Indian Journal of Fundamental and Applied Life Sciences ISSN: 2231-6345 (Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/jls.htm
2014 Vol. 4 (3) July-September, pp. 167-179/Nayaka and Saxena
Research Article

PHYSIOLOGICAL RESPONSES AND ECOLOGICAL SUCCESS OF LICHEN *STEREOCAULON FOLIOLOSUM* AND MOSS *RACOMITRIUM SUBSECUNDUM* GROWING IN SAME HABITAT IN HIMALAYA

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ABSTRACT
The surface reflectance, chlorophyll fluorescence and water relation of lichen *Stereocaulon foliolosum* and moss *Racomitrium subsecundum* co-occurring in Himalayan environment are studied *in vitro* during dehydration and rehydration stages. In both the species total reflectance in RED and NIR region decreased during dehydration and showed maximum recovery during rehydration. Lichen reflected more light than moss during fresh as well as dehydrated condition. Reflectance parameters were observed to be different in both species. Fv/Fm in case of moss showed up to 93% recovery while lichen attained 100% after rehydration. Relative Water Content in both the species followed a similar pattern during dehydration and rehydration though moss desiccated and recovered faster. The lichen emerged as better desiccation tolerant according to derivatives of PV curve by having low Osmotic Potential at full turgor, low apoplastic water content, low relative water content at turgor loss and low elasticity modulus. Possible mutual advantages to lichen and moss by co-occurrence is discussed.

Keywords: *Reflectance, Fluorescence, PV Curve, Water Relation, Photosynthesis, Cryptogams*

INTRODUCTION
The lichens and bryophytes though taxonomically two unrelated groups, share certain fundamental characteristics such as poikilohydrism, absence of cuticle, smaller thallus size, slow growth rate, predominance of sexual reproduction, ability to tolerate high irradiance and desiccation. The absence of well developed root system frees them from a dependency on substratum for nutrition. They often grow together on harsh substrates like rock which are mostly hostile to many other plants. The requirement of similar nutrition and microclimatic conditions are probably the reasons for lichens and bryophytes to co-occur on same habitat. During the ecological succession on rock lichens and bryophytes are the pioneer colonizers and make the habitat suitable for the growth of other plants through pedogensis. Their hygroscopic nature and moisture retaining capabilities complement each other as a fine microhabitat for existence. Many species of these groups frequently desiccate, but rapidly resume photosynthesis and respiration upon rewetting (During, 1992). In general, lichens appear to tolerate higher irradiances and more frequent desiccation than bryophytes (Bates and Farmer, 1992). However, co-occurrence many not be always advantageous; few reports on inhibition and destruction of mosses by lichens by production of allopathic metabolites are also available (Heilman and Sharp, 1963; Cocker, 1966; Faegri, 1980). It is observed in western Himalaya that a moss *Racomitrium subsecundum* (Hook and Grev.) Mitt., found to be a most common associate of lichen *Stereocaulon foliolosum* Nyl. growing luxuriantly over soil and rock. In the present study an attempt has been made to understand the physiological similarities among these two species at varied water and light conditions as clue for their comfortable coexistence. The aim is achieved *in vitro* using parameters such as surface reflectance, chlorophyll fluorescence and Pressure Volume relationships.

MATERIALS AND METHODS
The Species and their Habitat: The lichen *S. foliolosum* is a dimorphic species with pseudopodetia growing up to 4.5 cm height, sparingly branched and decorticated (Figure 1). Phyllocladia are flattened,

leafy, while cephalodia are protosacculate with *Nostoc* in lumina. It is mostly distributed in Himalayas (Awasthi, 2007). The moss *R. subsecundum* has a semi-procumbent shoot of about 4 cm height, which is branched and laxly tufted. The leaves are oval at base, lanceolate and ending in short acuminate, hyaline tip. It is widely distributed in South-east Asia (Gangulee, 1969-72). In Munsiyari (Pithoragarh, Western Himalayas) from where the samples are collected both the species were found growing together on rocks between altitudes 2200 to 3500 m above mean sea level. The diurnal temperature, light and relative humidity at Munsiyari during the study varied between 10 – 30º C, 08 – 2800 µmol m^{-2} S^{-1} and 20 – 40% respectively.

Figure 1: Lichen *Stereocaulon foliolosum* growing along with moss *Racomitrium subsecundum*

Collection and Processing of Samples: The lichen and moss samples collected from Munsiyari were maintained in growth chamber for at least one week before initiation of the experiment at 12º C temperature, 20 – 30 µmol m^{-2} S^{-1} of light (12 h light and dark cycle) and 70% of relative humidity. The species were watered once a day. During the experiment species were kept in Petri dishes on wet Whatman filter paper. For dehydration moss and lichen tufts were allowed for drying at room temperature (25º C) with relative humidity of 55% and during rehydration water was poured on the filter paper. The measurements of parameters mentioned below were taken both during dehydration and rehydration.

