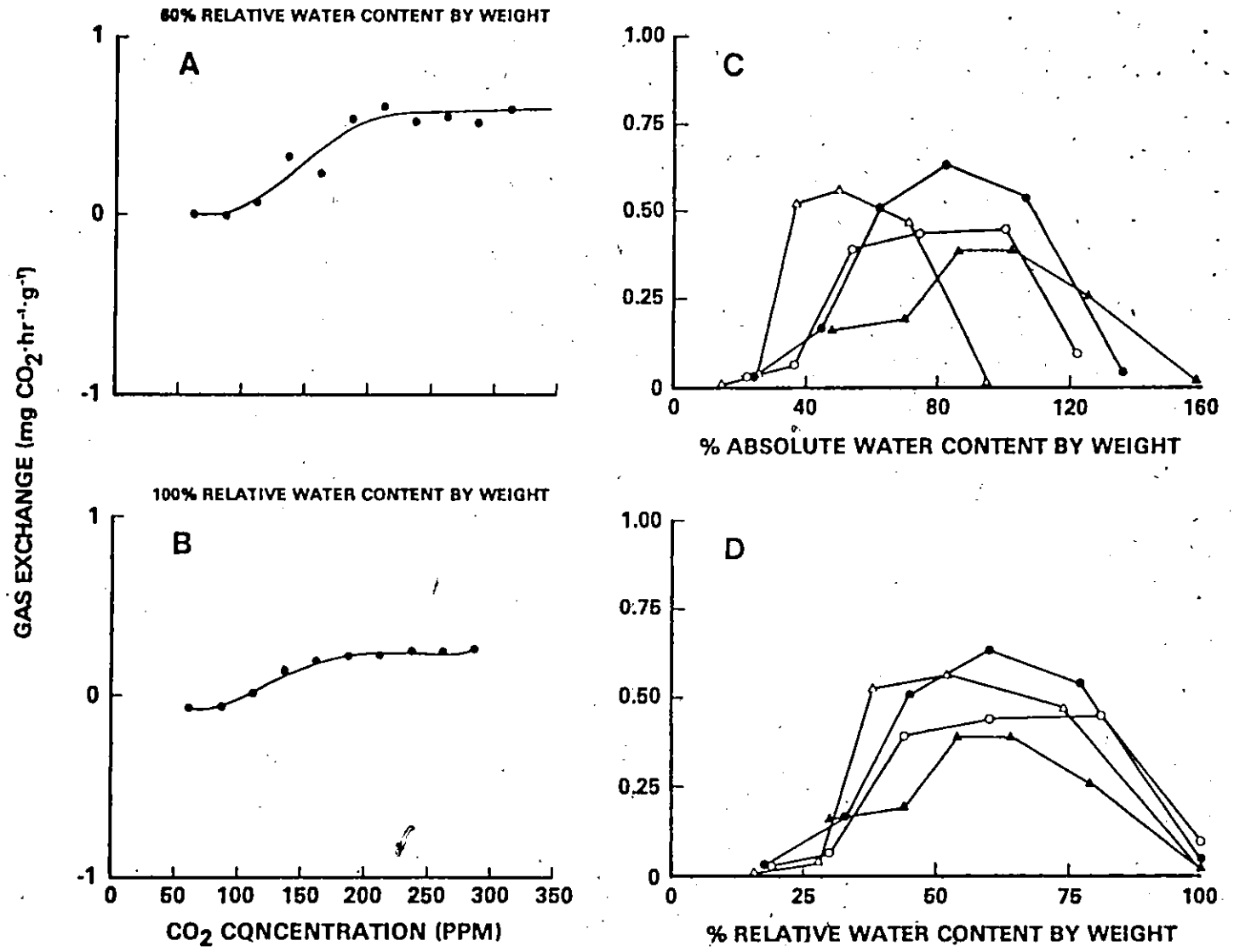

% THALLUS WATER CONTENT
BY WEIGHT
0
50
100
150
200
0
20
40
60
TIME (Minutes)

Figure 5

Net photosynthetic rates in R.superficiale as a function of: A) CO_2 concentration at 60% relative thallus moisture content ; B) CO_2 concentration at 100% relative thallus moisture content ; C) Percent absolute thallus moisture content by weight and; D) Percent relative thallus water content by weight. Each symbol in (C) and (D) denotes a seperate replicate followed over the course of the drying run.


60% RELATIVE WATER CONTENT BY WEIGHT
A
100% RELATIVE WATER CONTENT BY WEIGHT
B
GAS EXCHANGE (mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$)
1
0
-1
0 50 100 150 200 250 300 350
CO_2 CONCENTRATION (PPM)
C
D
1.00
0.75
0.50
0.25
0
0 40 80 120 160
% ABSOLUTE WATER CONTENT BY WEIGHT
0 25 50 75 100
% RELATIVE WATER CONTENT BY WEIGHT

(2.3) The Nitrogenase Assay

(2.3.1) Measurement and Control

Nitrogenase activity in N.commune was monitored using the acetylene (C_2H_2) reduction technique of Dilworth (1966) as modified by Crittenden and Kershaw (1979). Marginal lobes of about 0.75 g wet weight were incubated in 30 cm^3 gas exchange cuvettes under a 10% C_2H_4 atmosphere for 30 minutes. A 0.5 ml gas sample was then analysed for ethylene (C_2H_4) content using a Hewlett-Packard 5710A gas chromatograph with a Poropak-R column and flame ionization detector. Results were expressed in nmol C_2H_4 mg^{-1} h^{-1}, except for selected data sets expressed per mg Chl-a. Cumulative rates of nitrogenase activity (Fig. 48) are expressed both in uE m^{-2} s^{-1} PAR and in mg N m^{-2}, the latter through use of the theoretical conversion ratio 3:1 acetylene reduced to nitrogen fixed and measured densities (g m^{-2}). Although Millbank (1981) criticizes the 3:1 conversion ratio as being unrealistically low, his own comparitive data biases the ratio upward through equating long term continuous $^{15}N_2$ uptake rates with midday short term C_2H_2 reduction rates. Horstmann, et al.(1982) suggest that comparative short term assays will yield ratios quite close to theoretical. The present conversion also allows comparison of nitrogenase activity with older literature, expressed only in mg N m^{-2}. Temperature and light control within experimental cuvettes was as outlined above (Section 2.2.2).

(2.3.2) Seasonal Response to Temperature, Moisture, and Light in N.commune

The seasonal response of nitrogenase activity to temperature, light and moisture in N.commune was determined for the same factorial interactions as was CO_2 exchange (Section 2.2.2). However, as the initial response of nitrogenase activity to thallus moisture content was constant at all temperature and moisture conditions examined, most subsequent experiments were conducted with replicates held at thallus saturation. The interaction of nitrogenase activity with light intensity was followed in two different ways. In one method individual replicates were sequentially exposed to different light conditions, with acetylene reduction assays being repeated for the same material. Controls for time dependent acetylene exposure effects included keeping one set of control replicates under constant light conditions and exposing others to a reverse order of light treatment. The advantage of continued use of the same material was that effects of inter-replicate variability could be minimized over complex experimental manipulations. However, acetylene exposure can itself induce greater rates of ethylene production (Scherer, et al. 1980) and proper control treatments must distinguish these effects. Experiments where each set of acetylene reduction assays uses newly selected material, ie. destructive treatment, do not suffer from such marked time dependent interactions. Thus a second set of experiments utilizing destructive sampling was conducted over a full

range of light conditions. Standard pretreatment of N.commune thalli prior to C_2H_2 reduction assays involved misting of replicates for 12 hours with distilled water at 21 'C and 200 uE m^{-2} s^{-1} PAR. This contrasted with photosynthetic experiments where material was rehydrated under storage (ie. ambient seasonal) light and temperature conditions. However, experimental series defining the rehydration response of nitrogenase activity suggested that any seasonal changes in activity would be masked if pretreatment was variable (See Sections 3.2.3 and 3.2.4).

(2.3.3) Pretreatment Effects of Temperature, Light and Moisture on Nitrogenase Activity in N.commune

The rehydration response of nitrogenase activity in N.commune was first followed at 25 degree C for material over the full thallus moisture response curve. Material held at 200 uE m^{-2} s^{-1} PAR was examined for nitrogenase activity at 0.25, 0.5, 2, 3, 6, 10, 14, 24 and 42 hours after initial hydration. Destructive sampling of six replicate thalli at each time point precluded the above noted C_2H_2 pretreatment effects. Further experiments which were conducted at thallus saturation followed rehydration responses over two diurnal light/dark periods at 7, 14 and 21 'C. Again destructive sampling of 8 replicates at each time point minimized C_2H_2 interactions. Acetylene reduction assays for these experiments were conducted at 28 'C and 200 uE m^{-2} s^{-1} PAR, allowing

determination of maximal potential activity after rehydration.

(2.3.4) Laboratory Freeze-Thaw Interactions

The pattern of nitrogenase activity in N.commune over freeze thaw conditions following snowmelt was simulated through temperature manipulation in experimental growth chambers. For this experiment replicates were first given a standard rehydration pretreatent of misting with distilled water at 5 °C for 48 hours under a 350/0 uE m^{-2} s^{-1} PAR 12/12 hour day/night photoperiod. At the end of the second night period replicates were divided into 3 groups and transferred to the growth chamber conditions outlined in Table 3 for 14 days. This material was maintained at thallus saturation. A thin ice film covered the material held at subzero temperatures, as is commonly observed under winter field conditions. The rate of morning and nightime freeze-thaw temperature transition was held to 2.5 °C h^{-1}. At 2400 hours on Day 14 all material was put under growth chamber conditions outlined for Group A, ie. nightime subzero temperatures and daytime melting under a 350 uE m^{-2} s^{-1} PAR (Table 1). The course of nitrogenase activity was then monitored over the following 4 days. For Group A this furthur 4 day period was merely a continuation of the same storage regime, while for Groups B and C it simulated snowmelt emergence. C_2H_2 reduction assays were carried out at 20 °C and 200 uE m^{-2} s^{-1} PAR.

Table 3. Growth chamber conditions over 14 day treatment period for laboratory simulated snowmelt and freeze/thaw sequences.

GROUP	STORAGE TEMPERATURE °C		LIGHT INTENSITY ($\mu E\ m^{-2}\ s^{-1}$ PAR)		LENGTH OF LIGHT PERIOD HOURS
	NIGHT	DAY	NIGHT	DAY	
A	-5	+5	0	350	12
B	-5	-5	0	0	0
C	-5	-5	0	350	12

(2.3.5) Field Nitrogenase Activity

Field rates of nitrogenase activity by N.commune in Stipa-Bouteloa grassland were monitored both over winter snowmelt periods and under midsummer conditions using the C_2H_2 reduction assay outlined above (Section 2.3.1). However, gas samples from experimental cuvettes were stored in pre-evacuated rubber stoppered tubes for analysis at a later date in the laboratory. This allowed incubation of thalli in glass cuvettes at field sites, requiring only a source of purified C_2H_2. Briefly, under field conditions intact lobes of N.commune freshly removed from the soil surface were placed in 30 cm^3 incubation cuvettes and held under a 10% C_2H_2 atmosphere for 1 hour. During low radiation conditions incubation bottles were placed directly on the soil surface, but during direct radiation periods the incubation bottles were placed in a temperature controlled water bath, which allowed maintenance of thallus temperature inside the cuvettes to within 2 °C of thalli undisturbed on nearby soil surfaces. A continuous readout of the differential between thallus temperature inside the incubation bottles and those undisturbed on nearby soil surfaces was obtained by placing the sensing tips of fine wire thermopiles in thalli within the cuvettes and the ice-point tips in thalli on soil surfaces. Light intensity was only slightly reduced by submersion of cuvettes in the water bath (about 10 uE m^{-2} s^{-1} PAR). For some experiments thalli freshly removed from field conditions were incubated under C_2H_2 at 20 °C and 200 uE m^{-2} s^{-1} PAR. Thalli of

N.commune were destructively sampled at hourly intervals during field runs for gravimetric moisture determination. Unfortunately a number of attempts to follow thallus moisture content remotely, including use of micro-psychrometer probes, dewpoint hygrometers and comparison with dummy dry thallus references (following Larson, 1977) all failed due to gross data distortion under high solar insolation conditions.

The density of N.commune at this grassland study site was determined in June through random placement of 41 1 m^2 quadrats within a 1 ha area. All N.commune colonies visible within these quadrats were removed for weighing. These estimates will tend to be conservative, as some thalli always eluded detection among the densely tufted Bouteloa gracilis clumps. Surface mixed algal crusts in intimate contact with the soil were not removed, nor were surface cyanophilic lichens (eg. Collema tenax).

(2.4) Field Microclimate Instrumentation

Thallus temperature measurements were made with fine wire Cu/Cn thermocouples referenced against Omega TRC Ice Reference Cells (Tanner, 1963). Air temperature measurements were made with Cu/Cn thermocouples kept in shielded aspirated tubes at 15, 100 and 200 cm above the ground surface, while wind velocity measurements were made with cup anemometers at 200 cm. Temperature data is mainly presented as a sequence of measurements throughout an experimental period, each representing an average of 5 spot measurements over a 15 minute period from 40 individual

thermocouple tips (grouped into 8 thermopiles). The exception to this are the data from snowmelt periods and wind screen experiments where individual thermopiles were used. Variation between replicate thermopiles under constant full radiation conditions over the open soil surfaces was low (less than 5 °C), reflecting small differences in microtopographic relief.

A temperature profile was measured at depths of 2, 4 and 8 cm into the argillitic bedrock under surface R.superficiale colonies. Horizontal holes, 2 mm in diameter and 30 cm deep, were drilled into the sides of two large rock slabs. 30 gage Cu/Cn thermopiles were inserted into these holes, which were then filled with silicone sealant. Wire leads at the edge of the rock slab remained well below the soil surface for an additional 1 m to minimize thermal conductivity along the leads.

Incoming short wave radiation[1] (0.3 to 3.0 u m) was measured with an Eppley radiometer and is expressed in most figures as Energy Flux Density in $W\ m^2$. Photosynthetically Active Radiation was measured with a LI-Cor quantum sensor and is expressed in $uE\ m^{-2}\ s^{-1}$ PAR.

(1) The SI unit of radiant flux density is the watt (W). There is no SI unit of photon flux. The einstein is commonly used to designate Avogadro's number of photons, and it has been suggested that this quantity be called a mole of photons (6.022×10^{23} photons) since the mole is an SI unit. When this definition of einstein is used, the quantity of photons in a mole is equal to the quantity of photons in an einstein (1 einstein = 1 mole = 6.022×10^{23} photons). The einstein has also been used in radiation physics as the quantity of radiant energy in Avogadro's number of photons. This definition in not used in physiological studies. (From Li-cor Technical Note, 1979)

Section 3.

RESULTS

(3.1) CO_2 Gas Exchange

(3.1.1) Interaction of Net Photosynthesis with CO_2 Concentration

The limitation of net photosynthesis by declining concentration of ambient CO_2 in R.superficiale is shown in Figs. 5a and b. At optimal thallus water content, which is approximately 60% relative moisture content by weight, net photosynthesis remained constant to just below 200 ppm, after which it declined rapidly to the CO_2 compensation point of about 85 ppm. At full thallus saturation there is an identical pattern of response, but with maximum rates of net photosynthesis reduced to ca. 0.2 mg CO_2 h^{-1} g^{-1} from the optimal value of ca. 0.5 mg CO_2 h^{-1} g^{-1} at 14 °C and 600 uE m^{-2} s^{-1} PAR illumination.

By contrast, rates of net photosynthesis in C.trachyphylla at optimal thallus moisture content (75%) showed a strong dependence on ambient cuvette CO_2 concentration to over 800 ppm, although the slope of response is steepest below 300 ppm CO_2 (Figs. 6a and b). At full thallus saturation a biphasic response curve is seen, with an initially steep slope at low CO_2 concentrations followed by a lesser response at

intermediate CO_2 concentrations and a steeper response slope again at CO_2 concentrations approaching 1000 ppm (Figs. 6c and d). This response pattern was evident at both 7 and 21 °C, although lower absolute rates were seen over lower CO_2 concentrations at 21 °C. In Fig. 7 the photosynthetic CO_2 dependency regression line of summer collected C.trachyphylla is plotted alongside that of winter collected material assayed under the same conditions. The differences in rates of net photosynthesis evident near ambient CO_2 concentrations (19 uM) are even more pronounced at higher CO_2 concentrations. Further, the slope of the response curves at low CO_2 concentrations show marked differences. When this data is presented as a double reciprocal plot these differences are even more apparent, the winter stored material showing a V_{max} and K_c of 4.1 and 17.2 respectively, while for summer stored material corresponding values of 3.4 and 24.8 were calculated.

The photosynthetic CO_2 dependency curves for R.superficiale and C.trachyphylla confirm the validity of using the discrete sampling IRGA technique to measure net photosynthesis. At most, rates of net photosynthesis will deviate by up to .03 and .09 mg CO_2 h^{-1} g^{-1} for R.superficiale and C.trachyphylla respectively when compared to "instantaneous" rates derived from 3rd-order regression plots through data of Figs. 5 and 6 (See Appendix A for calculations).

In N.commune there is a very gradual decline of net photosynthetic response from 800 ppm CO_2 down to ca. 200 ppm, below which a very abrupt decline down to the CO_2 compensation point of ca. 10 ppm is seen (Fig. 8).

(3.1.2) The Seasonal Response Matrices of Net Photosynthesis and Respiration

The seasonal net photosynthetic and respiratory response matrix for R.superficiale is given in Fig. 9. Maximum rates of net photosynthesis of ca. 1.2 mg CO_2 h^{-1} g^{-1} were generated over a temperature range from 1 to 14 °C under high levels of illumination (900-1200 μE m^{-2} s^{-1} PAR). At 1 °C, rates of net photosynthesis were maximal with a gradual decline of rates down to ca. 0.75 mg CO_2 h^{-1} g^{-1} at 21 °C. Above 21 °C net photosynthetic rates declined rapidly and at 28 and 35 °C respiration completely dominated gas exchange. The difficulties inherent in working with a crustaceous species and the problems of adequate morphological control are evident within some cells of the seasonal response matrix for R.superficiale, particularly in comparing maximal rates of net photosynthesis (ie. at optimal moisture content) in the 14 °C and high light cells. The data of July 1980 within these cells was derived from experimental runs conducted near the end of the summer series which utilized a higher proportion of replicate chips with older senescent colony centers. The differences between optimal rates of net photosynthesis in the remainder of the matrix cells, including the remaining c[illegible]r July, fall within the range of within experimental SEM and it is concluded that there is no significant seasonal photosynthetic capacity changes in R.superficiale. Also evident in the data of Fig. 9 is differences in the apparent optimal moisture

content for net photosynthesis, for instance between December and May data in the 1 °C and 900 uE m^{-2} s^{-1} PAR matrix cell. These differences reflect methodological difficulties outlined above (Section 2.2.3) in determining R.superficiale thallus moisture content without detructive sampling during IRGA experiments.

Light saturation in R.superficiale occurred at approximately 900 uE m^{-2} s^{-1} PAR, reflecting the very exposed nature of this species habitat. The response of net photosynthesis to thallus hydration showed an optimum between 50 to 80% relative thallus saturation, with a considerable decrease of rates at full thallus saturation and very low rates of gas exchange below 20% relative water content. Respiratory rates were fairly low up to 14 °C, thereafter increasing substantially at the higher temperatures. Rates decline more or less linearly with decreasing thallus moisture.

The seasonal response matrix for C.trachyphylla is given in Fig. 10. The response of net photosynthesis to thallus hydration again showed a fairly sharp optimum at mid-saturation values near 75 to 100% thallus moisture content. The spring and summer collections showed a broad temperature optimum centered near 21 °C, with rates reaching nearly 3.0 mg CO_2 h^{-1} g^{-1} at light saturation. Rates of net photosynthesis declined sharply across all light levels at 35 °C. The winter collection, while showing a similar response to higher temperatures, is markedly different from the spring and summer collections in the 7 °C cells of the matrix. At light saturation rates reach nearly 3.0 mg CO_2 h^{-1} g^{-1}, a marked increase compared to summer net photosynthetic rates of 2.0 mg CO_2 h^{-1}

g^{-1}. However, no significant respiratory changes were evident between seasonal collections, although a slight trend to lower rates may be present in the winter collection. The seasonal changes shown in Fig. 10 were further confirmed by a March collection, which also had higher rates, at 7 °C, than summer collections (Table 4). When air dry thalli from the March collection were stored under summer growth chamber conditions for 1 week, the temperature response curve moved back to a summer pattern, ie. rates of net photosynthesis fell back to near 2.0 mg CO_2 h^{-1} g^{-1} at 7 °C, while control material under winter storage conditions maintained higher rates at 7 °C (Table 4). When this experimental sequence was repeated in July (Table 4) these changes could not be induced, pointing to an intrinsic seasonal component in the triggering mechanisms involved. Laboratory induction of these capacity changes was again attempted in the following January, successfully repeating the March experiments (Fig. 11). The January experimental series closely examined the quantum efficiency of winter/summer stored material at both 7 and 14 °C. Capacity changes at 7 °C were found not to involve changing quantum efficiency, but merely an upwards shift along the same response slope. Equally, experiments at 21 °C showed no changes in quantum efficiency between winter and summer storage groups, although the slope seen was lower than that at 7 °C. The point of light saturation, (outlined by a third order polynomial curve) remains near 1000 uE m^{-2} s^{-1} PAR in all experiments, except for the summer stored material run at 7 degrees, where light saturation falls to nearly 600 uE m^{-2} s^{-1} PAR. The same data set expressed per mg Chl-a is also given in

Figs. 11 and 12. No major differences are seen, with capacity changes still evident for summer stored material in net photosynthetic assays at 7 °C.

The response of CO_2 gas exchange in N.commune to changing thallus hydration levels is shown in Fig. 13. Full thallus saturation, taken as the point at which a thin water film still covered experimental material after light blotting, occurred between 2000 to 2500% moisture content by weight for N.commune. Rates of net photosynthesis and respiration remained largely constant from this point down to nearly 500% moisture content, falling off very rapidly below 100% moisture content. This pattern of response was very similar at all temperature and light levels examined, although only the results at 25 °C are presented here. Material of N.commune held at full thallus saturation showed maximal rates of net photosynthesis between 600 and 900 uE m^{-2} s^{-1} PAR, although the variation between replicates can be quite high (Figs. 14 and 15). The response of net photosynthesis and respiration to temperature is examined in Fig. 16. No marked seasonal changes in the pattern of response were evident, with respiration and net photosynthesis both rising almost linearly up to 35 °C. The higher magnitude of both net photosynthesis and nitrogenase activity seen in May collections of N.commune was reduced when results were expressed on a chlorophyll-a basis, following extraction with acetone (Table 6).

The rehydration response of net photosynthesis and respiration in N.commune differed considerably between replicates soaked up at 7 °C and those rehydrated at 21 °C (Fig. 17). At 21 °C net photosynthesis showed

full recovery after 80 minutes, while at 7 °C almost 6 hours are needed for full recovery. Respiratory differences, although not as marked, were also evident between the 7 and 21 °C experiments. At 21 °C a basal level of respiration was achieved in approximately 80 minutes, while at 7 °C nearly 180 minutes were required. An initial burst of CO_2 was seen upon initial rehydration at both temperatures, however when replicates were dryed in a CO_2 free airstream this burst was eliminated (Fig. 18). The rapid recovery of rates seen in the first hour after rehydration in Figs. 17 and 18 was confirmed over a further 12 hours in Fig. 31 for replicates held at 21 °C and 0 and 600 uE m^{-2} s^{-1} PAR.

(3.1.3) Response to Heat Stress

The response of summer collected R.superficiale thalli to heat stress treatments while air dry is given in Fig. 19. Exposure to a 3 hour midday stress period of 45 °C over a 7 day period reduces net photosynthesis to below compensation and after 21 days heat exposure very little photosynthetic capacity remained in the experimental replicates. At 35 °C however there is very little evidence of stress until day 21, when maximum rates of net photosynthesis had declined to ca. 0.15 mg CO_2 h^{-1} g^{-1}. Respiration rates however, remained unaffected throughout the entire 3 week stress period. In the January replicates a broadly similar pattern was evident (Fig. 20). At 45 °C there was an immediate small decline of photosynthesis after two days exposure and by day 14 little activity was found. However thalli exposed daily to a 35 °C midday

temperature maxima showed a continuous decline of photosynthetic capacity over the 21 day period.

Air dry thalli of both C.trachyphylla and N.commune exposed daily to temperature maxima of 60 °C showed no marked changes in photosynthetic or respiratory responses induced by the heat treatment conditions (Table 5, and Fig. 21 respectively).

Table 4. Gas exchange patterns in Caloplaca trachyphylla. (mg $CO_2 h^{-1} g^{-1}$).

Storage Conditions			Assay Conditions[a]		CO_2 Gas Exchange[b]				
					% Moisture Class Intervals				
No. of Days	Temperature °C	Day Length	Light Level[c]	Light Level[c]	Temperature °C	0-	25-	50-	75-	100-
1[d]	7	8	300	0	7	-.21	-.25	-.31	-.3	-.40
1	7	8	300	600	7	1.10	2.20	3.70	3.60	2.70
7	7	8	300	0	7	-.21	-.26	-.32	-.39	-.41
7	7	8	300	600	7	0.90	2.40	3.50	3.20	2.30
7	25	14	300	0	7	-.18	-.32	-.32	-.34	-.37
7	25	14	300	600	7	0.60	0.90	1.37	1.10	0.42
1[e]	25	14	300	0	7	-.20	-.25	-.29	-.35	-.36
1	25	14	300	600	7	0.87	1.30	1.76	1.73	1.62
7	25	14	300	0	7	-.16	-.20	-.27	-.30	-.33
7	25	14	300	600	7	0.79	1.12	1.70	1.64	1.55
7	7	8	300	0	7			-.23	-.35	-.37
7	7	8	300	600	7			1.50	1.52	.041

(a) Replicates held air dry under storage conditions until 12 hours prior to assay at which time thalli were misted, then returned to storage conditions.

(b) Each value is a mean of 4 replicate incubations, the SE of which less than 0.15 mg $CO_2 h^{-1} g^{-1}$ dry weight.

(c) $\mu E\ m^{-2} s^{-1}$ PAR.

(d) March collected material. Held previously at 7°C and 300 $\mu Em^{-2} s^{-1}$ PAR, 8 hour daylength.

(e) July collected material. Held previously at 25°C and 300 $\mu Em^{-2} s^{-1}$ PAR, 14 hour daylength.

Table 5. The response of CO_2 gas exchange (mg $CO_2 h^{-1} g^{-1}$) in Caloplaca tracyphylla to heat stress.

Days of Treatment	Treatment Group (a)	Gas Exchange	n=4 ±1 SE.	Light Level (b)	Temperature °C
0	CN	-0.73	0.059	0	28
0	CN	1.76	0.103	600	28
7	CN	-0.85	0.047	0	28
7	CN	1.85	0.076	600	28
7	HS	-0.77	0.058	0	28
7	HS	2.01	0.086	600	28
14	CN	-0.74	0.066	0	28
14	CN	1.92	0.087	600	28
14	HS	-0.78	0.105	0	28
14	HS	1.70	0.091	600	28

(a) CN - Control group held at 25°C, 600 $\mu Em^{-2} s^{-1}$ PAR, and 14 hour day. HS - Heat stress group held for 5 hours midday at 60°C, changing by 10°C h^{-1} down to a night temperature of 25°C. Photoperiod as in a.

(b) $\mu Em^{-1} s^{-1}$ PAR.

Figure 6

The response of net photosynthetic response to CO_2 concentration in summer collected C.trachyphylla at: a) 7 °C and 125% thallus moisture content (r=.90); b) 21 °C and 125% thallus moisture content (r=.96); c) 7 °C and 75% thallus moisture content (r=.95); d) 21 °C and 75% thallus moisture content (r=.97). Lines were fitted with a 3rd order polynomial regression.

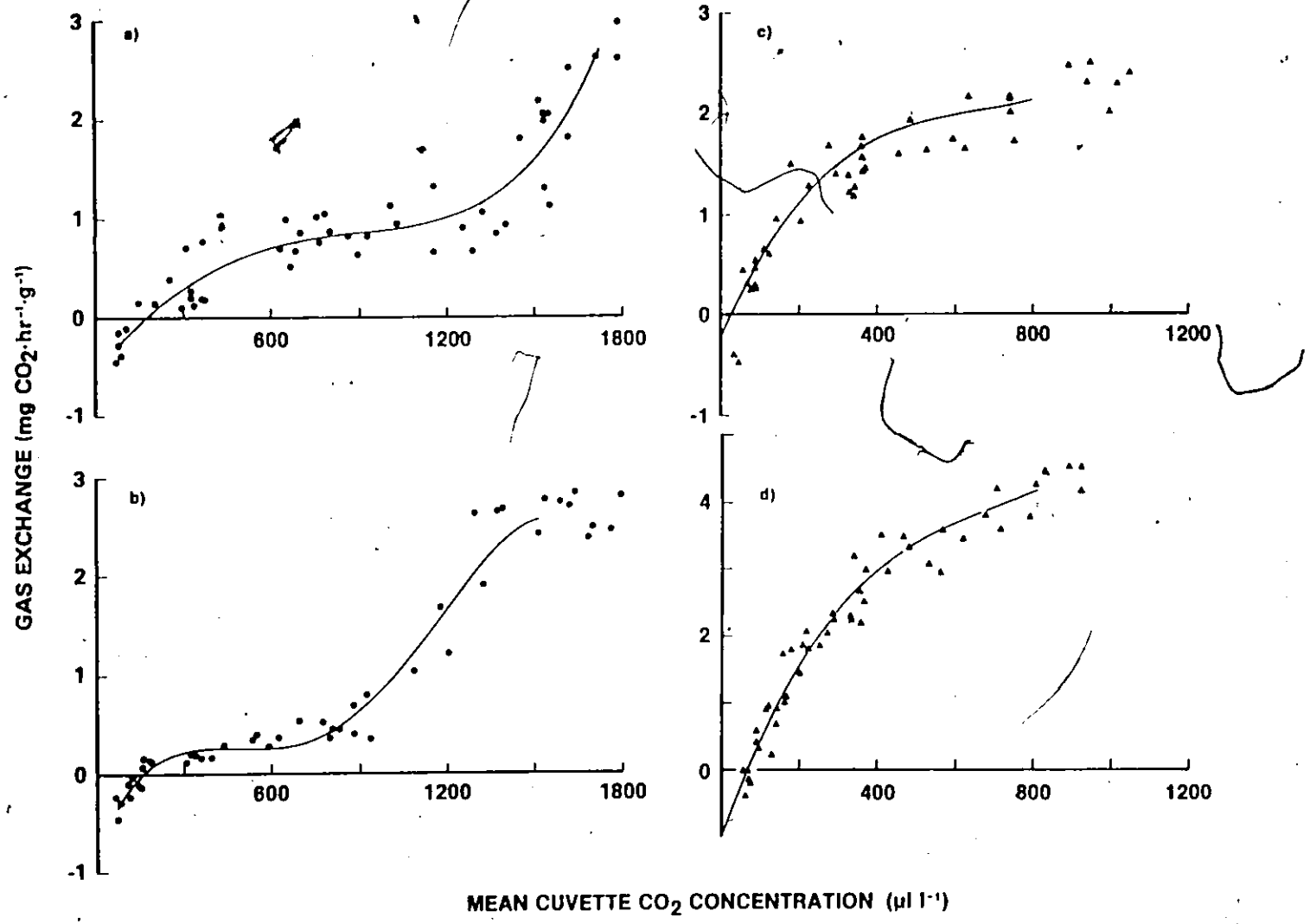

a)
b)
c)
d)
GAS EXCHANGE (mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$)
MEAN CUVETTE CO_2 CONCENTRATION ($\mu l\ l^{-1}$)

Figure 7

A) The response of net photosynthesis to CO_2 concentration for both winter and summer collected C.trachyphylla at 7 °C and 600 uE m^{-2} s^{-1} PAR. Only the 3rd order polynomial regression fit to data is presented. The summer raw data scattergram is shown in Fig. 6c. (r=.96) while the winter raw data scatter gram is not presented (r=.97). B) Double reciprocal plot of (A), including the kinetic parameters K_c and V_{max} derived from 1st order regression fit.

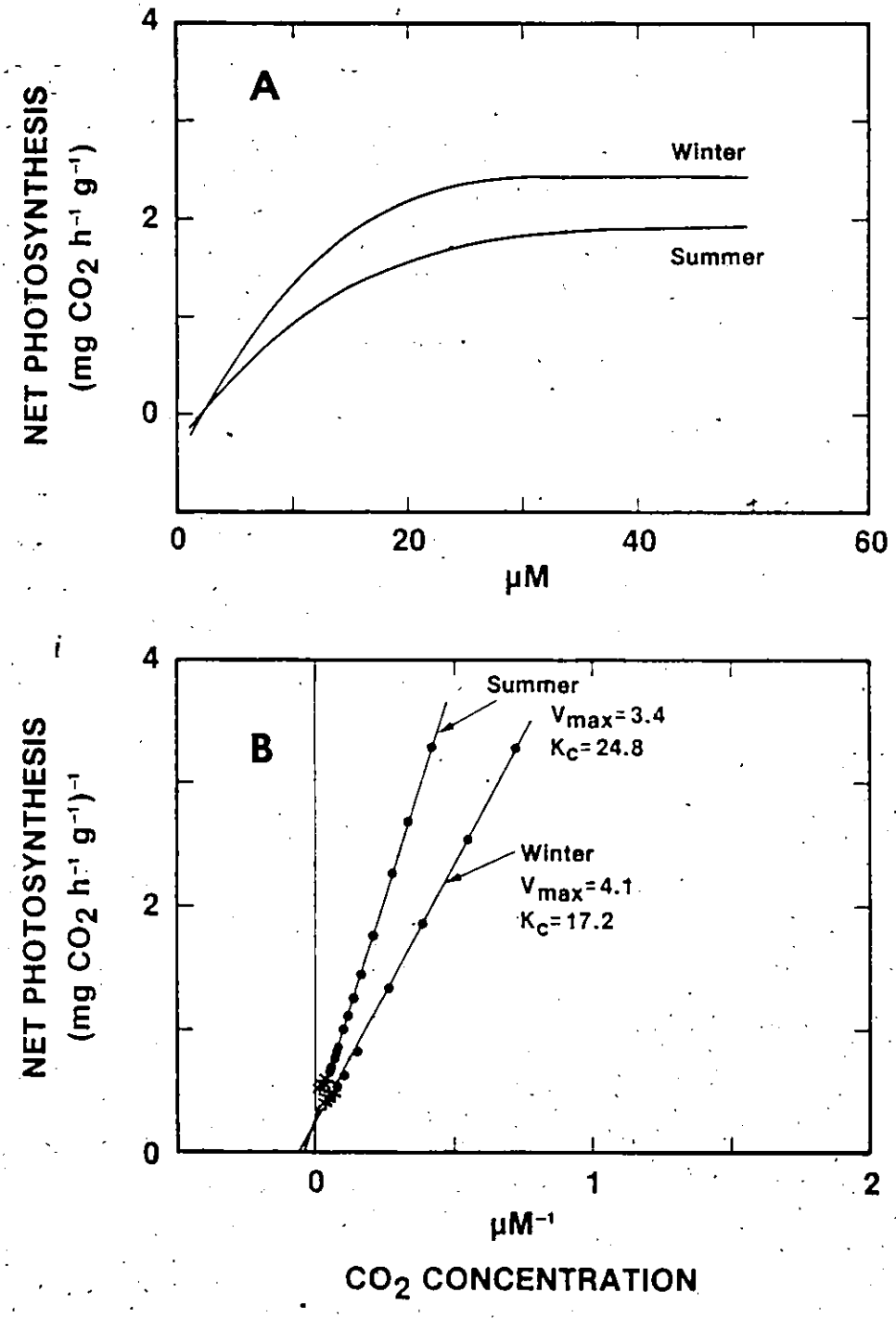

A
Winter
Summer
NET PHOTOSYNTHESIS
(mg CO_2 h^{-1} g^{-1})
0
2
4
0
20
40
60
μM
B
Summer
V_{max} = 3.4
K_c = 24.8
Winter
V_{max} = 4.1
K_c = 17.2
NET PHOTOSYNTHESIS
(mg CO_2 h^{-1} g^{-1})$^{-1}$
0
1
2
μM^{-1}
CO_2 CONCENTRATION

Figure 8

The relationship between net photosynthesis and CO_2 concentration in N.commune at full thallus saturation, 25 °C and 600 uE m^{-2} s^{-1} PAR. The CO_2 range from 300 to 250 ppm is outlined by vertical bars, while the inset plot enlarges the pattern of points near the origin.

