A provisional survey of the interaction between net photosynthetic rate, respiratory rate, and thallus water content in some New Zealand cryptogams

W. P. SNELGAR[1], D. H. BROWN[2], and T. G. A. GREEN[1]

[1]Department of Biological Sciences, University of Waikato, Hamilton, New Zealand
[2]Botany Department, The University, Woodlands Road, Bristol, U.K.

Abstract   The effect of water content on photosynthetic and respiratory rates in eight lichen species and one bryophyte species were studied using an injection infrared gas analyser technique. All species showed a strong relationship between net assimilation rate (NAR), respiration rate, and water content similar to relationships reported in published studies overseas. Species from moist habitats showed negative NAR at low water contents. Species from high-light areas showed a depression in NAR at high water contents which could be alleviated by higher light intensities. The experiments confirmed the suitability of New Zealand species for these studies.

Keywords   bryophytes; lichens; Stictaceae; photosynthesis; respiration; water content

INTRODUCTION

In the last decade considerable advances have been made in the understanding of gas exchange and productivity of lichens and bryophytes. Research has concentrated on species from relatively open habitats such as Canadian open woodland (Kershaw 1971, 1977a, 1977b; Kershaw & Smith 1978; Harris 1971; Busby & Whitfield 1978), deserts (Lange 1969), maritime Antarctica (Collins 1976), Canadian tundra (Kershaw & Rouse 1971), and English woodlands (Dilks & Proctor 1979). There is a paucity of research on species from dense forest, particularly rain forest in subtropical and tropical areas. In New Zealand a considerable biomass of lichens and bryophytes exists in rain forests and, to date, there appear to have been no physiological studies on the productivity or gas exchange of these plants. An initial study of nitrogen fixation by New Zealand lichens has been carried out (Green *et al.* 1980) and demonstrates the suitability of the plants for physiological studies.

In this work the relationship between carbon dioxide exchange and water content of eight lichens and one bryophyte was studied using the injection infrared gas analyser technique pioneered by Larson & Kershaw (1975). This technique provides considerable time advantages over a gas flow system when many samples are involved.

Seven of the lichens studied are members of the Peltigerinae (six in the Stictaceae) and were chosen to represent the ecological range found within this group. One lichen species (*Usnea* sp.) was included to provide the contrast of a lichen that does not fix nitrogen and occurs in an exposed habitat. Similarly, one species of bryophyte was included so that a comparison of the water relations of a different plant type growing in the same area could be made. It was considered that these comparisons would be of interest in this preliminary study of New Zealand species.

The lichens forming the central part of this study may be of great importance in New Zealand forests, particularly in their ability to fix nitrogen. This work is part of a major study on the productivity and ecology of this group in an attempt to assess their role in the nutrient cycles of forests.

MATERIALS AND METHODS

Lichens and bryophytes were collected from the localities listed in Table 1. The date of collection is also given and all plants, except *Pseudocyphellaria dissimilis*, were assayed on the same day. *P. dissimilis* was stored for 24 hr at 16°c, 100% r.h. 12-hr day at 70 μE m^{-2} s^{-1} before assay.

Plant material was thoroughly moistened with a distilled water spray and stored in polythene bags at

Table 1 Location and description of collection sites.

Species	Date of collection	Locality[1]	Locality description
Peltigera dolichorhiza (Nyl.) Nyl.	4.7.79 5.7.79	A	Ground, moist bank at side of track.
Pseudocyphellaria billardieri (Del.) Ras.	21.6.79	C	Branches of *Weinmannia racemosa*
Pseudocyphellaria colensoi (Bab. in Hook f.) Vain.	3.7.79 1.6.79	A	*Nothofagus menziesii* trunk, 2 m above ground.
Pseudocyphellaria dissimilis (Nyl.) D. Gall. et P. James *in litt.*	22.5.79	C	Ground, mossy wet bank.
Pseudocyphellaria homoeophylla (Nyl.) Dodge	31.5.79 2.6.79	A	*N. menziesii* trunk, 1 m above ground.
Sticta caperata Bory. in Nyl.	31.5.79 2.6.79	A	*N. menziesii* trunk, 1 m above ground.
Sticta latifrons Rich.	5.7.79 6.7.79	B	Hinerau's track, *N. menziesii*, 2 m above ground
Usnea sp.	4.7.79 5.7.79	A	*Coprosma* scrub, exposed branches 2 m above ground.
Weymouthia mollis (Hedw.) Broth.	4.7.79 5.7.79	A	Small *N. menziesii* by side of track, 2 m above ground.

[1]A: Clearing ("Paradise clearing") near Lake Waikareiti, altitude 900 m. The clearing is bordered with *Coprosma* scrub, and surrounded by mature forest dominated by *Nothofagus menziesii* and *N. fusca*. Map reference: NZMS 1 N96:565330.

B: Headquarters of Urewera National Park, Waikaremoana, altitude 620 m, forest of *N. fusca*, *N. menziesii*, and *Dacrydium cupressinum* emergents. Map reference: NZMS 1 N105:580295.