Measuring Surface Reflectance: Diffuse spectral reflectance were measured using Li-1800 spectroradiometer (LI-COR) attached to integrating sphere by fiber optics, using a barium sulfate block as a reference. The sphere illuminator (halogen lamp) was directed toward the moss or lichen tuft in the reflectance lamp port. Diffuse reflectance was calculated as a ratio in relation to the white reference data and five scans were averaged per reflectance spectrum. Spectra were determined from 400 to1100 nm at a scanning interval of 1 nm. Spectral reflectance was taken at every 1 ½ hour intervals during dehydration and rehydration and following indices were determined with Rn indicating reflectance at wavelength (λ)n.

Photosynthetic Reflectance Indices: PRI was calculated using formula; PRI = (R531-R570)/(R531+R570), where R531 is reflectance at 531 nm, shows xanthophylls cycle pigment and R570 is reflectance at 570 nm presenting the reference band (Gamon *et al.*, 1997). The reflectance at 531 nm is associated with epoxidation of xanthophylls cycle pigments (Gamon *et al.*, 1990, 1992) also measured as photochemical energy conversion, Fm´–F = ΔF/Fm´ (Genty *et al.*, 1989) and can be correlated with ΔF/Fm´ and non photochemical quenching-NPQ (Gamon *et al.*, 1997; Peñuelas *et al.*, 1995).

Normalized Difference Vegetative Index: NDVI is associated with the plant photosynthetic efficiency and calculated according to Schafleitner *et al.*, (2007) by using reflectance at 800 and 650 nm (formula NDVI = (R800-R650)/(R800+R650)). It is considered as index of chlorophyll content and correlated with maximal photochemical quantum yield Fv/Fm (Gamon *et al.*, 1997; Gamon and Surfus, 1999).

Cold Hard Band*:* CHB is calculated according to Lovelock and Robinson (2002) as CHB = (R750.R710)/(R750 + R710). It represents the chlorophyll protein complex formation in leaves which protects the plant against freezing (Gilmore and Ball, 2000).

Normalized Pigment Chlorophyll Index: NPCI calculated as NPCI = (R680-R430)/(R680+R430) following Peñuelas *et al.*, (1994). It is the ratio between total carotenoid and chlorophyll (Lovelock and Robinson, 2002).

Water Index: WI is a measure of water content and measured as WI = *R*900/*R*970 (Peñuelas *et al.*, 1997; Levizou *et al.*, 2004).

Structure Independent Pigment Index: SIPI is a measure of carotenoid to chlorophyll ratio similar to NPCI and calculated as SIPI = (R800-R445)/(R800+R445) following Peñuelase *et al.*, (1995) and Levizou *et al.*, (2004).

Indices of Photosynthetic Pigments: These are calculated as R_{717}/R_{770}, R_{731}/R_{770} and R_{696}/R_{770} respectively which corresponds to chlorophyll a, b and a/b ratio in the plants (Nicotra *et al.*, 2003).

Chlorophyll Fluorescence Imaging: Imaging-PAM Chlorophyll Fluorometer (Walz, Effeltrich, Germany) was used to investigate the spatial heterogeneity of the photosynthetic parameters (Schreiber *et al.*, 1994). The charge-coupled device (CCD) camera has a resolution of 1392 X1040 pixels. For maximal spatial resolution and the minimal working distance was chosen, which corresponds to an imaged area of 9 x 12 cm. Measuring light pulses were applied at low frequency (1 Hz) and 0.5 µmol quanta m^{-2} s^{-1} intensity for the measurement of F_o images (quasi-dark state). During actinic illumination and saturation pulses, the frequency of the measuring light pulses was automatically increased to 10 Hz and 2700 µmol quanta m^{-2} s^{-1} intensity. Associated with each measuring light pulse, two images were measured, one shortly before the light pulse and another during the light pulse. The two images were subtracted from each other, pixel by pixel, resulting is an image corrected for the ambient background light. In the absence of actinic illumination, on application of a saturation pulse, the dark-level fluorescence yield (F_o) and the maximum fluorescence yield (Fm) were determined, from which the optimal PSII quantum yield (Fv/Fm) was calculated. In the presence of actinic illumination, the current fluorescence yield (Ft) and the maximum light-adapted fluorescence (Fm_o) were determined, from which the effective PSII quantum yield (ΦPSII = (Fm_o-Ft)/Fm_o = ΔF/Fm_o) was derived (Y(II)). At a known flux of incident PAR, the relative rate of photosynthetic electron transport (ETR) was calculated as ETR = C x ΦPSII x PAR. For the coefficient C, which contains assumptions about the absorption of PAR by PSII, a value of 0.42 was assumed (Schreiber *et al.*, 1994). Non-photochemical quenching was calculated according to NPQ = (Fm-Fm_o)/Fm_o. The light response of photosynthetic electron transport was assessed with the help of a pre-programmed sequence of illumination steps at increasing PAR values (light curves). The illumination time at each step was 60 seconds. At the end of each illumination step, a saturation pulse was applied for the assessment of the fluorescence parameters. After the light curve areas of interest (AOI) were defined, over which the values of the selected fluorescence parameters were averaged. Fv/Fm of samples was taken at every 15 min during dehydration and samples were dehydrated until Fv/Fm became 0 in dark adapted samples. ETR and NPQ are measured at fresh (before dehydration) and rehydrated stages only.