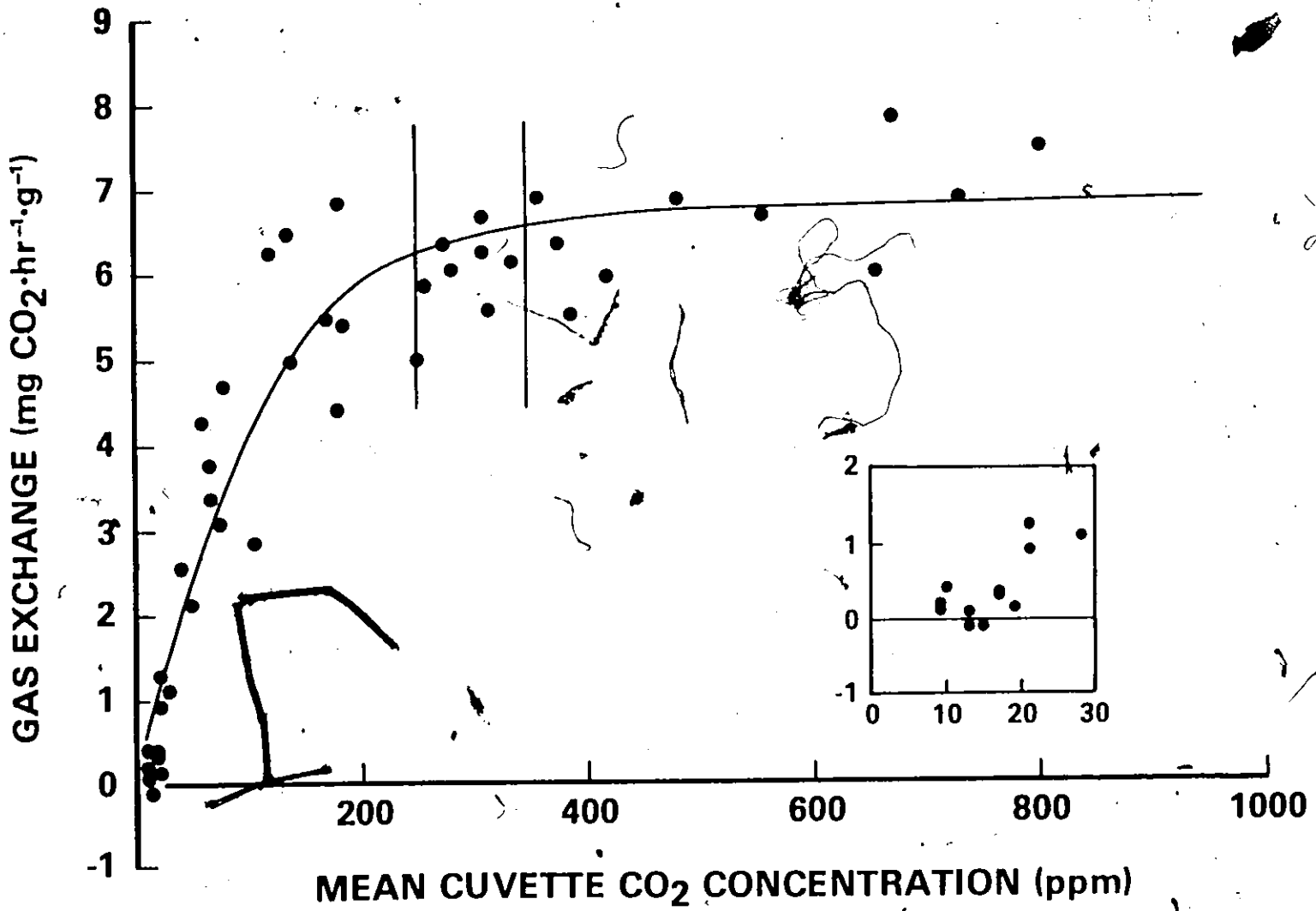

GAS EXCHANGE (mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$)
9
8
7
6
5
4
3
2
1
0
-1
200
400
600
800
1000
MEAN CUVETTE CO_2 CONCENTRATION (ppm)
2
1
0
-1
0
10
20
30

Figure 9

The gas exchange response matrix in R.superficiale at 1, 7, 14, 21, 28 and 35 °C and 0, 300, 600, 900 and 1200 uE m^{-2} s^{-1} PAR in December 1979, April, May and July 1980 across all levels of thallus hydration (expressed in percent relative terms with full thallus saturation equal to 100 percent, See Section 2.2.3). SEM of each 20% relative moisture class less than 0.08 mg CO_2 h^{-1} g^{-1} for 6 replicates.

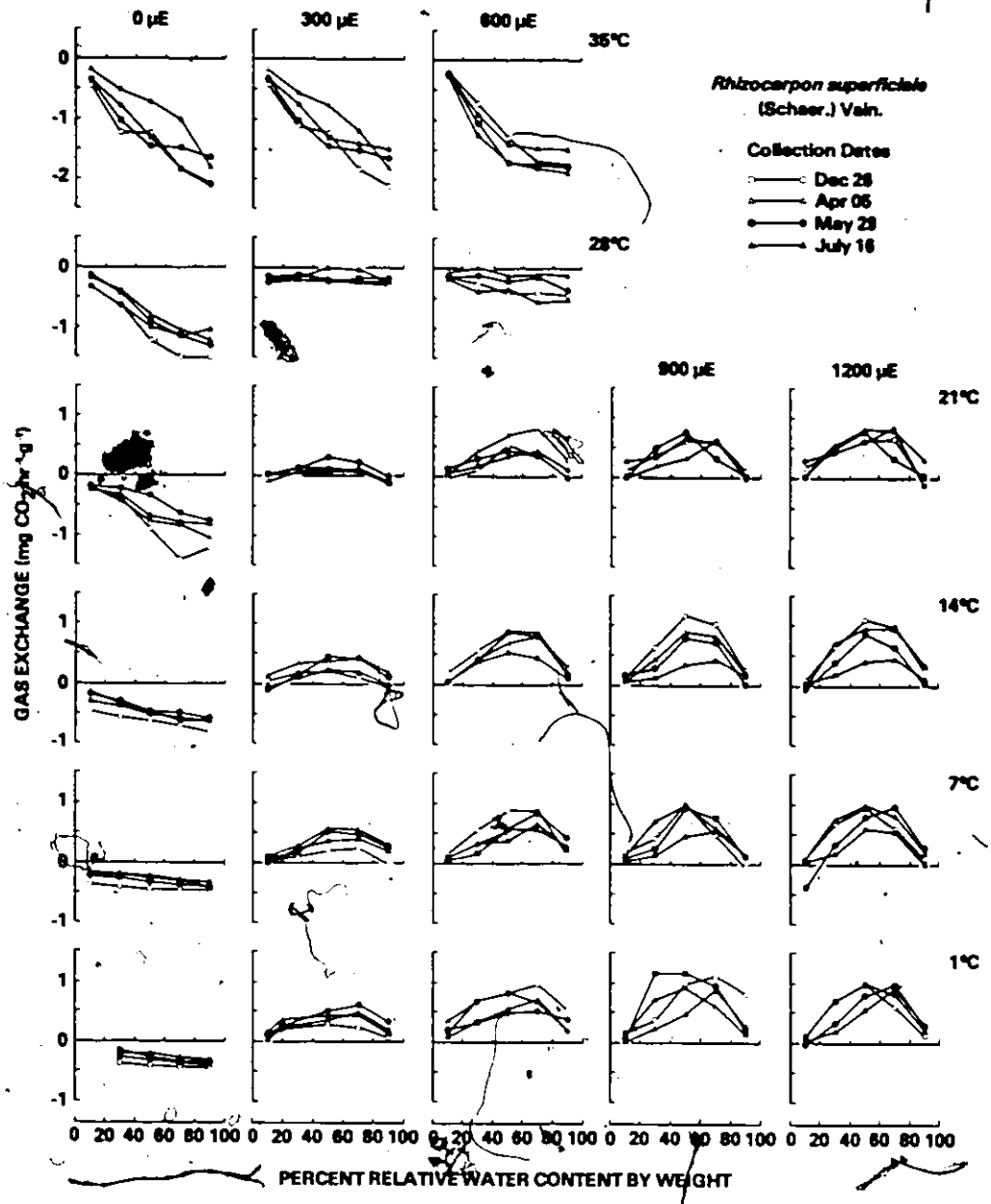

0 µE
300 µE
600 µE
900 µE
1200 µE
35°C
28°C
21°C
14°C
7°C
1°C
Rhizocarpon superficiale
(Schaer.) Vain.
Collection Dates
Dec 28
Apr 05
May 28
July 16
GAS EXCHANGE (mg CO2 hr-1 g-1)
PERCENT RELATIVE WATER CONTENT BY WEIGHT

Figure 10

The gas exchange response matrix in C.trachyphylla expressed as mg CO_2 h^{-1} g^{-1} (each y-axis) plotted against percent thallus moisture content by weight (each x-axis) over 25% moisture class intervals at 7, 14, 21, 28, and 35 °C and at 0, 300, 600, 900, and 1200 uE m^{-2} s^{-1} PAR. Collections were made in May and July 1981, and January 1982. The SEM of each 25% moisture class was less than 0.15 mg CO_2 h^{-1} g^{-1} for 6 replicates.

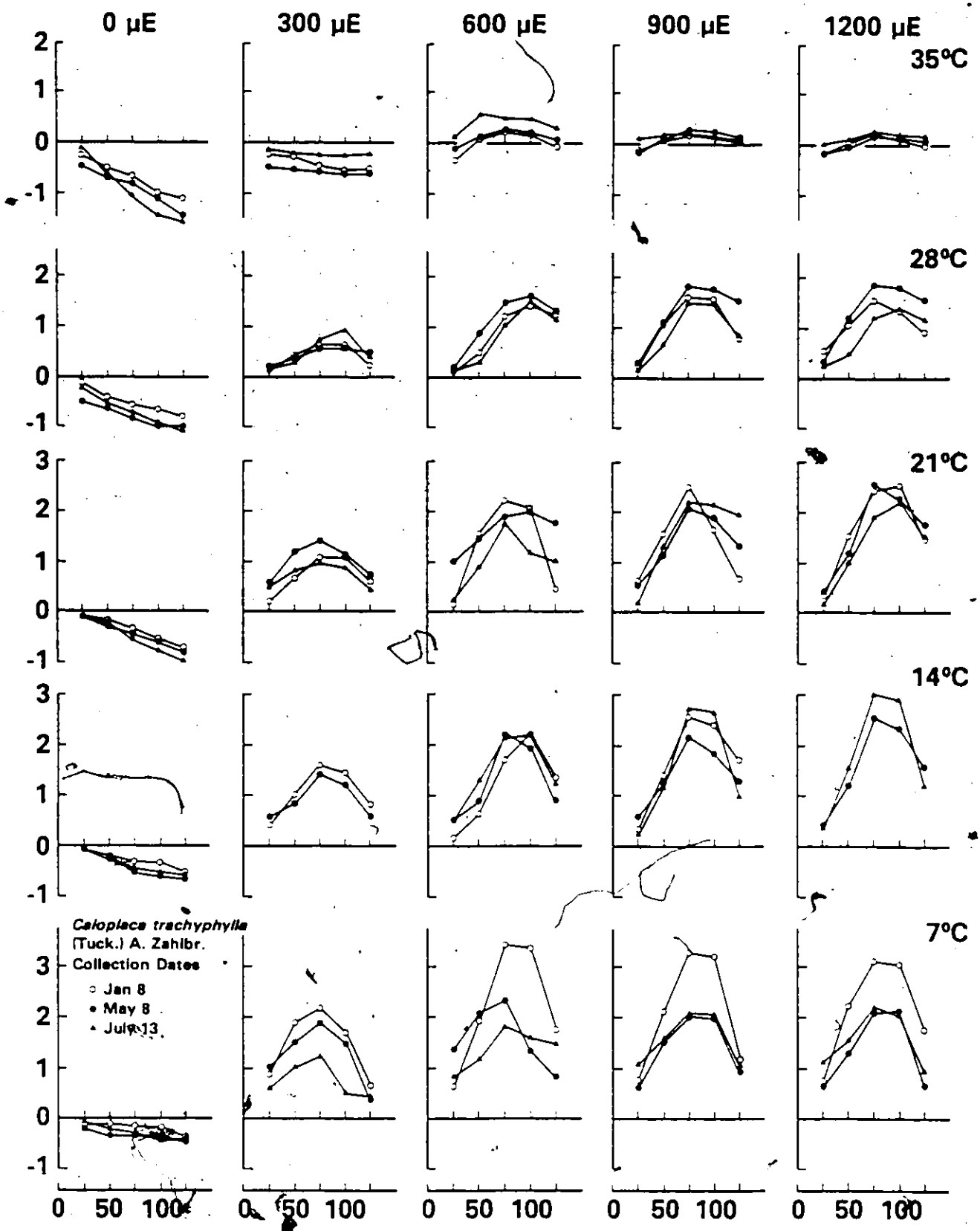

0 µE
300 µE
600 µE
900 µE
1200 µE
35°C
28°C
21°C
14°C
7°C
Caloplaca trachyphylla
(Tuck.) A. Zahlbr.
Collection Dates
Jan 8
May 8
Jul 13
0 50 100

Figure 11

The dependence of net photosynthetic rates on illumination levels (uE m^{-2} s^{-1} PAR) in C.trachyphylla collected in March, 1982. Replicates were stored air dry under winter storage conditions of 1/5 °C day/night temperature and 0/300 uE m^{-2} s^{-1} PAR over a 16/8 hour photoperiod (Plots a, b, e, and f) and summer storage conditions of 20/30 °C day/night temperature and 0/300 uE m^{-2} s^{-1} PAR over a 8/16 hour photoperiod (Plots c, d, g, and h). The response of CO_2 gas exchange (mg CO_2 h^{-1} g^{-1}) was followed at 7 °C (Plots a to d) and 21 °C (Plots e to h) after 7 days storage of dry thalli under both winter and summer storage conditions. Rehydration pretreatment consisted of 12 hours at 5 and 20 °C for winter and summer stored replicates respectively. A 1st order regression line through data points below 100 uE m^{-2} s^{-1} PAR (slope = a_1, correlation coefficient = r_1) intersects the line drawn through the mean of light saturated rates of net photosynthesis, while a 3rd order regression line is fitted to the entire data set (correlation coefficient = r_2). All experiments with January, 1983 collected replicates.

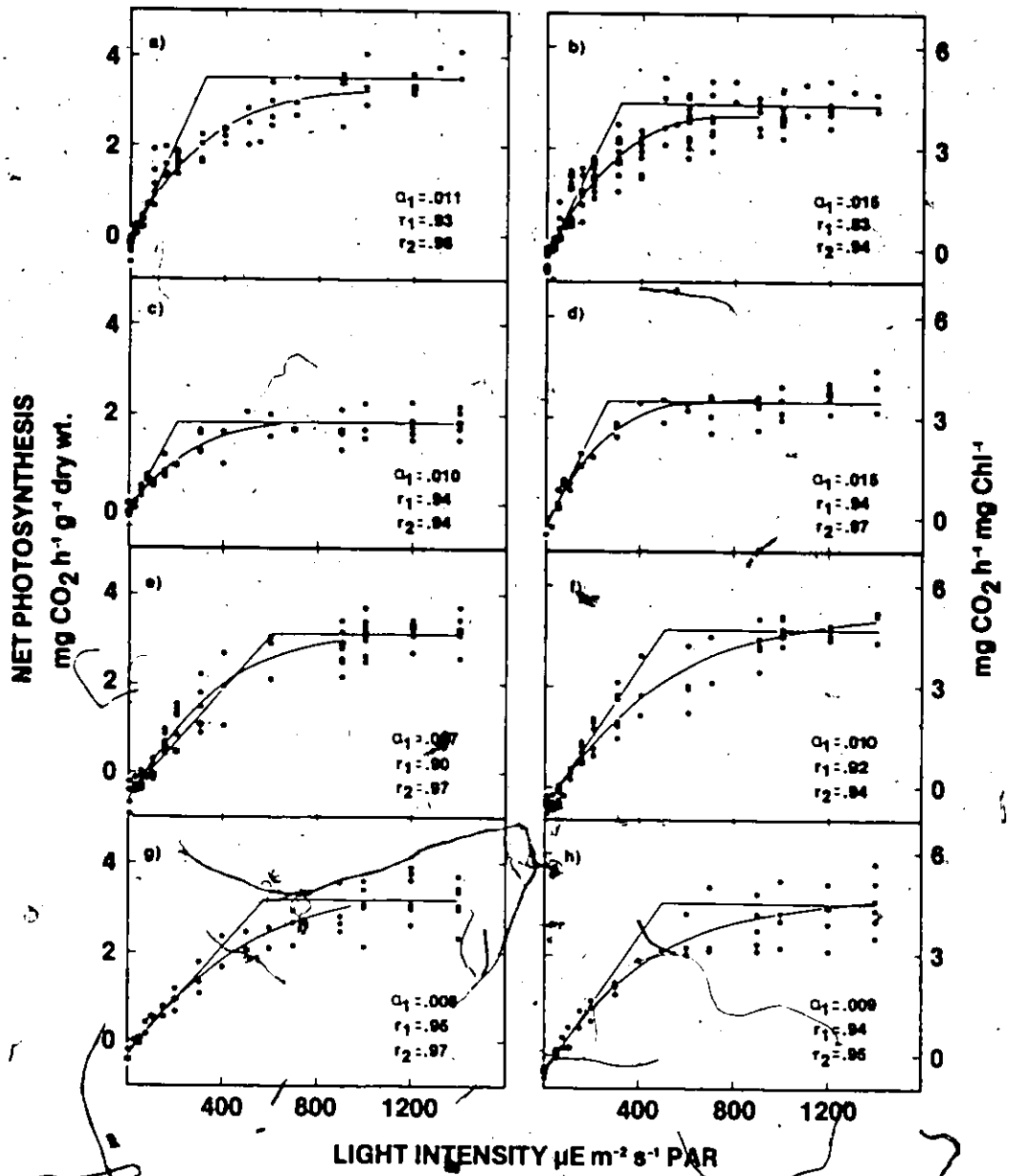

a)
b)
c)
d)
e)
f)
g)
h)
NET PHOTOSYNTHESIS
mg CO_2 h^{-1} g^{-1} dry wt.
mg CO_2 h^{-1} mg Chl^{-1}
LIGHT INTENSITY µE m^{-2} s^{-1} PAR
400
800
1200
0
2
4
3
6

Figure 12

The plot of regression slopes of light limited photosynthetic rates in C.trachyphylla (from Fig. 11), expressed both on a dry weight (top) and chl-a (bottom) basis. Replicate groups as follows: A) Winter stored 7 °C assay; B) Summer stored 7 °C assay; C) Winter stored 21 °C assay and D) Summer stored 21 °C assay.

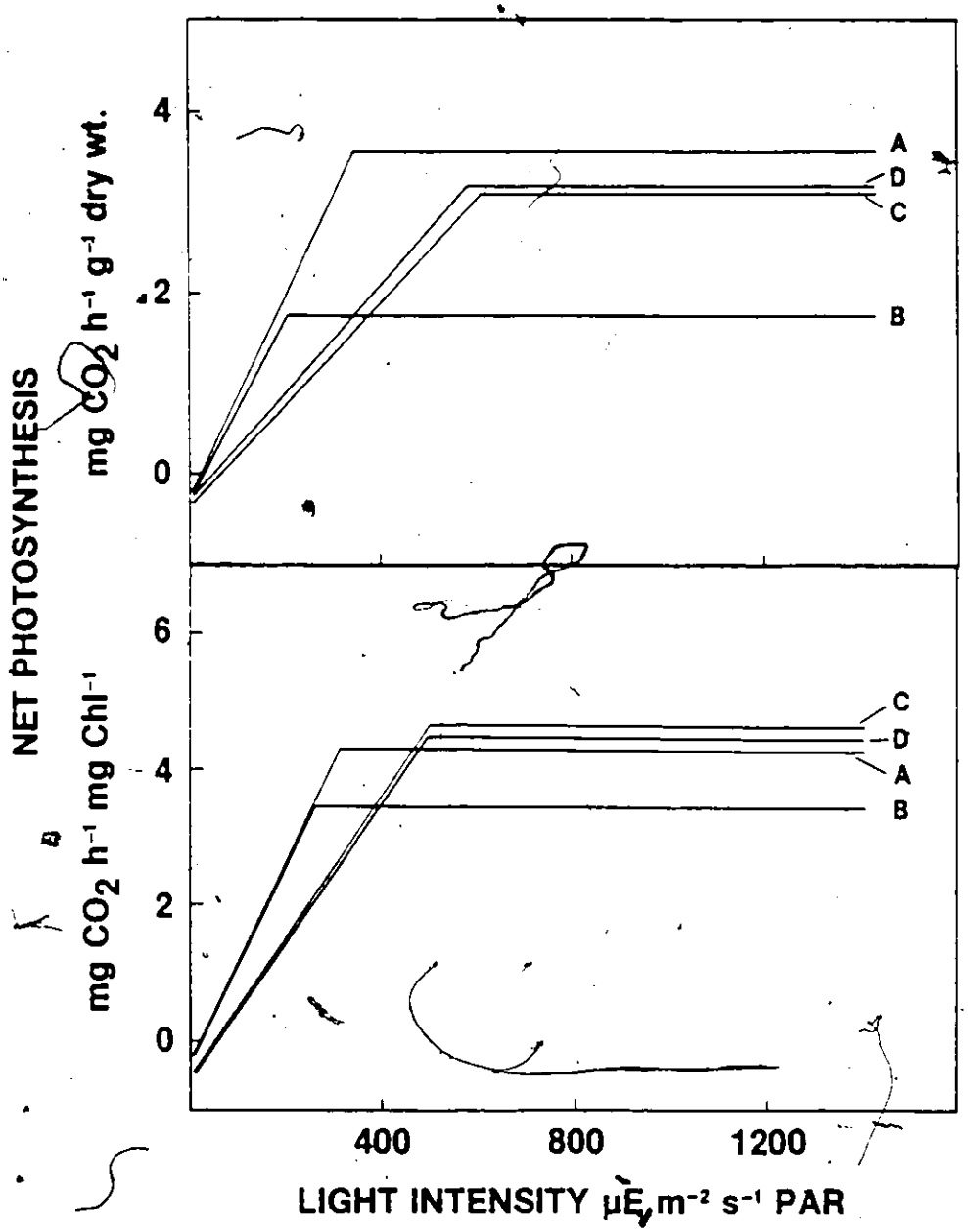

NET PHOTOSYNTHESIS
mg CO_2 h^{-1} g^{-1} dry wt.
4
2
0
A
D
C
B
mg CO_2 h^{-1} mg Chl^{-1}
6
4
2
0
C
D
A
B
400
800
1200
LIGHT INTENSITY μE, m^{-2} s^{-1} PAR

Figure 13

The effects of thallus hydration on gas exchange (mg CO_2 h^{-1} g^{-1}) at 25°C and 0 uE m^{-2} s^{-1} PAR (open symbols) and 600 uE m^{-2} s^{-1} PAR (closed symbols) in N.commune.

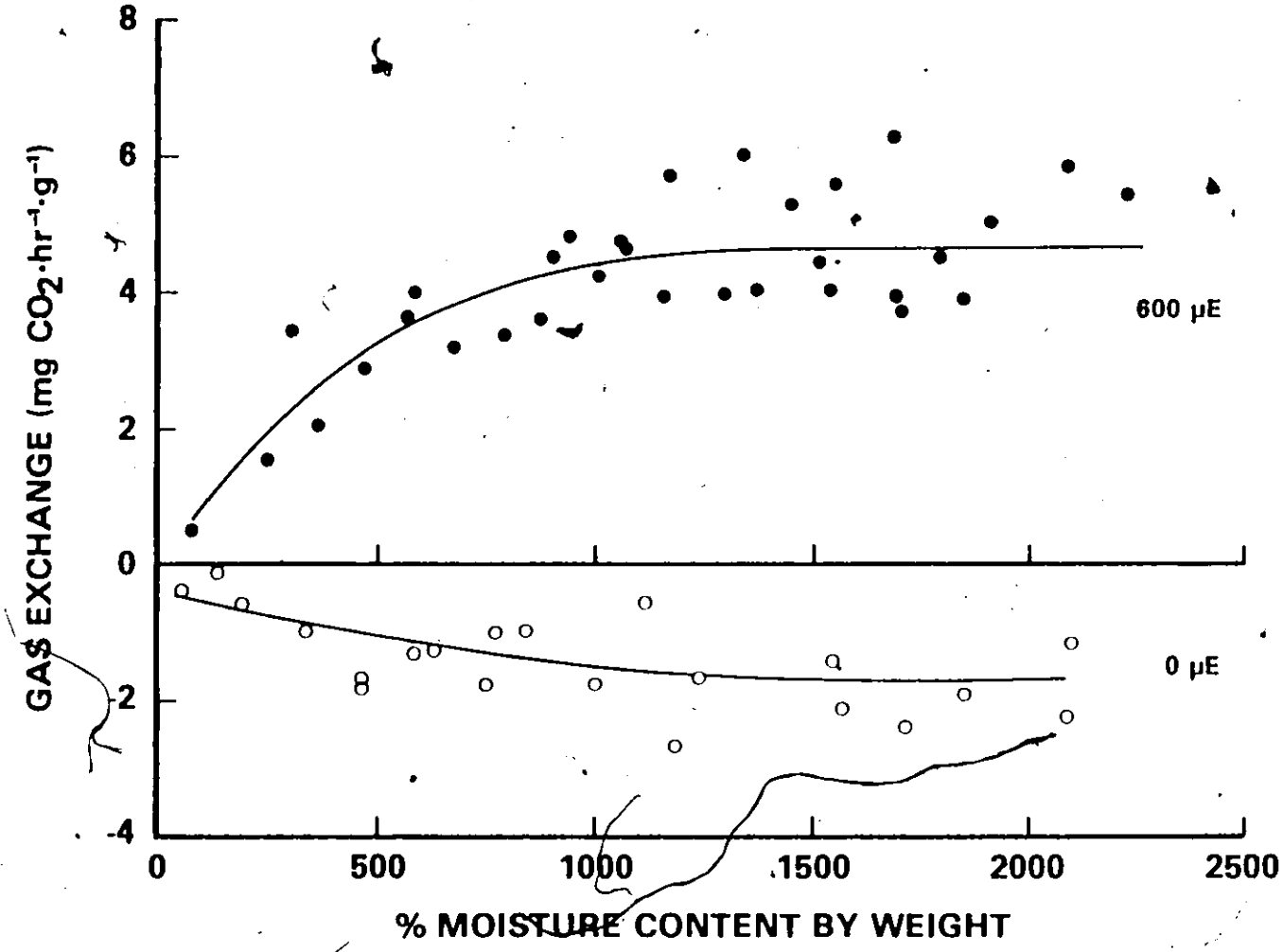

8
6
4
2
0
-2
-4
GAS EXCHANGE (mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$)
600 µE
0 µE
0
500
1000
1500
2000
2500
% MOISTURE CONTENT BY WEIGHT

Figure 14

The response of net photosynthesis (mg CO_2 h^{-1} g^{-1}) in N.commune to 0 (□), 300 (●) and 600 (○) uE m^{-2} s^{-1} PAR at 25 °C over 500% thallus moisture content class intervals. SEM bars given for each mean of 8 replicate incubations.

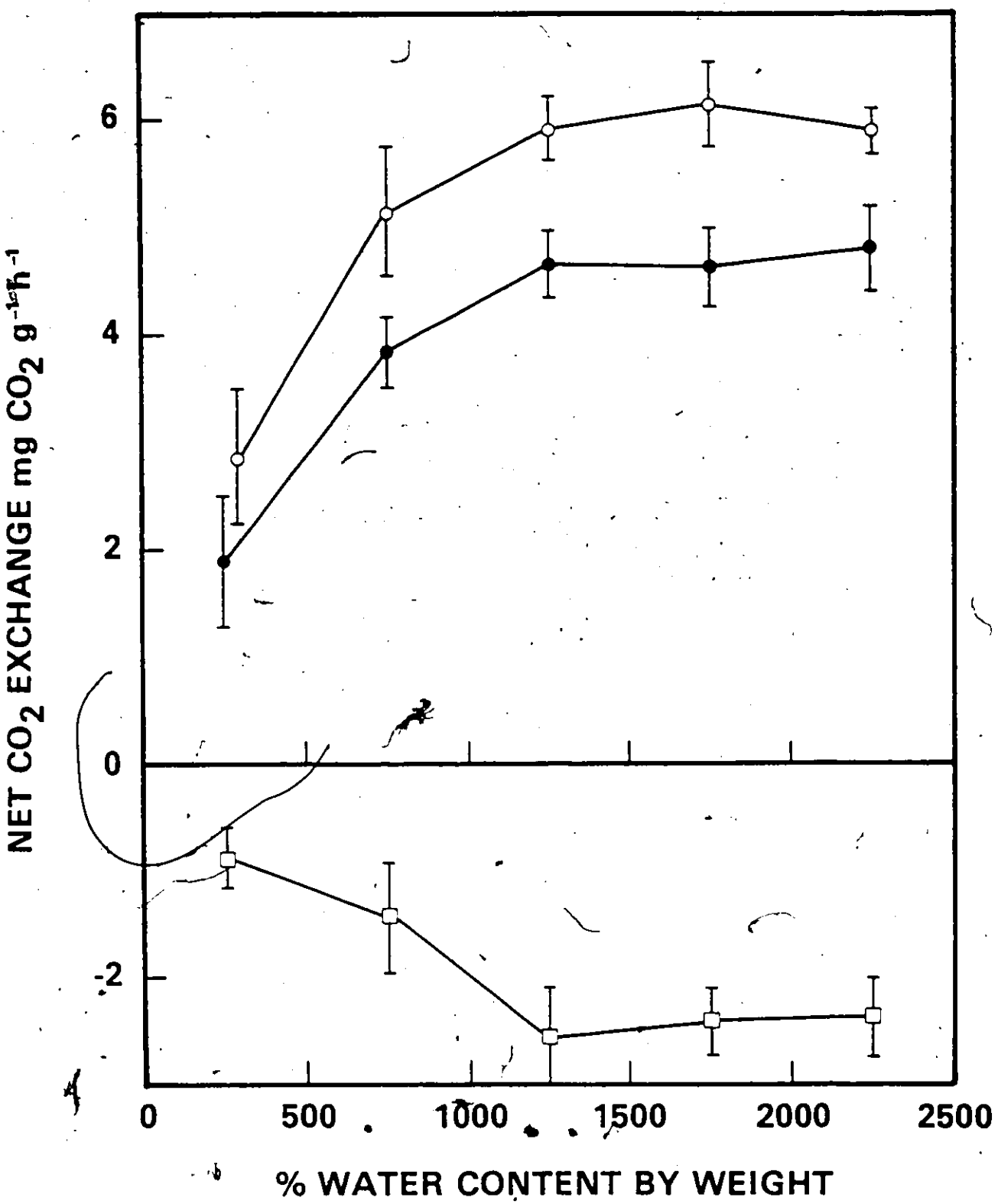

6
4
2
0
-2
0
500
1000
1500
2000
2500
NET CO_2 EXCHANGE mg CO_2 $g^{-1}h^{-1}$
% WATER CONTENT BY WEIGHT

Figure 15

The response of net photosynthesis (mg CO_2 h^{-1} g^{-1}) in N.commune to 50, 100, 300, 600, 900 and 1200 uE m^{-2} s^{-1} PAR at 21 °C and full thallus saturation. Each symbol refers to an individual replicate.

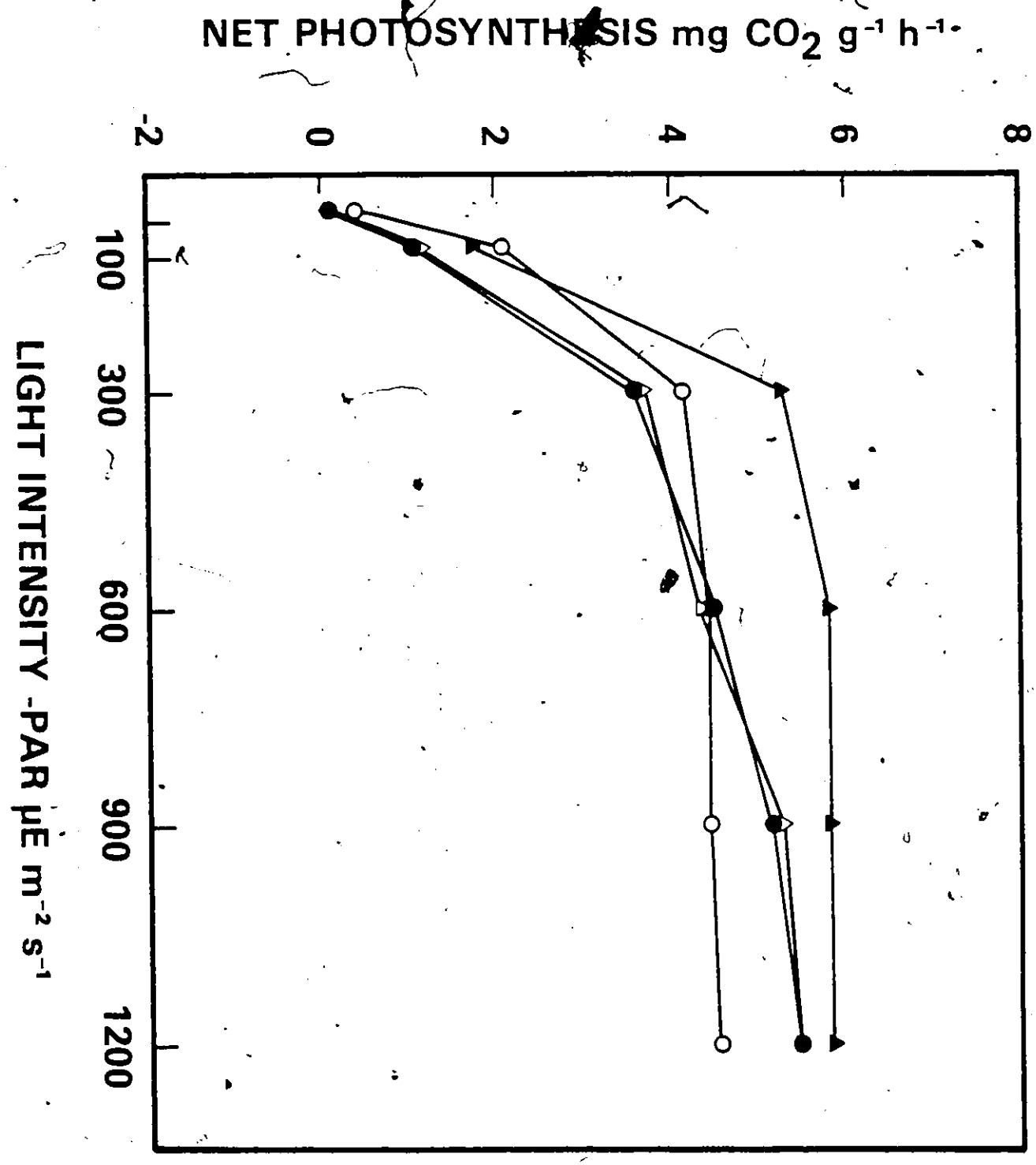

NET PHOTOSYNTHESIS mg CO_2 g^{-1} h^{-1}
-2
0
2
4
6
8
LIGHT INTENSITY -PAR µE m^{-2} s^{-1}
100
300
600
900
1200

Figure 16

The seasonal response of net photosynthesis, respiration and nitrogenase activity in N.commune. Material was collected in January (○), March (◇), May (△), July (□) and October (▽) 1981; and assayed at 7, 14, 21, 28 and 35 °C. A light intensity of 200 uE m^{-2} s^{-1} PAR was used during nitrogenase assays, while CO_2 exchange measurements followed rehydration pretreatment of 12 hours under seasonal temperature levels. Each point is a mean of 6 to 10 replicate determinations, SEM below 0.5 nmol C_2H_4 mg^{-1} h^{-1} and 0.4 mg CO_2 h^{-1} g^{-1}.

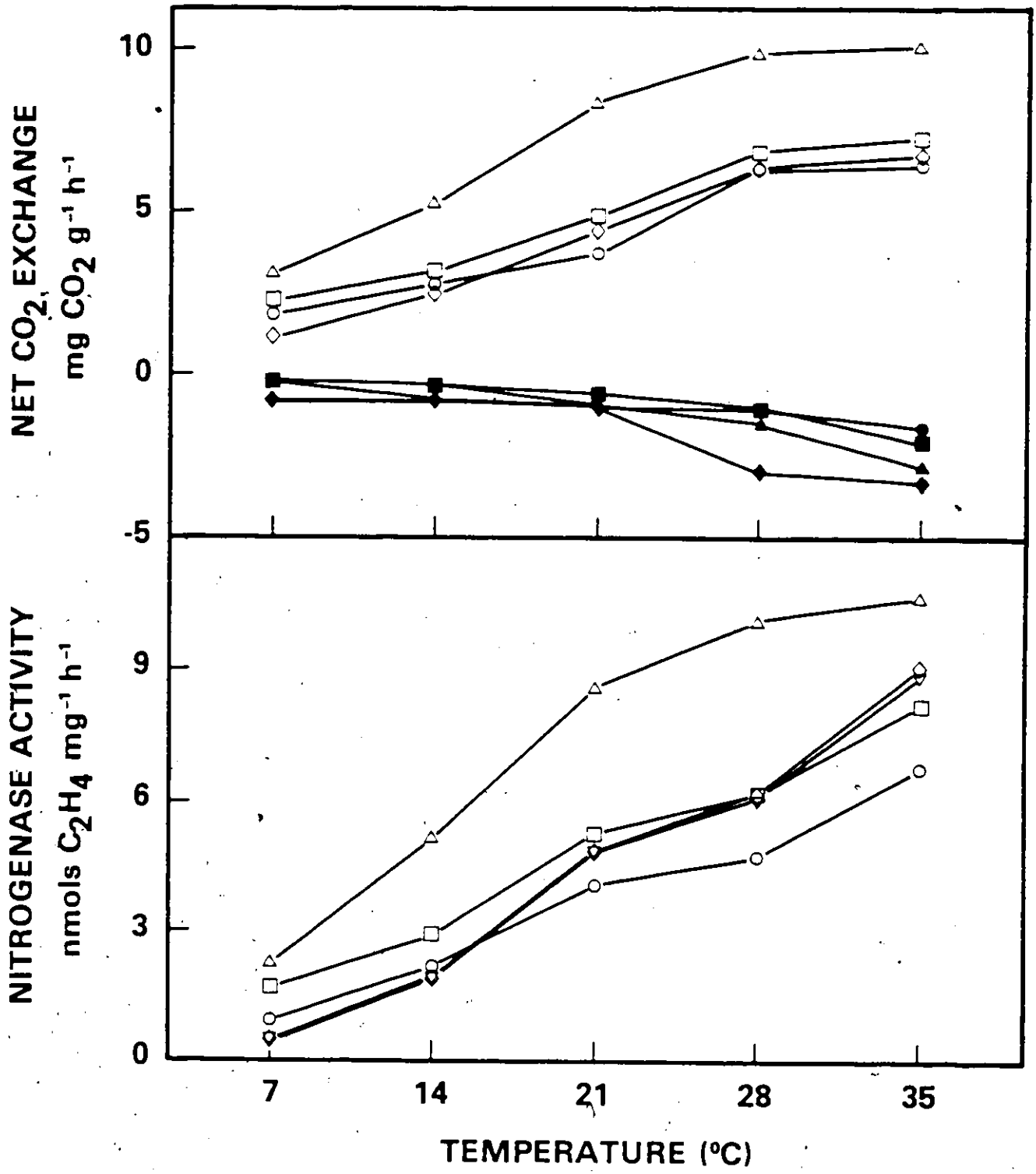

NET CO_2 EXCHANGE
mg CO_2 g^{-1} h^{-1}
10
5
0
-5
NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
9
6
3
0
7
14
21
28
35
TEMPERATURE (°C)

Figure 17

The rehydration response of net photosynthesis at 600 uE m^{-2} s^{-1} PAR (O) and respiration at 0 uE m^{-2} s^{-1} PAR (●) in N.commune. Gas exchange (mg CO_2 h^{-1} g^{-1}) was followed at both 7 and 21 °C following a 12 hour hydration period. The previous wetting/ drying cycle for this material incorporated a 5 hour "slow" dry after 48 hours hydration.