C: Hakarimata Range, Ngaruawahia, adjacent to water supply dam in moist valley; altitude 60 m. Major trees are *Weinmannia racemosa*, *Fuchsia excorticata*, *Leptospermum scoparium*. Map reference: NZMS 1 N56:645622.

ambient temperature until required. Healthy terminal portions of thalli were selected and excess surface moisture removed by gentle shaking or blotting. With *Sticta latifrons* older non-fertile portions of the thalli were used. Samples were placed in small, pre-weighed aluminium-foil boats to enable easy handling, then assayed.

Assays of both photosynthesis and respiration were carried out using an ADC series 225 infrared gas analyser (IRGA) operating on a sample injection system as shown in Fig. 1, which was similar to that described by Clegg *et al.* (1978) and Larson & Kershaw (1975). Modifications to previous systems included the use of CO_2-free air as carrier gas and a smaller injection volume of 1.0 ml. Signal output from the IRGA on 100 mV range was fed to a Servo-scribe chart recorder set on 20 mV range ($\times 5$ amplification). The IRGA was initially set up to produce full scale deflections when 500 ppm CO_2 were passed through the 5% analysis cell. The flow system was then altered to pass the CO_2-free carrier gas through the full 100% analysis cell as shown in Fig. 1. Injection of 1 ml of 203 ppm CO_2 produced a mean peak height of 39 chart units (recorder full scale = 100 chart units) so that 1 chart unit ≈ 5.2 ppm CO_2. For CO_2 concentrations >500 ppm the zero subtraction on the recorder of 100–400% could be used so that samples of up to 2500 ppm could be measured without loss of accuracy. Samples could be assayed at the rate of 2 per min and incubation times depen-

ded on the rate of gas exchange, varying between 3.5 and 20 min. Separate CO_2-free gas supplies to analysis and reference cells were used so that loss of CO_2 absorbancy could be rapidly detected. A major advantage of the system is that no gas cylinder is needed to provide the carrier gas. Gas flow rates were 900 ml min^{-1} analysis cell, 180 ml min^{-1} reference cell. Calibration was by injection of 1-ml volumes of known CO_2 mixtures (N.Z. Industrial Gases Ltd). Precision was estimated to be ± 2 ppm CO_2.

Plant samples were incubated in 30-ml universal bottles mounted by rubber O-rings in a stainless-steel water bath as shown in Fig. 2. Plant sample temperatures were monitored using a hypodermic thermistor probe attached to a plant sample in an extra incubation chamber. Temperature was maintained at 16 $\pm 0.5°$c by circulating the water over a cooling coil and thermostatically controlled heater. Light was provided by two No. 35 white 20 W fluorescent tubes suspended above the bath and intensity was measured using a Licor Quantum meter Model LI 185A. A light intensity of 70 μE m^{-2} s^{-1} was routinely used. Respiration assays were obtained with the tubes blacked out by placing a lid over the steel chamber. In some cases temperature was regulated by carrying out the assays in a 16°c controlled temperature room.

The standard incubation routine (prepared samples were assayed as shown in Fig. 3) used was a modification of Larson & Kershaw (1975) who dem-