Water Potential (Ψ) Measurement and Pressure Volume (PV) Curve Derivatives: About 15-20 mg of fresh samples was cleaned in distilled water and kept in tap water for 15 -30 min to obtain fully turgid samples. Then samples were thoroughly blotted using paper towels until they released almost no water, quickly weighed and placed in psychrometer chambers of Psypro Water Potential System. After equilibration for 4 h chambers are connected to a Wescor HR-33T micro voltmeter and measured the water potential. Samples were then allowed to lose about 5–20% of their water and allowed to equilibrate again. Measurements were repeated until the water potential fall to about –5 MPa. After the samples were dried for 70 hrs at 50° C in hot air oven weight was taken. Psychrometer chambers were calibrated with standard solution 0.5 M of NaCl at 25° C. Values of Ψ are corrected to a temperature of 25° C.

A typical PV curve was made by plotting 1/Ψ against relative water content (RWC) (Beckett, 1995, 1997). The resulting curve is initially concave but beyond the region where turgor is lost (i.e. where turgor no longer contributes to Ψ) the curve became linear. From the PV isotherm, turgor potential was calculated as the difference between the extrapolated linear portion of the curve and the actual curve, and turgor pressure (TP) was then plotted as a function of RWC. In most of the lower plants, unlike the angiosperms, TP do not fall with the initial loss of water. Water lost between 100% RWC and the RWC at which turgor started to fall was assumed to be intercellular. The RWCs for all the data were recalculated to exclude intercellular water as follows, RWCc = ((Fresh weight – Dry weight) / (Turgid weight – Dry weight)) – Weight of intercellular water)

Again corrected RWC was plotted as function of 1/Ψ. Osmotic potential (OP) at full turgor was calculated as the y-intercept of the linear portion of the PV curve. Regression line going through linear portion of the curve intercepts at x axis and yields the symplastic and apoplastic fraction of water. Tissue elasticity was calculated from the relationship between WP and RWCc (Stadelmann, 1984). The bulk elasticity modulus of tissue expresses the change in turgor of tissue cells for a unit change in the relative water content of the cells ($e = dP/dr$).

Statistical Analysis: Analysis of variance (ANOVA) was carried out for both the plants by using SAS 9.1 software. Water relation and reflectance are taken as separate set of parameter. ANOVA for each of the parameter was calculated and analyzed the difference in both of the plants and P value <0.05 is considered significant. Correlation was carried out using MS Excel 2007.

RESULTS AND DISCUSSION

Results

Both for lichen as well as moss total reflectance in RED and NIR region decreased during dehydration and showed maximum recovery during rehydration (Figure 2).

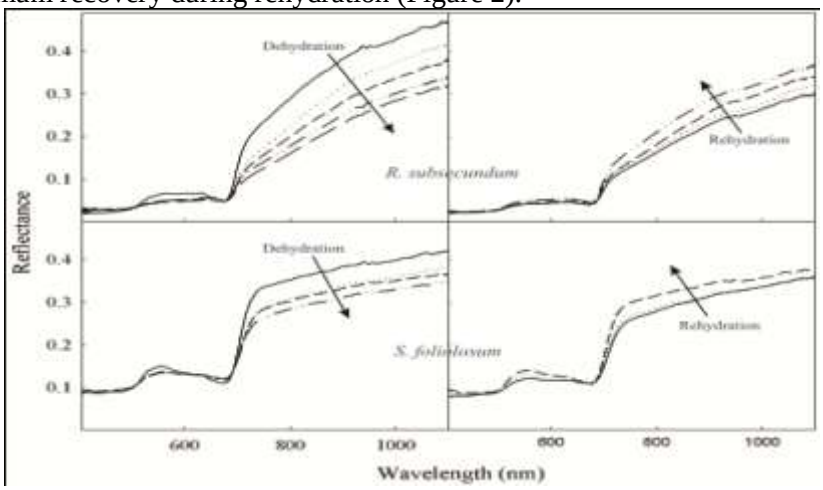

Figure 2: Changes in reflectance of the lichen and moss. Each line shows the average of 3 or more samples