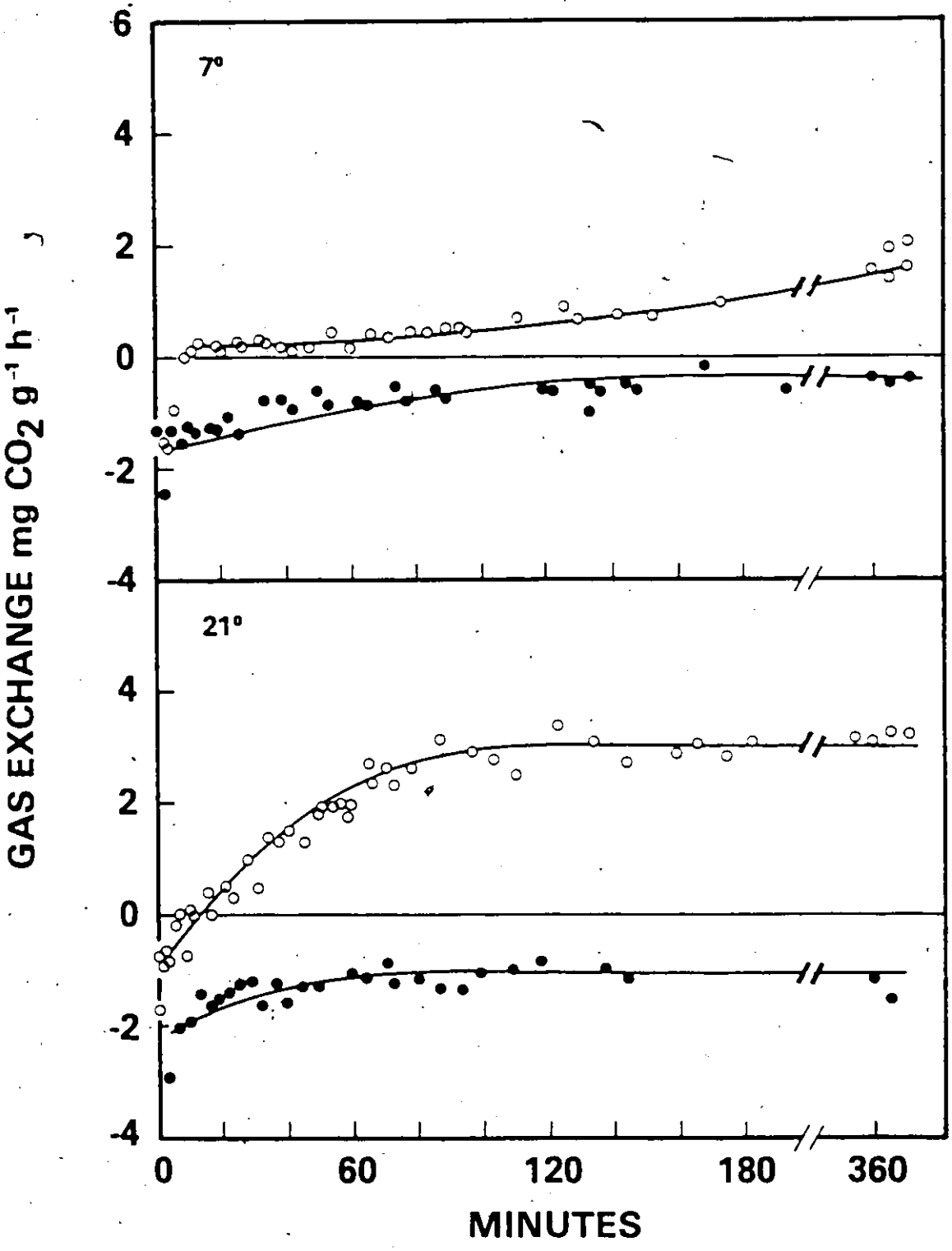

7°
21°
6
4
2
0
-2
-4
GAS EXCHANGE mg CO_2 g^{-1} h^{-1}
0
60
120
180
360
MINUTES

Figure 18

The time course of CO_2 evolution (mg CO_2 h^{-1} g^{-1}) following rehydration of N.commune at 21 °C and 600 uE m^{-2} s^{-1} PAR. Immediate pretreatment consisted of a 12 hour hydration period, while the previous wetting/ drying cycle incorporated a 5 hour "slow" dry under both normal (○) and CO_2 free (●) air after 48 hours hydration.

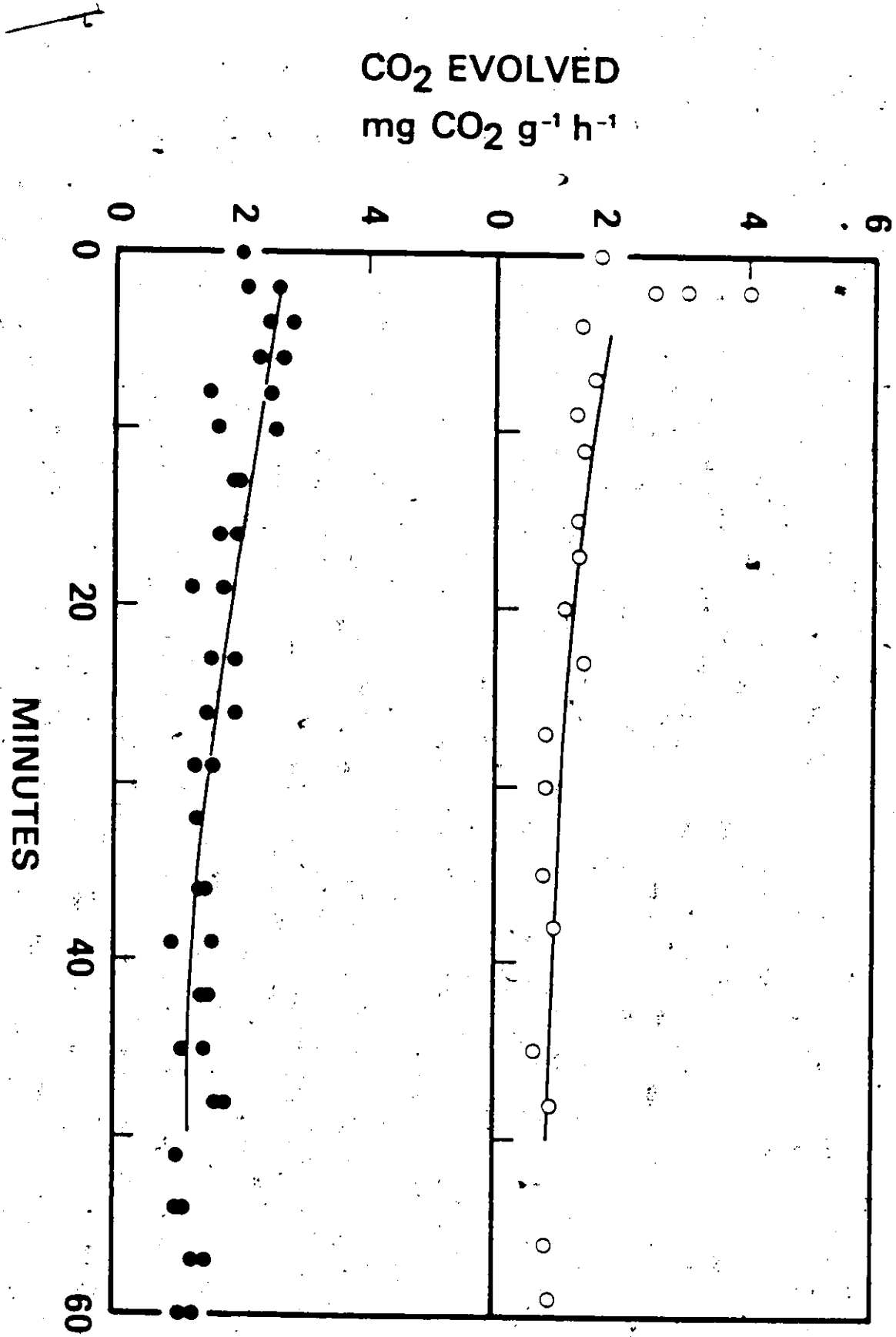

CO_2 EVOLVED
mg CO_2 g^{-1} h^{-1}
0
2
4
0
2
4
6
0
20
40
60
MINUTES

Figure 19

The response of net photosynthesis and respiration in July 1980 collected R.superficiale to continued heat exposure. Air dry replicates were exposed to midday temperatures of 35 and 45 °C for three hours daily over a 21 day experimental period and assayed for gas exchange following a 12 hour hydration period at days 2, 7, 14 and 21.

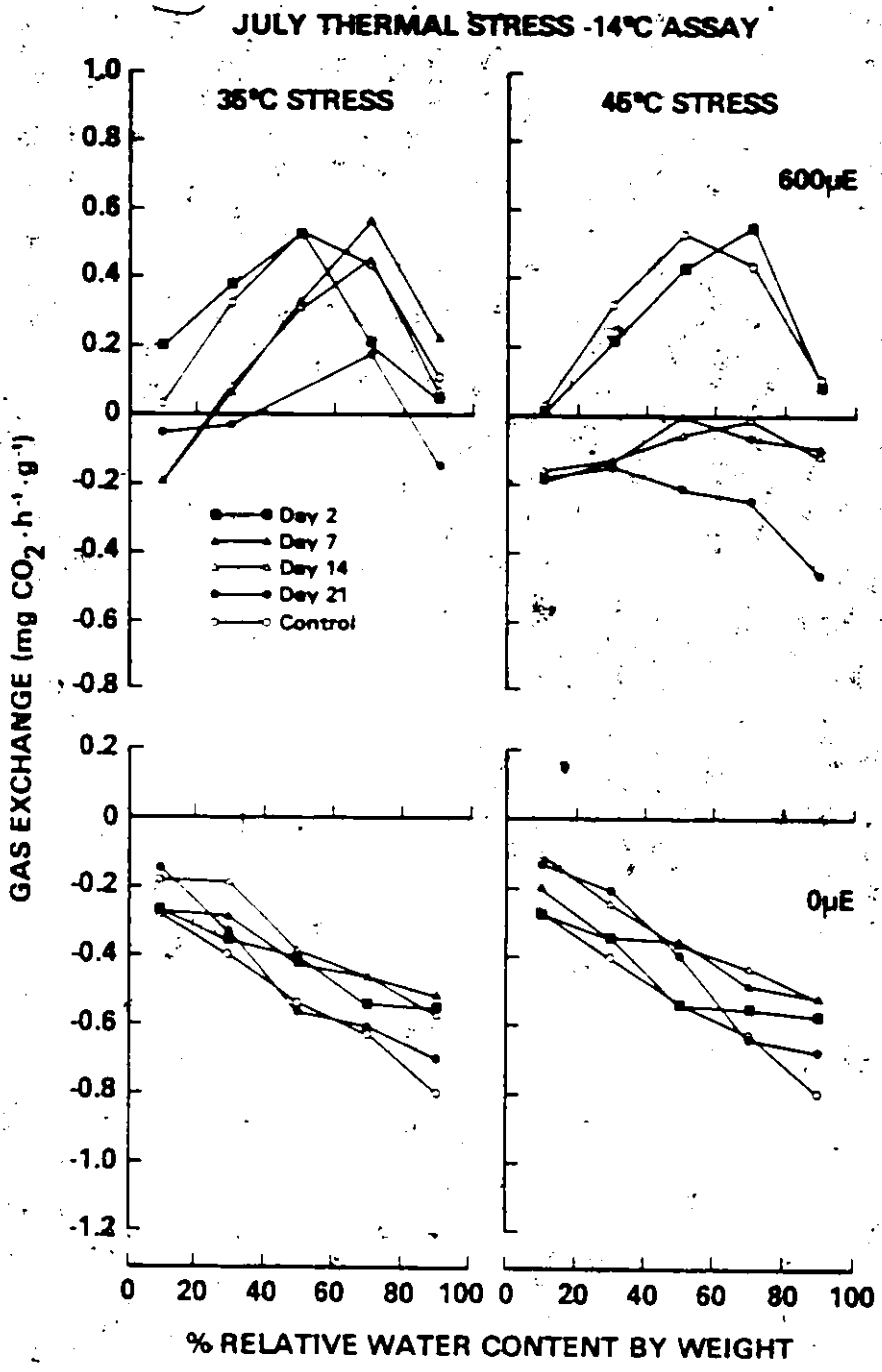

JULY THERMAL STRESS -14°C ASSAY
35°C STRESS
45°C STRESS
600µE
0µE
Day 2
Day 7
Day 14
Day 21
Control
GAS EXCHANGE (mg $CO_2 \cdot h^{-1} \cdot g^{-1}$)
% RELATIVE WATER CONTENT BY WEIGHT
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
0
20
40
60
80
100

Figure 20

Heat stress experiment as per Fig. 19, only for material of R.superficiale collected in January 1980.

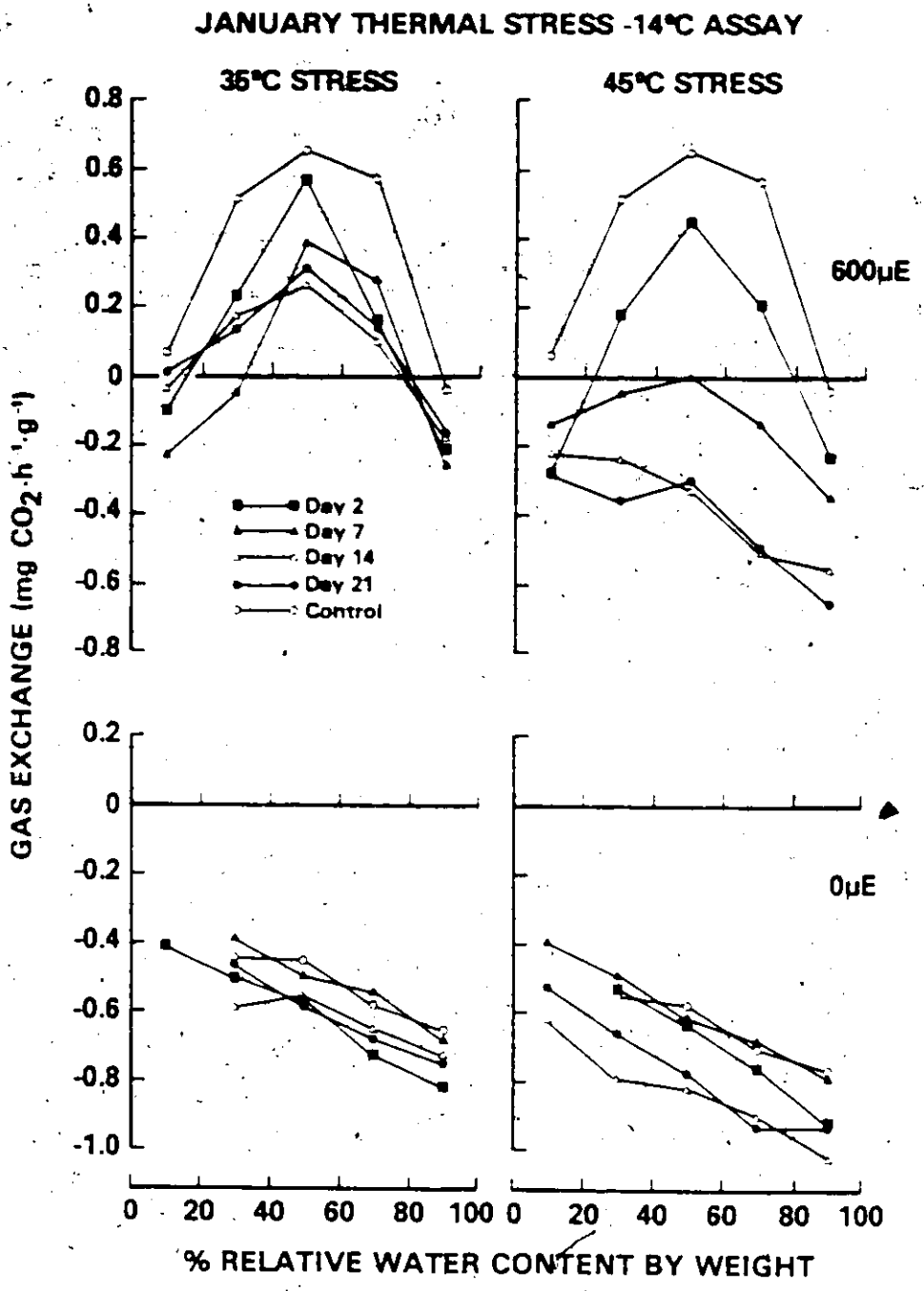
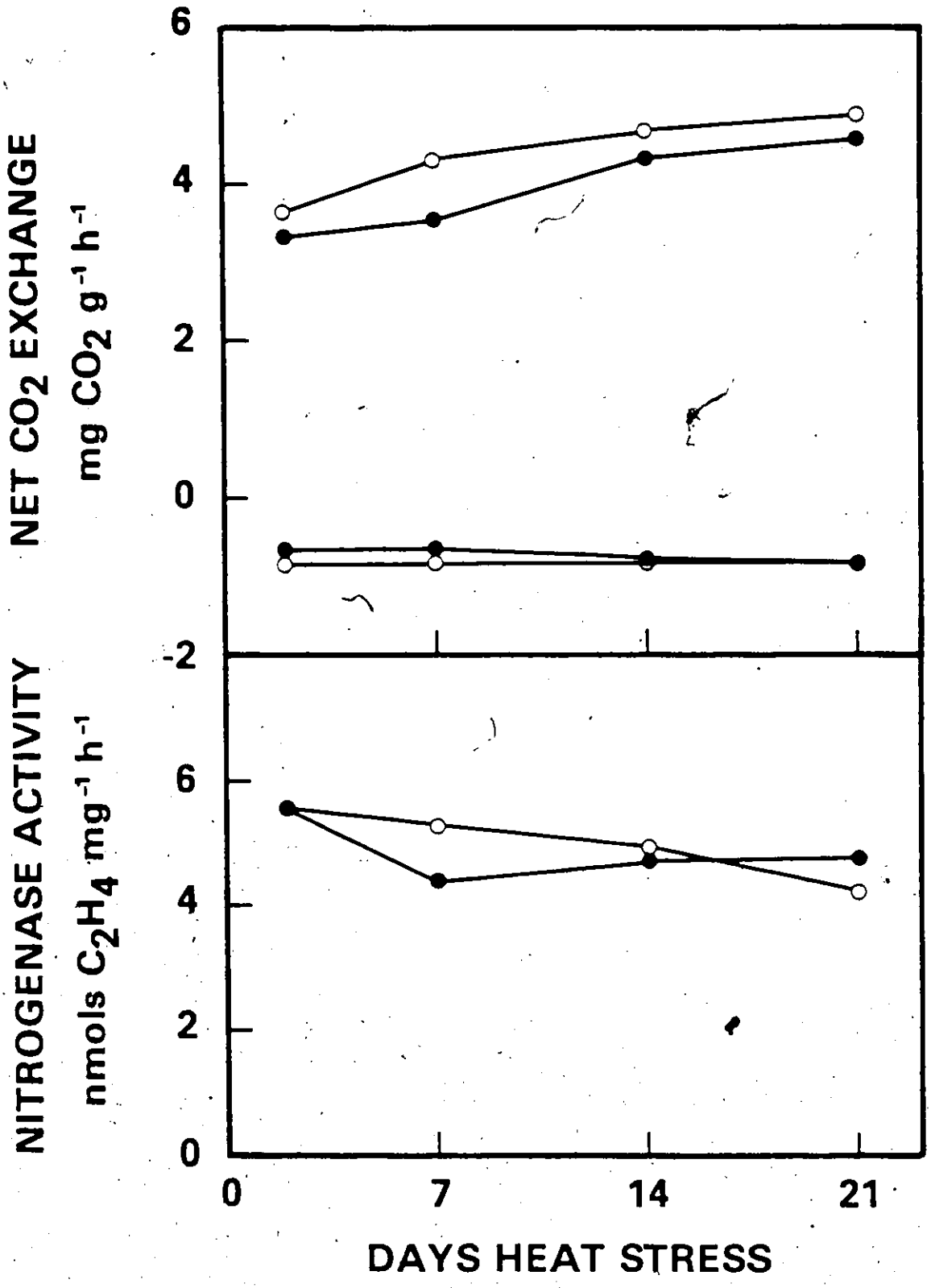

JANUARY THERMAL STRESS -14°C ASSAY
35°C STRESS
45°C STRESS
600µE
0µE
Day 2
Day 7
Day 14
Day 21
Control
GAS EXCHANGE (mg $CO_2 \cdot h^{-1} \cdot g^{-1}$)
% RELATIVE WATER CONTENT BY WEIGHT
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
0 20 40 60 80 100

Figure 21

The response of N.commune to continuous heat stress whilst dry over a 21 day period. Midday temperatures were held at 60 °C for 5 hours each day, changing by 10 °C h^{-1} from a 25 °C night time temperature regime. Both nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) and CO_2 exchange (mg CO_2 h^{-1} g^{-1}) were assayed at 1, 7, 14 and 21 days after initiation of high temperature storage (●), with additional assays of control replicates (○) held at 25 °C conducted simultaneously. Assay conditions were 21 °C and 600 uE m^{-2} s^{-1} PAR after 6 hours rehydration pretreatment under these same conditions. SEM as in Fig. 16.


NET CO_2 EXCHANGE
mg CO_2 g^{-1} h^{-1}
6
4
2
0
-2
NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
6
4
2
0
0
7
14
21
DAYS HEAT STRESS

(3.2) Nitrogenase Activity

(3.2.1) Temperature, Light and Moisture Interactions

The short term response of nitrogenase activity to temperature in N.commune is given in Fig. 16. There were no marked seasonal differences in the response pattern, all four collections showing steady increases in activity with increasing temperature. Although the magnitude of response was higher for the May collection, this difference was reduced when results were expressed in mg Chl a $^{-1}$ h^{-1} (Table 6). Fig. 16 illustrates short term C_2H_2 reduction assays only. Continued exposure to high temperature (Fig. 22) showed that 28 °C is actually the long term temperature optimum for nitrogenase activity, as rates declined very rapidly at 40 °C. The response of nitrogenase activity to declining thallus moisture content parallels that seen for CO_2 gas exchange (Fig. 23), with constant rates from 2500 down to 500% thallus moisture content, falling very quickly below 100% moisture content.

Light saturation of nitrogenase activity in N.commune occurs at approximately 900 uE m^{-2} s^{-1} PAR. Destructive sampling and incubation of replicates at various light levels gave generally higher rates of nitrogenase activity at higher light intensities, however, inter-replicate variability tended to obscure any definitive interaction of nitrogenase activity with light intensity (Fig. 24). A more clear cut

light dependency was seen when individual replicates were followed sequentially through changing light levels (Fig. 25). Although rates of nitrogenase activity were higher at the 100 uE m^{-2} s^{-1} PAR after 5 hours acetylene exposure, there were still marked light interactions of even greater magnitude in material transferred up to 900 uE m^{-2} s^{-1} PAR and then back to 100 uE m^{-2} s^{-1} PAR. These values are expressed in relative terms for each replicate, so that inter-replicate variability does not hide the individual response patterns to light.

The rate with which nitrogenase activity declined on transfer of experimental replicates into darkness is shown at 5, 15 and 25 °C in Fig. 26. Replicates were pretreated at 200 uE m^{-2} s^{-1} PAR and 25 °C for 12 hours. A strong temperature dependence was noted, with most rapid elevation of C_2H_2 reduction rates occurring at the highest temperatures. The pattern of nitrogenase activity after addition of 10 uM DCMU at 2 and 12 hours into the daily photoperiod is shown in Figs. 27 and 28 respectively. These results are expressed in both nmol C_2H_4 mg^{-1} h^{-1} and in nmol C_2H_4 mg Chl-a^{-1} h^{-1}.

(3.2.2) Response to Thermal Stress

When dry, N.commune showed extreme resistance to extended desiccation and heat exposure. After 21 days exposure to 60 degree C temperatures midday, no significant changes in nitrogenase activity were evident following a standard 6 hours pretreatment period (Fig. 21). This contrasted markedly with the sensitivity to thermal extremes shown when

replicates were hydrated (Fig. 22), noted above in Section 3.2.1.

(3.2.3) Response to Freeze-Thaw Periods

Material of N.commune exposed to growth chamber freeze-thaw cycles showed rapid recovery of nitrogenase activity on morning melting, in agreement with field acetylene reduction rates in winter (Section 3.3.2). Replicates of N.commune held previously under a growth chamber freeze/thaw environment for 14 days showed substantial daily nitrogenase activity, rates rising from 0.8 nmol C_2H_4 mg^{-1} h^{-1} on thawing to near 6.0 nmol C_2H_4 mg^{-1} h^{-1} after 8 hours (Group A replicates, Fig. 29a). Group B and C replicates pretreated at -5 °C for 14 days showed a different response pattern, taking nearly 3 days before full recovery of nitrogenase activity to the levels shown by Group A was reached (Fig. 29a). Exposure to higher temperatures upon initial melting greatly accelerated the recovery rate of Group B and by 12 hours at 20 °C recovery was complete (Fig. 29b). A marked interaction of higher temperature with the pattern of light recovery was also seen.

(3.2.4) Pretreatment Interaction Between Temperature, Light and Photoperiod

A strong interaction was noted between the rehydration response of nitrogenase activity and experimental temperature in N.commune. At 25 °C, nitrogenase activity shows almost full recovery after 6 hours

rehydration and by 14 hours rates had reached maximal values (Fig. 30). This recovery response was similar across the full range of thallus moisture contents. Further interactions of nitrogenase rehydration response with temperature and photoperiod are given in Figs. 31 to 33, where material after rehydration was maintained under a 12/12 hour photoperiod at different temperatures. At 21 °C the response immediately following rehydration in the morning (Line C, Fig. 31) confirms the previous time sequence data (Fig. 30). After 24 hours prior hydration under a 12/12 hour photoperiod nitrogenase activity was immediately detectable and increased rapidly over following light periods (Line A, Fig. 31). When replicates were illuminated after only being hydrated for the previous 12 hours dark period (Line B, Fig. 31), their response is intermediate between the other two groups. This last rehydration sequence (Line B, Fig. 31) is especially common under summer field conditions, where after late evening thundershowers, material remains wet well into the following day (Section 3.3.2). Concurrently at 21 °C there was a virtually immediate recovery of respiratory and photosynthetic activity, confirming previous results (Section 3.1.2; Figs. 17 and 18). The same pattern of photoperiod rehydration recovery was seen at 14 °C (Fig. 32). In direct contrast however, at 7 °C very little recovery of nitrogenase activity was evident after even 36 hours hydration. The above recovery patterns are evident both for nitrogenase activity expressed in nmol C_2H_4 mg^{-1} h^{-1}, or in nmol C_2H_2 mg Chl-a^{-1} h^{-1} (Fig. 33).

Table 6 Seasonal changes in mg Chl_a per g oven dry weight of *Nostoc commune* (N=8) and comparison of C_2H_2 Reduction rates expressed on both a dry weight and chlorophyll basis.[a]

Season	mg $Chl_a\ g^{-1}$	SE	nmols C_2H_4 per $mg^{-1}\ h^{-1}$	nmols C_2H_4 per mg $Chl_a^{-1}\ h^{-1}$
January	0.85	0.035	4.6	5.4
March	0.78	0.015	5.1	6.5
May	1.64	0.047	11.9	7.2
July	0.84	0.042	5.1	6.0
October	0.90	0.027	5.9	6.5

(a) Assayed at 28°C and 600 $\mu Em^{-2}\ s^{-1}$ PAR.

Figure 22

The time course of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune over an 8 hour period in replicates held at 28 (▲), 35 (○) and 40 (●) °C. Material was pretreated for 14 hours at 28 °C and 200 uE m^{-2} s^{-1} PAR and assayed at 28 °C and 200 uE m^{-2} s^{-1} PAR. All replicates were maintained at full thallus saturation over course of experiments. Each value plotted is the mean of 6 replicate incubations, the SEM of which fell under 0.5 nmol C_2H_4 mg^{-1} h^{-1}.

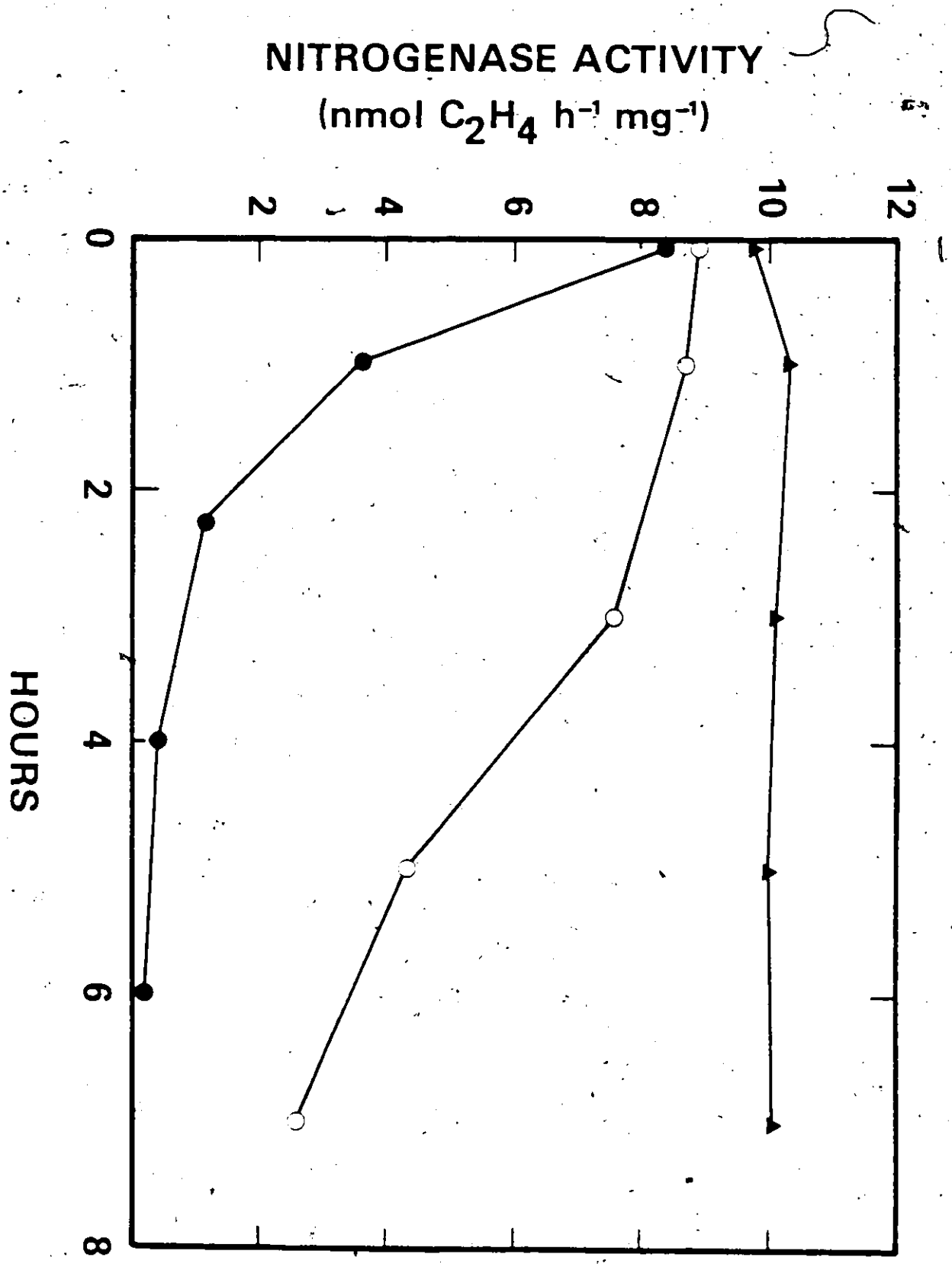

NITROGENASE ACTIVITY
(nmol C_2H_4 h^{-1} mg^{-1})
2
4
6
8
10
12
0
2
4
6
8
HOURS

Figure 23

The response of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune to level of thallus hydration. Replicates were assayed for C_2H_2 reduction at 21 °C and 200 uE m^{-2} s^{-1} PAR. A third order regression through data points is depicted by line.

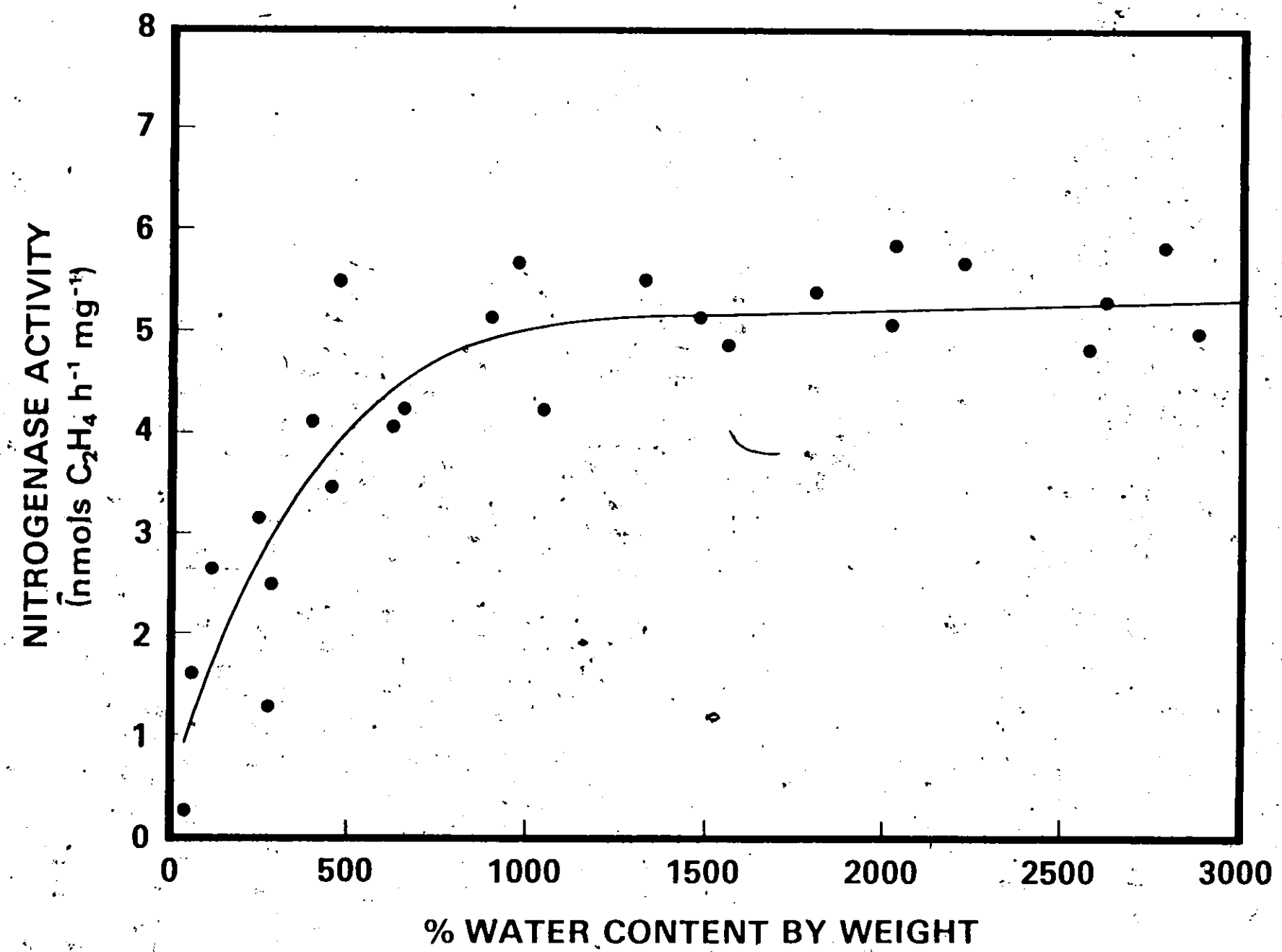

NITROGENASE ACTIVITY
(nmols C_2H_4 h^{-1} mg^{-1})
8
7
6
5
4
3
2
1
0
0
500
1000
1500
2000
2500
3000
% WATER CONTENT BY WEIGHT

Figure 24

The response of nitrogenase activity to light intensity over the full range of thallus moisture content. Activity was assayed at 0 (△), 100 (▲), 300 (●) and 600 (○) uE m^{-2} s^{-1} PAR in N.commune. Each value plotted is the mean of 6 replicate incubations (destructive sampling) within 500% moisture class interval, with the SEM indicated by bar. Material was rehydrated 12 hours at 21 °C and 200 uE m^{-2} s^{-1} PAR prior to experimental runs.

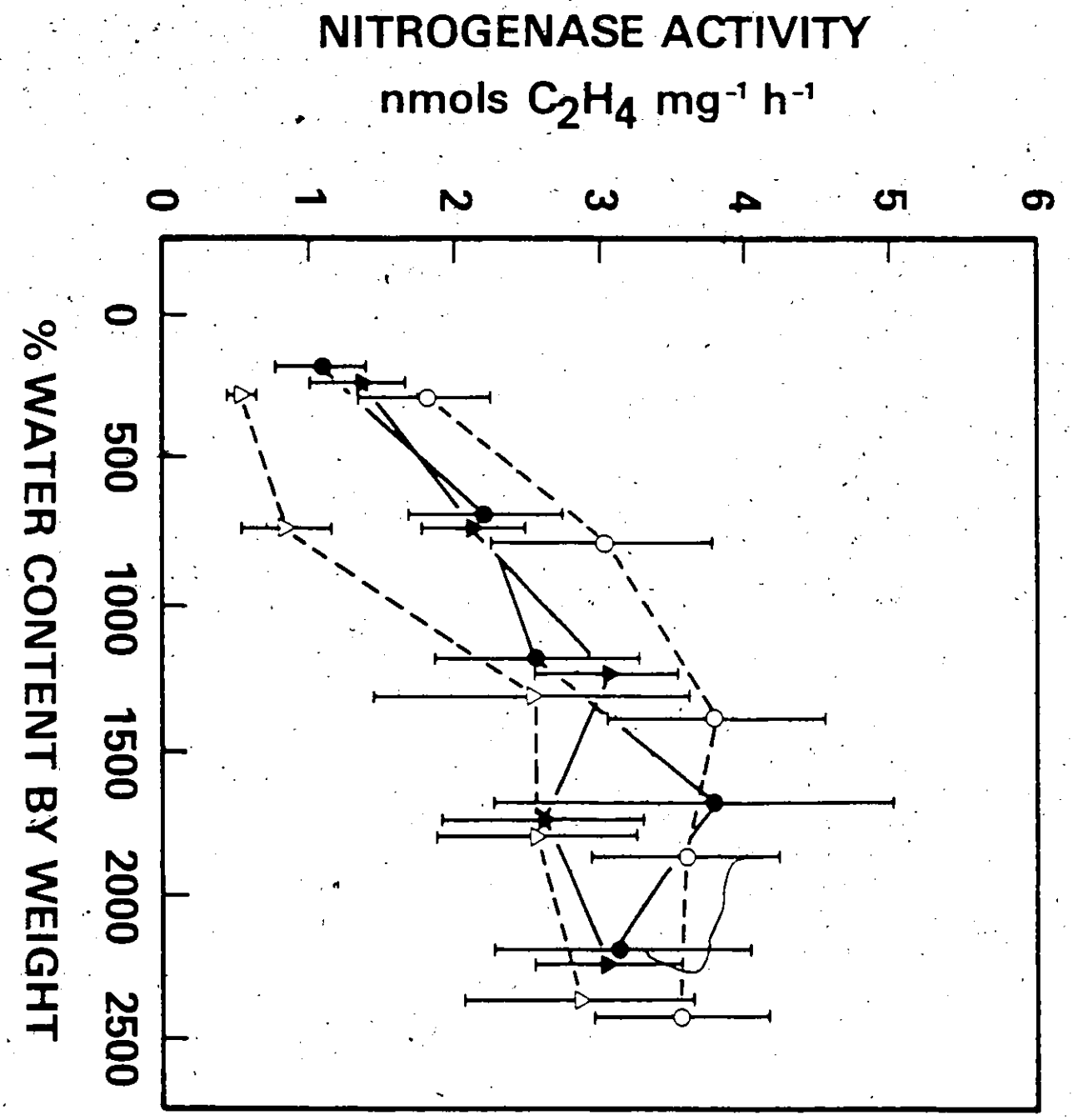

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
0
1
2
3
4
5
6
% WATER CONTENT BY WEIGHT
0
500
1000
1500
2000
2500

Figure 25

The light saturation response of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune. The maximum rates of C_2H_2 reduction for each replicate over the experimental run was regarded as 100% relative activity and other rates scaled accordingly. Standard error of the mean, denoted by bars for each group of six replicates, was calculated from relative values. Two groups of experimental replicates were given standard 14 hour light pretreatments (Section 2.3.1). Group A material was run through 10 sequential 30 minute incubations from 100 to 900 uE m^{-2} s^{-1} PAR and back to 100 uE m^{-2} s^{-1} PAR, while Group B replicates were sequentially exposed to the reverse order of light treatment.