Fig. 1 Diagramatic representation of gas flow system. A: carbasorb column; B: air pump; C: gas flow meter; D: analysis cell of IRGA; E: gas sample injection point through suba seal; F: reference cell of IRGA; G: CO_2-free air from internal supply in IRGA. Gas flow rates were 900 ml min^{-1} through analysis cell, 180 ml min^{-1} through reference cell.
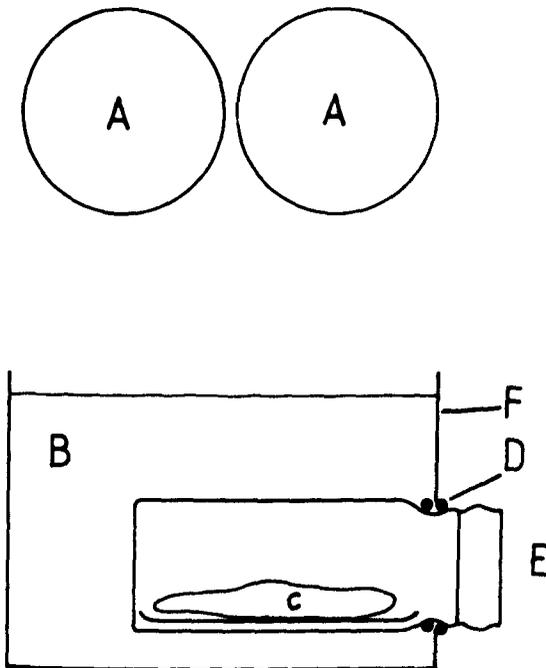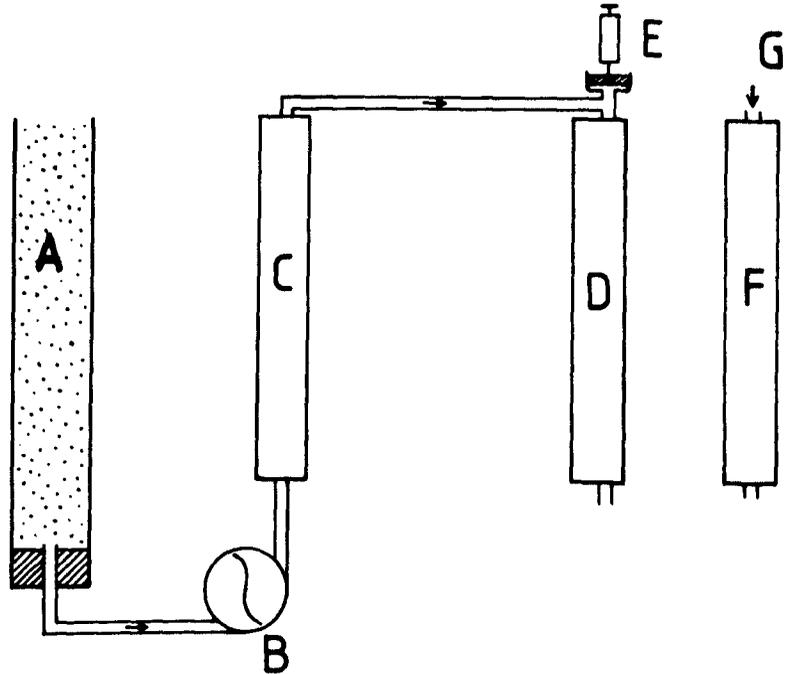
Fig. 2 Photosynthetic incubation vial positioned in temperature controlled stainless-steel water bath. A: fluorescent tubes above water bath; B: circulated water at constant temperature; C: plant sample on aluminium-foil boat; D: rubber O-ring seals; E: screw cap with butyl rubber septum-seal on universal bottle; F: stainless-steel water bath.
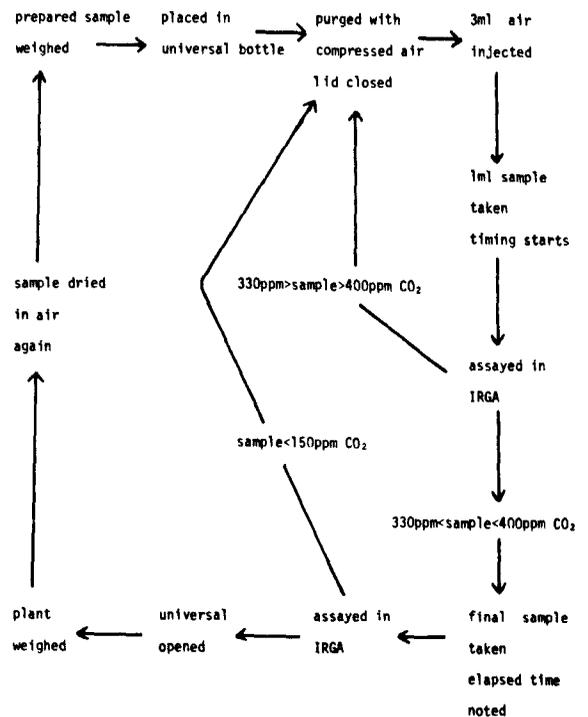
Fig. 3 Standard assay routine indicating decision points necessary to maintain a constant CO_2 concentration range. The decision points do not need to be applied during respiration assays.

onstrated that under the conditions shown CO_2 concentration and ventilation had a negligible effect on the rates obtained.

Dry weights of samples were obtained by drying to a constant weight at 100°c. In all instances CO_2 exchange rates are given in units of mg CO_2/g dry weight/hr. Similarly, all water contents are in mg water/mg dry weight.

RESULTS

Peltigera dolichorhiza (Fig. 4a)

This species was commonly found on the wet banks of tracks or where there was an ample ground-water supply as seepage and also a low to moderate light level. Saturated plants had a very high water content (maximum c. 6.0*) and showed no clear depression of net assimilation rate (NAR) at these levels. Maximum NAR (6.5 mg CO_2 g^{-1} hr^{-1}) was high compared with other species tested. NAR was negative below a water content of 1.8 and remained so until gas exchange ceased at a water content of c. 0.4. Respiration rates remained nearly constant at c. 2.5 mg CO_2 g^{-1} hr^{-1} over a wide range of water contents from 2.5 to 6, with a steady decline with water content below 2.5. In comparison with other lichens assayed, the thallus of P. dolichorhiza appeared to be much more delicate and less robust.

Pseudocyphellaria billardierii (Fig. 4b)

The species is normally epiphytic, growing horizontally as large thalli across small branches in the lower canopy or subcanopy; relatively open forest areas appear to be favoured. Maximum water content (c. 1.8) is much lower than that of Peltigera dolichorhiza but approximates that of the other lichen species. The NAR shows a much higher rate of increase with water content and appears to approach a maximum rate of c. 3.0 mg CO_2 g^{-1} hr^{-1} at a water content of 1.0. Positive NAR was attained at a water content as low as 0.15 and this, together with a high NAR value at low water contents, indicates a tolerance of drying conditions.

Pseudocyphellaria colensoi (Fig. 4c)

P. colensoi is typically found on branches in the tree canopy, occurring high up tree trunks but lower down on trees fringing open areas. Such an environment would have reasonably high light intensities and drying conditions. Respiration rate increased steadily with water content and the maximum rate occurred at the maximum water content studied. NAR, however, increased to a maximum value of 1.2 mg CO_2 g^{-1} hr^{-1} at a water content of 0.9 and declined at higher water contents. At the highest water content the NAR was c. 60% of the maximum rate.