Table 2: Pressure volume derivatives for lichen and moss

	S. foliolosum			*R. subsecundum*			ANOVA (P values)				
Parameters	**Fresh**	**Dehydrated**	**Rehydrated**	**Fresh**	**Dehydrated**	**Rehydrated**	**Moss: Fresh vs rehydrated**	**Lichen: Fresh vs rehydrated**	**Fresh: Lichen vs moss**	**Dehydrated: Lichen vs moss**	**Rehydrated: Lichen vs moss**
PRI	-0.021±0.01	-0.035±0.001	-0.03±0.007	-0.09±0.004	-0.06±0.011	-0.08±0.007	0.0645	0.5447	**0.0004**	**0.013**	**0.001**
NDVI	0.531±0.043	0.421±0.015	0.502±0.096	0.733±0.031	0.671±0.060	0.721±0.033	0.673	0.663	**0.0028**	**0.0383**	**0.0201**
CHB	0.159±0.021	0.139±0.013	0.146±0.051	0.162±0.008	0.149±0.009	0.152±0.008	0.2192	0.7028	0.8768	0.4658	0.8505
NPCI	0.119±0.030	0.161±0.037	0.110±0.059	0.461±0.091	0.290±0.111	0.396±0.026	0.302	0.8133	**0.0035**	0.0851	**0.0015**
SIPI	1.104±0.033	1.204±0.033	1.130±0.103	1.130±0.009	1.151±0.051	1.129±0.011	0.8787	0.7092	0.265	0.8224	0.9926
WI	0.979±0.003	0.960±0.001	0.978±0.012	0.924±0.016	0.905±0.051	0.915±0.019	0.5578	0.8927	**0.0041**	0.121	**0.0076**
NPQI	0.021±0.006	0.016±0.004	0.020±0.007	-0.02±0.001	0.116±0.093	-0.036±0.01	0.1305	0.8628	**0.0002**	0.4818	**0.0009**
R_{727}/ R_{770}	0.895±0.014	0.881±0.011	0.893±0.027	0.802±0.002	0.793±0.013	0.806±0.009	0.491	0.8897	**0.0003**	**<0.0001**	**0.0064**
R_{731}/ R_{770}	0.919±0.010	0.904±0.008	0.915±0.020	0.824±0.002	0.815±0.012	0.828±0.009	0.5366	0.7541	**<0.0001**	**<0.0001**	**0.0024**
R_{696}/ R_{770}	0.473±0.048	0.555±0.008	0.507±0.105	0.428±0.019	0.478±0.024	0.453±0.027	0.2628	0.6442	0.2034	0.4931	0.443

Significant P value of ANOVA are presented in bold.
Each value represents average of 3-4 samples with standard deviation.
PRI = Photosynthetic Reflectance Index, NDVI = Normalized Difference Vegetative Index, CHB = Cold Hard Band, NPCI = Normalized Pigment Chlorophyll Index, SIPI = Structural Independent Pigment Index, WI = Water Index, NPQI = Normalized Pheophytinisation Index

The reflectance parameters such as PRI, NDVI, NPCI, WI, NPQI, R_{727}/R_{770} and R_{731}/R_{770} compared at fresh and rehydrated conditions indicates that both the species are physiologically different (P value <0.05), which is obvious because they belong to completely two different taxonomic groups (Table 1). When fresh and rehydrated samples of moss and lichen compared among themselves for all parameters did not show any significant difference indicating that the recovery pattern after dehydration is similar in these species. In both the species CHB and SIPI did not show any significant difference in fresh as well rehydrated samples showing their full recovery after rehydration.