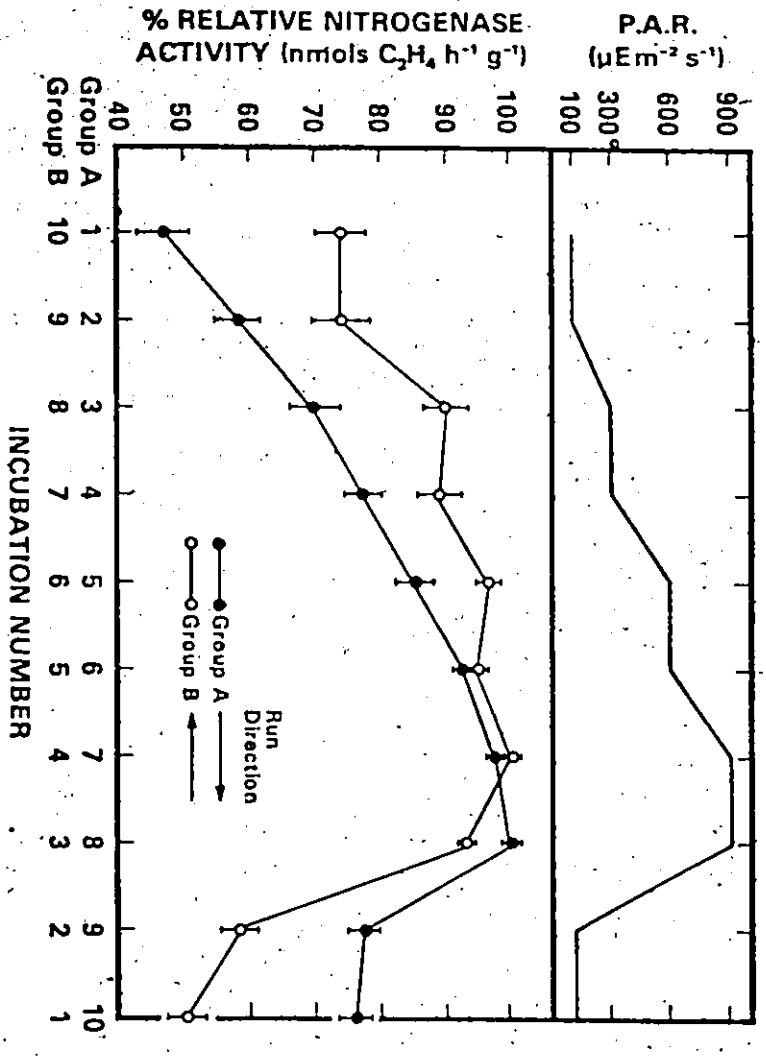

% RELATIVE NITROGENASE ACTIVITY (nmols C_2H_4 h^{-1} g^{-1})
P.A.R. ($\mu E m^{-2} s^{-1}$)
40
50
60
70
80
90
100
100
300
600
900
Group A
Group B
10
9
8
7
6
5
4
3
2
1
INCUBATION NUMBER
Group A
Group B
Run Direction

Figure 26

The time course of nitrogenase activity in N.commune after transfer to darkness (at time zero) for material held at 5 (△,▲), 15 (○,●) and 25 (□,■) °C. Rates are expressed in both absolute terms (open symbols) and relative terms (closed symbols). C_2H_2 reduction assays were conducted at each storage temperature and light level (200 uE m^{-2} s^{-1} PAR at time 0). Standard errors of the mean for 8 replicate incubations did not exceed 0.5 nmol C_2H_4 mg^{-1} h^{-1}. Material was held at the indicated temperature and 200 uE m^{-2} s^{-1} PAR for 14 hours prior to the start of the nitrogenase assays.

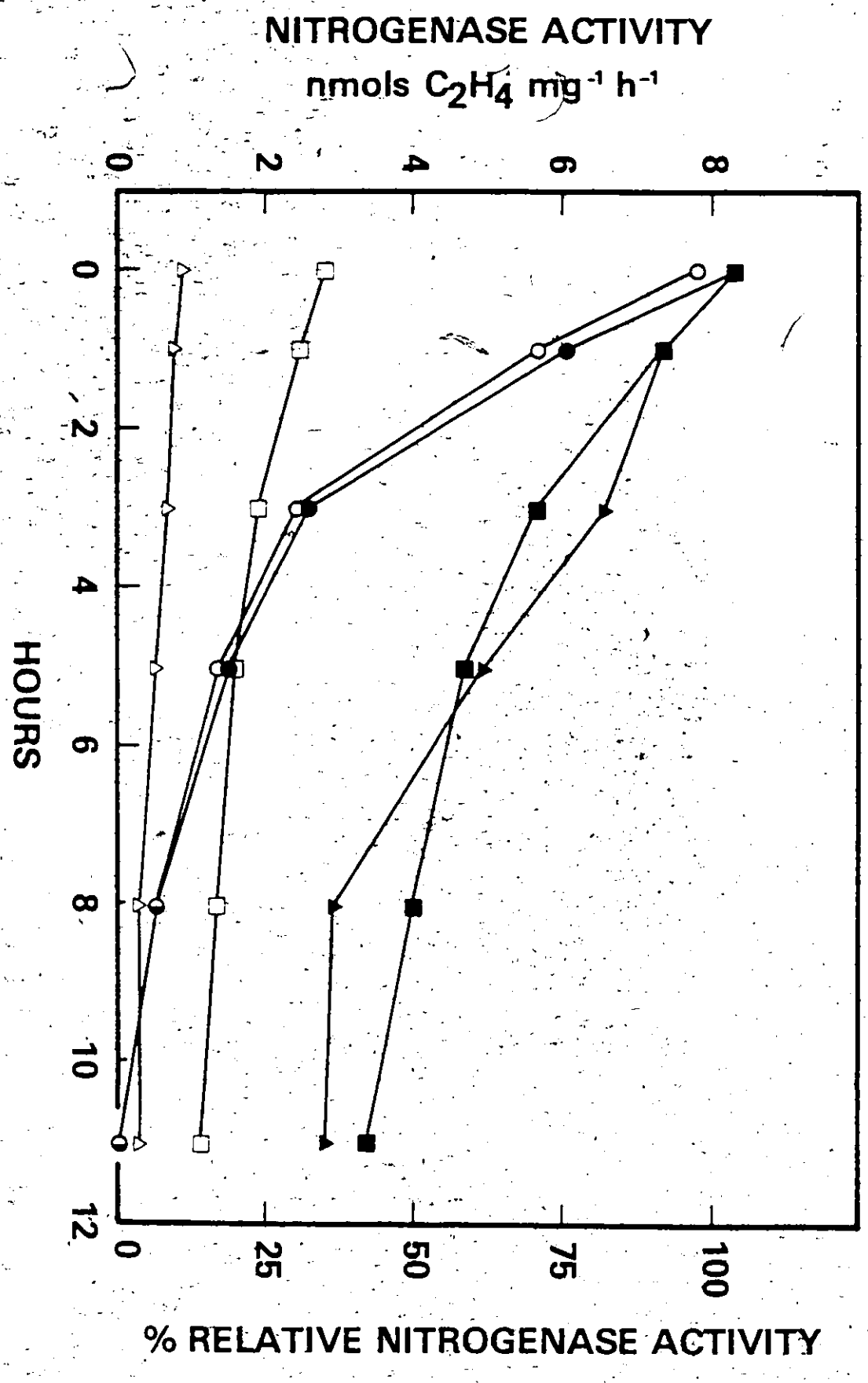

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
0
2
4
6
8
HOURS
0
2
4
6
8
10
12
0
25
50
75
100
% RELATIVE NITROGENASE ACTIVITY

Figure 27

The response of nitrogenase activity in N.commune to cessation of net photosynthetic uptake caused by addition of 10 uM 3-(3,4-dichlorophenyl)-1, 1-dimethylurea (DCMU) or transfer to darkness. Experimental treatments were initiated at 2 hours into the daily photoperiod (denoted by arrow) for material held at 21 °C under a 12/12 hour 0/200 uE m^{-2} s^{-1} PAR light regime. Results are expressed in both nmol C_2H_4 mg^{-1} h^{-1} and nmol C_2H_4 mg Chl-a^{-1} h^{-1} for control replicates (Δ and ▲ respectively) and for DCMU treated replicates (○ and ● respectively). The above groups were assayed at 21 °C and 200 uE m^{-2} s^{-1} PAR. Nitrogenase assays for material transfered to darkness (■) were at 21 °C and 0 uE m^{-2} s^{-1} PAR and are expressed in nmol C_2H_4 mg^{-1} h^{-1}, as are rates for material transfered to darkness, but put into 1% glucose solution (*). All sampling was destructive and + or - 1 SEM bar is shown for the mean of 8 incubations.

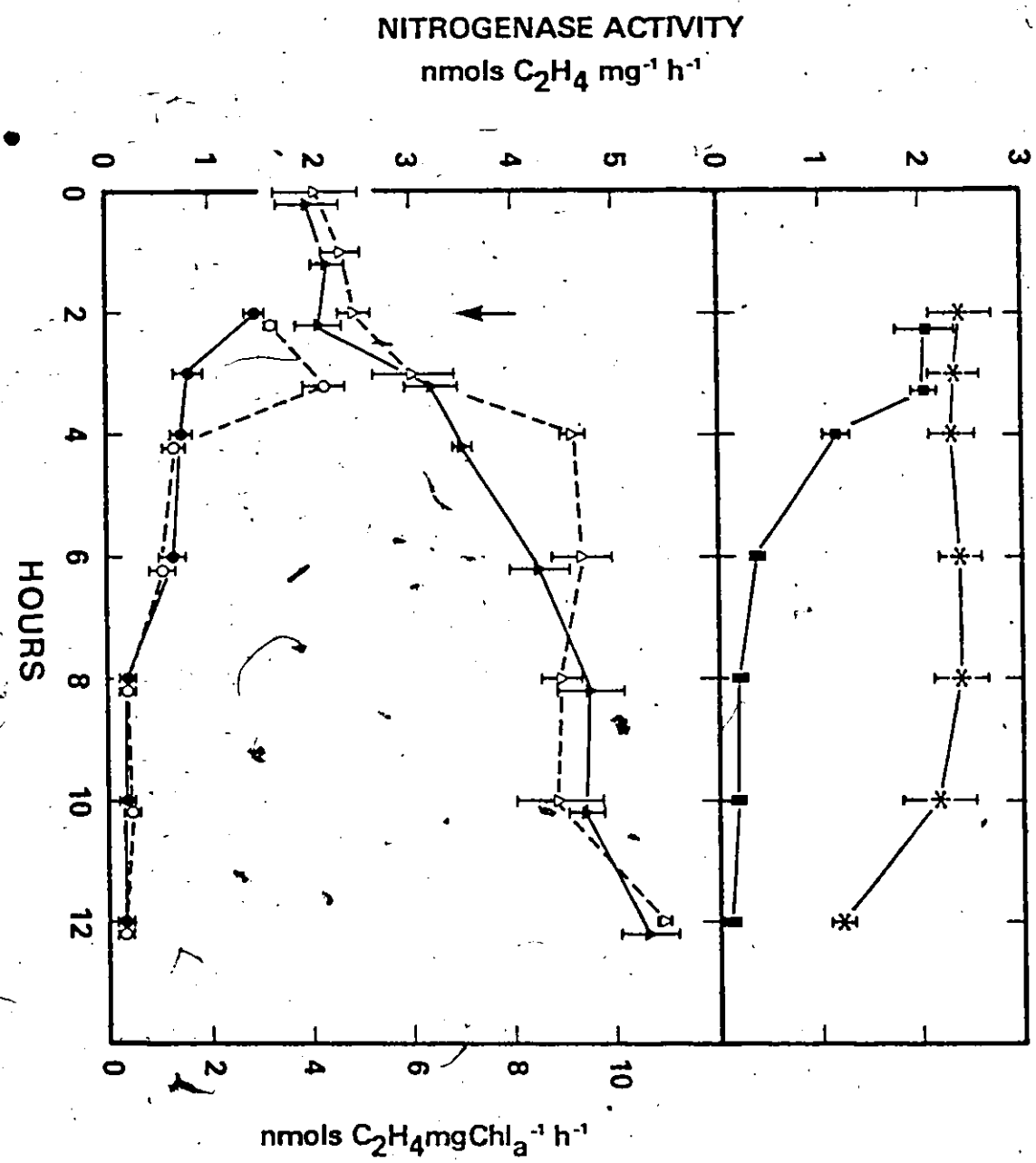

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
0 1 2 3 4 5
0 1 2 3
HOURS
0 2 4 6 8 10 12
0 2 4 6 8 10
nmols C_2H_4 $mgChl_a^{-1}$ h^{-1}

Figure 28

The time response of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune to addition of DCMU after 14 hours in the light (○), transfer of material to darkness (▲) and continued light exposure in water (●). Assay and treatment conditions otherwise as in Fig. 27.

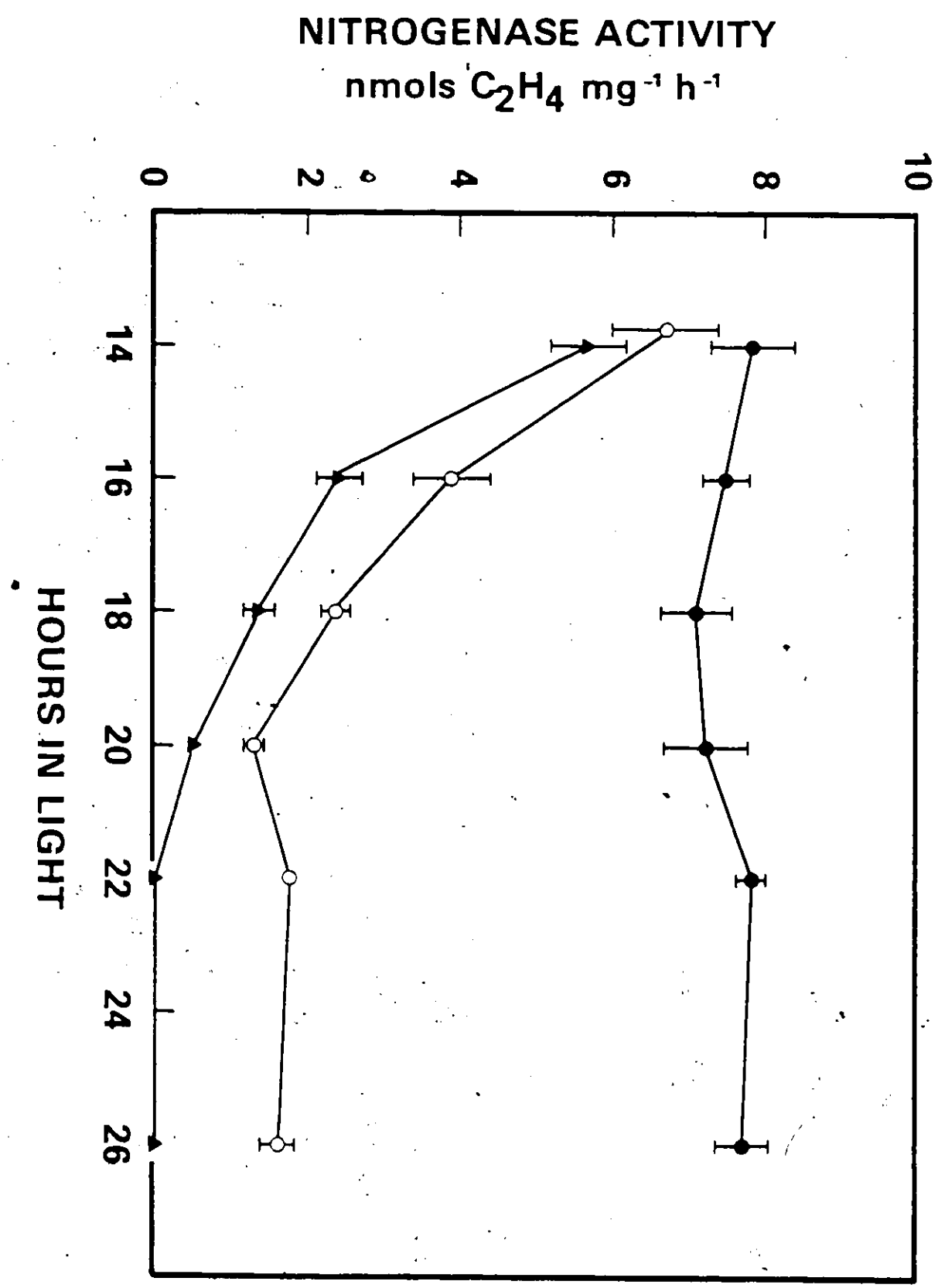
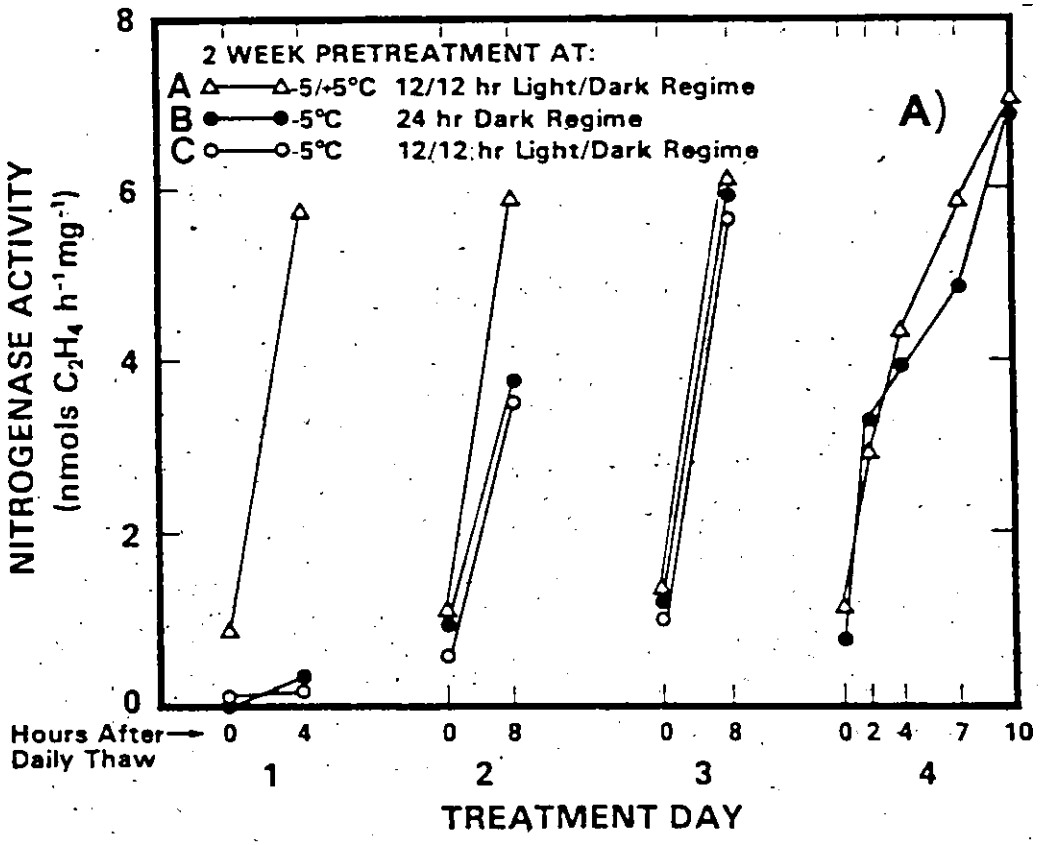

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
0
2
4
6
8
10
14
16
18
20
22
24
26
HOURS IN LIGHT

Figure 29

Top: The pattern of nitrogenase activity in N.commune (nmol C_2H_4 mg^{-1} h^{-1}) over laboratory simulated chinook snowmelt sequence. All replicates were stored during the four day experimental period under a -5/+5 °C thermoperiod and a 350/0 uE m^{-2} s^{-1} PAR 12/12 hour photoperiod. C_2H_2 reduction assays were carried out at 20 °C and 200 uE m^{-2} s^{-1} PAR for destructively sampled replicates. The various pretreatment storage conditions are outlined in Table 3. Bottom: The recovery of nitrogenase activity in N.commune after 2 weeks pretreatment as per Table 2, but for material then transfered to a 20 °C and 200 uE m^{-2} s^{-1} PAR storage regime, C_2H_2 reduction assays under these same conditions. SEM as in Fig. 16.


2 WEEK PRETREATMENT AT:
A -5/+5°C 12/12 hr Light/Dark Regime
B -5°C 24 hr Dark Regime
C -5°C 12/12 hr Light/Dark Regime
A)
NITROGENASE ACTIVITY
(nmols C_2H_4 $h^{-1}mg^{-1}$)
Hours After Daily Thaw
0 4 0 8 0 8 0 2 4 7 10
1 2 3 4
TREATMENT DAY

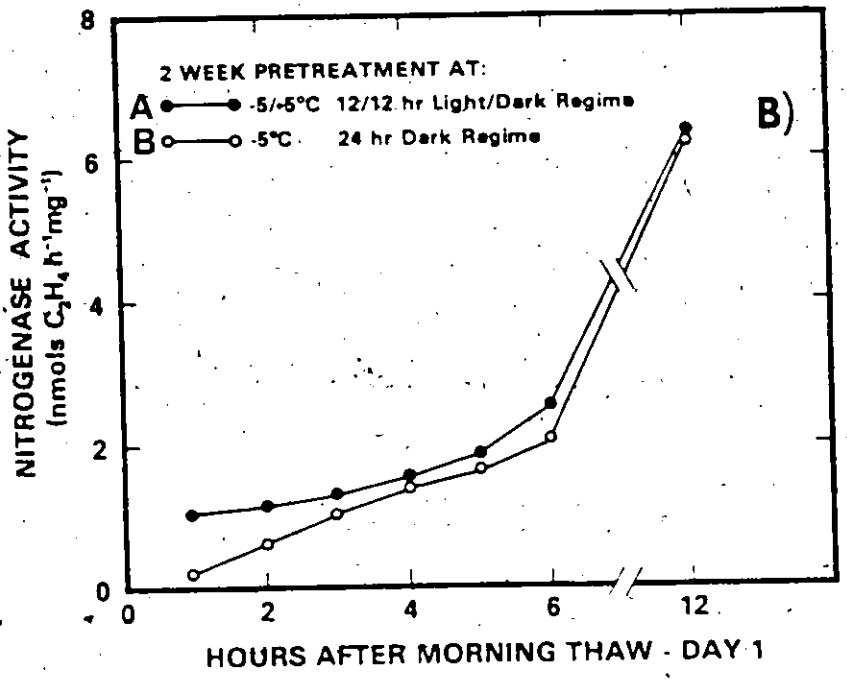

2 WEEK PRETREATMENT AT:
A -5/+5°C 12/12 hr Light/Dark Regime
B -5°C 24 hr Dark Regime
B)
NITROGENASE ACTIVITY
(nmols C_2H_4 $h^{-1}mg^{-1}$)
0 2 4 6 12
HOURS AFTER MORNING THAW - DAY 1

Figure 30

The rehydration response of nitrogenase activity in N.commune (nmol C_2H_4 mg^{-1} h at 25 °C over the full range of thallus moisture content. Activity at 0.25 (—·—), 0.5 (·····), 2 (—··—), 3 (- - - -), 6 (——), 10 (▲—▲), 14 (○–○), 24 (●—●) and 42 (△–△) hours after initial hydration for material held at 200 uE m^{-2} s^{-1} PAR is given. SEM bars for 6 replicate incubations within each 800% moisture class interval are given. The first class interval excludes thalli below 400% moisture content.

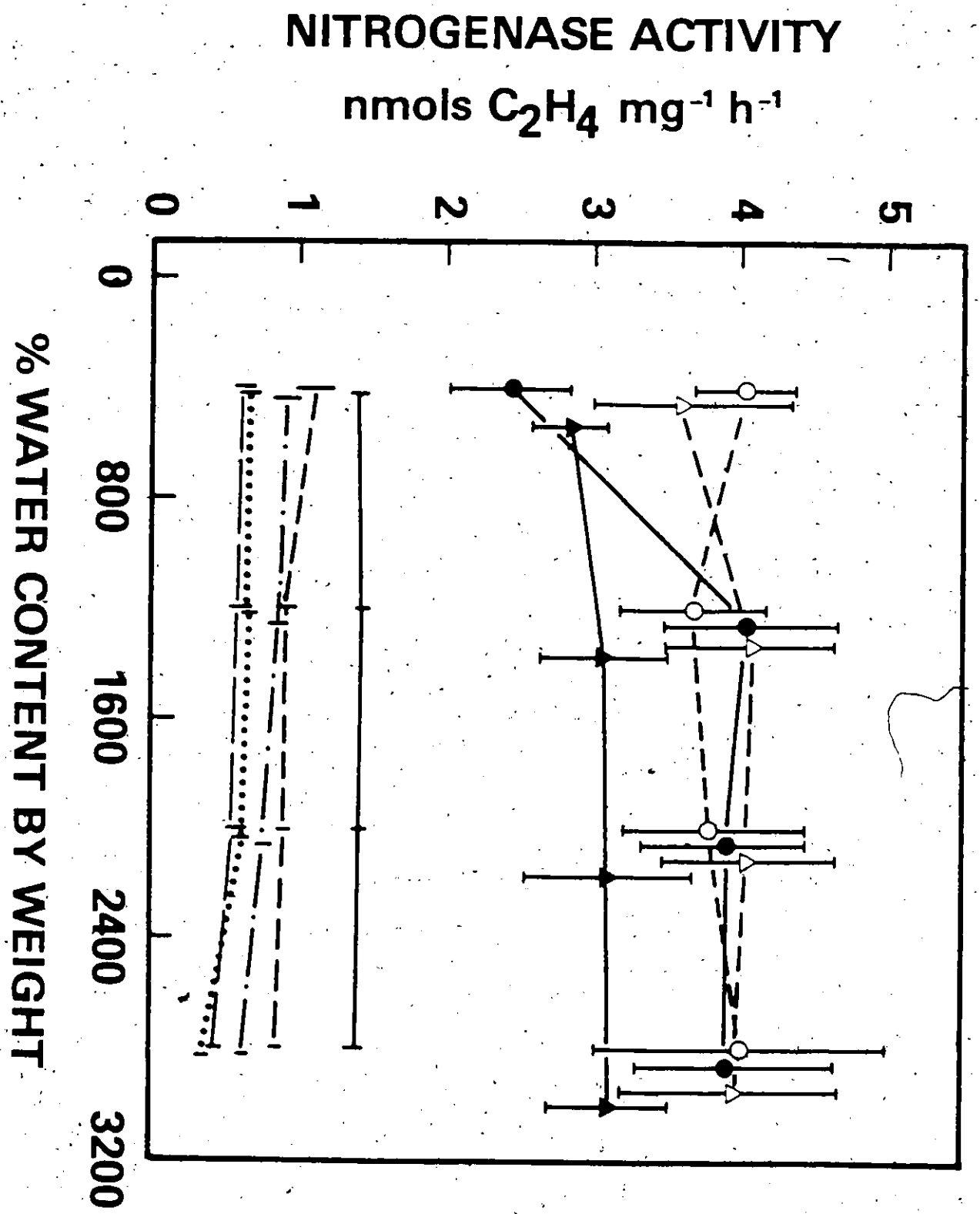

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
0
1
2
3
4
5
% WATER CONTENT BY WEIGHT
0
800
1600
2400
3200

Figure 31

The time course of nitrogenase activity, net photosynthesis and respiration for N.commune rehydrated at 21 °C. Nitrogenase activity was monitored over the final 12 hour period of the following diurnal light cycles: A) 12/12/12 hrs light/dark/light (△); B) 12/12 hrs dark/light (□); and C) 12 hours light (◇). Rehydration in all cases was at start of diurnal periods. CO_2 exchange was followed at 0 (●) and 600 (○) uE m^{-2} s^{-1} PAR at 28 °C, while nitrogenase activity was followed at 200 uE m^{-2} s^{-1} PAR and 28 °C.

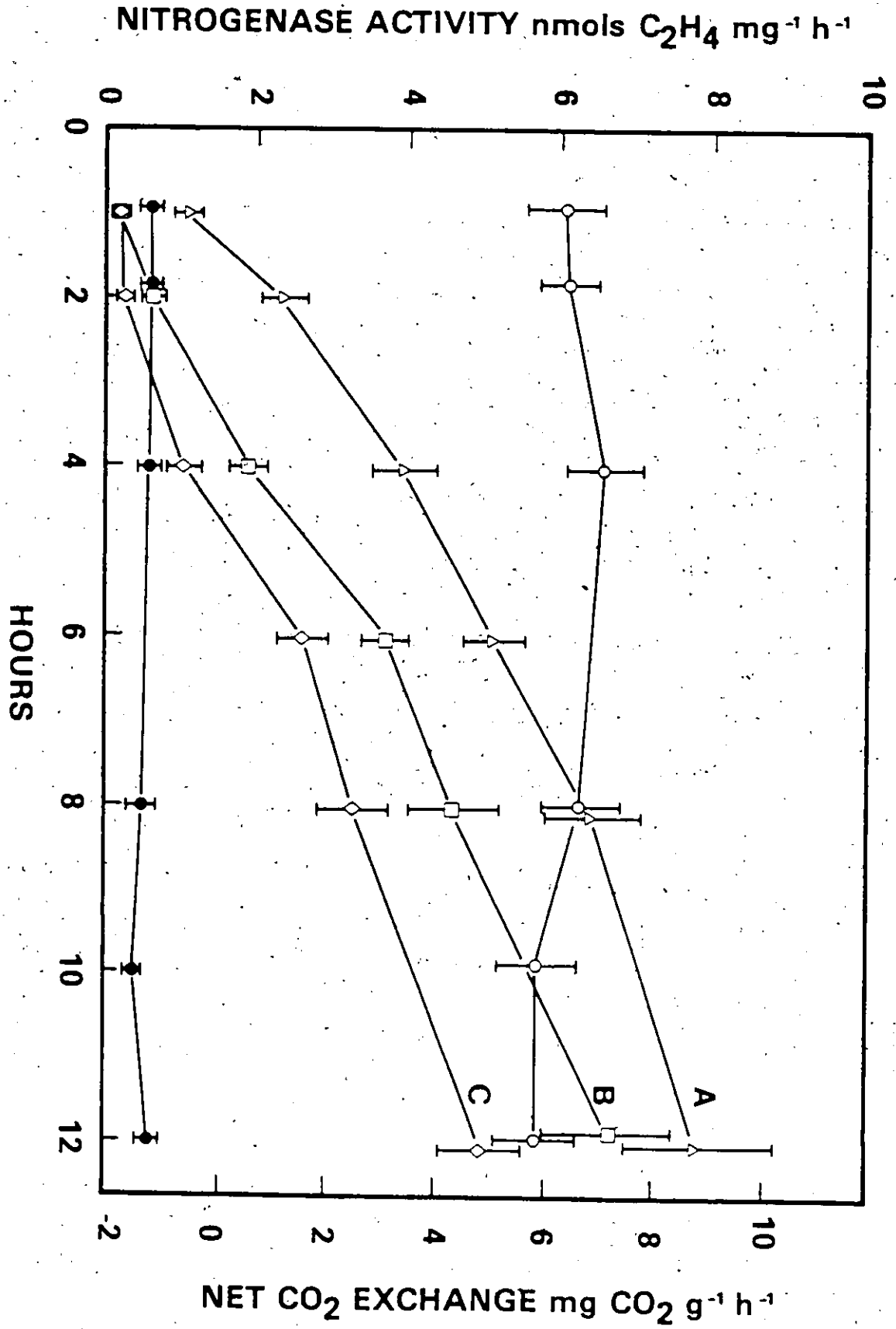

NITROGENASE ACTIVITY nmols C_2H_4 mg^{-1} h^{-1}
0
2
4
6
8
10
HOURS
0
2
4
6
8
10
12
A
B
C
D
-2
0
2
4
6
8
10
NET CO_2 EXCHANGE mg CO_2 g^{-1} h^{-1}

Figure 32

The recovery of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune following rehydration at 7 and 14 °C under the following diurnal light conditions: A) 12/12/12 hrs light/dark/light (7 °C ▲ ; 14 °C □); B) 12/12 hrs dark/ light (7 °C ● ; 14 °C ■); and C) 12 hrs light (7 °C ○ ; 14 °C △). Activity was followed over the final 12 hour light period in each case through destructive sampling with subsequent assays at 28 °C and 200 uE m^{-2} s^{-1} PAR. Mean values from 8 replicate incubations are plotted for each treatment group, the SEM of which is less than 0.5 nmol C_2H_4 mg^{-1} h^{-1}.

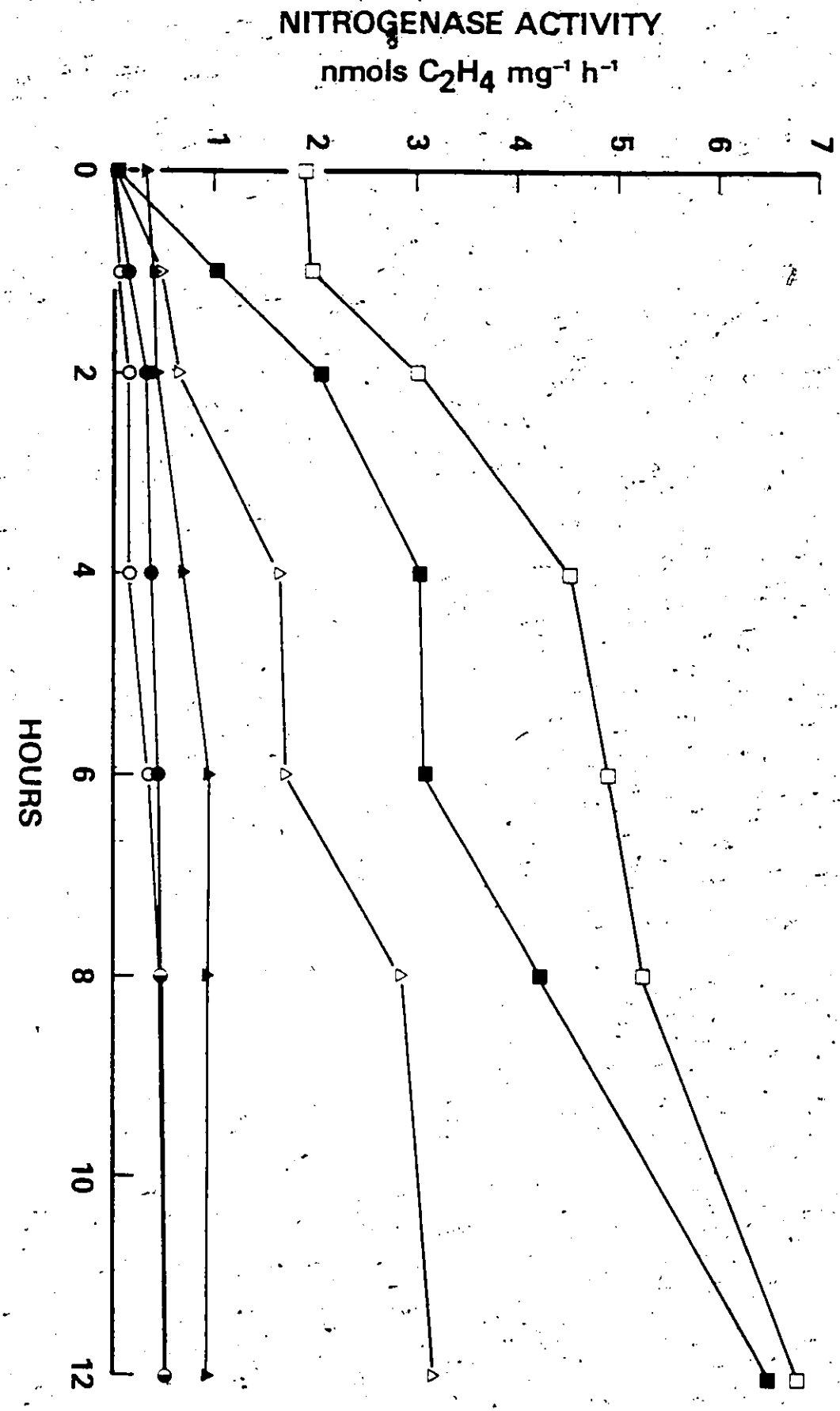
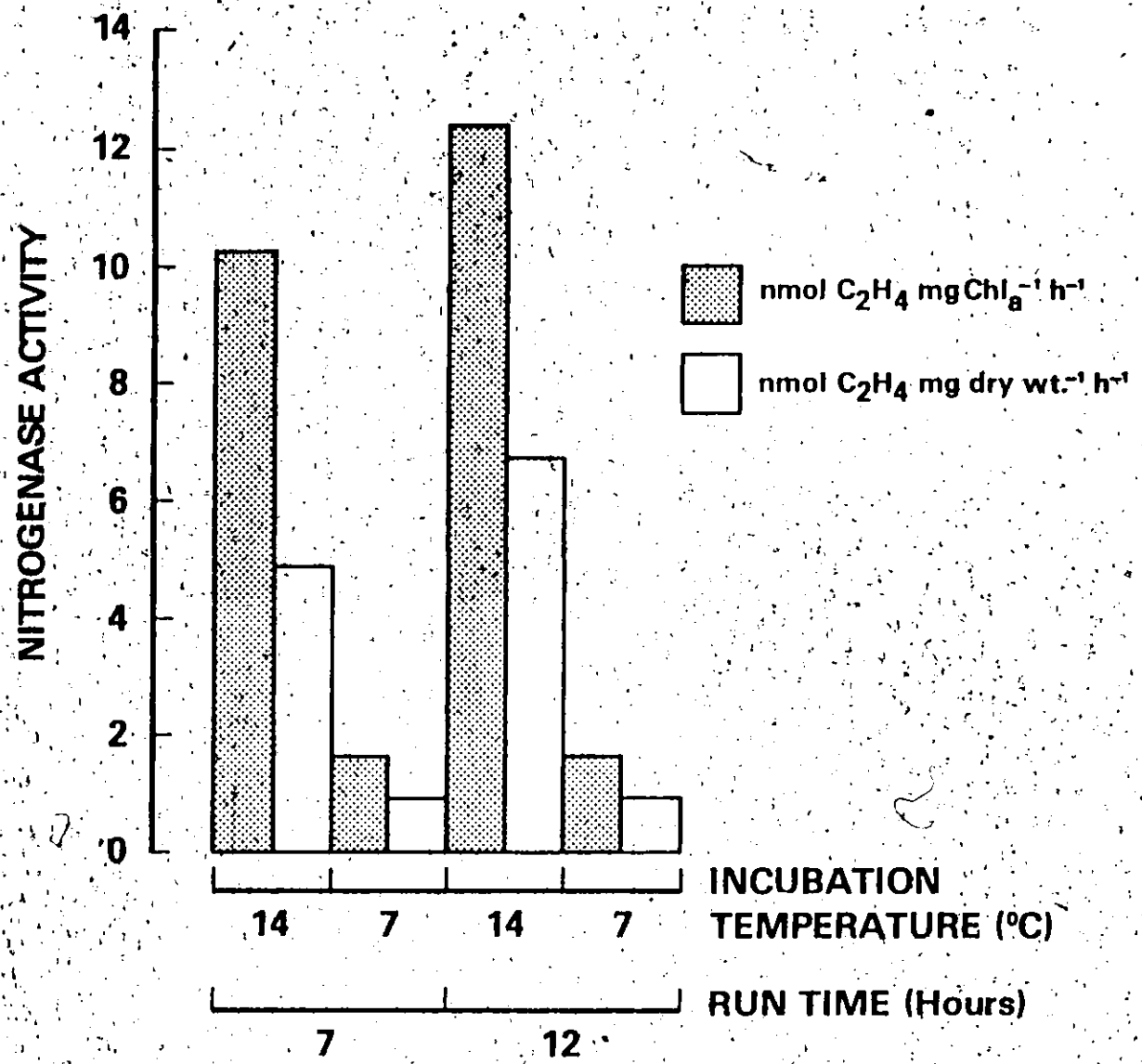

NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
1
2
3
4
5
6
7
HOURS
0
2
4
6
8
10
12

Figure 33.