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*All water contents are mg water/mg dry weight.

Pseudocyphellaria dissimilis (Fig. 4d)

P. dissimilis is normally found growing on the forest floor in very low light regimes. It is generally epiphytic on the exposed roots or lower trunks of trees, although it is sometimes found growing on rocks and mosses in very moist habitats.

The NAR graph for this species is unusual in that the increase is almost linear with water contents up to saturation point. This is the only species which did not show a levelling off or a decrease in NAR at high water content. At water contents below 0.8 NAR is negative and has a response similar to that of Peltigera dolichorhiza. The respiratory response is also unusual in that it appears to be asymptotic rather than linear, and again no obvious maximum was found. Asymptotic respiratory responses have also been found by Kershaw (1977a, b) for Peltigera canina var. praetextata and P. polydactyla.

Pseudocyphellaria homoeophylla (Fig. 5a)

This is by far the most abundant lichen found in the mixed beech forest surrounding Lake Waikareiti. It is invariably epiphytic on the lower trunks of large trees (most often Nothofagus menziesii) or on the well developed buttresses of Nothofagus fusca. In these positions the plants receive c. 5% of the incident light and an ample water supply from rain and stem flow. In these forests P. homoeophylla is rare at altitudes below 900 m, being replaced by P. delisia, a similar, but isidiate, lichen.

The NAR increases rapidly with water content and reaches a constant rate of 1.6 mg CO_2 gm^{-1} hr^{-1} at a water content of c. 1.2. There appears to be little evidence for negative NAR at very low water contents, indicating simultaneous cessation of respiration and photosynthesis.

The respiratory rate increases steadily with water content over the range investigated, with some indication of a slowing in the rate of increase at the higher water contents.

Sticta caperata (Fig. 5b)

This species appears to occupy an almost identical habitat to that of P. homoeophylla. In this investigation both species were collected from the same tree, within 30 cm of one another. The response of NAR to water content is very similar to that of P. homoeophylla, with the main difference being a slightly higher maximum rate, 2.0 mg CO_2 g^{-1} hr^{-1}, which is attained at a higher water content of 1.5. Negative NAR values were rarely obtained at low water contents. Respiration rate increases steadily with water content, reaching a maximum rate of 0.9 mg CO_2 g^{-1} hr^{-1} at water contents of 1.5 and higher.

Sticta latifrons (Fig. 5c)

S. latifrons differs from the other lichen species studied in possessing a stalk and in growing out horizontally, particularly when young, on tree trunks normally some metres above the ground. Also, in