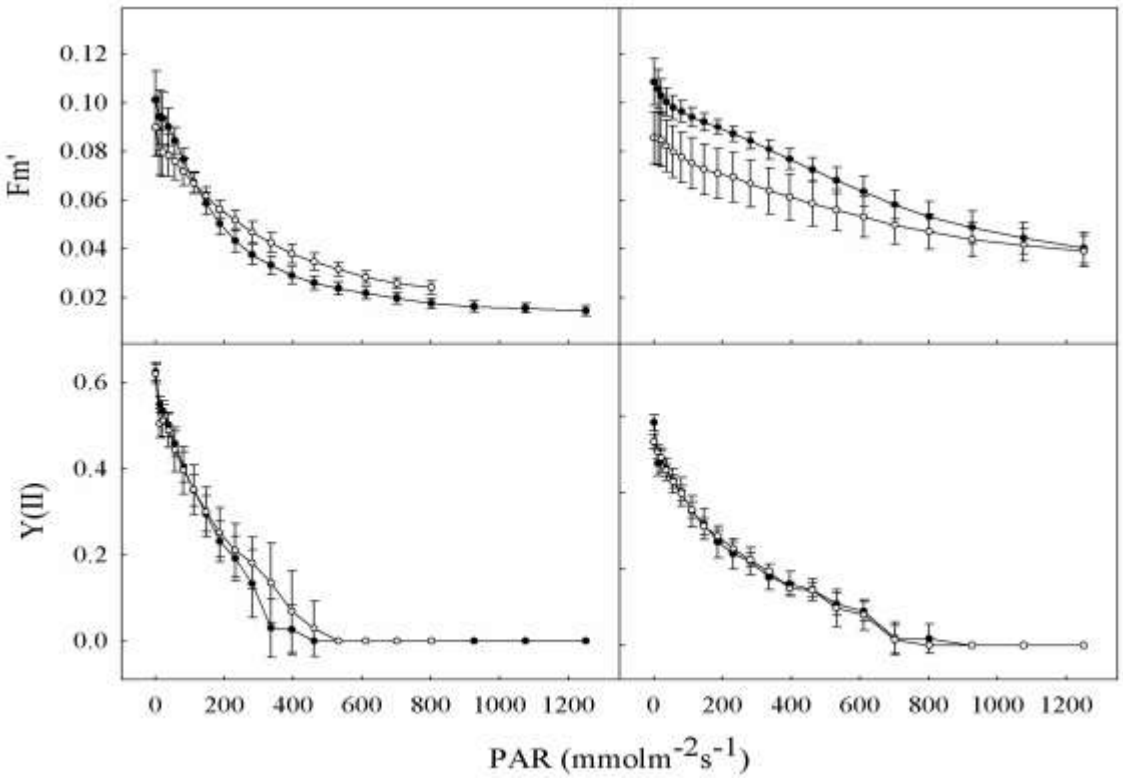

Figure 3: Maximal fluorescence yield (Fm') and effective photochemical quantum yield (YII) of the fully turgid fresh (•) and rehydrated samples (o) of lichen and moss during changing light conditions

Chlorophyll fluorescence of both moss and lichen decreased during dehydration and showed recovery during rehydration. At low PAR, in comparison to fresh samples of moss in the rehydrated samples less reaction centers were opened, but at high PAR more number of reaction centres were opened as indicated by their Fm´ and Y(II) values. It may be possible due to slow re-reduction of reaction centre after light treatment. In case of lichen at low and high PAR the Fm´ values were more in fresh samples, however it did not effect yield Y(II) (Figure 3).

ETR in lichen and moss in fresh and rehydrated samples showed slight, insignificant variation, whereas NPQ decreased considerably in rehydrated samples (Figure 4). This is due to regulation of energy dissipation via xanthophylls cycle has decreased.

The maximal photochemical quantum yield (Fv/Fm) in case of moss showed slightly less recovery (93%) during rehydration in comparison to lichen (100%). Further, Fv/Fm of moss goes down to zero at a faster rate than lichen (Figure 5).

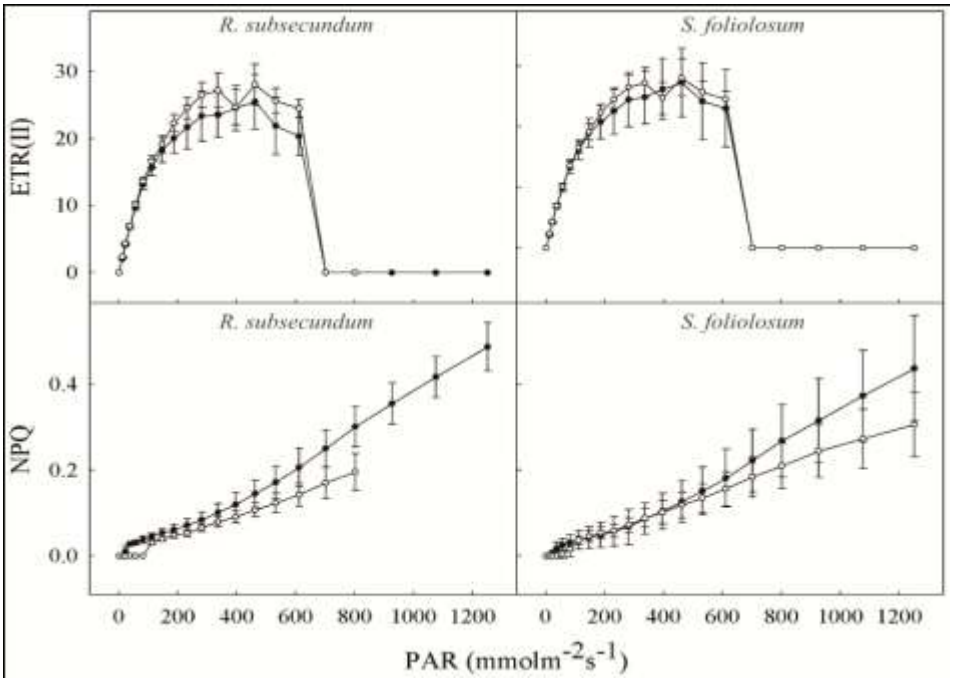

Figure 4: Electron transfer rate (ETR) and non photochemical quenching in PSII reaction centers of moss and lichens at fully turgid fresh (•) and rehydrated (o) states during increasing light intensities