The recovery of nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) in N.commune at 7 and 14 °C after 7 and 12 hours light exposure on the second day after rehydration (12/12 hrs light/ dark). Nitrogenase activity was assayed at 28 °C and 200 uE m^{-2} s^{-1} PAR for destructively sampled replicates. Rates are expressed in both nmol C_2H_4 mg^{-1} h^{-1} and nmol C_2H_4 mg Chl-a $^{-1}$ h^{-1}. SEM as in Fig. 32.


NITROGENASE ACTIVITY
14
12
10
8
6
4
2
0
nmol C_2H_4 mgChl_a^{-1} h^{-1}
nmol C_2H_4 mg dry $wt.^{-1}$ h^{-1}
14
7
14
7
INCUBATION TEMPERATURE (°C)
RUN TIME (Hours)
7
12

(3.3) Field Microclimate Observations and Nitrogenase Activity

(3.3.1) The Alpine Environment

Field microclimate observations at the Prairie Bluff study site were conducted in the spring and summer of 1980. Selected data sets characteristic of the range of general synoptic weather conditions encountered in the alpine environment are presented below.

The pattern of incoming radiation, air temperature at 2 m height and R.superficiale thallus temperatures for May 17 and 18, characteristic of high radiation conditions, are given in Fig. 34. There was a marked interaction between thallus temperature and energy flux density. On both days cumulus cloud activity resulted in alternating sun-shade conditions. Thallus temperatures reached 30 °C under full solar insolation, but dropped immediately by more than 10 °C upon even momentary shading.

The data for May 22 followed a period of shower activity throughout the night and early morning and represents very typical conditions of cumulus buildup, with sporadic shower activity (Fig. 35b). Thallus temperatures of R.superficiale obtained for this day are contrasted with those of Umbilicaria kraschenninnikovii (a low black foliose lichen intermingled with R.superficiale thalli). With increasing radiation levels following early morning shower activity, hydrated R.superficiale thalli rapidly reach near 23 °C, finally desiccating

(below 25% relative moisture content) near 1015 hours. The dessicated thalli continue to rise in temperature, exceeding that of air considerably by 1500 hours. The temperature of R.superficiale thalli remained several degrees C warmer than that of the black U.krascheninnikovii thalli (Fig. 36). U.krascheninnikovii also showed a more dramatic decline in temperature when incoming direct short wave radiation was interrupted at midday by cumulus buildup.

Data for low radiation conditions, during heavy precipitation and low ambient temperatures on May 23, 1980 are given in Fig. 35a. Even under these extremely low energy conditions there is a modest thallus temperature elevation compared with air values, but otherwise the data calls for little comment, the entire vertical temperature profile being nearly isothermal.

The storm system followed in Fig. 35a subsequently intensified, resulting in the accumulation of over 25 cm of snow, followed by gradual melt conditions. The data of Fig. 37 document the development of snowmelt pockets under high radiation spring conditions, immediately after snowfall deposition. Throughout the snowmelt period air temperatures remained low, while PAR ranged from values above the solar constant (as a result of multiple reflection effects) down to 800 $uE.m^{-2}s^{-1}$ PAR. The initial melting resulted in development of "closed" snowmelt pockets above the soil surface as radiation penetration elevated the substrate temperature (though still under continuous snow cover). These "closed" snowmelt pockets accentuated the melting process, resulting in the rapid formation of "open" snowmelt craters as the snow

surface was breached. In the early morning, under 25 cm snowcover R.superficiale thalli temperatures remained at 0 °C. With development of surface heating the "closed" snowmelt pockets formed in which R.superficiale thalli show small but significant temperature elevation. With further melting of the pockets and final collapse of the snow "roof" there was a substantial increase in thallus temperatures, thalli within the large "open" pockets reaching 20 °C while still hydrated from the surrounding snow margins.

By July 10, mid-summer thunderstorm activity was common. A typical data set showing periods of low radiation levels during each shower period alternating with high radiation conditions is given in Fig. 38. Thallus temperatures closely paralleled the pattern of incoming short wave radiation, resulting in the exposure of hydrated thalli to high temperature and light levels over repeated short bursts. The corresponding rock thermal profile (Fig. 39b) showed a classical dampening of temperature fluctuations with depth, marked temperature inversions developing during short precipitation periods.

Under high radiation conditions there was a remarkable temperature profile developed below 15 cm. On July 5 strong surface heating occurred under continuous full radiation conditions, with thalli air dry throughout the experimental period. The complete air, surface and rock profiles are shown sequentially in Fig. 40 and effectively summarize the thermal events under maximum radiation conditions. In early morning a strong temperature inversion was evident, with the rock surface/ R.superficiale interface showing the lowest absolute temperature

in the profile. Strong surface heating developed through the morning until by 1400 hours a temperature profile of over 20 °C had developed. By 1800 hours declining solar angle had diminished short wave radiation input and the temperatures of the black U.kraschenninikovii thalli were now slightly higher than those of the yellow R.superficiale thalli. By 2300 a full temperature inversion has been re-established with continued long wave heat loss.

This was examined experimentally on July 8th under windy (25 km h^{-1}), but virtually cloudless conditions when the highest temperatures of the summer field period were recorded. Thallus temperatures reached 35 °C briefly, a 20 degree differential above air temperature, but remained above 30 °C throughout a four hour period around solar noon (Fig. 41). The concurrent profile development in the underlying rock substratum showed an equivalent response (Fig. 39a), with a maximum temperature of 29 °C recorded at 8 cm in depth. At 1300 hours one thermopile monitoring temperature of an air dry R.superficiale colony was sheltered with wind screening, yet without reducing incoming short wave radiation. Thallus temperatures climbed steeply, reaching 45 °C in just over 1 hour. Removal of the shelter and the re-establishment of convective cooling quickly returned the thallus to the temperatures of surrounding unshielded replicates (Fig. 41).

Figure 34

A) Energy Flux Density ($W\ m^{-2}$) for May 17, 1980. Bottom: Air temperature at 2 m (○), R.superficiale thallus temperatures (●). Plotted from 15 minute averages. B) As above, but for May 18, 1980. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

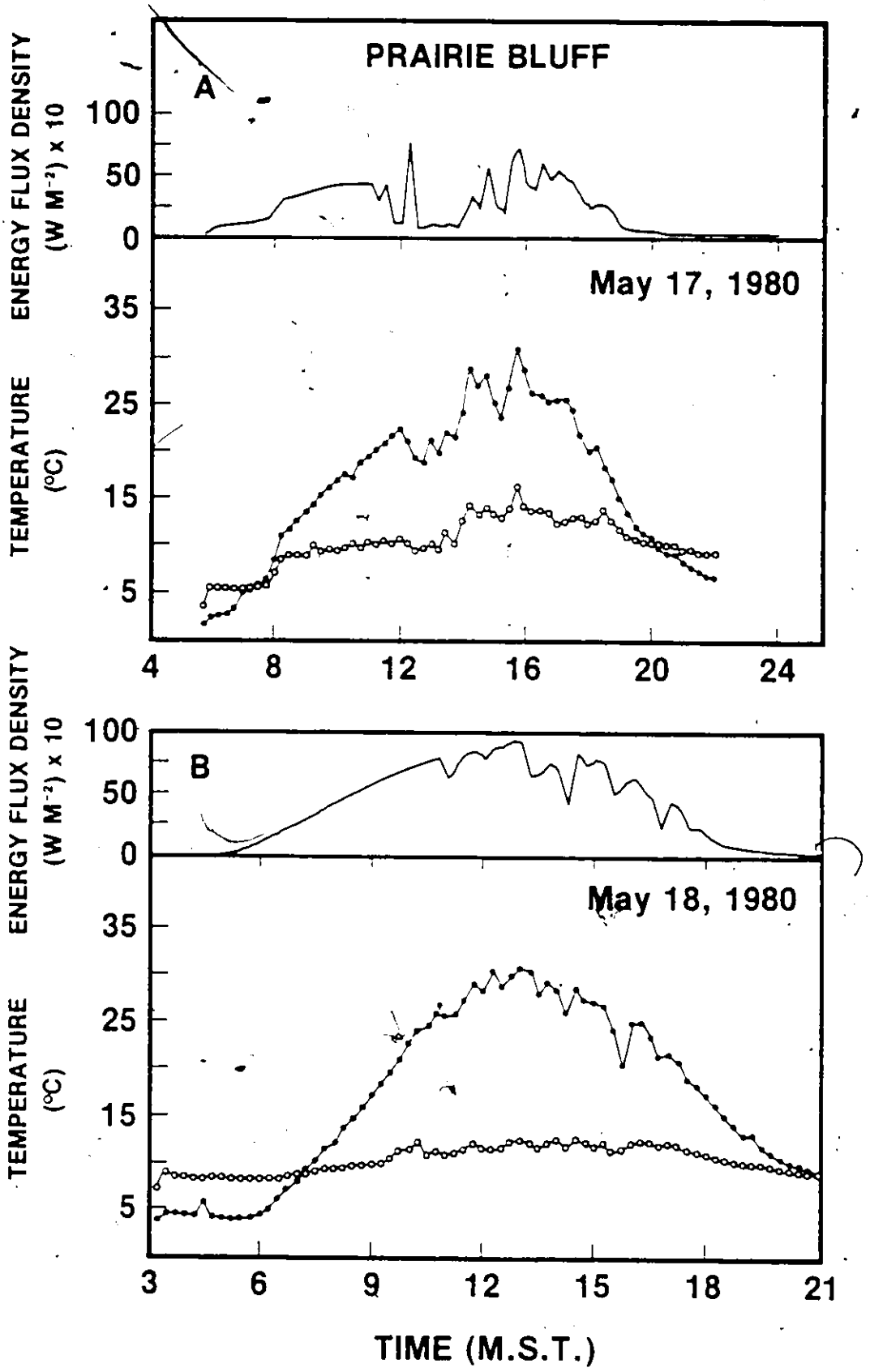

PRAIRIE BLUFF
A
ENERGY FLUX DENSITY (W M⁻²) x 10
100
50
0
May 17, 1980
TEMPERATURE (°C)
35
25
15
5
4
8
12
16
20
24
B
ENERGY FLUX DENSITY (W M⁻²) x 10
100
50
0
May 18, 1980
TEMPERATURE (°C)
35
25
15
5
3
6
9
12
15
18
21
TIME (M.S.T.)

Figure 35

A) Energy Flux Density ($W\ m^{-2}$) for May 23, 1980. Bottom: Air temperature at 2 m (O), R.superficiale thallus temperatures (●). Plotted from 15 minute averages. Note that arrow denotes time at which mean R.superficiale relative moisture content fell below 25%. B) As above, but for May 22, 1980. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

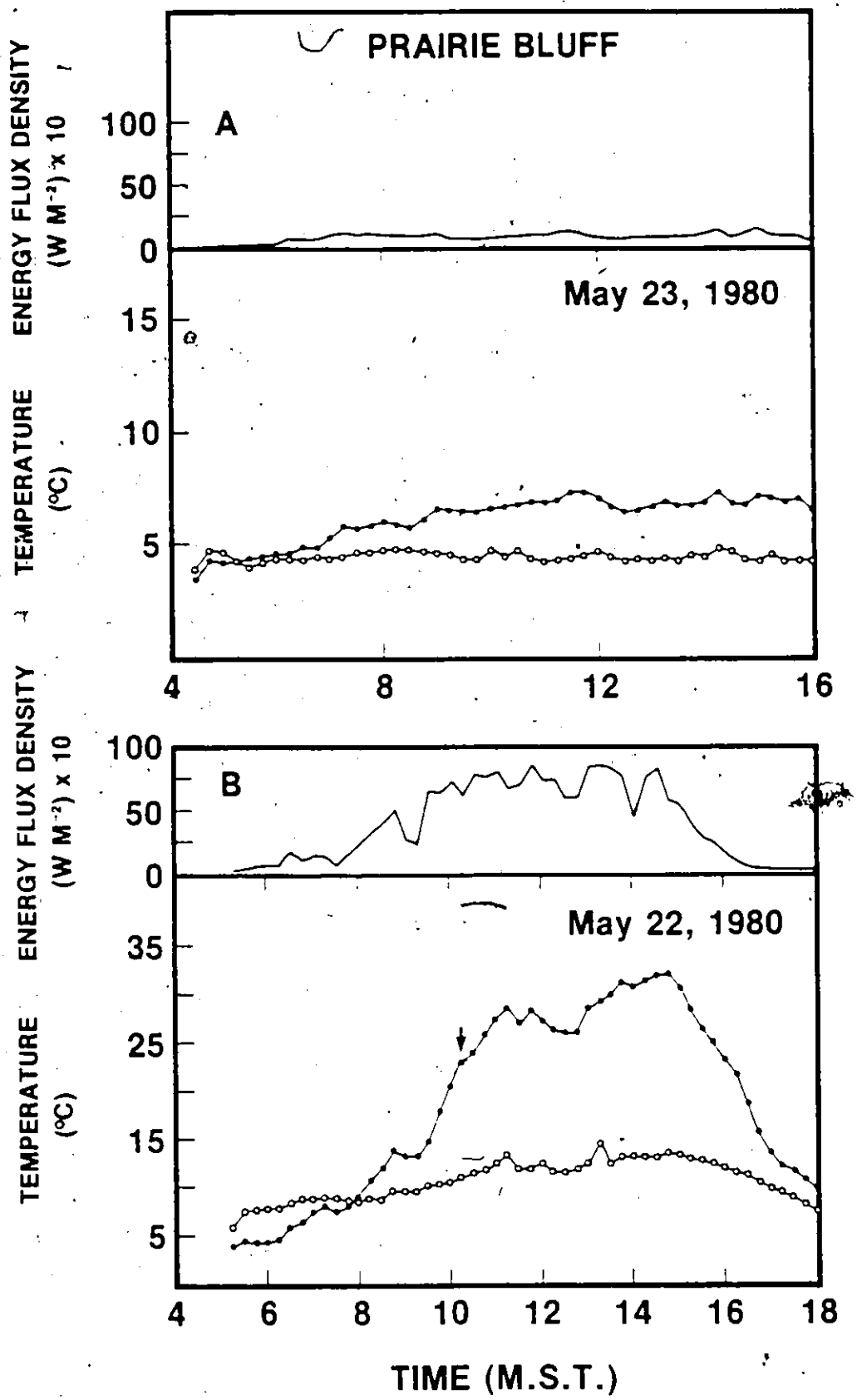

PRAIRIE BLUFF
A
ENERGY FLUX DENSITY (W M⁻²) x 10
100
50
0
May 23, 1980
TEMPERATURE (°C)
15
10
5
4
8
12
16
B
ENERGY FLUX DENSITY (W M⁻²) x 10
100
50
0
May 22, 1980
TEMPERATURE (°C)
35
25
15
5
4
6
8
10
12
14
16
18
TIME (M.S.T.)

Figure 36

15 minute temperature averages for May 22, 1980. R.superficiale thallus temperatures (△), U.kraschenninikovii thallus temperatures (●), air temperature at 2 m (○). Arrow denotes time at which afternoon shower activity commenced. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

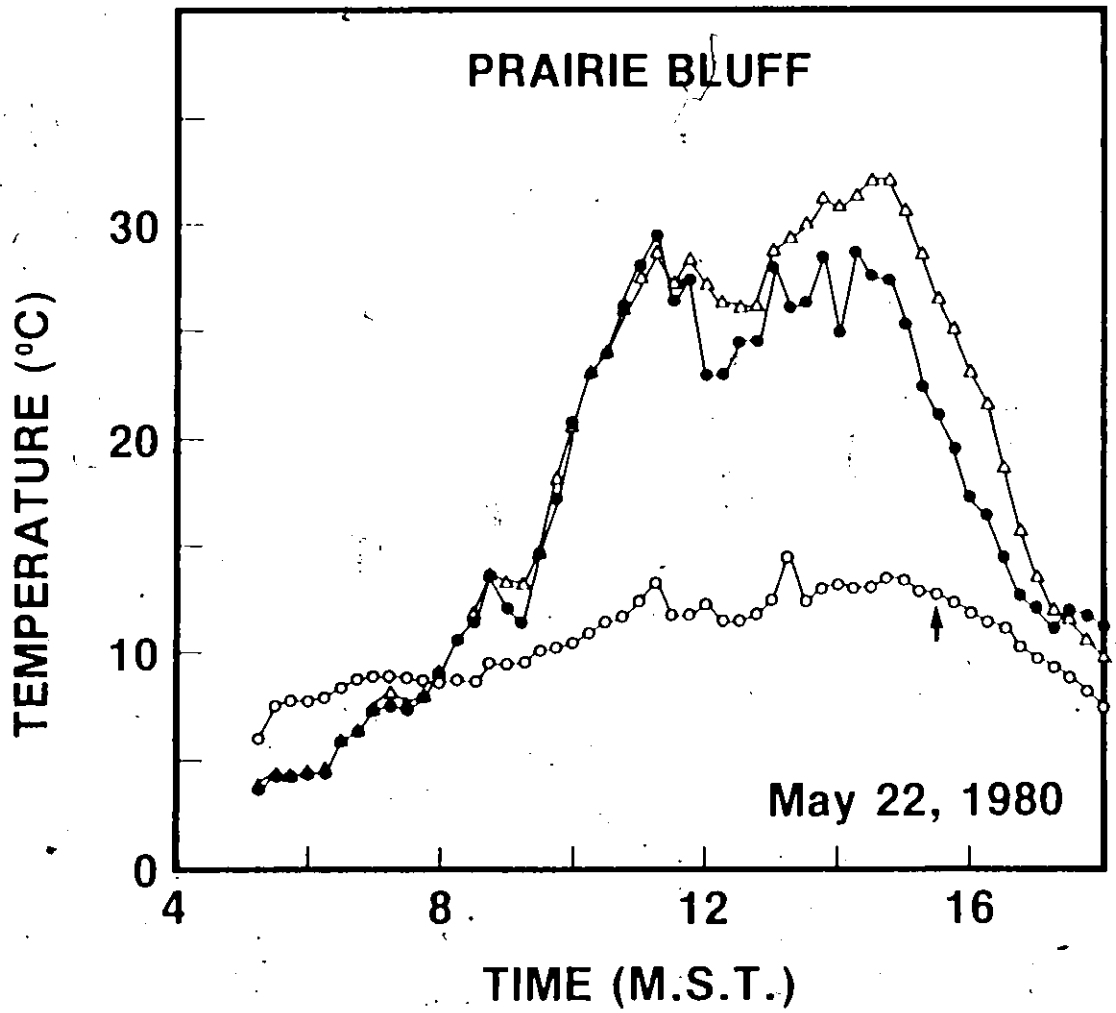

PRAIRIE BLUFF
TEMPERATURE (°C)
0
10
20
30
4
8
12
16
TIME (M.S.T.)
May 22, 1980

Figure 37

From top: A) Light Intensity (uE m^{-2} s^{-1} PAR) for May 28, 1980. B) R.superficiale thallus temperatures at center of large 30 cm "open" snowmelt pocket (□); R.superficiale thallus temperature at center of small 10 cm "open" snowmelt pocket (○); Rock temperature profile under small "open" snowmelt pocket at 2 cm (●), 4 cm (▲), and 8 cm (■) depth; Air temperature at 2 m height (△). c) R.superficiale thallus temperature under 20 cm snow (○); Rock temperature profile under 20 cm snow at 2 cm (●) and 4 cm (▲) depth; Air temperature at 2 m height (△). D) R.superficiale thallus temperature in "closed" snowmelt pocket under 15 cm of snow (○); Air temperature at 2 m (△). All values plotted from 15 minute averages. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

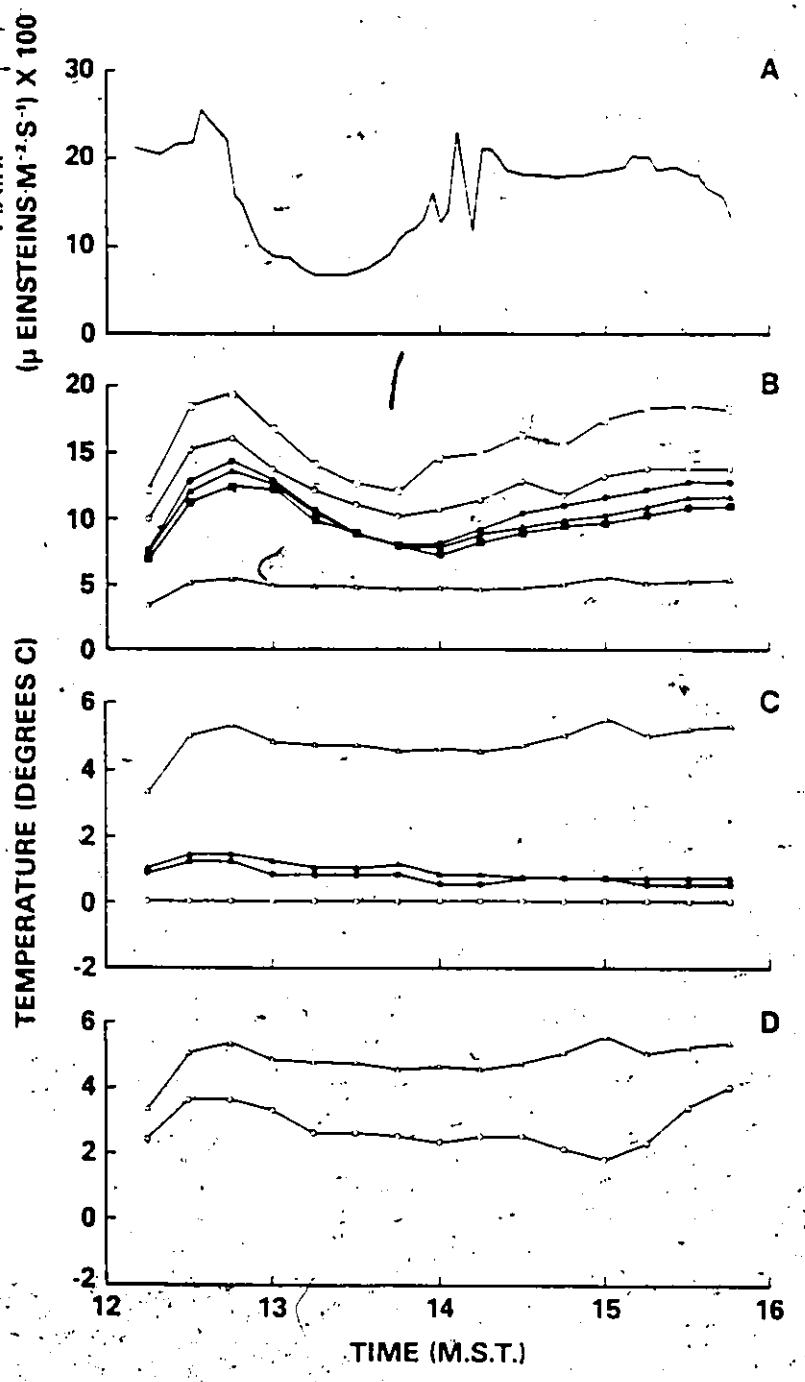

P.A.R.
(μ EINSTEINS·M⁻²·S⁻¹) X 100
A
B
C
D
TEMPERATURE (DEGREES C)
TIME (M.S.T.)
12
13
14
15
16

Figure 38

From top: A) Energy Flux Density ($W\ m^{-2}$) for July 10, 1980, Prairie Bluff. B) R.superficiale thallus temperature (Δ); Air temperature at 2 m height (O). All values 15 minute averages. C) R.superficiale thallus percent moisture content by weight (absolute values) (●). SEM denoted by bars. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

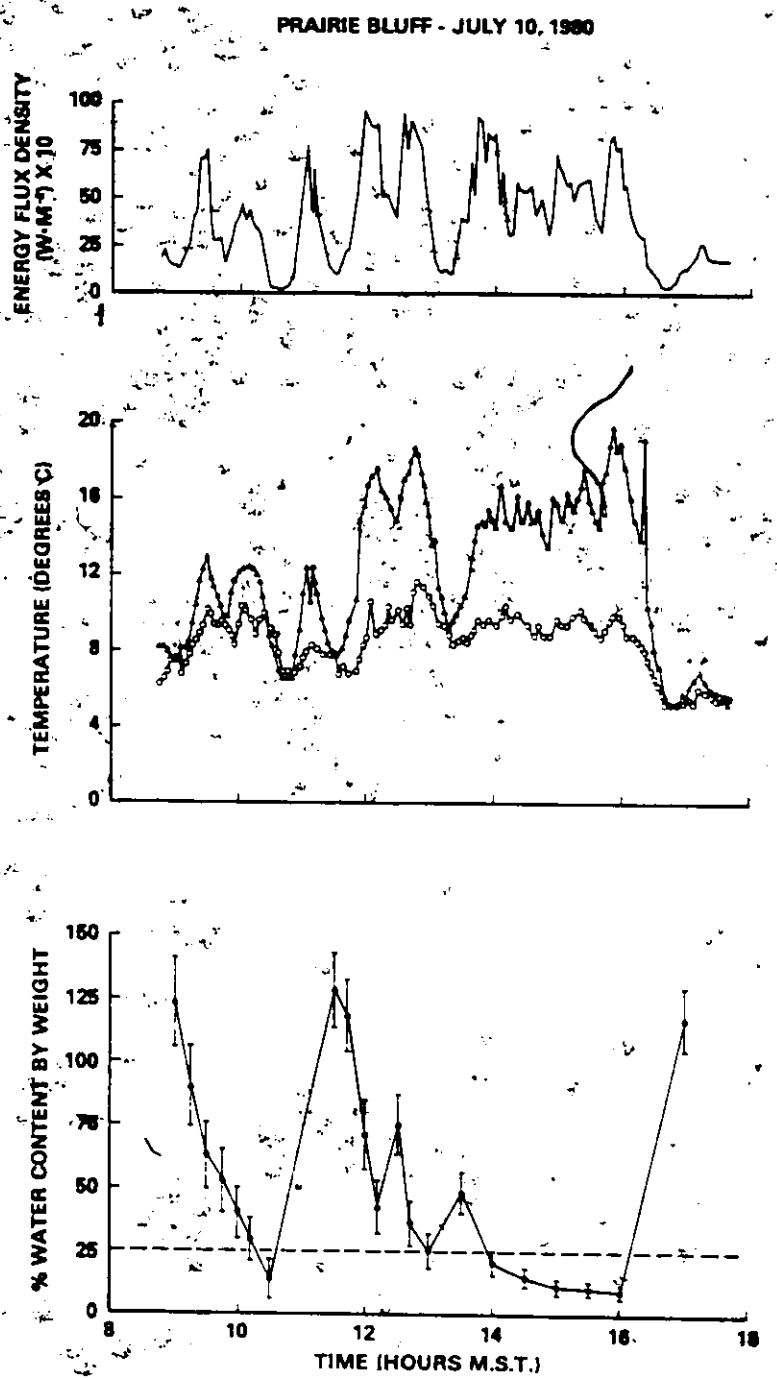

PRAIRIE BLUFF - JULY 10, 1980
ENERGY FLUX DENSITY (W·M⁻²) X 10
100
75
50
25
0
-1
TEMPERATURE (DEGREES C)
20
16
12
8
4
0
% WATER CONTENT BY WEIGHT
150
125
100
75
50
25
0
8
10
12
14
16
18
TIME (HOURS M.S.T.)

Figure 39

A) 15 minute temperature averages for July 8, 1980, Prairie Bluff. R.superficiale thallus temperatures (O); Rock temperature profile at 2 cm (▲), 4 cm (●) and 8 cm (□) depth. B) As above, but for July 10, 1980. All values plotted from 15 minute averages. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

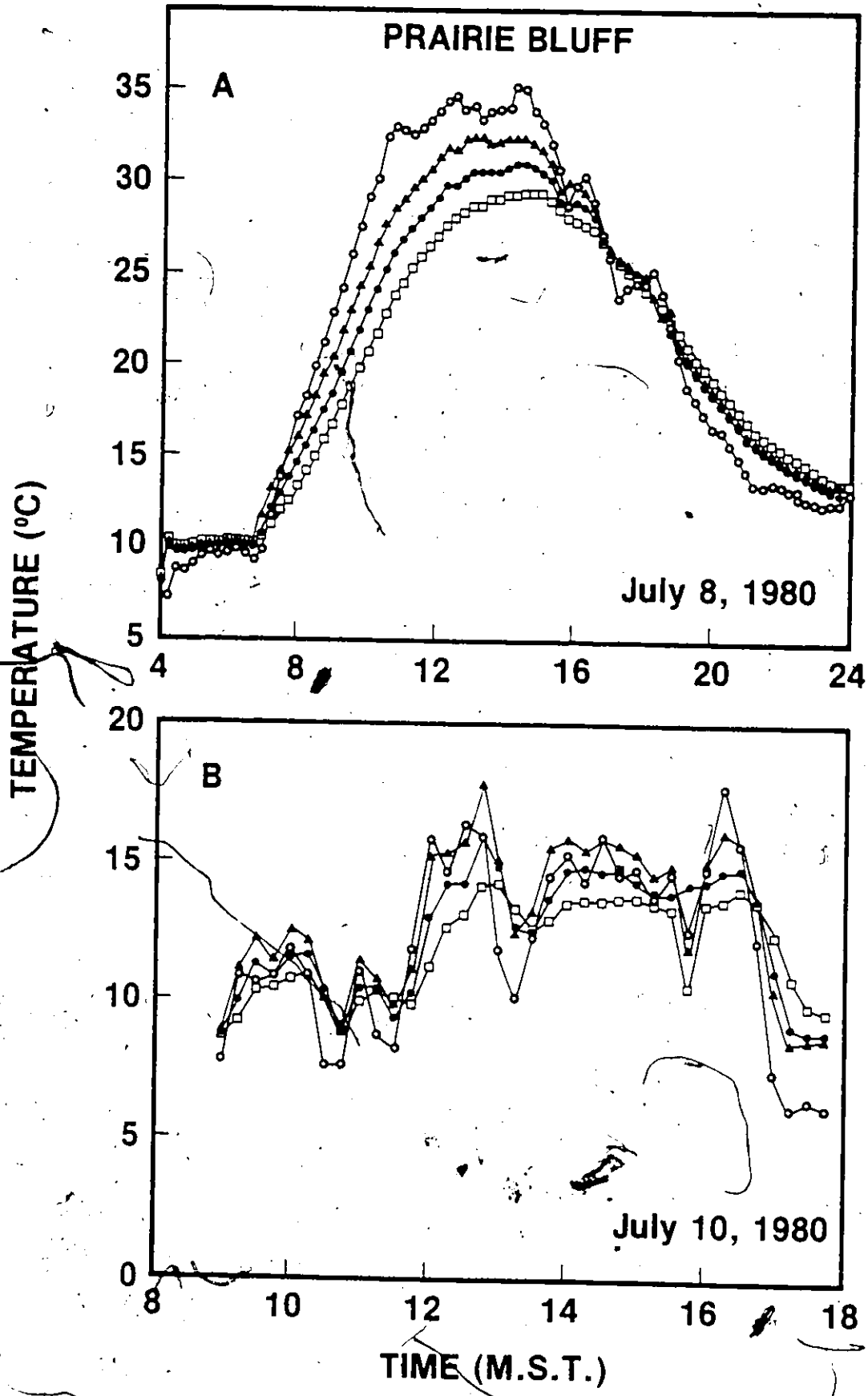

PRAIRIE BLUFF
A
35
30
25
20
15
10
5
July 8, 1980
4
8
12
16
20
24
B
20
15
10
5
0
July 10, 1980
8
10
12
14
16
18
TEMPERATURE (°C)
TIME (M.S.T.)

Figure 40

The temperature profile for Prairie Bluff on July 5, 1980; for 0600, 0700, 1000, 1400, 1800 and 2300 hours (M.S.T.). Profile measurement points, from top to bottom as follows: 1) Air temperature at 200 cm; 2) Air temperature at 100 cm; 3) Air temperature at 15 cm; 4) Air temperature at 2 cm; 5) U.krascheninnikovii thallus temperature; 6) R.superficiale thallus temperature; 7) Rock temperature at 2 cm depth below surface; 8) Rock temperatures at 4 cm depth; and 9) Rock temperature at 8 cm depth. Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).