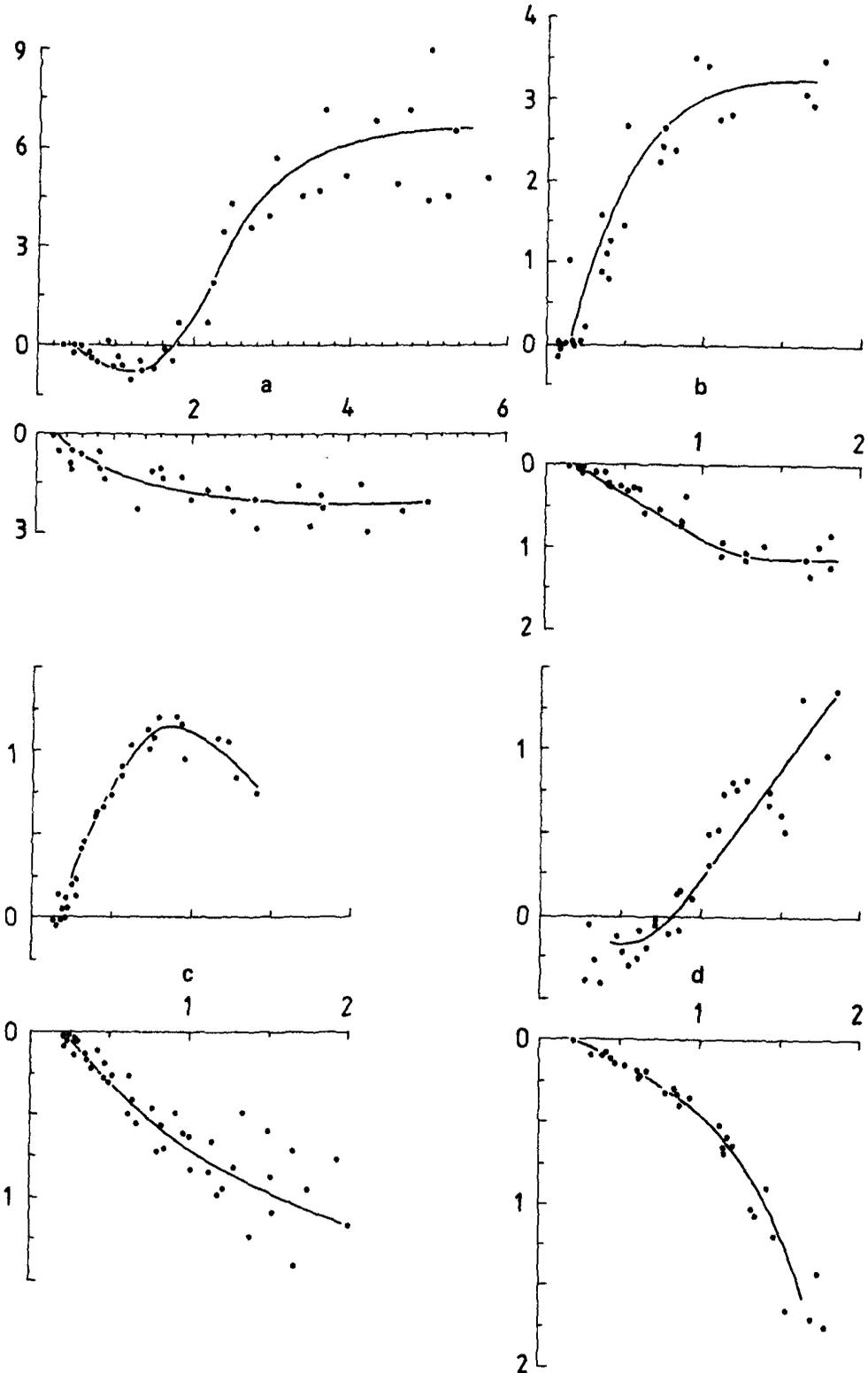**Fig. 4** Net assimilation rates (upper graph) and respiration rate (lower graph) in mg CO_2 g^{-1} hr^{-1} with respect to water content for (a) *Peltigera dolichorhiza*, (b) *Pseudocyphellaria billardierii*, (c) *Pseudocyphellaria colensoi*, (d) *Pseudocyphellaria dissimilis*. Experimental details in text. Horizontal axis of all graphs is water content in mg water/mg dry weight.
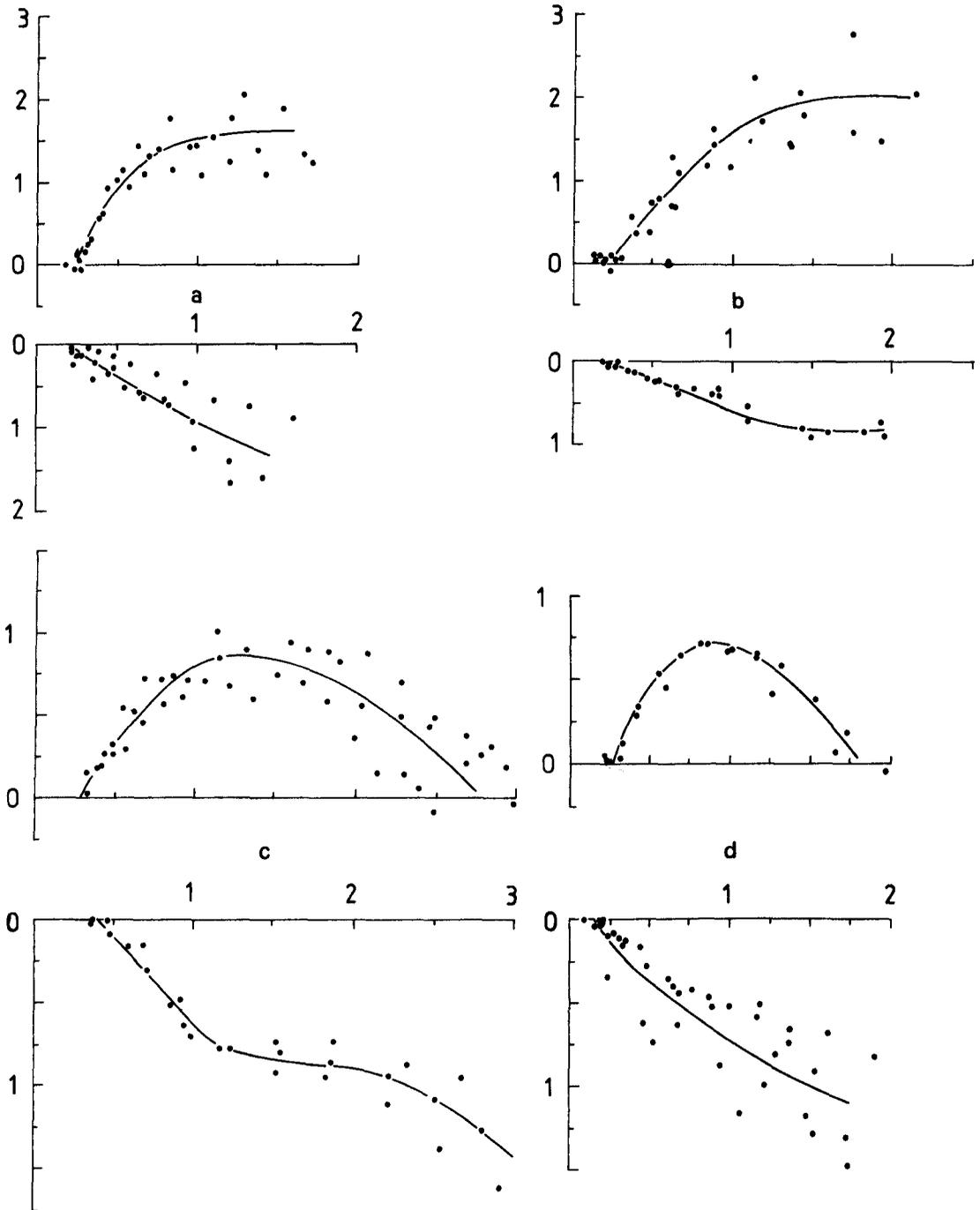
Fig. 5   Net assimilation rates (upper graph) and respiration rate (lower graph) in mg CO_2 g^{-1} hr^{-1} with respect to water content for (a) *Pseudocyphellaria homoeophylla*, (b) *Sticta caperata*, (c) *Sticta latifrons*, (d) *Usnea* sp. Experimental details in text. Horizontal axis of all graphs is water content in mg water/mg dry weight.