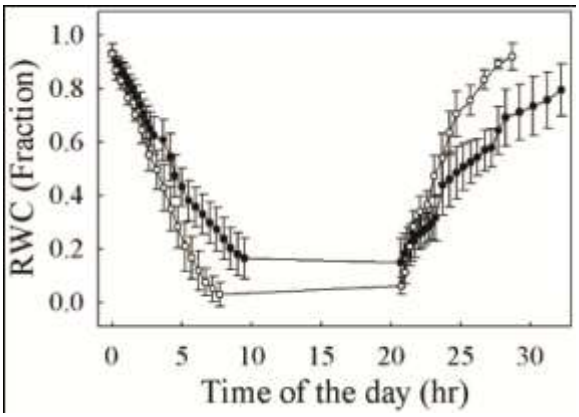

Figure 5. Maximum photochemical quantum yield (Fv/Fm) of lichen (•) and moss (o) during dehydration and rehydration

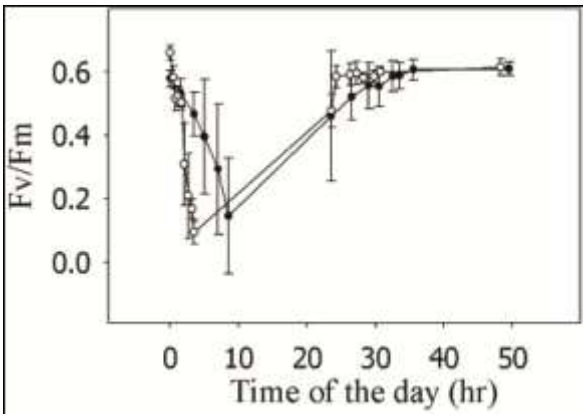

Figure 6: Dehydration and rehydration curves of lichen (•) and moss (o)

The RWC of moss and lichen during dehydration as well as rehydration exhibited similar pattern without any significant difference in slopes of curves (Figure 6). The moss loses water faster and also reabsorbs faster than the lichens. Both the species showed maximum recovery after rehydration with respect to RWC. The intercellular water fraction was more in moss (20.88 ± 4.76) than lichen (13.25 ± 3.37). It is clear from the table 2 that there is significant difference in the all the derivatives of PV curve between lichen and moss. The lichen have low elasticity modulus, maximum symplastic water, low apoplastic water content, more osmotic potential at full turgid, low turgor loss potential, low water content at turgor loss point and low effective solute concentration, where as in moss all these parameters showed opposite trend. The typical PV curve of lichen and moss from which these parameters are derived are given in Figure 7.