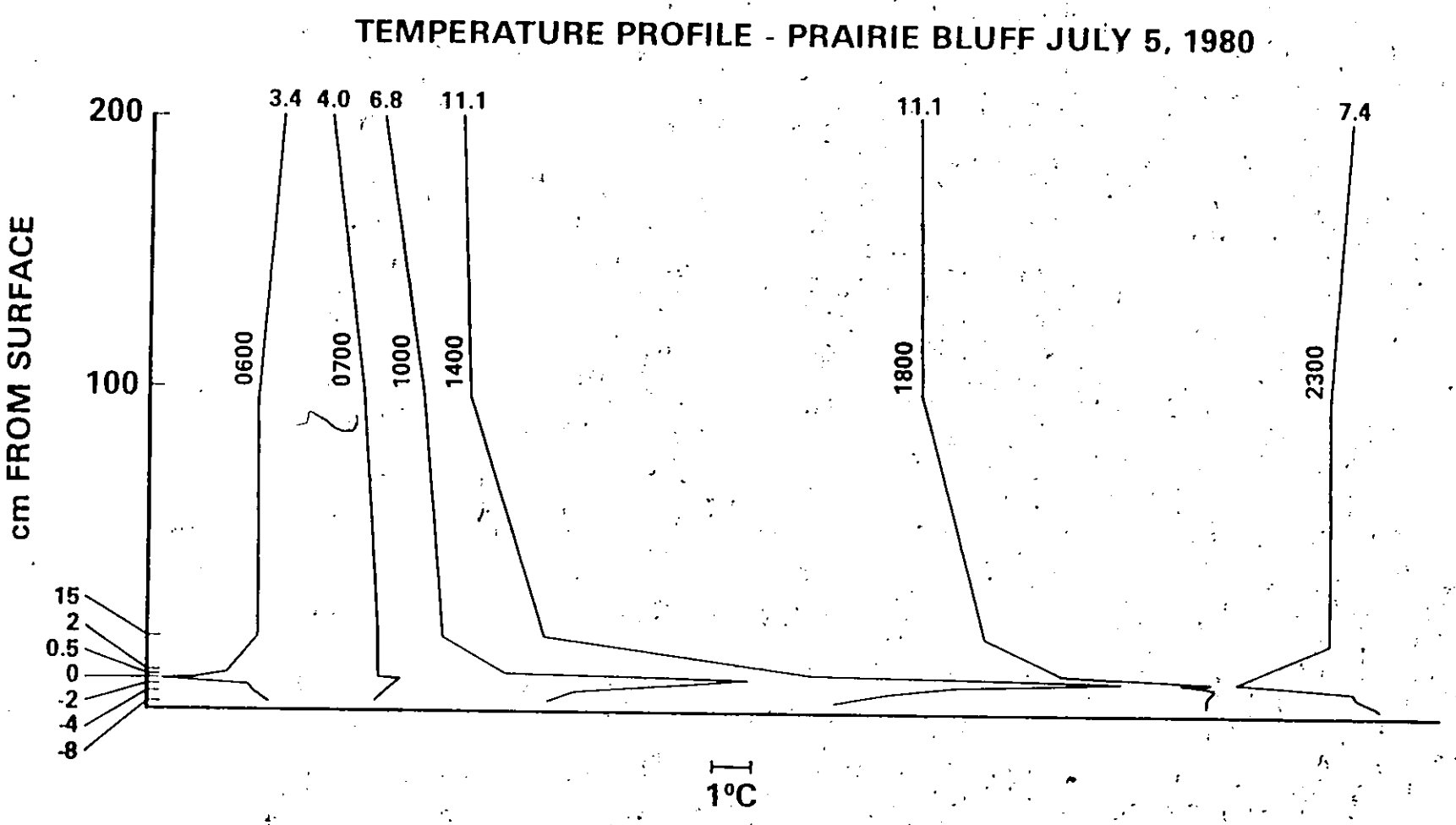
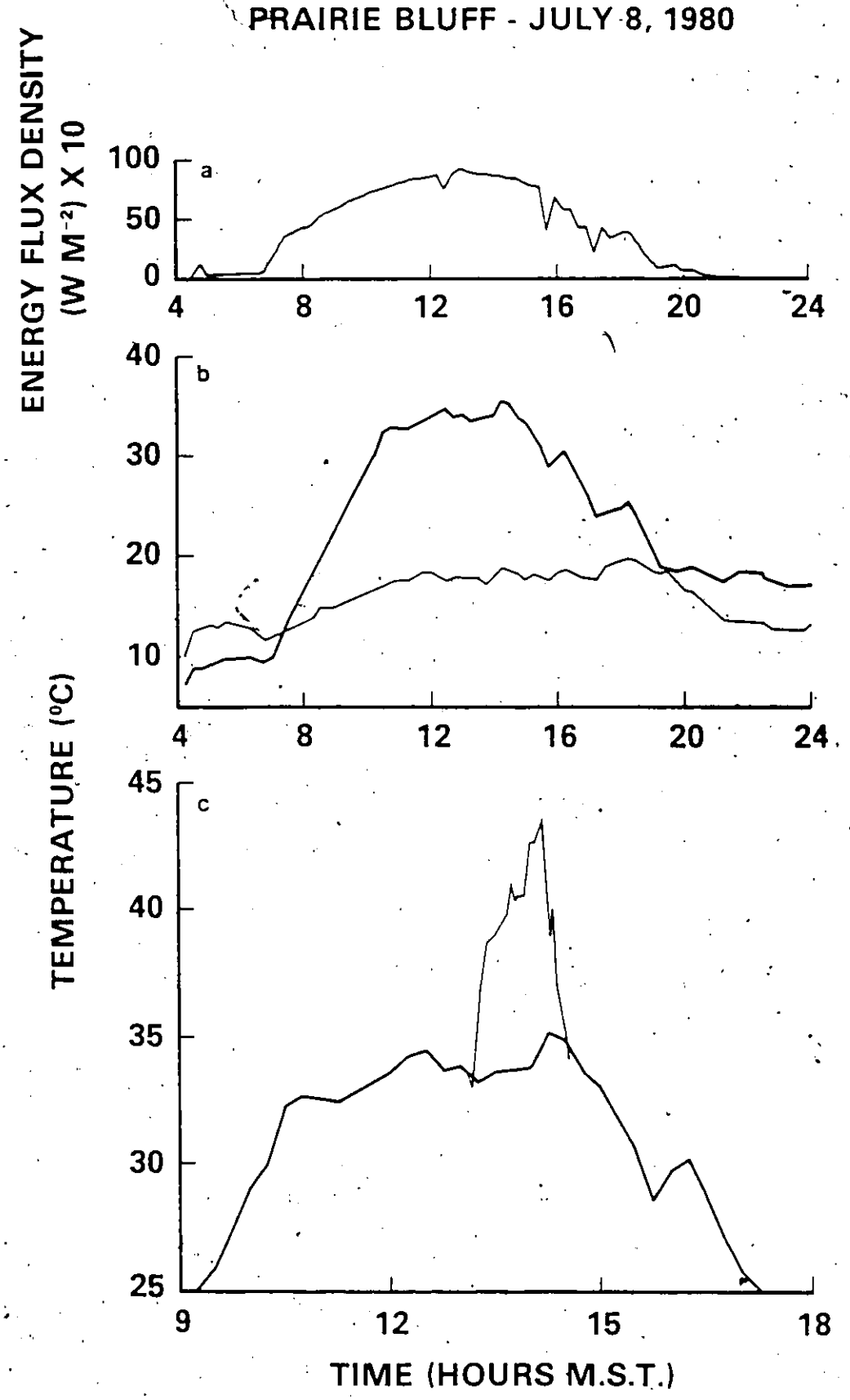

TEMPERATURE PROFILE - PRAIRIE BLUFF JULY 5, 1980
cm FROM SURFACE
200
100
15
2
0.5
0
-2
-4
-8
3.4
4.0
6.8
11.1
11.1
7.4
0600
0700
1000
1400
1800
2300
1°C

Figure 41

Top: Energy Flux Density ($W\ m^{-2}$) for July 8, 1980, Prairie Bluff. Middle: Air temperature at 2 m (thin line); R.superficiale thallus temperature (thick line). Bottom: R.superficiale thallus temperatures under normal exposure (thick line) and sheltered by windscreen for one hour (thin line). Time along the x-axis is expressed in hours Mountain Standard Time (M.S.T.).


PRAIRIE BLUFF - JULY 8, 1980
ENERGY FLUX DENSITY
(W M⁻²) X 10
100
50
0
a
4
8
12
16
20
24
40
30
20
10
b
4
8
12
16
20
24
TEMPERATURE (°C)
45
40
35
30
25
c
9
12
15
18
TIME (HOURS M.S.T.)

(3.3.2) The Grassland Environment

A typical sequence of temperatures that can accompany a winter snow-deposition/ Chinook snowmelt period is given in Fig. 42. The data set starts on Dec. 16 under Chinook conditions, with both air and C.trachyphylla thalli temperatures exceeding 15 °C. The re-establishment of cold continental air masses over the site on Dec. 17 resulted in a rapid temperature drop, air temperatures falling below -20 °C, while C.trachyphylla thalli under a fresh snowcover hovered near -10 °C. Return of warmer maritime air to ground level on Dec. 24 and again Dec. 26 resulted in an immediate rise of ambient air temperatures. However, thallus temperatures showed a much slower rate of increase over the melt period. Snowmelt pockets over the exposed ridge crests occupied by C.trachyphylla developed slightly on Dec. 24 and by Dec. 26 thalli were all largely exposed, though still hydrated from surrounding snow margins (Illustrated in Plate 1). The snow depths given in Fig. 42 refer to average values from the surrounding grassland, depths over C.trachyphylla thalli typically being less then those shown. A more detailed examination of the periods Dec. 22 to 23 and Dec. 25 to 26 is presented in Fig. 43, including thalli temperatures of both C.trachyphylla and N.commune as well as air temperature at 2 m. Under cold conditions, the thalli of N.commune remained considerably warmer than those of C.trachyphylla, their deeper snowpack providing greater insulation. However under melt conditions, the greater insulation afforded N.commune

considerably delayed snowmelt pocket establishment. Thus throughout most of Dec. 26 C.trachyphylla thalli were fully hydrated and metabolically active, whilst N.commune thalli remained frozen beneath the snow surface. Data from a further snowmelt period, this time in mid-March is presented in Fig. 44. Again, prior to snowmelt substantial insulation was provided by the subnivean environment. Large snowmelt pockets developed quickly upon the establishment of Chinook conditions, the higher incoming solar flux of early spring allowing rapid elevation of surface temperatures. Again thalli of N.commune show delayed melting under deeper snow cover. However once exposed, their black colouration and more sheltered position allows higher temperature extremes to be reached. The pattern of nitrogenase activity followed over this period for N.commune is shown in Fig. 45., both under natural field temperature and illumination levels and at 20 °C and 200 uE m^{-2} s^{-1} PAR for destructively sampled replicates. C_2H_2 reduction assays on snowmelt Day 1 (under controlled conditions) found levels of 0.42 nmol C_2H_4 mg^{-1} h^{-1}, rising to near 1.1 nmol C_2H_4 mg^{-1} h^{-1} after 7 hours exposure. Field activity under natural conditions was lower, only reaching 0.9 nmol C_2H_4 mg^{-1} h^{-1} by the end of Day 1. Nitrogenase activity was not detected whilst the thalli were frozen, but was detectable immediately upon thawing Day 2, when field rates reaching 0.8 nmol C_2H_4 mg^{-1} h^{-1} while laboratory rates reached 1.2 nmol C_2H_4 mg^{-1} h^{-1}. Nitrogenase activity declined on Day 3 as surface drying proceeded.

Measured temperature, moisture, hydration and nitrogenase activity in N.commune over the period May 28 to June 25, 1982 are shown in Figs. 46 to 48. Several points of interest emerge. Under full

radiation conditions the mean temperature of the black N.commune thalli frequently exceeded 55 °C, with diurnal fluctuations exceeding 50 °C not being uncommon (eg. the morning of May 31). A marked diurnal fluctuation in the moisture content of N.commune was also noted, even in absence of dewfall or precipitation, as the thalli rehydrated after extreme midday dessication throughout the cooler relatively more humid nights (eg. May 31 to June 2). However no C_2H_2 reduction was noted, except after direct precipitation or dewfall condensation periods. Following wetting N.commune thalli quickly reached over 1500% moisture content, drying relatively slowly thereafter. For example, on June 8 thalli of N.commune required nearly 8 hours under full radiation conditions to fall from saturation to air dry moisture levels (at ca. 1500 hours). In contrast, thalli of C.trachyphylla were fully air dry by 0900 hours (Fig. 49), each having been brought to saturation the previous night. Marked diurnal patterns of nitrogenase activity were noted in N.commune. From June 4th to the 8th midday maxima of up to 4.7 nmol C_2H_4 mg^{-1} h^{-1} were reached, with rates declining gradually throughout the night until sunrise, when rates again rose rapidly.

The instantaneous rates of nitrogenase activity in Figs. 46 and 47 are summarized in cumulative form in Fig 48. Cumulative nitrogenase activity over the period May 28 to June 28, 1982 exceeded 350 nmols C_2H_4 mg dry $weight^{-1}$, or over 80 mg N m^{-2} (using a 3:1 ratio C_2H_2 reduced to N_2 fixed, See Section 2.3.1) in localized microsites with high surface density of N.commune.

Rainfall frequency and intensity over the summer field study

period are also given in Fig. 48. The precipitation on May 26 to 28 and June 5 to 7 resulted from major synoptic storm centers, while other rainfall events were largely due to localized thundershower activity.

Mornings with dewfall deposition, as evidenced both by visible condensation on equipment and foliage, together with an early morning rise in N.commune thallus moisture content in the absence of precipitation events are given in Table 7. It is noteworthy that 5 out of 12 dewfall periods had been preceeded the previous day by rainfall. However only on June 8 and 17 was there any substantial carry-over of thallus moisture content in N.commune. Maximum thalli moisture levels resulting from dewfall condensation were usually recorded around 0600 hours, followed by a peak of C_2H_2 reduction several hours later. The rapidity of drying after dewfall hydration was influenced by surface microtopography, those thalli which remained shaded longest being the last to dry out. Frost on the mornings of May 30, 31 and June 8 melted soon after sunrise and did not effect subsequent nitrogenase activity. Nitrogenase activity was quite variable, depending on the intensity of dewfall condensation and thallus hydration. On June 14, although thalli were slightly wetted by dewfall condensation, moisture levels failed to rise to a level sufficient to allow the onset of detectable nitrogenase activity.

The cover estimates used in converting nitrogenase activity from a weight to an area basis are given in Fig. 51. The cover values reflect the patchy nature of the distribution of N.commune, ranging from near 0 to over 24 g m^{-2}, resulting in a mean cover value of 4.3 g m^{-2}.

The repeated destructive sampling required for accurate thallus moisture content determination in C.trachyphylla severely restricted the number of periods over which this parameter could be followed. The limited data available (Table 8, Fig. 49) strongly suggest that in summer thalli of C.trachyphylla experience only resticted metabolic activity. For example, on June 8 N.commune remains hydrated for twice as long as C.trachyphylla. Rapid drying of C.trachyphylla following shower activity was also documented on June 5 and 16 (Table 8), N.commune again retaining thalli moisture for a much longer period. Clearly the colloidal nature of N.commune enables considerable moisture retention, well after thalli of C.trachyphylla are completely dessicated. The thermal regimes of C.trachyphylla and N.commune also differ considerably in summer months. Thalli of C.trachyphylla typically remain much cooler well into the midday period and conversely much warmer through the night than do thalli of N.commune (Fig. 50). Further the thalli of N.commune experience much higher temperature extremes, both midday maxima and nightime minima. This contrast between the crustaceous surface cryptogam C.trachyphylla and foliose N.commune is opposite in pattern to that of R.superficiale and U.kraschenninikovii. However, C.trachyphylla and N.commune are not immediately adjacent, the C.trachyphylla thalli being located on slightly higher rock slabs as outlined above.

Table 7. Thallus Moisture content and resultant nitrogenase activity (nmols C_2H_4 $mg^{-1}h^{-1}$) in *N. commune* during morning dewfall periods from May 28 to June 28, 1982.

Date	Deposition Type Frost or Dew	Maximum Deposition Period Time	% Moisture Content HI	% Moisture Content Mean	Maximum Nitrogenase Activity Period Time	% Moisture Content HI	% Moisture Content Mean	Rate[A]	Previous Moisture[B] Content
May 30*	F	0600	280	68	0830	235	62	304	25
31	F	0700	80	47	0830	70	38	18	12
June 8*	F	0500	1168	1052	1000	940	836	2836	990
9	D	0600	294	95	1100	185	60	1857	81
10*	D	0530	219	103	0900	180	60	955	38
11	D	0600	74	50	0900	69	51	52	27
12	D	0500	93	57	0830	90	25	108	18
14	D	0600	42	35	No detectable activity				12
15	D	0600	89	57	0800	54	38	30	5
17*	D	0530	1075	115	1000	511	83	2345	127
19	D	0600	62	50	0800	40	16	10	8
24*	D	0700	118	105	0800	113	97	165	64

* Denotes precipitation periods during previous day.

A. Rate in nmols C_2H_4 g^{-1} h^{-1}. Mean value from 8 replicate incubations.

B. % Moisture Content at 2100 hours previous evening. Mean of 6 determinations.

Table 8. Comparative thallus moisture content of Caloplaca trachyphyla and Nostoc commune.

DATE	TIME	THALLUS MOISTURE CONTENT (% of oven dry weight) C. trachyphylla	N. commune	SYNOPSIS
June 5	1700	75	1100	Overcast, light
	1900	47	1089	Cool and windy.
June 9	2300	8*	103	Clear skies.
June 10	0600	12*	98	Morning dewfall,
	0700	17	99	full solar insol-
	0800	12*	84	ation conditions.
	0900	9*	60	
	1000	3*	45	
June 12	0500	9*	57	As June 10.
	0530	9*	49	
	0600	7*	47	
	0630	8*	44	
	0700	7*	39*	
	0730	7*	33*	
	0800	6*	25*	
	0900	1*	16*	
	1000	1*	8*	
June 16	0930	69	741	Morning showers.
	1100	95	1091	
	1200	59	845	Clearing skies.
	1300	46	547	
	1330	36	410	
	1400	14*	215	
	1430	9*	80	
	1530	10*	54	

*Thallus moisture content below threshold of CO_2 gas exchange (c.a. 15% for C. trachyphylla and 40% for N. commune).

Figure 42

Top: Snowcover (cm) in open Stipa-Bouteloa grassland, Dec. 16-29, 1981. Middle: Energy Flux Density ($W m^{-2}$). Bottom: Air temperature at 2m (thick line); C.trachyphylla thallus temperature (thin line).

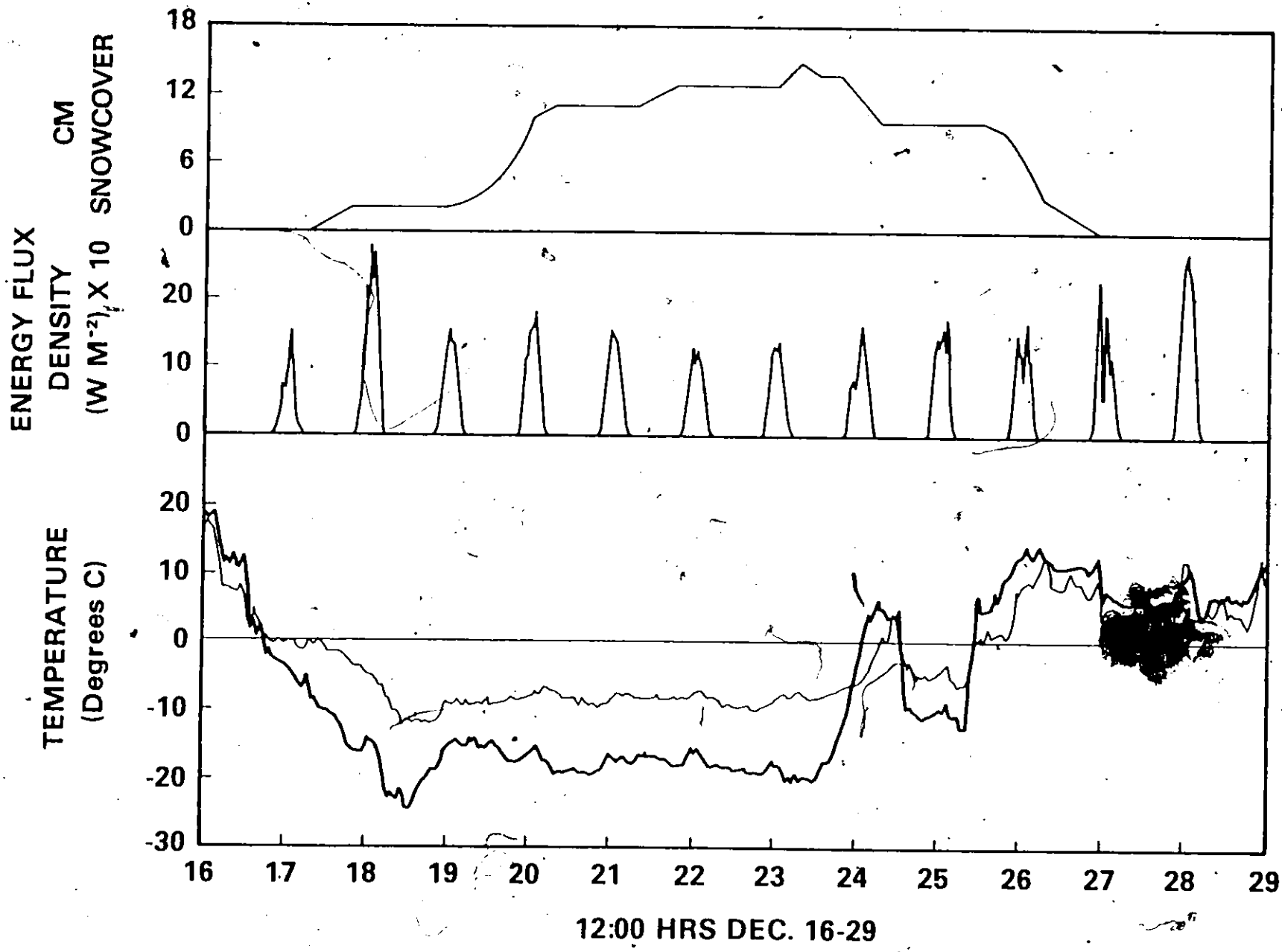

CM SNOWCOVER
18
12
6
0
ENERGY FLUX DENSITY (W M⁻²) X 10
20
10
0
TEMPERATURE (Degrees C)
20
10
0
-10
-20
-30
16
17
18
19
20
21
22
23
24
25
26
27
28
29
12:00 HRS DEC. 16-29

Figure 43

Top: Thallus temperature for N.commune (Line A) and C.trachyphylla (Line B) and air temperature at 2 m (Line C) for the period Dec. 25 to 26, 1981, Pearce, Alberta. Bottom: As above, but for Dec. 22 to 23, 1981.

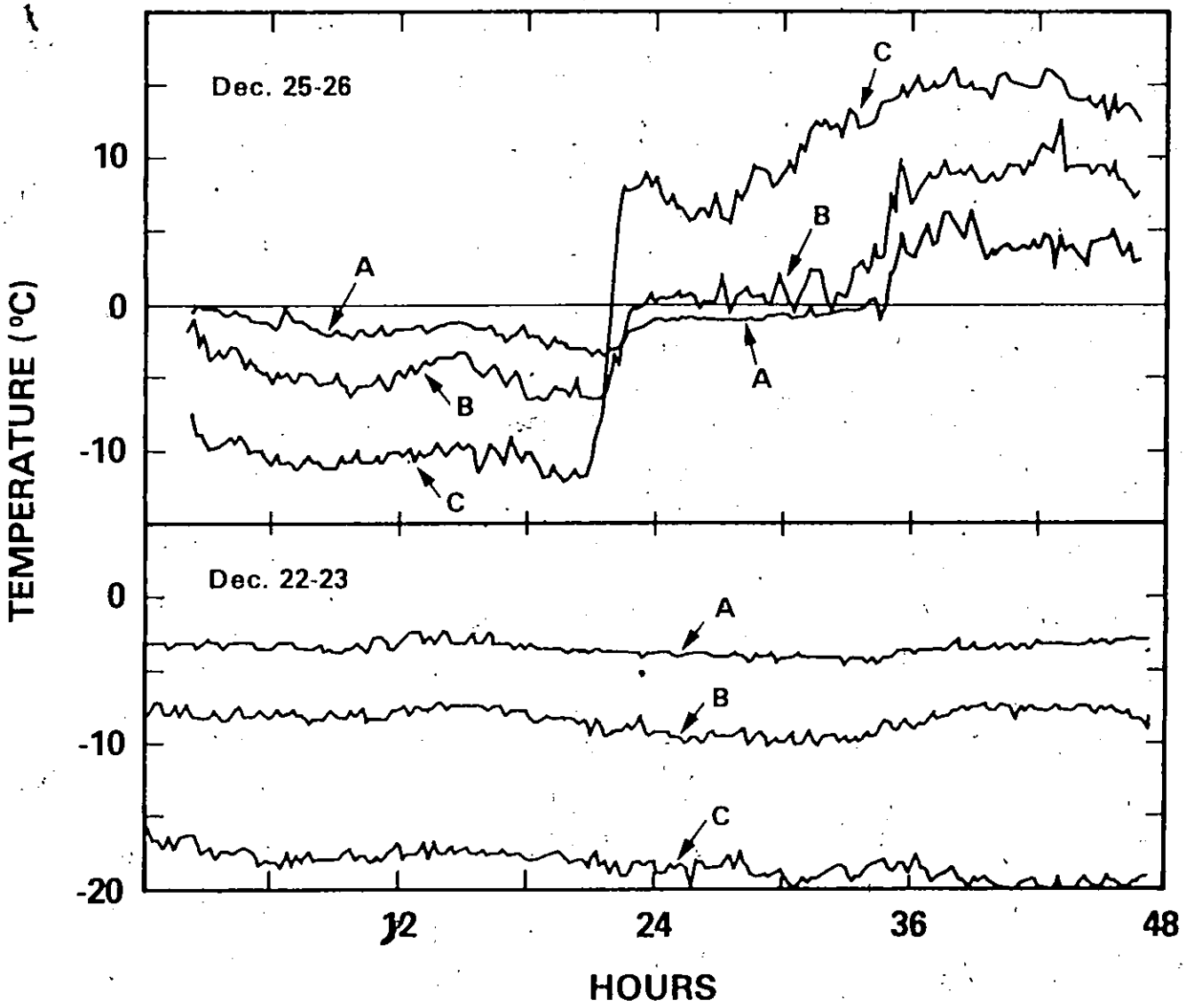

Dec. 25-26
Dec. 22-23
TEMPERATURE (°C)
10
0
-10
0
-10
-20
12
24
36
48
HOURS
A
B
C
A
B
C
A
B
C

Figure 44

Top: Energy Flux Density ($W\ m^{-2}$) for March 22 to 23, 1982, Pearce, Alberta. Bottom: Air temperature (thick line) and C. trachyphylla thallus temperature (thin line).

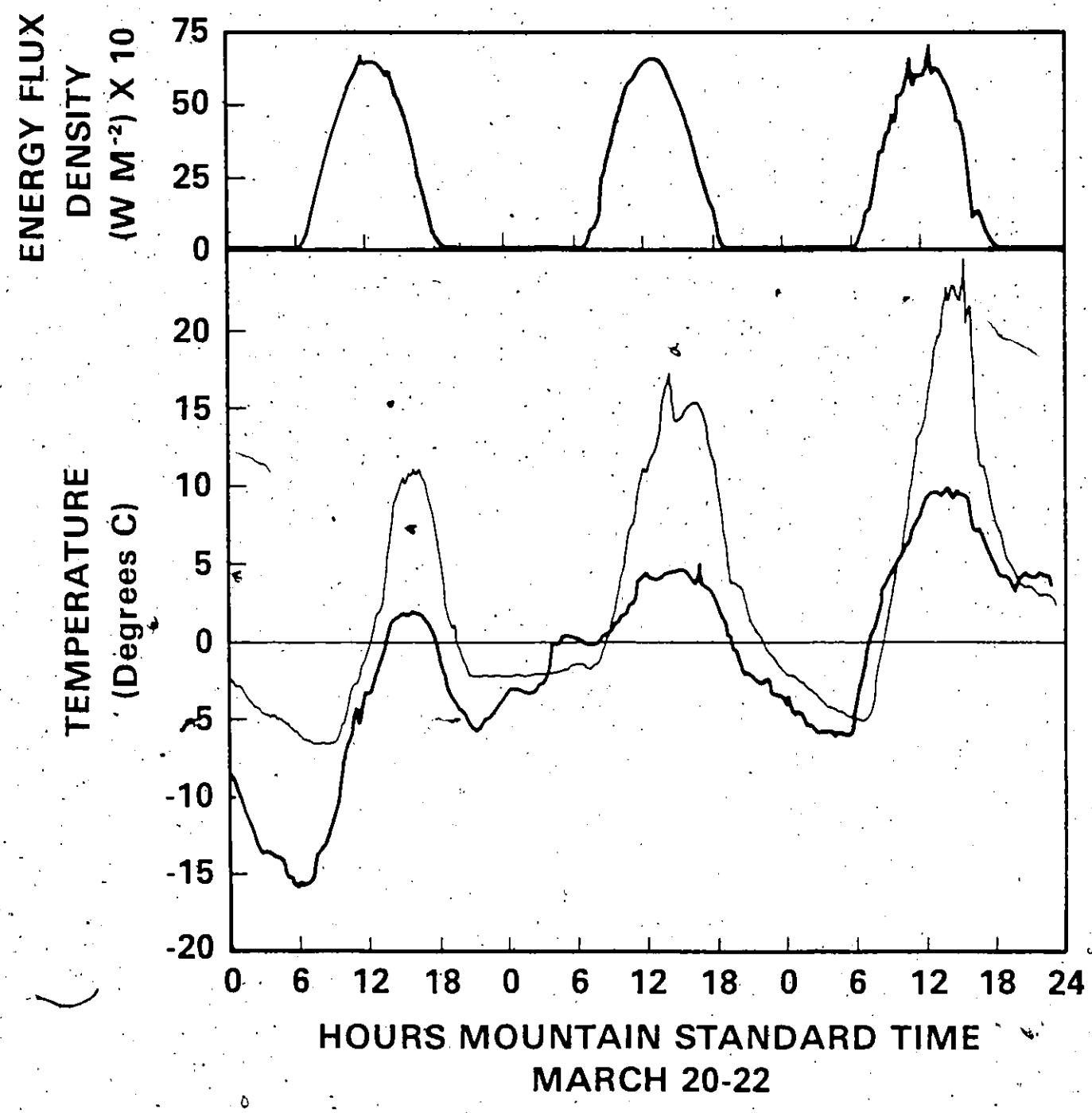

ENERGY FLUX DENSITY (W M⁻²) X 10
75
50
25
0
TEMPERATURE (Degrees C)
20
15
10
5
0
-5
-10
-15
-20
0
6
12
18
0
6
12
18
0
6
12
18
24
HOURS MOUNTAIN STANDARD TIME
MARCH 20-22

Figure 45

Pattern of nitrogenase activity in N.commune and environmental parameters over the Chinook snowmelt sequence of March 20 to 22, 1982, Pearce, Alberta. From top: A) Nitrogenase activity (nmol C_2H_4 mg^{-1} h^{-1}) measured under field conditions of light, temperature and moisture (O), contrasted with experimental rates at 20 °C and 200 uE m^{-2} s^{-1} PAR (●) for freshly collected replicates. Standard error of the mean less than 0.5 nmol C_2H_4 mg^{-1} h^{-1}. B) Radiant Energy Flux Density. C) Air temperature at 2 m and N.commune thallus temperatures. D) Percent relative moisture content by weight for experimental replicates (□).

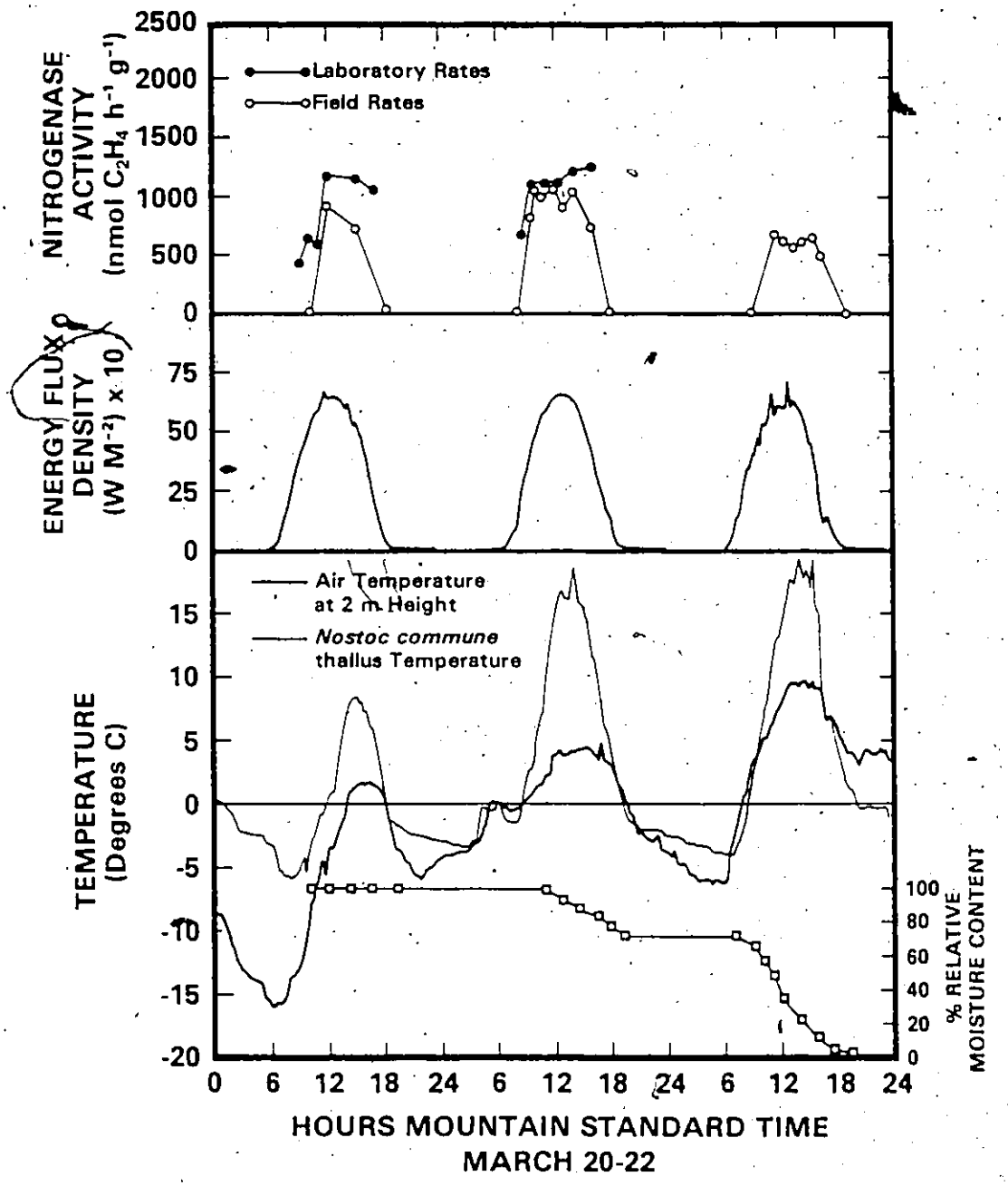

NITROGENASE ACTIVITY (nmol C_2H_4 h^{-1} g^{-1})
2500
2000
1500
1000
500
0
Laboratory Rates
Field Rates
ENERGY FLUX DENSITY (W M^{-2}) x 10
75
50
25
0
TEMPERATURE (Degrees C)
Air Temperature at 2 m Height
Nostoc commune thallus Temperature
15
10
5
0
-5
-10
-15
-20
% RELATIVE MOISTURE CONTENT
100
80
60
40
20
0
0 6 12 18 24 6 12 18 24 6 12 18 24
HOURS MOUNTAIN STANDARD TIME
MARCH 20-22

Figure 46

From top: A) Radiant Energy Flux Density ($W\ m^{-2}$) for May 28 to June 11, 1982, Pearce, Alberta; B) N.commune thallus temperatures and air temperature at 2 m; C) N.commune thallus moisture content expressed on both logarithmic (1-1000) and linear (0-2000) scales; and D) nitrogenase activity measured under ambient temperature, moisture and light conditions. Each point is the mean of 8 to 12 replicates (hourly), SEM under 0.1 nmol $C_2H_4\ mg^{-1}\ h^{-1}$.

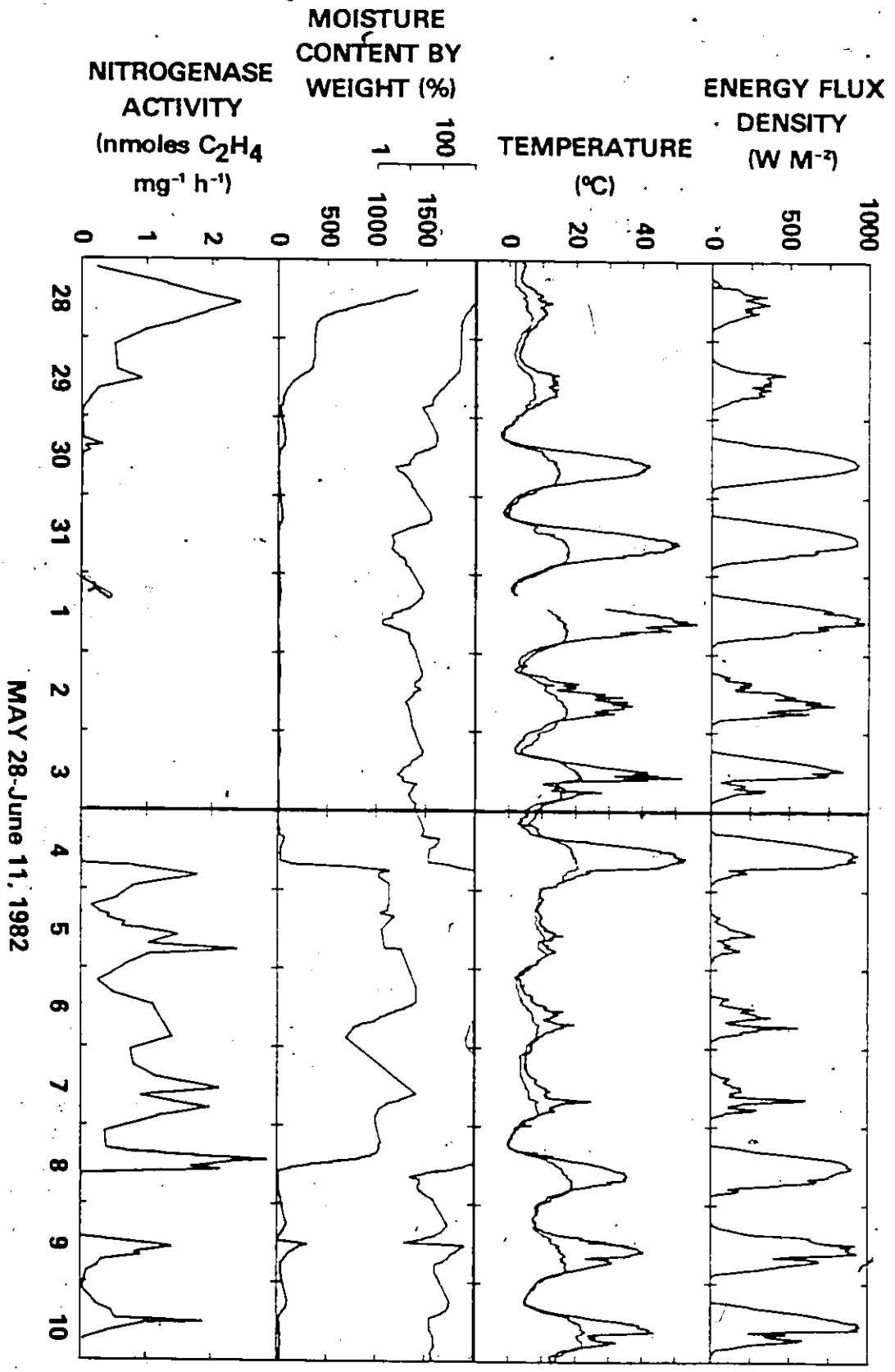

NITROGENASE ACTIVITY (nmoles C_2H_4 mg^{-1} h^{-1})
MOISTURE CONTENT BY WEIGHT (%)
TEMPERATURE (°C)
ENERGY FLUX DENSITY (W M^{-2})
0
1
2
500
1000
1500
100
20
40
28
29
30
31
1
2
3
4
5
6
7
8
9
10
MAY 28-June 11, 1982

Figure 47

As for Fig. 46, but for the period June 11 to 25, 1982.