contrast with the other species, older sections of the thalli were studied to avoid inclusion of ascocarps which commonly crowd the upper surface. NAR was zero at both high and low water contents, with a maximum rate of 0.8 mg CO_2 g^{-1} hr^{-1} at the intermediate water content of 1.3. Respiration rate shows a biphasic response to water content, increasing rapidly between water contents of 0.4–1.5 and 2.0–3.0 but remaining nearly constant between water contents of 1.5 and 2.0. *S. latifrons* and *Pseudocyphellaria dissimilis* are the only two species studied which show an asymptotic respiration increase at high water contents.

Usnea sp. (Fig. 5d)

Usnea sp. was the only lichen studied from outside the Peltigerineae, and was thus the only nitrogen non-fixer (Green *et al.* 1980). Plants are found on the exposed terminal twigs of trees and shrubs and are clearly visible from outside the canopy, obviously growing at a higher light level than any of the other species studied. NAR rises from nil at a water content of *c.* 0.25 to a maximum rate of 0.7 mg CO_2 g^{-1} hr^{-1} at a water content of 0.9 and declines to zero or slightly negative values at water contents >1.9. No evidence was found of negative NAR values at low water contents. The respiration response to water contents is almost identical to that found for *Pseudocyphellaria colensoi*, reaching a maximum value of 1.1 mg CO_2 g^{-1} hr^{-1} at the highest water contents studied.

Weymouthia mollis (Fig. 6)

W. mollis was the only bryophyte studied and was chosen because of its widespread occurrence in close proximity to many of the lichen species in the forests. Plants of *W. mollis* hang vertically from horizontal branches and twigs and are typical of many bryophytes in possessing a far greater water content at saturation than lichens. Both NAR and respiration rate show almost constant rates over most of the range of water contents (respiration above 2.0 and NAR above 4.0). Below these levels both NAR and respiration rates decline rapidly with lowering of water content. Maximal rates of NAR (2.0 mg CO_2 g^{-1} hr^{-1} at 10.0) and respiration (1.0 mg CO_2 g^{-1} hr^{-1} at all water contents above 2.0) are similar to those obtained for the lichens studied.

Effect of light intensity

Certain species, *Sticta latifrons*, *Pseudocyphellaria colensoi*, and *Usnea* sp. were found to show decreased NAR at the higher water contents. This effect is most marked in *Usnea* sp. and *S. latifrons* where slightly negative NAR was found. Since the NAR is the sum of photosynthetic CO_2 uptake by the alga and CO_2 release by the alga and fungus, it is possible that this decrease is a result of photosynthesis reaching maximal values at moderate to high water contents whilst respiration continues to
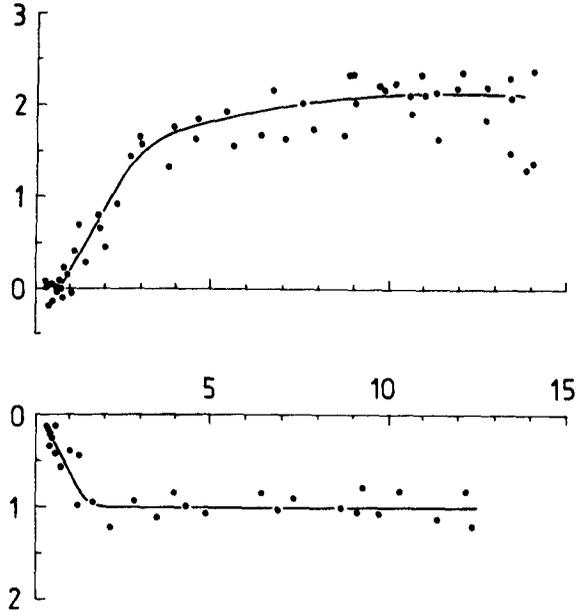

Fig. 6 Net assimilation rate (upper graph) and respiration rate (lower graph) in mg CO_2 g^{-1} hr^{-1} with respect to water content for *Weymouthia mollis*. Experimental details in text. Horizontal axis is water content in mg water/mg dry weight.

increase with water content. A possible photosynthetic limitation was the light level used, set at 70 μE m^{-2} s^{-1} for all assays, which may be suboptimal for these three species, all of which come from moderate to high light areas. To investigate this possibility *Usnea* sp. was assayed at a higher light level, 280 μE m^{-2} s^{-1}, and a lower level, 37 μE m^{-2} s^{-1}. *P. colensoi* was also assayed at 280 μE m^{-2} s^{-1}.