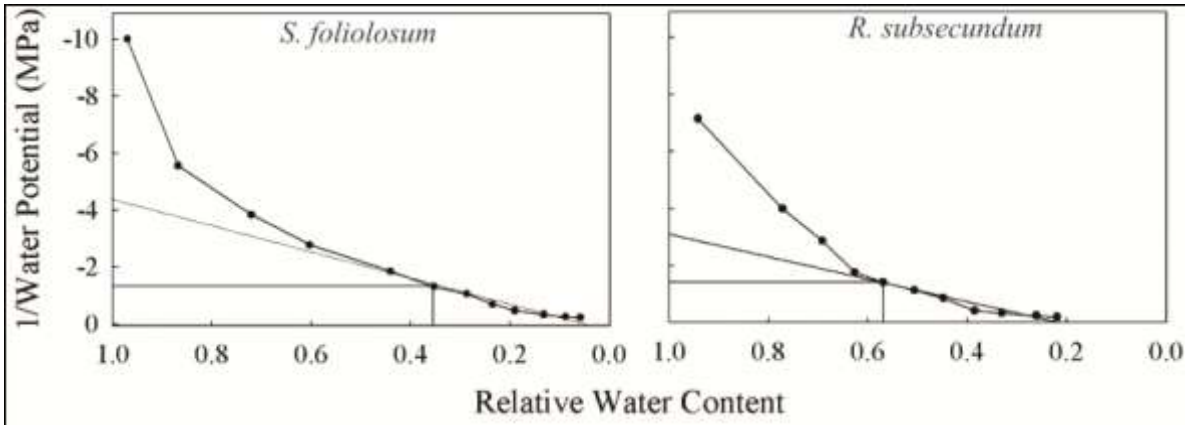

Figure 7: Typical pressure volume curve for lichen and moss

Table 2: Pressure volume derivatives for lichen and moss

Parameter	Lichen	Moss	ANOVA (P Value)
OP (MPa)	–0.30 ± 0.06	–0.46 ±0.05	p<0.0001
Symplastic water (%)	95.50 ± 1.51	81.50 ± 4.38	p<0.0001
Apoplastic water (%)	4.50 ± 1.51	18.50 ± 4.38	p<0.0001
Elasticity modulus (MPa)	0.24 ±0.10	7.13 ± 0.66	p<0.0001
Water potential at TLP	–1.54 ± 0.39	–2.60 ± 0.30	p<0.0001
Water content at TLP	23.75 ± 5.90	42.00 ± 6.50	p<0.0001
Effective solute concentration	0.20 ± 0.05	1.05 ± 0.32	p<0.0001

Discussion

Several studies on spectral reflectance of higher plants are available, while such studies are meager for cryptogams. In higher plants spectral reflectance can provide a remote indication of photosynthetic function, leaf water content, approximate leaf pigment content, changes in photosynthetic efficiency and capacity. For example xanthophylls cycle pigments can be detected in intact leaves with subtle changes in absorbance at 505-515 nm (Bilger *et al.*, 1989) or reflectance at 531 nm (Gamon *et al.*, 1990, 1993). Because xanthophylls cycle pigments are regulatory pigments closely linked to PSII light use efficiency. Recent studies have proved that PRI is correlated with ΔF/Fm′, fluorescence based indicator of PSII light use efficiency (Gamon *et al.*, 1997; Genty *et al.*, 1989). Lovelock and Robinson (2002) found significant correlation between xanthophylls pigment concentrations and chlorophyll fluorescence parameters (Fv/Fm) in Antarctic mosses. In the present study PRI of moss and lichens have shown significant correlation with Fv/Fm at both dehydration and rehydration stage (moss r^2 = 0.791 during dehydration, r^2 = 0.504 rehydration; lichen r^2 = 0.856 dehydration, r^2 = 0.983 rehydration). In *in vivo* (fresh) condition lichens reflect more light than moss but it is more in near infrared region which helps in temperature maintenance. During dehydration lichen lowered 17% reflectance while moss decreased 21% (Figure 1). In desiccation stage lichen avoid accepting more light. It is helpful in protecting the organism from photo inhibition because photosynthetic machinery is less efficient due to deficiency of water. The difference in the reflectance behavior of species can also be presumed on the basis of their colour. The moss thallus is green and of lichen is whitish-grey, hence lichen reflect more light during desiccation and protects itself during desiccation. CHB is the reflectance of the cold tolerant proteins, which protect the species from against freezing and hence did not show any significant difference either during dehydration or rehydration (Gilmore and Ball, 2000). NPQI is the index of chlorophyll degradation or pheophytinisation. In the present study there is no significant chlorophyll degradation either in lichen or moss due to dehydration. This is also exhibited by photosynthetic pigment indices R_{727}/R_{770}, R_{731}/R_{770} and R_{696}/R_{770}. However, during dehydration the indices value changes significantly which is due to presence of complex

photoprotection mechanism in the plants. In case of *Tortula ruralis* laboratory studies suggested that chlorophyll or carotenoid contents does not alter during desiccation and dehydration cycles (Tuba *et al.,* 1996). NPCI and SIPI are the reflectance ratio between carotenoid and chlorophyll pigment. Their value increases as dehydration increases with decreasing quality of chlorophyll as evident in the present study both for lichen and moss. NDVI indicates the ratio between photosynthetic area and total area. The photosynthetic area shrinks during dehydration and expands while rehydration. Both in lichen and moss NDVI reduces during dehydration and tries to recover during rehydration with maximum recovery in case of moss (98.3%) than lichen (94.5%). WI is the reflectance as a measure of water content in the plant body. RWC in both lichen and moss decreases during dehydration and increases during rehydration, which is reflected in WI and shows recovery up to 99%. However, figure 5 depict >100% recovery in RWC of moss and comparatively less in case of lichen. This is because in case of moss extra cellular water is more than that of lichens which is unavoidably accounted during RWC calculation. Gloser and Gloser (2007) studied the changes in the spectral reflectance of foliose lichen *Umbilicaria hirsuta* (Sw. ex Westr.) Hoffm. during desiccation. Similar to *S. foliolosum* WI and NDVI decreased during desiccation and there was no significant change in SIPI. Yamano *et al.,* (2006) examined the spectral indices NDVI, PRI and chlorophyll fluorescence Fv/Fm in soil crust containing moss and lichens. The hydrated crusts showed significantly higher F_v/F_m values than dry crusts and a significant correlation between the PRI and F_v/F_m was found in moss and lichen dominated crusts.