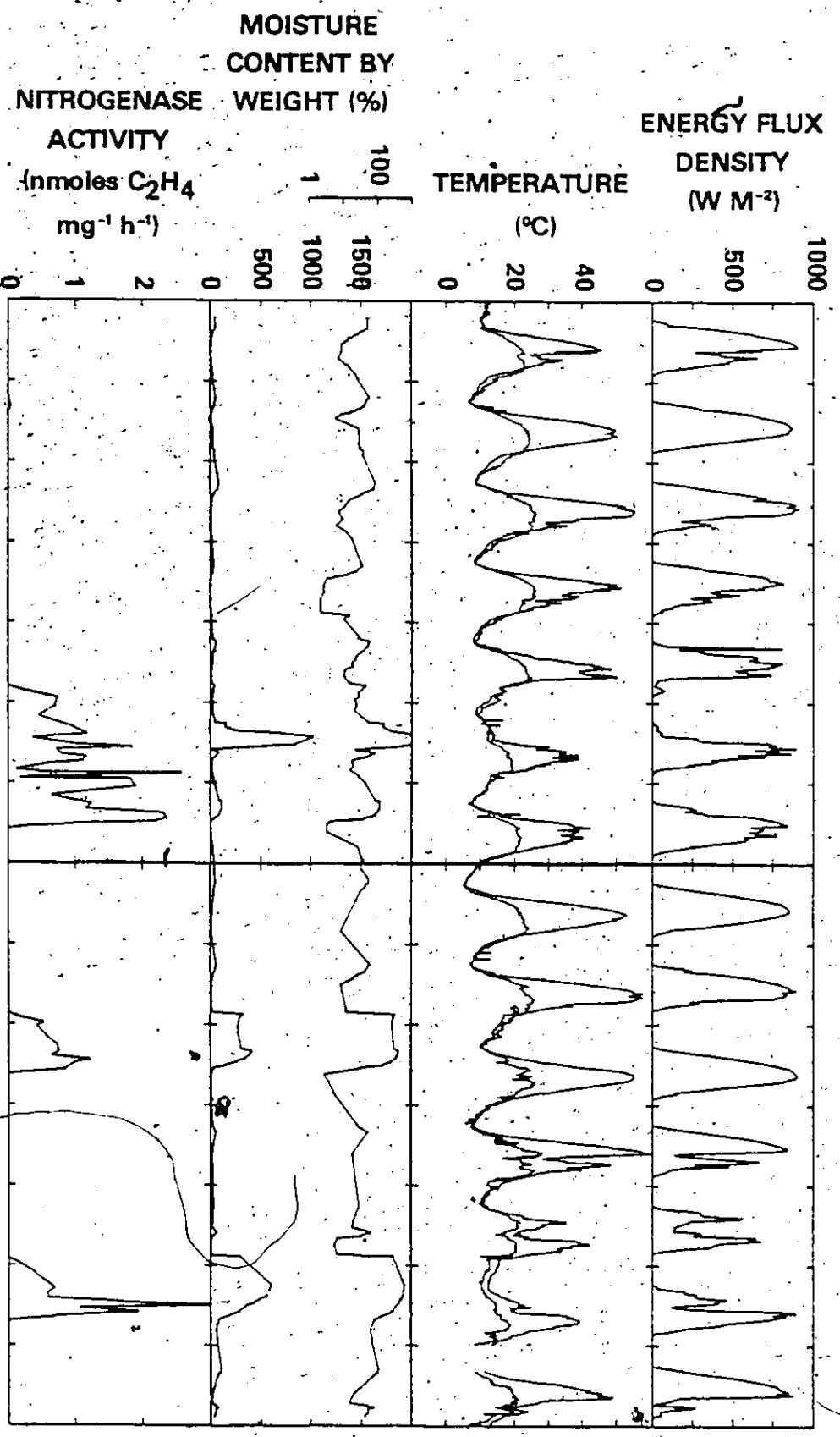

NITROGENASE ACTIVITY (nmoles C_2H_4 mg^{-1} h^{-1})
MOISTURE CONTENT BY WEIGHT (%)
TEMPERATURE (°C)
ENERGY FLUX DENSITY (W M^{-2})
0
1
2
500
1000
1500
100
20
40
11
12
13
14
15
16
17
18
19
20
21
22
23
24
JUNE 11-25, 1982

Figure 48

The pattern of nitrogenase activity and precipitation events for May 28 to June 28, 1982, Pearce, Alberta. From Top: Rainfall (cm) per 24 hour period (trace amounts denoted by *); maximum rate of nitrogenase activity in replicate set incubated under ambient temperature, light and moisture conditions; and cumulative nitrogenase activity with A) maximum, B) mean, and C) minimum values from each set of field incubations expressed. Results are plotted in both nmols C_2H_4 mg^{-1} and mg N m^{-2}, the latter over 2 scales, 0- 90 (at a density of 23.9 g m^{-2}) and 0-16 mg N m^{-2} (at a density of 4.3 g m^{-2}). Results in mg N m^{-2} assume a 3:1 ratio C_2H_4 evolved per mole N_2 reduced.

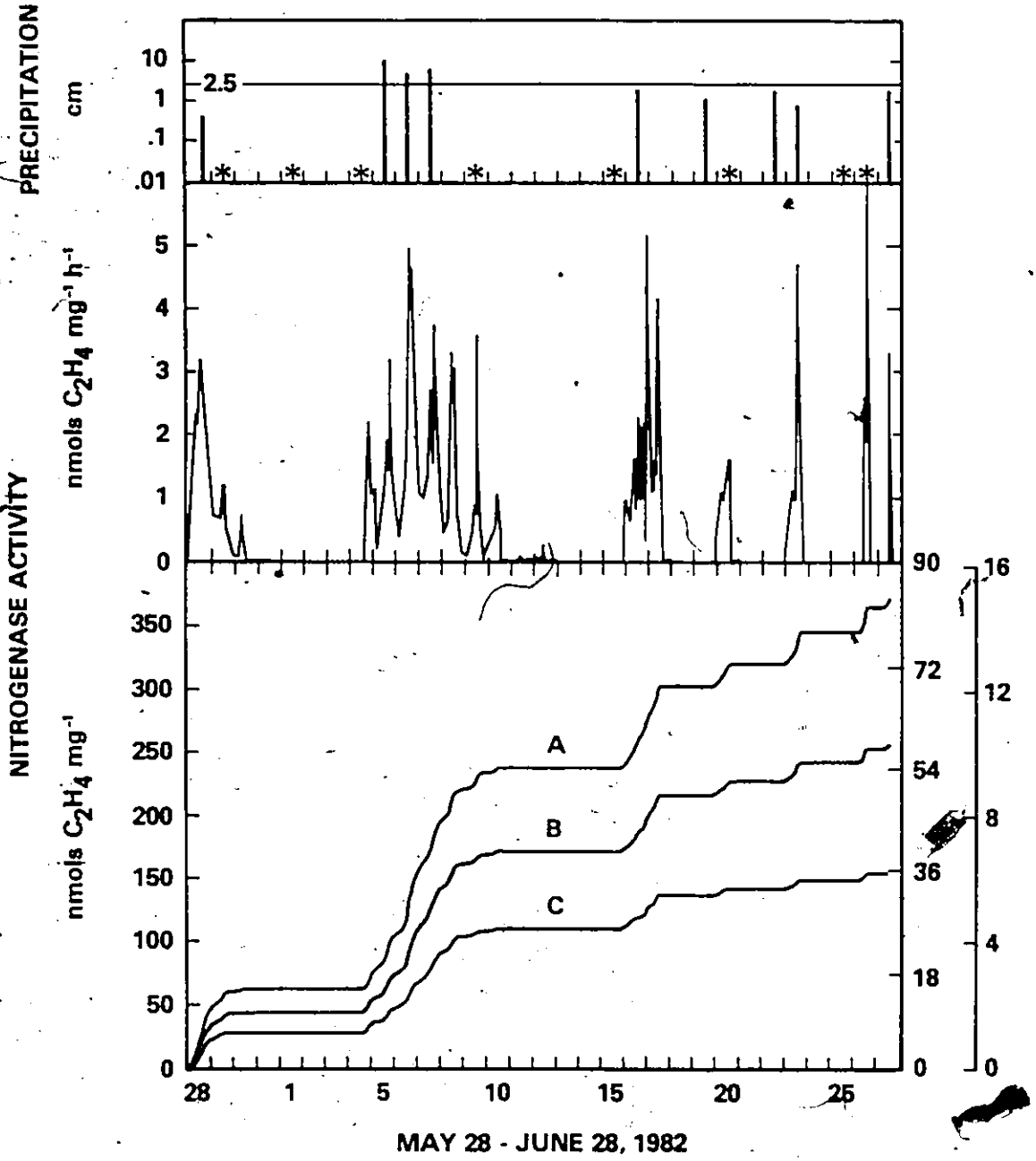

PRECIPITATION
cm
10
1
.1
.01
2.5
NITROGENASE ACTIVITY
nmols C_2H_4 mg^{-1} h^{-1}
5
4
3
2
1
0
nmols C_2H_4 mg^{-1}
350
300
250
200
150
100
50
0
A
B
C
90
72
54
36
18
0
16
12
8
4
0
28
1
5
10
15
20
25
MAY 28 - JUNE 28, 1982

Figure 49

The pattern of solar radiation, temperature and thallus moisture content for June 8, 1982, Pearce, Alberta. From top: A) Radiant Energy Flux Density ($W\ m^{-2}$); and B) N.commune (thick line) and C.trachyphylla (thin line) thallus temperatures; and C) N.commune (thick line) and C.trachyphylla (thin line) thallus moisture contents by weight. Arrows denote time at which thallus moisture contents fell below thresehold values at which continued CO_2 gas exchange is usually detectable (See Sections 4.3 and 4.4.1).

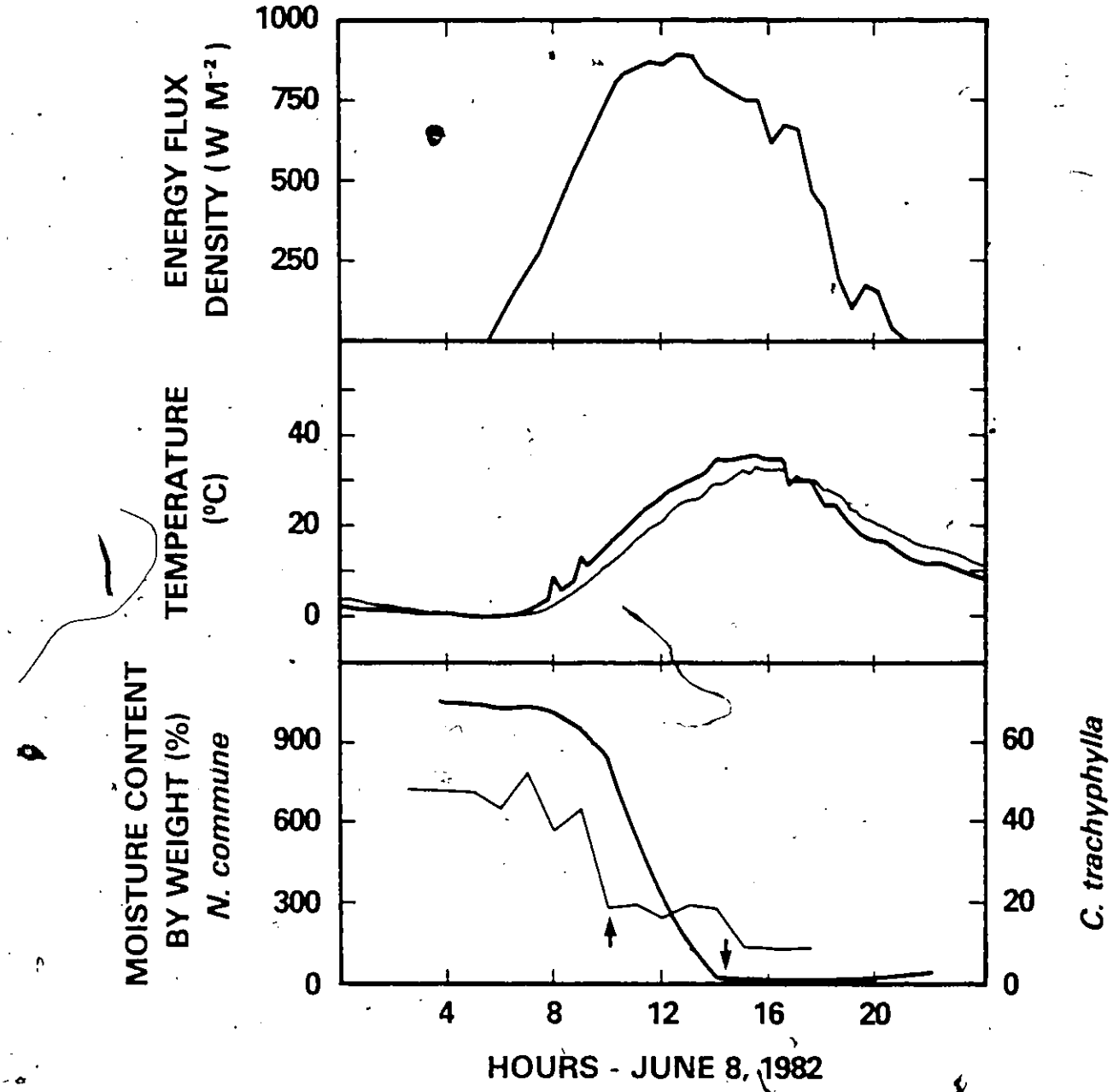

ENERGY FLUX DENSITY (W M⁻²)
1000
750
500
250
TEMPERATURE (°C)
40
20
0
MOISTURE CONTENT BY WEIGHT (%)
N. commune
900
600
300
0
C. trachyphylla
60
40
20
0
4
8
12
16
20
HOURS - JUNE 8, 1982

Figure 50

The pattern of N.commune (thick line) and C.trachyphylla (thin line) thallus temperatures from May 28 to June 24, 1982, Pearce, Alberta.

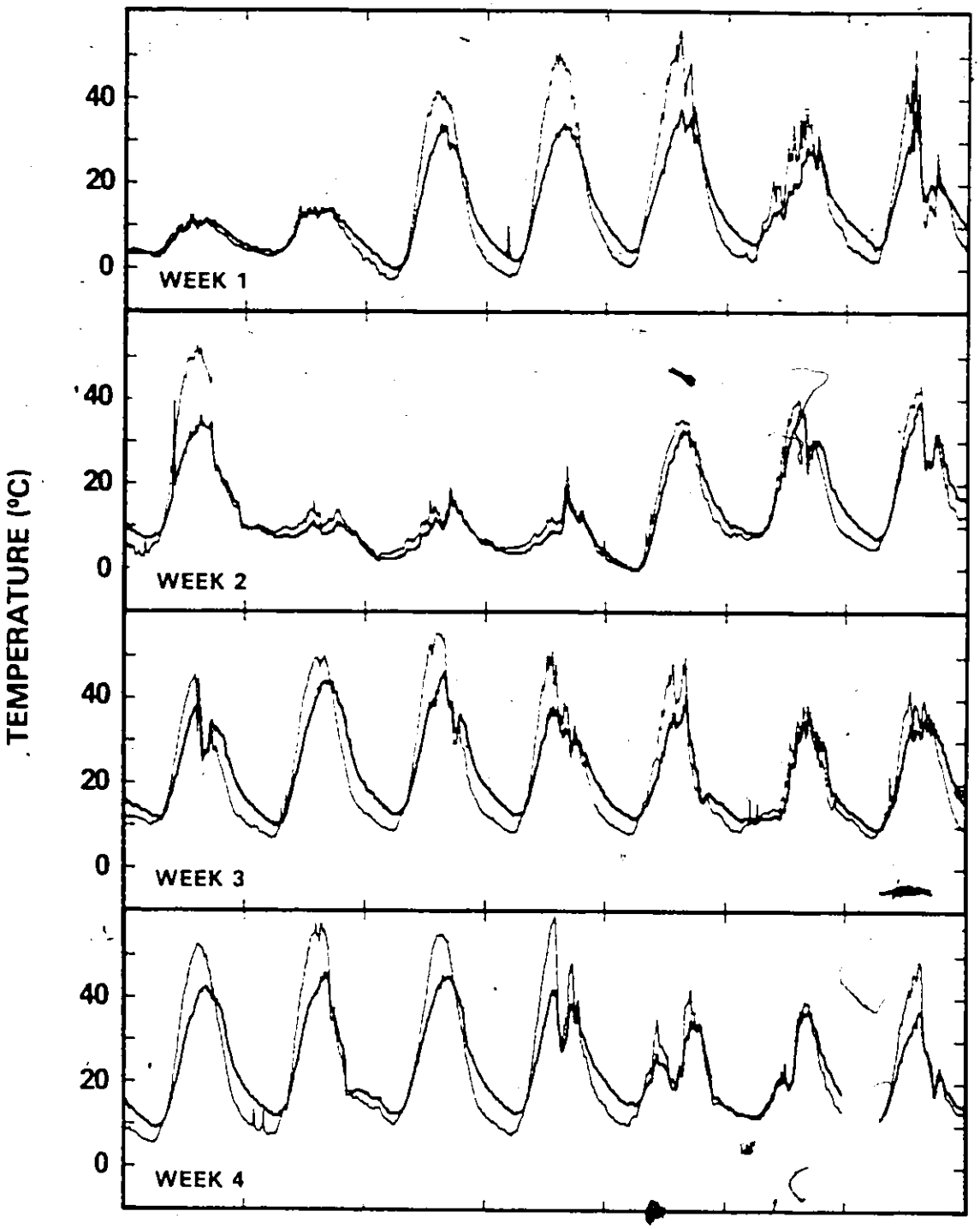
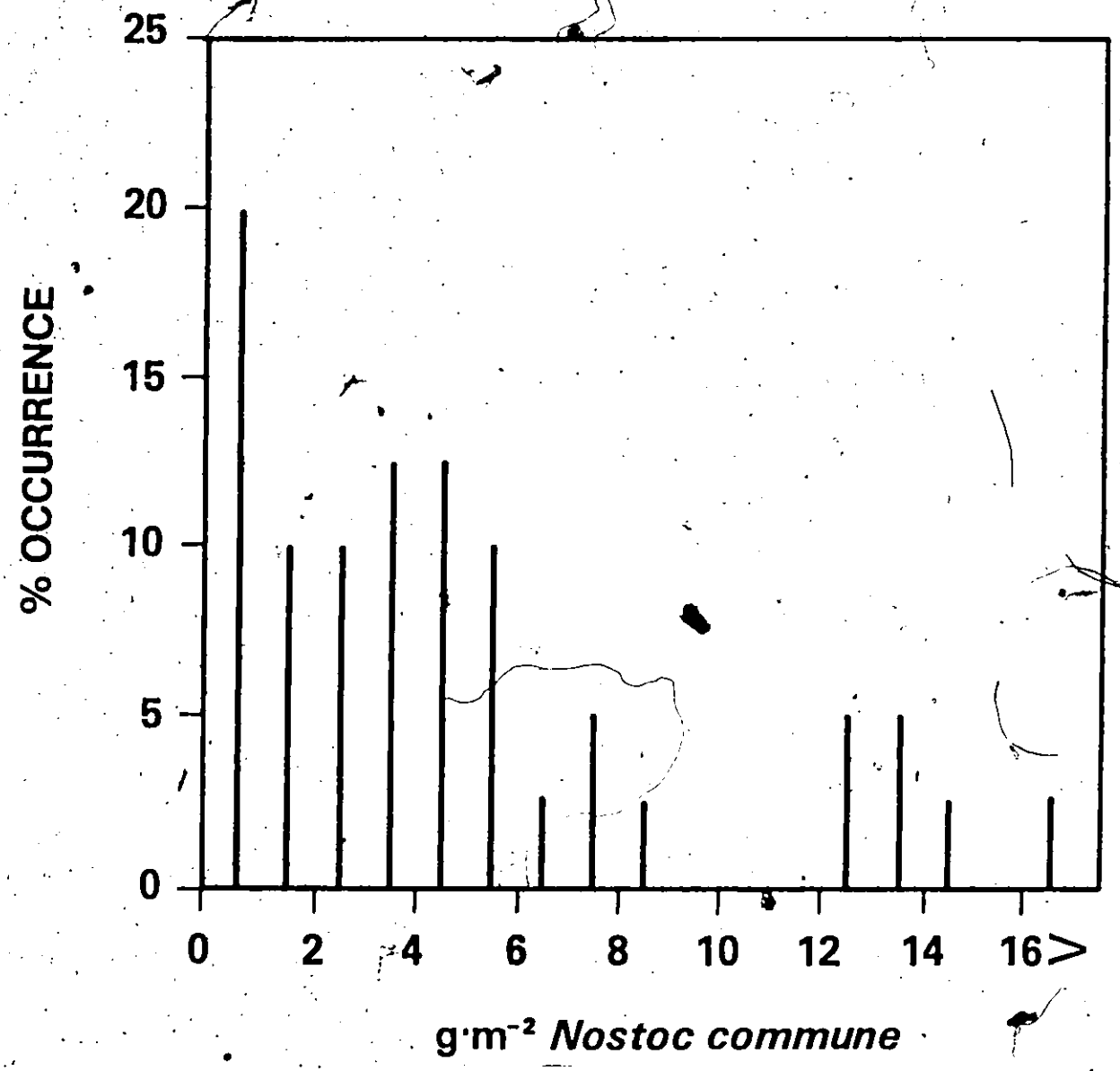

TEMPERATURE (°C)
40
20
0
WEEK 1
WEEK 2
WEEK 3
WEEK 4
MAY 28 - JUNE 24

Figure 51

The frequency distribution of N.commune biomass in Stipa-Bouteloa grassland over 1 g class intervals. Biomass determinations (g oven dry weight) are from destructive sampling within 41 randomly placed 1 m^2 quadrats. Mean cover equals 4.3 g m^{-2}, while high and low values were respectively 23.94 and 0.01 g m^{-2}.


25
20
15
10
5
0
% OCCURRENCE
0
2
4
6
8
10
12
14
16>
g·m⁻² Nostoc commune

Section 4.

DISCUSSION

(4.1) The Pattern of Gas Exchange in R.superficiale in Context of the Physical Environment

Maximal rates of net photosynthesis in R.superficiale were seen between 0 and 10 °C , with the temperature compensation point being reached near to 28 °C (Fig. 9). This temperature optimum is similar to those of a wide range of other alpine lichens, including: Cladonia elongata, C.alcicornus, Stereocaulon alpinum, Letharia vulpina, Parmelia encausta (Lange, 1965), Alectoria ochroleuca, Thamnolia vermicularis, Cetraria cucullata, C.islandica, and C.ericitorum (Turk, 1981). Equally many arctic lichens such as: Cetraria nivalis, Parmelia olivacea, Nephroma arcticum, and Solorina crocea (Kallio and Heinonen, 1971; Kallio, 1973), and also antarctic species, for example, Parmelia coreyi (Lange, 1965), Beullia frigida (Lange and Kappen, 1972) and Xanthoria mawsonii (Gannutz, 1970) show a similar low temperature optima of net photosynthesis. The optimal rates of net photosynthesis observed here in R.superficiale agree well with those given by Ried (1960) for alpine populations of R.geographicum in Germany. Reid found rates of net photosynthesis ranging from 0.46 to 1.26 (mean=0.73) mg CO_2 h^{-1} g^{-1}. However, only summer material was examined and experimental pretreatment and storage conditions were not detailed. In common with most of the above mentioned species, R.superficiale shows a general trend towards

lower net photosynthetic temperature optima at lower light intensities. This stems largely from the marked temperature dependency of respiration, a response common to most surface cryptogams. Although Turk (1981) regards this trend towards higher light compensation points at higher temperatures as an adaptation to cool-temperature and low-light conditions, the relationship is so widespread that any adaptive development relative to a specific habitat is questionable. This concept should not be confused with the specific adaptations to low light intensities found in some surface cryptogams and free living algae (See Section 4.2.1).

The most striking feature of the physical operating environment of R.superficiale is its dynamic nature. During the winter months the alternating influence of Arctic continental and Pacific maritime air masses results in repeated snow deposition/snowmelt sequences over the southern Alberta frontal mountain ranges. Over midwinter Chinook snowmelt periods the temperature of fully hydrated thalli of R.superficiale can exceed 5 °C , as observed during December 1979 collections on Table Mtn.. Under the higher radiation conditions of late spring hydrated thalli temperatures exceed 20 °C during snowmelt periods (Fig. 37). During these periods sunfleck activity and the diurnal temperature wave can act in concert to produce even hourly freeze thaw transitions. In midwinter particularly, hydrated thalli can within hours drop from ca. +5 to -30 degree C. A contributing factor to the severity of winter temperature fluctuations experienced by R.superficiale is the lack of subnivean insulation afforded thalli on their typically windswept ridge crest habitats (Fig. 2). Larson (1979) suggested that for the ridge crest surface cryptogams of arctic tundra, the spring snowmelt period

might well represent the major period of carbon gain. In R.superficiale, with snowmelt providing thallus hydration in all months of the year, this hypothesis assumes an even greater significance.

During major storm periods R.superficiale thalli temperatures remain quite low, generally close to air temperature (Fig. 35). This is in agreement with microclimate data of Tegler and Kershaw (1980) and Kershaw and Watson (1983) for northern boreal sites. However, even short sunny breaks between precipitation periods result in dramatic temperature elevation. Field miroclimate data indicates that the thalli of R.superficiale can remain hydrated at levels sufficient for metabolic activity for several hours after rainfall cessation (Fig. 38). The high frequency of convective shower activity observed over the alpine study site means that repeated cycles of thallus wetting, followed by gradual drying under full radiation conditions and high temperature are a very common occurence for R.superficiale thalli (Fig. 35).

It is also evident from the field microclimate data that the thallus temperature of R.superficiale growing closely adpressed to the rock surface can be significantly higher than that of adjacent foliose surface cryptogams projecting further above the boundary layer zone. This can be seen in comparison of R.superficiale with U.kraschenninnikovii thallus temperatures (Figs. 36 and 40). Even though thalli of U.kraschenninnikovii are much darker in colour than those of R.superficiale they are consistently cooler under high radiation conditions, a pattern opposite to that predicted by Kershaw (1975a) for light versus dark coloured thalli. These temperature differences likely reflect the resistance of still air in the boundary layer to the transfer of sensible heat fluxes. In an analagous way the transfer of latent heat

from a hydrated thallus is similarly impeded by boundary layer conditions.

A further potential advantage provided by the closely adpressed morphology of R.superficiale thalli is the improved moisture retention after hydration periods through the equilibrium with the subsurface moisture reserves of the porous sedimentary rock. The water content held by the argillitic substratum reaches ca. 1.4 % by weight at saturation (Fig. 3b), a value higher than that that documented by Kappen et al. (1981) for antarctic sandstones colonized by cryptoendolithic lichens, where the rock substrate provides the major protection from desiccation. A clear relationship is seen between the thallus moisture content of R.superficiale and the substrate moisture content for 30 g rock chips under controlled wind tunnel conditions, after an initial period of high evaporation from free water surfaces (Fig. 3c). This suggests that under field conditions of lower air temperature and higher humidity R.superficiale thalli adpressed to argilitic slabs of many tons in size, would experience attenuated drying cycles, relative to thalli of non-crustaceous surface cryptogams.

The kurtosis of the temperature response curve in R.superficiale differs considerably in form from those of the other species mentioned above (Fig. 9). Instead of a typically bell shaped response curve, there was virtually no change in net photosynthetic rates from 1 up to 21 °C, the curve being platykurtic in form (Ferguson, 1976). On first examination, such a broad range of response would seem anomalous in the context of general trends shown by alpine tundra species. However, closer examination of the specific thermal operating environment experienced by R.superficiale reveals that only during major storm

periods does R.superficiale experience the stereotypic alpine climate, ie. cold and wet. The extreme thermal fluctuations experienced by hydrated R.superficiale thalli are probably a major factor in the breadth of the photosynthetic temperature response curve. Thus the photosynthetic response matrix does indeed represent an adaptation to the alpine tundra environment, correlating well with the breadth of boundary layer temperature fluctuations documented.

As in C.trachyphylla and many other cryptogamic species, R.superficiale shows a sharp peak of net photosynthesis relative to thallus moisture content at between 40 to 60 percent moisture content by weight. Both Snelgar et al. (1981a, b) and Lange and Tenhunen (1981) recently examined this phenomena in a range of lichen species. They attributed the depressed net photosynthetic rates to a high physical transport resistance to diffusive passage of CO_2 through the surface water films and water filled internal spaces of the lichen thalli. The thick upper cortex of R.superficiale and other crustaceous surface cryptogams, whilst providing protection for the phycobiont from both solar radiation and excessive desiccation (Runemark, 1956; Rundel, 1978; Kershaw and MacFarlane, 1980), also creates a high internal resistance to CO_2 diffusion when fully saturated. Similarly, Snelgar et al. (1980) found that in finely branched epiphytic lichens from tropical mist forests, no such depression of net photosynthesis was evident at full thallus saturation, diffusive resistances being lower through their thinner fungal cortex. Equally specialized gas exchange structures, ranging from pseudocyphellae to pores and cortical cracks can provide increased access of CO_2 in other surface cryptogams (Hale, 1981).

The response of respiration in R.superficiale to changing thallus

moisture content is very similar to that documented for Peltigera polydactyla and P.praetextata by Kershaw (1977a, b). At low temperatures, respiration rates remain constant as thallus moisture content declines until very low levels are reached. With increasing temperature levels respiration rates show an almost proportional change with thallus moisture content. A slight trend toward increased respiration is seen in the winter collections of R.superficiale. This may reflect in part a "winter-hardening" of physiological processes, as seen in the increased winter respiration rates in Umbilicaria deusta and U.mamulata (Larson, 1980). However, in other surface cryptogams a winter hardened state is variously accompanied by decreasing respirations rates, as in U.vellea and Cladonia rangiferina (Larson,1980; Tegler and Kershaw, 1980), or no change in rates, as seen in P. polydactyla and U.papulosa (Kershaw, 1977a; Larson, 1980). Interpretation of these changes in context of their adaptive significance remains obscure at present.

The pattern of response to light in R.superficiale is interesting in that saturation of net photosynthesis does not occur until ca. 900 uE m^{-2} s^{-1} PAR. Typical light intensities under even overcast field conditions often reach 600 uE m^{-2} s^{-1} PAR, whilst hydrated R.superficiale thalli are frequently exposed to over 2000 uE m^{-2} s^{-1} PAR. A high light saturation point would be expected from these values, although the actual light intensities at the chloroplast level may be considerably lower due to screening by the highly pigmented upper cortex (Runemark, 1956). Pigmentation in crustaceous surface cryptogams is widely regarded as protecting the phycobiont against irradiation damage (Kappen, 1973), particularly in alpine environments where a high ultra-violet component is present (Billings and Mooney, 1968).

The factorial data set closest in pattern to that of R.superficiale is that recorded for Collema furfuraceum in subarctic boreal forest of Northern Ontario (Kershaw and MacFarlane, 1982). It also shows a broad pattern of temperature response with little seasonal variation. In contrast to R.superficiale it's physical environment is quite stable, being located on shaded north facing Populus balsamifera tree trunks where its thallus temperatures closely follows that of ambient air. The foliose lichen Parmelia disjuncta, common on exposed rocky outcrops of low arctic environments, also shows a response pattern quite similar to that of R.superficiale. Over most of the year, it shows a temperature optimum of about 7 °C and a temperature compensation point at about 28 °C. However, over the midsummer period P.disjuncta shows marked increases in maximum photosynthetic rates (P_{max}) at high light levels and moderate to high temperatures. Unfortunately the thermal operating environment of this lichen has only been documented while dry under full radiation conditions and during major precipitation periods. The importance of snowmelt periods and convective shower activity to annual carbon gain in P.disjuncta remaining unknown. Rouse (1982) notes that convective showers occur frequently in midsummer over the coastal ridges on which P.disjuncta is located. Thus the rapid fluctuations in temperature typical of R.superficiale's habitat may also play a role in the ecology of P.disjuncta. The major immediate difference between their environments is that P.disjuncta remains snow covered over the winter period, whilst R.superficiale experiences frequent melt conditions. It is interesting to note that the beach ridge lichens Alectoria ochroleuca and Cetraria nivalis, which experience conditions similar to that of P.disjuncta, also show midsummer capacity changes at higher temperature

(Larson and Kershaw, 1975c, d). The above noted seasonal changes in P_{max} have been referred to as examples of photosynthetic acclimation, as they allow continued homeostasis of carbon gain over seasonal periods (Kershaw, 1977a, b; Larson, 1980; Turk, 1981). In light of the widespread nature of the seasonal changes in P_{max} in these low arctic surface cryptogams, Larson and Kershaw (1975a) suggested that acclimatory changes would prove common in other extreme environments. The constancy of seasonal response in R.superficiale does not substantiate this premise. Instead, a case by case comparison of physiology relative to physical operating environment appears to be necessary for the interpretation of operating strategies. This comparison is discussed further in Section 4.2.

During periods of thallus hydration a major avenue of heat dissipation for R.superficiale is through latent heat loss, following the partitioning of net radiation (Q^*) into latent ($L\dot{E}$), sensible (H) and conductive (G) heat terms according to the equation:

$$Q^* = LE + H + G$$

However, when thalli are dry only G and H are available as avenues of heat loss. The strong diurnal substrate heat wave (Fig. 39) points to some loss through G. However the larger proportion of energy dissipation probably occurs as H, as evidenced by up to 30 degree C elevation of thalli temperatures over that of ambient air and the close coupling of thalli temperatures to convective cooling (Fig. 41). A similar partitioning is common to exposed sub-arctic soil surfaces, particularly during early phases of fire succession (Kershaw and Rouse, 1971). The absolute recorded temperature maximum of R.superficiale thalli during the summer field period was nearly 35 °C, a value recorded on July 10, 1980

when air temperatures reached near 20 °C. This temperature limit is reflected in the response of R.superficiale thalli to laboratory heat stress experiments. In July, after 14 days of midday high temperature storage at 35 °C, there was no apparent decline in either net photosynthetic or respiratory rates. However, even a few days exposure of air dry thalli thalli to midday 45 °C temperature extremes results in severe reduction of net photosynthetic capacity (Fig. 19). In midwinter, an exposure of even 35 °C at midday results in a slight decline of photosynthetic capacity, whilst the 45 degree treatment immediately results in a total loss of photosynthetic capacity (Fig. 20). A clear threshold of thermal lability appears to exist between 35 and 45 °C. The data of Fig. 45 suggests that convective transport of sensible heat from the boundary layer surface is an important component of the energy balance of R.superficiale. Removal of this convective dissipation of energy by physically screening the thalli from wind rapidly results in temperature values which are clearly quite deleterious after even a few hours exposure. The very circumscribed distribution of R.superficiale in the study area to completely exposed and wind-swept alpine tundra areas correlates well with the potential requirement for a strong convective term in the energy balance of R.superficiale. MacFarlane and Kershaw (1980) suggested that the tolerance range to heat stress in surface cryptogams correlates closely with their environment. This postulate appears to hold true for R.superficiale, despite the earlier belief that surface crustaceous lichens were practically immune to temperature extremes when dry (Kappen, 1973). As with a priori determination of photosynthetic temperature optima, the assignment of thermal tolerance limits without specific reference to parameters of the surface cryptogams

operating environment can be highly misleading.

(4.2) The Pattern of Gas Exchange in C.trachyphylla in Context of the Physical Environment

A very different pattern of CO_2 gas exchange was found in C.trachyphylla, compared to that of R.superficiale. The temperature optimum of net photosynthesis is much higher, from 14 to 21 °C, while the temperature compensation point is only reached above 35 °C (Fig. 10).

The net photosynthetic response to levels of thallus hydration in C.trachyphylla again shows a marked optimum at intermediate thallus water contents (about 60 to 80 percent by weight), a pattern characteristic of many lichen species, and interpreted by Snelgar et al. (1981a, b) as representing diffusive resistance to CO_2 transport at thallus saturation. This interpretation is strengthened by the response of net photosynthesis to increasing CO_2 concentrations in C.trachyphylla. Replicates held at optimal water content show a steep initial slope of photosynthetic response to increasing CO_2 concentrations (up to near 350 ppm), above which rates continue to rise only slowly. At optimal water content diffusive resistance to CO_2 transport is low and only a moderate CO_2 gradient is required to saturate the sites of carboxylation. In marked contrast, replicates held at full thallus saturation require a very high CO_2 gradient to overcome physical transport resistance, with cuvette CO_2 levels of 1100 ppm achieving the same net photosynthetic rates previously seen at 350 ppm in drier thalli. A similar pattern of response to CO_2 concentration was evident in the data of Lange and Tenhunen (1981) and Snelgar et al. (1981b). The CO_2 response curve for C.trachyphylla points

to the need for careful control over the draw-down of cuvette CO_2 levels during the course of "discrete" IRGA incubations. At high thallus moisture contents in particular, the "discrete" sampling IRGA system will tend to slightly underestimate the magnitude of net photosynthesis, as net assimilation rates decline in direct proportion to the length of incubation. This problem was not as severe for R.superficiale, whose response curve to CO_2 concentration is less marked near ambient atmospheric values. These interactions of net photosynthesis with declining CO_2 levels will potentially be most severe at higher temperatures, where photorespiratory gas exchange assumes greater importance (Coxson et al. ,1982; Bidwell, 1977; Lloyd et al., 1977).

The most interesting difference in physiological response curves between R.superficiale and C.trachyphylla was the dramatic increase in photosynthetic capacity evident at low temperatures in winter collected material of C.trachyphylla. This was first noticed in December, 1981 collections of C.trachyphylla and subsequently reconfirmed in January, 1982 (Fig. 10), March, 1982 (Table 4) and January, 1983 collections of C.trachyphylla (Figs. 11 and 12). Equally the lower net photosynthetic capacity seen in summer collected C.trachyphylla was documented in both July, 1981 (Fig. 10) and July, 1982 (Table 4). The temperature response curve for C.trachyphylla thus has more degrees of freedom than most other studies with surface cryptogams. These capacity changes which were evident at low temperature could also be induced by pretreatment storage conditions in both January and March (Figs. 11 and 12, Table 4). In both cases photosynthetic capacity at 7 °C fell back to summer levels after one week of storage of the air dry thalli at higher temperatures and longer photoperiod. The maintenance of continued photosynthetic

homeostasis at 21 °C for this material indicates that the induced change at 7 °C is not simply a thermal stress effect. Further, these changes were induced while thalli were air dry, with control experiments rehydrating summer stored replicates under both winter and summer storage conditions yielding identical results.

Detailed examination of the light response curve associated with these winter summer capacity changes showed that no shift in quantum efficiency was apparent between storage groups (Figs. 11 and 12). The capacity change at 7 °C instead stems from a rise of P_{max} along the same light limiting response slope, resulting in a higher point of light saturation for the winter state material. At 21 °C, while both quantum efficiency and P_{max} show no difference between the winter and the summer state material, there is a lower quantum efficiency overall than that found at 7 °C. A mechanistic interpretation of these changes in photosynthetic efficiency is discussed further below (Section 4.2.1).