Comparison of the NAR response of *Usnea* at the three light levels shows that

(a) increasing light produces an increased maximum NAR,

(b) the water content at which NAR was maximal is similar at all three light levels,

(c) the depression of NAR at high water contents is decreased by increasing light level. At 37 μE m^{-2} s^{-1} there is considerable negative NAR at water contents >1.4 (note that results are variable) whereas at 280 μE m^{-2} s^{-1} no negative NAR was recorded; NAR at the highest water content exceeded the maximum NAR at 70 μE m^{-2} s^{-1} (Fig. 7 a, b, c.).

The same features are found for *P. colensoi* when comparing NAR AT 70 μE m^{-2} s^{-1} and 280 μE m^{-2} s^{-1}. However, when the maximal NAR values obtained at each light level are compared the two species differed in the size of increase. NAR (max.) of *Usnea* sp. was directly proportional to the light level (i.e., 400% increase in light gives a 400% increase in NAR (max) whereas the same increase in
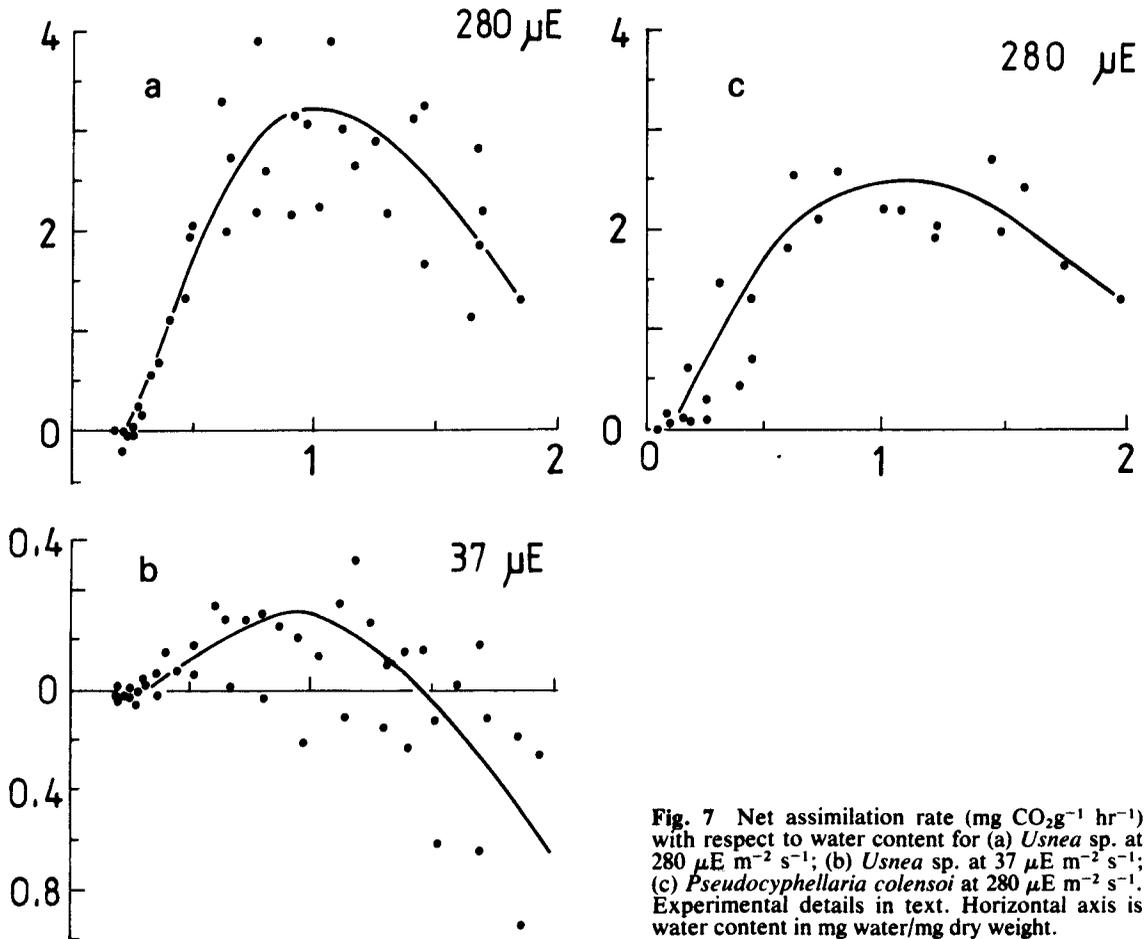
Fig. 7 Net assimilation rate (mg CO_2g^{-1} hr^{-1}) with respect to water content for (a) *Usnea* sp. at 280 μE m^{-2} s^{-1}; (b) *Usnea* sp. at 37 μE m^{-2} s^{-1}; (c) *Pseudocyphellaria colensoi* at 280 μE m^{-2} s^{-1}. Experimental details in text. Horizontal axis is water content in mg water/mg dry weight.

light level for *P. colensoi* gives a smaller increase in NAR (max.) (400% increase in light gives a 200% increase in NAR (max.)).

DISCUSSION

All species investigated showed a strong relationship between NAR and water content. The form of the responses of the lichen species, as shown in Figs 4-6, can be divided into three main groups.

GROUP 1: *Peltigera dolichorhiza, Pseudocyphellaria dissimilis:* species showing pronounced negative NAR at low water contents, a high minimum water content for positive NAR, and no depression of NAR at high water contents. The responses of this group correlate with the observed ecology. These species are found in constantly wet conditions (though not necessarily low light) where very low water contents would be infrequent. *Peltigera dolichorhiza* may be capable of tolerating more open areas by means of a water supply from the soil through the rhizines, although no direct evidence is available to support this suggestion.

GROUP 2: *Pseudocyphellaria homoeophylla, Sticta caperata, Pseudocyphellaria billardierii:* species showing just detectable negative NAR at low water contents, low minimum water contents for positive NAR, and a constant NAR at moderate to high water contents. *P. homoeophylla* and *S. caperata* are both found at the base of tree trunks whereas *P. billardierii* grows on branches. All receive low light levels and a greater and more frequent drying stress than do Group 1 species. *P. billardierii*, in particular, grows in more exposed conditions, and is almost equivalent to a fruticose lichen in being free from the substrate, and has a very low minimum water content for positive NAR.

GROUP 3: *Pseudocyphellaria colensoi, Sticta latifrons, Usnea* sp.: none or very little negative NAR at low water contents, low minimum water content for positive NAR, depression of NAR at high water contents. These species grow in exposed conditions of moderate to high light and consequent higher desiccation stress. Maximum NAR is reached at low water contents and is depressed at high water content.

There is also a trend for water contents at which maximum NAR occurs to be in the order Group 1>Group 2>Group 3.

The negative NAR of *Usnea* sp. at high water contents is a result of the failure of photosynthesis to counter the effects of increasing respiration (Harris 1976). This effect can be alleviated by increasing the light intensity and thus increasing photosynthesis, although it is possible that the depression may not be completely removed. This alleviation indicates that the Group 3 species are being assayed under suboptimal conditions with regard to light, which again correlates well with the observed ecology.

A similar alleviation of depression at high water content by high light intensity is also shown for *Stereocaulon paschale* by Kershaw & Smith (1978). Kershaw (1977a, b), however, shows this NAR depression for *Peltigera polydactyla* and *P. canina* var. *praetextata* and with no alleviation at higher light intensities, although maximum water contents are lower than those found for *P. dolichorhiza* in the present investigation. Comparison of NAR and respiration responses with water content (Kershaw 1977a, b) show that in this case NAR depression is not a result of increased respiration and must result from some other factor which affects photosynthesis, possibly carbon dioxide diffusion (Harris 1976). The maximum NAR values obtained by Kershaw (1977a, b) of 2.0 mg CO_2 g^{-1} hr^{-1} at 100 μE m^{-2} s^{-1}, 15°c are much less than those obtained here (6.5mg CO_2 g^{-1} hr^{-1} at 70 μE m^{-2} s^{-1}, 16°c. This, together with the enhancement with higher light intensities obtained by Kershaw suggests that the species which he tested were from more open environments than those of *P. dolichorhiza*.

The maximum NAR values obtained for lichens in the present investigation agree well with maximal rates published elsewhere (Kershaw 1977a, b; Larson & Kershaw 1975, Kershaw & Smith 1978), indicating the validity of the present technique. Respiration values obtained are also comparable. In assays of both NAR and respiration a noticeably greater variability between replicates was found at the higher water contents. This may reflect uneven distribution of liquid water content and location at these water contents (Smith 1962).

The fall in NAR at low water contents has been accepted to be a result of physiological changes in the lichen. However, it is difficult to understand why respiration (negative NAR) should continue to much lower water contents in *Peltigera dolichorhiza* and *Pseudocyphellaria dissimilis*. It is known that the photosynthetic pathways are more sensitive to decreasing water content than respiratory pathways (Cowan et al. 1979), however, such differences are not obvious for the Group 2 and Group 3 lichens. A further constraint that could apply to photosynthesis is the increasing opacity of the lichen cortex to light

at low water contents. Evidence that this might be important is present in the data of Kershaw (1977b) where increasing light intensity lowered the minimum water content for positive NAR in *Peltigera polydactyla* and *P. praetextata*.

Weymouthia mollis was the sole bryophyte studied and clearly demonstrates the major differences between bryophytes and lichens in water relations. *W. mollis* had a far greater water content at saturation than any of the lichens (15.0 against 6.0 for *Peltigera dolichorhiza*.) Most of the water is held externally on the surface of the leaves, so that NAR and respiration behave independently of water content until external and internal liquid water reserves are lost. This agrees with the results of Busby & Whitfield (1978) for four bryophyte species. *Ptychomnion aciculare* also shows this photosynthetic pattern (unpublished data). Similar external storage of water may occur in some species of *Pseudocyphellaria* (Snelgar & Green 1980).

The results demonstrate that New Zealand species of cryptogams provide excellent experimental material for gas exchange studies. Interpretations of the responses to water content changes are similar to those proposed in published overseas work. Certain differences are, however, very clear; these include the abundance of species from low light, moist habitats in contrast with those of more open areas described elsewhere. Also, the genus *Pseudocyphellaria* contains species which collectively span an extremely wide ecological range and thus provides material for comparative ecophysiological studies not available elsewhere.

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