These seasonal changes in P_{max} over the winter period can be correlated with the frequency distribution of thallus hydration periods in C.trachyphylla. The Chinook phenomena, described above in context of the alpine study site, is even more pronounced at the grassland research area, where it occurs on average with 30% greater frequency (Longley, 1967). The C.trachyphylla thalli, located on slightly exposed rock slabs, are among the first surface cryptogams of the grassland environment to experience free thallus meltwater with the onset of Chinook warming. Recorded thalli temperatures of C.trachyphylla rose from near -15 °C to over 10 °C with development of Chinook conditions during the period Dec. 16 to Dec. 29, 1981 (Fig. 42), while an even greater temperature elevation was documented for early spring Chinook

snowmelt (Fig. 44). The earlier development of snowmelt pockets on exposed rock outcrops where C.trachyphylla grows is evident in Fig. 43, where C.trachyphylla thalli are exposed to free meltwater almost 14 hours before N.commune thalli on surrounding soil surfaces. These differences, when integrated over the entire winter period, must result in considerably more metabolic activity at low temperatures for C.trachyphylla, even though it grows only meters from N.commune. In contrast, during summer months C.trachyphylla experiences far less metabolic activity then does N.commune, the latter retaining moisture much longer after precipitation events. The exposed position of the C.trachyphylla thalli on their sandstone substrate results in both higher drying rates after precipitation events and a reduced frequency of dewfall condensation events, reflecting the greater convective exchange present with topographic exposure. Further, the collodial like nature of the N.commune thalli allows much greater moisture retention after precipitation events (Discussed further below in Section 4.3). Equally, R.superficiale thalli also experience greater metabolic activity over the summer period than do C.trachyphylla thalli, precipitation periods being more frequent over the alpine tundra and subsequent drying periods longer under lower air temperature and higher humidity conditions. Clearly, the maintenance of photosynthetic homeostasis at lower temperatures by C.trachyphylla enhances its potential yearly carbon gain, as most hydration periods occur in the winter months. During the summer months thalli of C.trachyphylla remain largely dehydrated, often exceeding 40 °C under full insolation conditions. However, in marked contrast to R.superficiale, these temperature extremes have no effect on the resumption of photosynthetic activity on hydration. Even after 3 weeks

continuous midday exposure of air dry thalli to 60 °C under laboratory conditions, full photosynthetic activity is apparent upon rehydration (Table 5).

The carbon gain patterns of Sonoran desert lichens followed by Nash et al. (1982a, b) closely parallel those of C.trachyphylla in seasonal frequency. Again, they are metabolically active mainly during the winter months, in this case during winter rainfall periods. In summer thalli largely remained dehydrated , dewfall hydration only infrequently allowing carbon gain. The net photosynthetic temperature optimum for the two species examined, Parmelia kurokawae and Acarospora schleicheri, occurred at approxiamtely 20 °C at 750 uE m^{-2} s^{-1} PAR. Unfortunately, only fall collections were examined by Nash et al., thus potential seasonal responses to periods of hydration periods frequency remain unknown. The optimal net photosynthetic rates in A.schleicheri are higher than those of C.trachyphylla, at about 4.0 mg CO_2 h^{-1} g^{-1}, whilst in P.kurokawae optimal rates are almost double, at ca. 10.0 mg CO_2 h^{-1} g^{-1}. However, direct comparison of rates is difficult, as different ratios of marginal lobes to older central thalli can bias net photosynthetic rates considerably, particularly for interspecific comparisons (Nash et al., 1980; Kershaw, 1977a).

The most well known example of carbon gain patterns in desert crustaceous lichens is that documented by Lange et al. (1970) for Caloplaca ehrenbergii in the Negev desert. In this environment, most metabolic activity results from early morning dewfall hydration periods, precipitation events only infrequently resulting in thallus hydration. Unfortunately net photosynthetic rates for C.ehrenbergii are expressed on a per area basis and thus are not comparable with current results

expressed per g dry weight.

(4.2.1) Capacity Changes in C.trachyphylla. A Conceptual Framework

Seasonal changes of photosynthetic capacity have been widely documented in many surface cryptogams found in extreme environments. Understanding of the mechanistic basis for such changes has advanced considerably in recent years, steming largely from photosynthetic studies with free-living algae. Recent reviews by Harris (1978) and Prezelin (1981) in particular, discuss these concepts at length.

The production of sugars by the Calvin cycle is the end step of several distinct biochemical and photochemical processes, each of which may potentially be a rate limiting step controlling the maximal rates of net photosynthesis under optimal light, temperature, and moisture conditions (P_{max}). Photosynthetic energy conversion is initiated when pigments of the thylakoid membrane absorb light energy, which is then transferred to paired reaction centers (Photosystems I and II). These first steps are performed by a complex generally denoted as the "Photosynthetic Unit" (PSU), often defined as the smallest portion of the thylakoid membrane which can carry out the light reactions of photosynthesis (Prezelin and Sweeney, 1977). It is composed of a core of ca. 180 Chl-a molecules associated with photosystems I and II and includes accessory pigments (chlorophylls, phycobilins, and carotenoids) which can expand the spectral range of light energy that can be absorbed and transfered to Chl-a (Vierling and Alberte, 1980; Prezelin and Alberte, 1978; Prezelin, 1981). At the core of this complex is P700, a

chlorophyll dimer that serves as the reaction center of Photosystem I (Prezelin, 1981). Absorbed light energy, on transfer to the phototraps of its reaction centers, triggers an excited singlet state where both P680 (PS-II) and P700 (PS-I) eject an electron which is rapidly transferred to primary electron acceptors and ultimately NADP (Prezelin, 1981). The spatial configuration of the components across the thylakoid membrane, with the primary electron donors near the inner thylakoid surfaces, the reaction centers central and the electron acceptors near the outer stromal surface (cytosol in procaryotes), allows light energy to be stored as an electrochemical gradient (Prezelin, 1981; Gregory, 1977).

Several distinct categories of change in the components of these steps are proposed by Prezelin (1981), each being reflected in various patterns of photosynthetic-irradiance (PI) curves. These are outlined as follows into four general patterns.

A) Alteration of PSU size, ie. the amount of pigment per PS-I/PS-II quantum trap as reflected in the ratio of chl-a/P700, or often as chl-a/O_2 evolved. Since the number of discrete traps remains the same, P_{max} should remain unaltered, although quantum efficiency should rise, as a given amount of light energy will be intercepted more efficiently when expressed on a per cell basis. The key to elucidation of PSU size changes from PI relations is the expression of results on both a per cell (or dry weight) and on a total pigment (chl-a or accessory pigments as needed) basis. Increases in PI quantum efficiency per cell will not be reflected in the slope of PI plotted on a per pigment basis, the larger denominator cancelling out increased CO_2 uptake. These changes have been documented in higher plants grown under

low light conditions (Brown et al., 1974; Alberte et al., 1976), in diatoms (Perry et al., 1981), dinoflagellates (Prezelin and Sweeney, 1977, 1978) and blue-green algae (Jorgenson, 1969). At present no examples are clearly documented for terrestial surface cryptogams.

B) Changes in PSU density will also lead to increased quantum efficiency per cell, but in addition will be directly proportional to changes in P_{max}. Chl-a/p700 ratios and Chl-a/O_2 evolution ratios will remain unchanged, while P700/cell will rise (Vierling and Alberte, 1980). PI curves will show greater quantum efficiency when expressed on a cellular or dry weight basis, but not when plotted on a whole piment or chl-a basis. Such PI response curve changes have been seen in dinoflagellates, green algae and higher plants (Prezelin, 1981; Jorgenson, 1970; Perry et al., 1981; Patterson et al., 1977). Kershaw and MacFarlane (1983) found increased quantum efficiency and higher P_{max} in Peltigera praetextata responding to changes in deciduous forest canopy closure. PSU density changes were diagnosed on the basis of increased quantum efficiency on a per dry weight basis, while no such change was apparent on a per chl-a basis. Other examples of changes in PSU density changes are not clearly documented in surface cryptogams.

C) Changes in quantum efficiency can also be due to reduced energy flow through existing PSU's, ie. a coupling/uncoupling of electron flow between the photosystems (Prezelin, 1981). No pigmentation changes are observed, but both light limited and light saturated rates of photosynthesis are affected. On a cellular or dry weight basis these changes are indistinguishable from PSU density changes in form of their respective PI response curves. However, when PI responses are plotted on a pigment basis, the altered quantum efficiency and P_{max} relationships

remain intact, allowing differentiation from changes in PSU density where these differences vanish when similarly plotted: This coupling/uncoupling of electron flow is basic to diurnal and phenological changes observed in dinoflagellates, diatoms and blue-green algae (Prezelin et al., 1977; Prezelin and Ley, 1980; Senger, 1970). Prezelin and Sweeney (1977) postulate that circadian ion fluxes across the thylakoid membrane generate reversable conformational changes reflected in photosynthetic capacity. Energy transduction changes are often observed in association with photosynthetic acclimation to temperature in higher plants. Armond et al. (1978) found that pretreatment storage conditions of 20/15, 32/25, or 45/33 day/night temperature induced respectively greater stability of interactions between light harvesting pigments and quantum traps. P_{max} changes associated with these quantum yield differences have been documented by Badger et al. (1982) for the desert shrub Nerium oleander on acclimation of photosynthetic temperature optimum to a high temperature regime (45/32 °C day/night). In surface cryptogams, winter/summer changes in Cladonia rangiferina and C.stellaris, previously interpreted as acclimatory changes (Tegler and Kershaw, 1980; Carstairs and Oechel, 1978; Lechowicz, 1978), have now been interpreted as reversable coupling/uncoupling by MacFarlane et al. (1983) and Kershaw et al. (1983). Winter/summer capacity changes prior to leaf canopy emergence have also been documented for P.praetextata (Kershaw and Webber, 1983). Distinguishing between changes in PSU density and reversible coupling/uncoupling requires the simultaneous expression of CO_2 effluxes on both a per cell or weight basis and on a per pigment basis. Unfortunately this data is not available in the majority of current literature examining acclimatory changes in surface cryptogams.

D) The final pattern of change involves events "downstream" from the photochemical reactions, ie. changes in enzymatically rate limiting steps of the Calvin cycle. Theoretically these changes, being independent of light limiting reactions, will involve no alteration of quantum efficiency, either on a cellular or pigment basis, but will only result in altered P_{max}. A similar pattern of change is seen in the winter acclimated thalli of C.trachyphylla at low temperature, where quantum efficiency remains constant while P_{max} rises sharply (Figs. 11 and 12). Unfortunately, the mechanistic basis of photosynthetic acclimation has only been closely examined to date in context of high temperature responses. Badger et al. (1982) for instance, examined the enzymes of the Calvin cycle concurrent with acclimatory changes in the desert shrub N.oleander. Only activity of Fru-P_2 phosphatase showed any appreciable change with a shifting photosynthetic optimum. However, interpretation of this acclimatory change was complicated by simultaneous coupling/ uncoupling of electron transport, as reflected by changes in the slope of light limiting PI curves. Armond et al. (1978) considers these changes in quantum efficiency with acclimation to high temperatures as a "heat hardening" response, with the altered membrane configuration both reducing heat lability of photosynthetic processes and changing electron transport efficiency. Photosynthetic acclimation of other hot-desert plants, for example Atriplex sabulosa and Tidestroma oblingifolia (Bjorkman and Badger, 1977), may also involve changes in both membrane configuration (reducing heat lability) and increased enzymatic activity (allowing higher P_{max}). A further complicating factor is the interaction of quantum efficiency with temperature in C_3 plants, due to stimulation of oxygenation of RUP_2 as temperature increases (Berry

and Bjorkman, 1980). Measuring quantum efficiency at high CO_2 or low O_2 concentrations is one possible means of resolving the relative role of photorespiratory vs. coupling/uncoupling (of PSU electron flow) caused changes in quantum efficiency. Examples of changes in rate limiting enzymatic rates only, without coupling/uncoupling (viz. Armond et al., 1978) at present are documented only at the level of PI response curves. The summer capacity changes at high light levels in Parmelia disjuncta discussed above, are a potential example of enzymatic adaptation to higher summer temperatures. Unfortunately, seasonal acclimatory changes in the adjacent beach ridge species Bryoria nitidula and Alectoria ochroleuca (Kershaw, 1975b; Larson and Kershaw, 1975d) are too incomplete to interpret in the context of PI relationships. The best example to date of high temperature acclimation in surface cryptogams is that of Peltigera rufescens. Brown and Kershaw (1983) showed marked summer capacity changes at 35 °C, without any concomitant changes in quantum efficiency. Furthermore, these changes could be induced by manipulation of storage temperature and photoperiod conditions.

The capacity changes in C.trachyphylla at low temperature may also fall into this catagory of enzymatic changes. Winter state material of C.trachyphylla showed both a lower K_c and higher V_{max} (Fig. 7), suggestive of increased affinity for CO_2 by RuBP carboxylase at low temperatures (Monson et al., 1982). Although Larson (1980) suggested that low temperature acclimation occurred in Umbilicaria deusta, his data set does not allow a full interpretation in context of PI/P_{max} interactions. Increased affinity of RuBP carboxylase for CO_2 at low temperatures has been found in both winter acclimated rye and potatoe plants (Huner and MacDowall, 1979; Huner et al., 1981). Graham and

Patterson (1982) suggest that higher substrate affinity of enzymes at low temperatures may be a more widespread adaptive strategy than presently documented. Simon (1979) demonstrated K_m changes in the respiratory enzyme NAD malate dehydrogenase in response to pretreatment storage at 7/15, 15/25 and 22/30 °C day/night temperatures, a higher low temperature substrate affinity evident in cold stored material. The higher P_{max} evident in C.trachyphylla at low temperature, in absence of shifts in quantum efficiency (either on a per weight or a pigment basis), may thus reflect photosynthetic acclimation in the present strict sense of "downstream" enzymatic events only.

The above four catagories provide possible mechanistic interpretations for most capacity changes and acclimatory responses seen in surface cryptogams. While these interpretations cannot at present be made from most photosynthetic studies with surface cryptogams, re-examination of acclimatory changes in the context of PI response curves seem a probable next step. Obviously, both coupling/ uncoupling (C above) and strictly enzymatic changes (D above) can result in acclimation in the sense of Prosser (1955), ie. an adaptation resulting in homeostasis of carbon gain. Use of the term "photosynthetic acclimation" in the current sense (viz. Prezelin, 1981), where changes in P_{max} above light saturation must be documented on both a cellular and pigment basis, would alleviate considerably the current ambiguity of interpretation of photosynthetic changes. Such usage would remove the need for distinguishing between the "total" (Larson,1980), "partial" (Kershaw and Watson, 1983), or "incomplete" (Carstairs and Oechel, 1978) acclimatory responses of net photosynthesis to temperature regime.

(4.3) The Pattern of Gas Exchange in N.commune in Context of the Physical Operating Environment

(4.3.1) Physiological Response Matrix of Gas Exchange

The temperature response curve of both nitrogenase activity and net photosynthesis in N.commune (Fig. 16) does not differ substantially from that of other soil surface blue-green algal crusts (Rychert and Skujins, 1974; Jones, 1981; Lynn and Cameron, 1973; Paul et al., 1971; Sheriden, 1983). The optimal long term temperature response of nitrogenase activity falls near 28 °C, while net photosynthesis shows optimal rates at 35 °C. No marked seasonal differences were apparent in net photosynthetic or nitrogenase rates, except in May collected material. However, expression of results per mg Chl-a reduces the magnitude of this difference, possibly reflecting higher cell densities or increased chlorophyll content in spring. Seasonal changes in functional chlorophyll density have also been noted by Lynn and Cameron (1973) in surface cyanophyte mats.

The light saturation level for nitrogenase activity in N.commune, at or near 900 mg CO_2 h^{-1} g^{-1}, is much higher than typically observed in most studies with lichens, where increases in activity with increasing PAR are common up to only 75 uE m^{-2} s^{-1} PAR (Cox and Fay, 1969). Stewart (1974) summarized the information on effects of light intensity on terrestial cyanophytes by suggesting that there is a general, but not always very direct correlation between light intensity and nitrogen fixation in natural ecosystems. The data of Figs. 24 and 25 would

suggest a more direct transfer of the recent products of photosynthesis to the nitrogenase enzyme complex in N.commune, perhaps through smaller pool sizes for recent photosynthates. The time dependent increases in C_2H_2 reduction observed concurrently with the light dependencies in Fig. 25 have also been noted by Scherer et al. (1980), who suggested that conformational changes induced by acetylene exposure can enhance nitrogenase activity. Considerable variability was observed in the inter-replicate response to light saturation (Fig. 24). This may reflect uneven light penetration through the gelatinous sheath surrounding algal cell populations. Light intensity was measured only at the outer surface of the colony sheaths in the present studies.

There is a strong interaction of C_2H_2 reduction with continued exposure to light in N.commune. Activity continued to rise steeply after initial light exposure for up to ca. 14 hours (Figs. 31 and 32). This may reflect a depletion of carbohydrate pools during prior dark periods, which are not fully replenished until after several hours in the light. The decline of nitrogenase activity in the dark is directly proportional to increases in thallus temperature (Fig. 26). Presumably, at higher temperatures high respiratory demands quickly deplete substrate pools, while at lower temperatures these pools support nitrogenase activity over a longer time period. As in other blue-green algae, the reductant for nitrogenase activity is ultimately derived from photosynthetic activity, with phosphorylation being the major source of ATP (Gallon, 1980). This dependence on photophosphorylation is illustrated well by the rapid decline in nitrogenase activity on addition of DCMU (Figs. 27 and 28). As rates of nitrogenase activity in the DCMU treated replicates remained higher than those of replicates placed in darkness, cyclic

phosphorylation may play a role in heterocyst ATP provision through activity of Photosystem I (Gallon, 1980).

Comparison of the moisture response curve of N.commune with that of other surface algal crusts is difficult due to the discrete morphological form of this species. It occurs as large thalloid clumps on the soil surface, with little intermingling with soil particles and on drying tends to form tight clumps, very much like the lichen Chondropsis semiviridis (Rogers, 1971). The mucilagenous sheath holds up to 3000% moisture content by weight and on drying shows a response curve very similar to that of the gelatinous lichen Collema furfuraceum (Kershaw and MacFarlane, 1982). Both species show little response to declining thallus moisture content down to very low levels (Figs. 13, 14, and 23). Paul et al. (1973) found a sharp peak of nitrogenase response near 450% moisture content for surface algal crusts, but these populations were in intimate contact with the soil column. No metabolic activity was detected here in N.commune thalli held in a water vapour saturated (100% R.H.) cuvette for 12 hours (either in CO_2 exchange or C_2H_2 reduction), contact with water droplets being required for resumption of metabolic activity. Jones (1977) also found that cyanophyte soil surface crusts showed no resumption of nitrogenase activity after being held in a saturated environment for 3 days, although Brock (1975) reported metabolic activity in crusts held 4 days in a saturated environment. However humidities that high are rarely seen over extended periods at the present grassland research site and it is concluded that most periods of metabolic activity in N.commune, as in C.trachyphylla, will require direct precipitation or dewfall condensation.

(4.3.2) Rehydration Recovery

The rapid resumption of physiolgical activity at 14 and 21 °C (Figs. 31 to 33) agrees with a large body of literature on surface blue-green algal mats (Paul et al ., 1971; Hitch and Stewart, 1973). Jones (1977) found resumption of C_2H_2 reduction within 1 hour of wetting algal mats, whilst Rychert and Skujins (1974) reported low intial C_2H_2 reduction within minutes. More critical examination of controlled desiccation (and the often concurrent heat extremes) are far fewer. Kershaw and Dzikowski (1977) found sharply reduced rates of C_2H_2 reduction in Peltigera polydactyla upon rehydration following extremes of desiccation, whilst MacFarlane and Kershaw (1978) correlated extremes of summer heat exposure with sharply reduced levels of nitrogenase activity on subsequent rehydration. Thus the very rapid recovery of nitrogenase activity in N.commune was initially suprising, although centrally important to its survival, as midday surface temperatures in the Southern Alberta grassland frequently exceed 60 °C.

The pronounced respiration burst often noted on rehydration of surface cryptogams is largely absent in N.commune. Certainly, respiration is not effected to the extent reported for the lichen Peltigera polydactyla (Smith and Molesworth, 1973). There is an initial burst of CO_2 on wetting in N.commune, but as this burst can be eliminated by previous drying of replicates under a low CO_2 airstream, it's nature appears to be purely physical and does not involve metabolic carbon (Fig. 18). The gradual decline of respiration over the first few hours after rehydration seen in N.commune may represent initially higher metabolic activity as cellular integrity is restored, but equally likely, may

reflect the slow depletion of respiratory substrates with continued time in the dark. A similar decline of respiratory rates was documented for N.commune by Coxson et al. (1982) on transfer of material to darkness, following a 12 hour light exposure. This slow decline in respiration is common in procaryotes, whose respiratory activity is not as tightly coupled to cytoplasmic energy charge as that of eukaryotes (Coxson et al., 1982). Although other workers have increased the magnitude of the resaturation respiratory burst through faster drying of material (Brown et al., 1983; Krochko et al., 1979), when N.commune was given a very fast (30 minutes) drying period, there was no significant increase in respiration on subsequent rehydration compared to slowly dried material (unpublished data). This is not an unexpected response, for species where metabolic activity is confined to very short intervals would soon deplete any available carbon reserves if there was a large cost to each wetting/ drying cycle. Studies on desert lichens, which also experience repeated short periods of metabolic activity, showed little or no respiratory burst on rewetting (Rogers, 1971; Kappen et al., 1980).

Most studies examining the rehydration response of net photosynthesis and nitrogenase activity have followed recovery under room temperature conditions, or over midsummer field conditions. Of those that have examined physiological activity at low temperature (MacFarlane and Kershaw, 1977; Alexander et al ., 1978; Kallio, 1974; Kallio et al., 1976; Rychert and Skujins, 1974; Malek and Bewley, 1978), most have used material previously hydrated for some time and had not examined initial rehydration responses. The results presented here show slow recovery of photosynthetic activity and even slower recovery of nitrogenase activity on rehydration at low temperature (Figs. 17, and 30 to 33). As

laboratory controlled low temperature and freeze-thaw transitions do not effect nitrogenase activity in previously hydrated material, the slow recovery on rehydration (Figs. 32 and 33) may reflect the inhibition of de-novo protein synthesis over the initial period of membrane integrity restoration. Malek and Bewley (1978) found marked low temperature effects on protein synthesis in the moss Tortula ruralis, with incorporation of radioactive leucines slowed by up to 90% at 2 °C compared with controls at 20 °C. Equally, the restoration of reductant or ATP flow on rehydration may be temperature sensitive. Ono and Murata (1981) and Simon (1974) have each noted the temperature dependency of membrane bilayer lipid structure, the integrity of which is critical to both reductant and ATP flow (Haaker et al., 1980; Postgate, 1974). However, critical studies on low temperature membrane rehydration effects are lacking, particularly with respect to heterocyst membrane structure. The inhibition of nitrogenase activity on low temperature rehydration could reduce potential nitrogen fixation over the winter months in Stipa-Bouteloa grassland. However, this would require full dehydration of N.commune thalli between rehydration periods, a relatively rare occurance in winter at the grassland site.

(4.3.3) Freeze-Thaw Interactions

The pattern of nitrogenase activity in terrestial cyanophytes immediately following snowmelt has been examined by a number of workers (Alexander and Kallio, 1976; Crittenden and Kershaw, 1979; MacFarlane and Kershaw, 1980). Typically only very low rates of nitrogenase activity are detected initially. However, upon transfer to controlled laboratory

conditions rapid recovery of nitrogenase activity is usually seen. MacFarlane and Kershaw (1980) show a doubling of C_2H_2 reduction rates in Peltigera canina within 4 days after transfer from under snow pack conditions to a 15/10 °C thermoperiod and 350 uE m^{-2} s^{-1} PAR photoperiod. This recovery was both light dependent and temperature enhanced.

The pattern of recovery of nitrogenase activity in N.commune during and after field snowmelt conditions, when daily freeze/ thaw cycles often occur is less well documented. Kallio et al (1976) found very low rates of nitrogenase activity after repeated frosts in September, while both MacFarlane and Kershaw (1980) and Crittenden and Kershaw (1979) suggest that repeated freeze/ thaw cycles both before and after snowmelt would limit most N_2-fixation to spring and summer precipitation periods. Huss-Danell (1977) found marked differences in nitrogenase activity between replicates collected at different stages after snowmelt and then given a 1 or 12 hour pretreatment incubation. Those exposed longest to moderate temperature and light conditions, in either field or laboratory pretreatment, supported the highest subsequent C_2H_2 reduction rates. Unfortunately, the difference between replicates at different stages of snowmelt is only briefly described and no information regarding field temperature and light levels is presented. Thus interactions of cold lability and temperature and light pretreatment cannot clearly be distinguished, a problem common to much of the literature in this area.

Under controlled laboratory conditions the daily rise of nitrogenase activity in N.commune after repeated freeze/thaw cycles or even after continuous subzero exposure is rapid (Fig. 29), confirming the patterns seen in other surface cyanophytes. The present work, in showing

that freeze/thaw cycles have less effect on nitrogenase activity than does continued metabolic inactivity, either from darkness or freezing, provides further support for the concept that the status of the internal carbohydrate pools, reflecting, as they do, an integration of previous metabolic activity, play a large role in determining realized nitrogenase activity. Clearly no inactivation of the in vivo nitrogenase enzyme complex was evident in the present study. This was confirmed by the equally rapid recovery of nitrogenase activity documented under field snowmelt conditions, a recovery which accelerated with increasing time in the light and higher temperature (Fig. 45). The typically short duration of snowcover in the Southern Alberta grassland site may in part account for the differences seen between this and other studies after snowmelt. In northern boreal regions, cyanophytic surface cryptogams typically experience snowmelt after many months continued darkness and/ or metabolic inactivity. Thus on melting reductant and ATP pools, being severely depleted, cannot support full potential nitrogenase activity, a phenomenon often mistaken for cold lability. In contrast, N.commune is not snow covered all winter and thus on melting rapidly resumes full rates of nitrogenase activity, as allowed by ambient temperature and photoperiod conditions.

(4.3.4) In-situ Summer Nitrogenase Activity

The extreme resistance of dry N.commune thalli to heat stress treatments under experimental conditions (Fig. 21) was confirmed by in-situ incubations in summer at the grassland field site. For example on June 16 (Fig. 46) rates of nitrogenase activity climbed rapidly on

rehydration, despite extremes of soil surface temperature during the previous week exceeding 60 °C at midday. The faster recovery rates of nitrogenase activity under these higher field levels of temperature and light (near 35 °C and 1500 to 2000 uE m^{-2} s^{-1} PAR compared with a maximum of 25 °C and 200 uE m^{-2} s^{-1} PAR examined experimentally) confirms the previously noted interactions of C_2H_2 reduction with temperature and light on rehydration at 7, 14, 21 and 25 °C. Under field conditions C_2H_2 reduction rates typically rise very rapidly until midday temperature maxima are reached, desiccation usually then curtailing continued activity (Figs. 46 and 47). Under overcast conditions or over precipitation periods nitrogenase activity continued to rise to near sunset, followed by a gradual decline over the night period, which again confirmed laboratory induced experimental patterns. Jones (1981) observed similar patterns of field nitrogenase activity by surface blue-green algal mats in Florida grass swards in incubations under cool or cloudy conditions. However, Jones reported marked reduction of nitrogenase activity under midday conditions of full solar insolation. As no control over cuvette temperatures was maintained by Jones, this may simply reflect overheating of thalli. Certainly thalli of N.commune are quite sensitive to temperature extremes when hydrated (Fig. 22). Nitrogenase activity in N.commune, being quite temperature dependent, was closely coupled to patterns of incoming solar radiation, due to its influence on soil surface temperatures. Rychert and Skujins (1974) similarly present a very limited data set showing the dependence of field C_2H_2 reduction rates on incoming radiation patterns. The rapidity of the recovery of nitrogenase activity on rehydration in N.commune allows utilization of early morning dewfall condensation (Table 7), while after

evening thundershower activity, moisture retention by the colloidal-like thalli enables continued metabolic activity well into the next day. This contrasts markedly with the hydration regime of C.trachyphylla, whose crustaceous morphology and slightly more exposed position limits moisture retention after precipitation periods (Table 8).

The estimates of nitrogen fixation by N.commune reported here, range from a mean of 0.01 g m^{-2} $month^{-1}$ up to 0.077 g m^{-2} $month^{-1}$ (Fig. 48). This extreme range of nitrogenase activity, reflects both the variability of within replicate C_2H_2 reduction rates and the wide range of surface biomass densities recorded for N.commune (Fig. 51). If an average diurnal N_2 fixation cycle (for example, June 6) for fully hydrated thalli is multiplied by a 120 day yearly period of metabolic activity (following Rychert and Skujins, 1974), then total estimates of N_2 fixation reach 1.4 g m^{-2} yr^{-1}, a very high value compared with most other works, excluding the Great Basin Desert studies (Paul et al., 1973; Rychert and Skujins, 1974; Woodmansee, 1978).

Section 5.

Summary

(5.1) The Role of Environmental Constancy in Ecophysiological Strategies

The environments examined in the current work, namely alpine tundra and semi-arid grassland, both show a predominance of surface cryptogams and are commonly regarded as being "extreme" environments. The abundance of their surface cryptogams is often thought to stem from absence of competition from higher vascular plants, which are unable to survive these extremes. Yet this raises the question as to why surface cryptogams can themselves continue to exist in these habitats. Although anabiosis, the avoidance of stress while in a metabolically inactive state, may in part explain the abundance of poikilohydrous surface cryptogams, continued long term existance and reproduction requires at least some periods of metabolic activity. The process of acclimation provides one pathway by which physiological processes can be maximised during periods of metabolic activity. Berry and Bjorkman (1980) define photosynthetic acclimation as "environmentally induced changes in photosynthetic charcteristics that result in an improved performance under the new growth regime". Implicit in this definition is response to environmental change. What remains to be defined is the response time required for these physiological changes to occur and the scale of environmental change acting as the driving parameter.

As laboratory induced changes of P_{max} in C.trachyphylla were only examined after 7 days storage pretreatment, the minimum possible response time remains undefined. Brown and Kershaw (1983) found that a minimum exposure of one full photoperiod to newly changed environmental conditions was required to induce photosynthetic capacity changes in the lichen Peltigera rufescens. Similarly, Kershaw (1977a) found that after 2 days of warm storage, photosynthetic rates of winter collected P.praetextata showed a marked increase in rates of net photosynthesis, corresponding in magnitude to seasonally induced winter/summer P_{max} changes. However, subsequent return of these "summer" acclimated P.praetextata replicates to cold storage conditions did not result in a corresponding drop in P_{max} for nearly 4 days. Without further understanding of the mechanisms involved in these induced changes in photosynthetic temperature responses, the time required to trigger physiological changes cannot clearly be distinguished from the subsequent lag period before measurable photosynthetic attributes change. Although photosynthetic capacity changes associated with altered quantum efficiency can be completed within hours in free-living aquatic algae (Prezelin, 1981), adjustment of downstream biochemical events in the Calvin cycle may take much longer, corresponding to the turnover time of specific enzymes (Bjorkman, 1981). Equally one can speculate that a finite energetic cost is associated with these acclimatory changes in photosynthetic patterns, although to date no such cost/benefit analysis has been completed (Bjorkman, 1981; Kershaw, 1984).

In C.trachyphylla the higher net photosynthetic rates evident at low temperatures over the winter months allow increased net annual carbon gain through maintenance of photosynthetic homeostasis over winter

hydration periods. However, continued maintenance of this broader temperature reponse curve year around would not be energetically cost effective (assuming a finite cost to maintaining this higher P_{max}), as temperatures of hydrated thalli in summer do not usually fall into this lower range where P_{max} capacity changes are observed. A similar photosynthetic strategy has been adopted by the lichen Peltigera rufescens, but in this species the winter period is one of metabolic inactivity, while in summer, hydrated thalli regularly experience high temperatures The photosynthetic response of P.rufescens to these seasonal changes is a higher P_{max} at high temperature over the summer period (Brown and Kershaw, 1983), totally opposite in pattern to C.trachyphylla, where a higher P_{max} is seen at lower temperatures only in winter. In both species these seasonal changes in the P_{max} temperature response curves allows homeostasis of seasonal carbon gain in an environment where the amplitude of thermal changes (experienced by hydrated thalli) is high, but is experienced over monthly time scales.

The amplitude of change in the physical operating environment of R.superficiale is also high, only for this species the frequency of change is quite rapid. The current data set points to a highly variable thermal environment, where hydrated thallus temperatures can range from below 5 to over 20 °C several times daily. This time scale may well fall below that which photosynthetic acclimation can track. We instead observe a strategy of maintaining a broad range of response to temperature, encompassing the amplitude of environmental change at all times.

Curiously the same response pattern, ie. optimizing carbon gain over a wide temperature range year around, is seen in Collema

furfuraceum, a low arctic epiphyte found in shaded habitats which only rarely experiences marked short term temperature fluctuations. Although the frequency of long term environmental changes is quite predicatable for C.furfuraceum, their amplitude may fall below the threshold values at which acclimation of net photosynthetic temperature optimum would yield higher carbon gain.

In N.commune both nitrogenase activity and net photosynthesis essentially show no change in seasonal response to either temperature, moisture, or light. In the context of the dramatic shifts observed in C.trachyphylla, this lack of response at first seems anomalous. However, N.commune experiences an operating environment quite different from that of C.trachyphylla. In winter it remains longer in a frozen state beneath the snow cover, whilst in summer it remains longer in a hydrated state over high temperature periods. The physiological strategy of N.commune is superficially quite similar to that of the Bouteloa gracilis grass mat within which it grows. In B.gracilis C_4 acid transfers and decarboxylation combine with spatial separation of carboxylation enzymes to enhance CO_2 uptake at high temperatures (Kemp and Williams III, 1980), the majority of carbon gain occuring in midsummer following small precipitation events (Sala and Laurenroth, 1982). Although Coxson et al. (1982) could detect no photorespiratory gas exchange in N.commune, the presence of C_4 metabolic pathways remains unresolved without examination of ribulosebiphosphate carboxylase to phosphoenolpyruvate carboxylase ratios. Seasonal changes of photosynthetic temperature optima have been noted in the C_4 higher plants Atriplex sabulosa and Tidestroma oblongifolia, of the American Southwest Desert habitats (Bjorkman and Badger, 1977). However the alternation of winter-cool and summer-hot

seasonal conditions there allows greater metabolic return from the strategy of seasonal photosynthetic temperature acclimation. The absence of any winter capacity changes in N.commune may in part be due to the very limited periods of metabolic activity in winter (relative to C.trachyphylla), those few periods not justifying the expenditure of energy in acclimatory mechanisms. However, this argument remains speculative in absence of acclimatory cost accounting.

In general, the operating environments within which acclimation of net photosynthetic processes result in greater net annual carbon gain can be visualized as intermediate in both their frequency and amplitude of environmental change (largely thermal in present context). After environmentally induced changes in photosynthetic processes occur, the new environmental regime must re-occur with sufficient frequency and duration to recoup any metabolic costs associated with acclimatory changes). Equally, the magnitude of these environmental changes must be high enough to trigger the orginal alteration of photosynthetic mechanisms.

(5.2) Overview

The ecophysiological investigation on each of the three surface cryptogams studied, R.superficiale, C.trachyphylla and N.commune was designed so that that factorial interactions of light, temperature and moisture could be examined concurrently, allowing the identification of secondary and tertiary interactions. In R.superficiale examination of the physical operating environment led to recognition of the role played by short term thermal fluctuations in defining this species physiological

response curves. The temperature response of CO_2 exchange, initially puzzling in light of general climatic trends, was readily interpretable as a specific strategy allowing optimization of carbon gain once the boundary layer environment was characterized, yet these same boundary layer parameters favouring carbon gain in R.superficiale also imposed potentially severe distributional limits, due to the limited tolerance for thermal stress in this species. By contrast, in C.trachyphylla the primary factor limiting carbon gain was not temperature, but frequency of hydration. However, changes in carbon gain patterns during these restricted periods of metabolic activity, particularly during winter snowmelt periods, allowed potentially much higher net annual carbon gain in C.trachyphylla. The slight difference in aspect between C.trachyphylla and N.commune at the grassland site, combined with the unique morphology of N.commune proved sufficient to alter the operating environment of N.commune quite considerably from that seen in C.trachyphylla. These changes were reflected in the physiological response curves of N.commune, the carbon gain of which is maximized under full summer radiation conditions due to it's high water retention capacity. The differences in operating strategies between C.trachyphylla and N.commune, located as they are, only meters apart on exposed grassland surfaces, clearly emphasizes the need for close examination of the full operating environment of surface cryptogams and highlights the difficulties in predicting the species metabolic responses of surface cryptogams from general climatic and phytosociological parameters.

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APPENDIX A

Table 1

Photosynthetic interactions with CO_2 concentration in R.superficiale and C.trachyphylla using the discrete sampling IRGA technique.

Assay Temperature	Thallus Moisture Content**	Gas Exchange (mg CO_2 h^{-1} g^{-1}) A	B	C	D	E
R. superficiale						
01	Optimal	1.11	1.19	1.16	0.03	3.0
14	Optimal	.62	.64	.63	.02	2.2
14	Saturation	.25	.26	.25	.05	2.0
21	Optimal	.24	.28	.26	.02	5.9
C.trachyphylla						
07	Optimal	1.37	1.44	1.41	.03	2.4
07*	Optimal	2.07	2.17	2.13	.04	2.0
07	Saturation	.32	.37	.35	.03	7.1
21	Saturation	.23	.24	.24	.01	2.7
21	Optimal	2.40	2.60	2.50	.09	3.7

* Winter collected material, all other values for summer collections.
** See Section 3.1.2 for definition of optimal and saturating thallus moisture contents.

A) Predicted value of net photosynthesis (at 300 ppm CO_2, 600 mg CO_2 h^{-1} g^{-1}, and indicated temperature) from 3rd order polynomial regression equations (from raw data scattergrams of Figs. 5 and 6, except for winter material whose scattergram was not presented).

(Continued on next page)

B) As (A), but for 330 ppm CO_2.

C) Predicted value of CO_2 exchange following discrete sampling technique IRGA technique with a 30 ppm CO_2 drawdown over each "discrete" incubation (from 330 ppm), ie. value of y at which half the area under

$$\int_{x_i}^{x_{i+n}} y = ax + bx^2 + cx^3 + d$$

is reached, where x_i=300, n=30 and a, b, c and d are respectively 1st to 3rd order coefficients and constant of equations used in (A) and (B) above.

D) (B)-(C), ie. departure of "discrete" sampling net photosynthetic rates from predicted "instantaneous" rates. The rates predicted from (A) and (B) will deviate slightly from theoretical instantaneous rates (by up to 5%) due to the small errors inherent in the 10 to 15 ppm CO_2 drawdown of Figs. 5 and 6. This effect however, is insignificant on (D) and (E) (less than 1% difference).

E) (D) represented as a percentage difference.

Numbers presented above in columns (A) to (E) are values rounded to second decimal place.