Chlorophyll fluorescence is a noninvasive technique to assess the photosynthetic performance of the plant or leaves. It has become one of the most powerful and widely used techniques available to plant physiologist and ecophysiologists (Maxwell and Johnson, 2000). A single parameter Fv/Fm exhibit capacity of the organism for the photosynthesis either in dark adapted sample or light adapted. It also shows strong quantitative relationship with the quantum yield of CO_2 assimilation (Genty *et al.,* 1989). Chakir and Jensen (1999) showed remarkable capacity of lichen *Lobaria pulmonaria* L. to regain photosynthetic activity after progressive desiccation. In case of mosses *Rocomitrium lanuginosum* (Hedw.) Brid., *Anamodon viticulosus* (Hedw.) Hook., and *Rhytidiadelphus loreus* (Hedw.) Warnst., Proctor and Smirnoff (2000) reported that Fv/Fm of few days air dry samples reached two third or more value within few minutes of remoistening in dark. Initial phase of recovery was very fast and further change was slow. Similarly, in the present study Fv/Fm of *R. subsecundum* attain c. 90% of its value within 30 – 40 minutes, later on slows down and takes longer duration to attain 100%. In case of *S. foliolosum,* recovery of Fv/Fm is gradual and finally attains 100% of its value. Heber *et al.,* (2007) studied the reflectance and chlorophyll fluorescence in some desiccation tolerant moss and lichens and often found increase in the reflectance of light and simultaneous quenching of fluorescence during desiccation. Increased reflectance lowers light pressure on the photosynthetic apparatus, thereby it contributes to photoprotection. It is also observed in *Umbilicaria hirsuta* total reflectance increased during desiccation (Gloser and Gloser, 2007). However, in the present study both the reflectance and fluorescence in lichen and moss decreased during dehydration and we offer no explanation for the same at the moment. According to Veerman *et al.,* (2007) decreased yield of fluorescence in lichen can be attributed to sunscreen-type photoprotection mechanism that decreases the amount of light absorbed by the photobiont and/or an excitation energy-quenching mechanism that safely dissipates energy absorbed by the photosynthetic apparatus as heat. There are also changes in the morphology of the thallus of lichens upon desiccation that increase light scattering and decrease the transmission of light to the photobiont. Increased scattering could both decrease the amount of light reaching the photobiont and increase the reabsorption of emitted fluorescence.

Unlike vascular plants, lichens and mosses can stay longer in desiccation state and their metabolic activity can recover after their tissues have been reduced to very low RWC. Such plants are called ‘‘resurrection plants’’ and have evolved desiccation tolerance; can retain chlorophyll and the intact photosynthetic structures although changes in contents of photosynthetic pigments can occur (Bartels, 2005; Tuba *et al.,* 1998; Alamillo and Bartels, 2001). Psychrometric technique explores new possibilities to elucidating the water status of plants including cryptogams such as lichens, bryophytes, pteridophytes and PV isotherm is

one of the widely used tools for characterizing water status (Becket, 1997). PV isotherm has proved useful in assessing desiccation tolerance and the distribution of tree species in Malay-Thai peninsula (Baltzer *et al.,* 2008). Many useful parameters such as OP at full turgor, TLP, RWC at TLP, elasticity modulus, solute concentration, symplastic, apoplastic and intercellular fraction of water are measured with the PV curve. An ideal desiccation tolerant cryptogam would have low OP at full turgor, low apoplastic water content, low RWC at turgor loss and more importantly low elasticity modulus. In the current study moss has high elasticity modulus (7.13 ± 0.66), in other words its cells are less elastic, where as lichen cells are more elastic due to less elasticity modulus (0.24 ± 0.1). In general, elasticity modulus is thought to be determined by the mechanical properties of cell walls (Tyree and Hammel 1972; Cheung *et al.,* 1975). In leaf cells that have turgor elasticity modulus has a critical role in water relations. Advantage of the small elasticity modulus in the drought environment is that it contributes to the turgor maintenance of the leaf cells under conditions of low leaf water content (Kozlowski *et al.*, 1991). This is also evident as water potential at TLP of lichen is –1.54 ± 0.39 at RWC 23.75% ± 5.9 while moss has –2.6 ± 0.3 at RWC 42% ± 6.5. *S. foliolosum* fulfils all these characteristics and emerges as desiccation tolerant plant in comparison to moss (Table 2). The lichen and moss lack cuticle to impede entry of water in to the thallus and hence they have good amount of water in intercellular spaces. Further, presence of many dead or empty cells is the reason for larger portion intercellular water in tissue of *R. subsecundum*. Such condition was also visible in moss *Sphagnum* where the external, capillary water fraction considerably exceeds the symplastic water fraction held within the fully turgid cells (Hájek and Beckett, 2008). Further, mosses have their main pathways of water movement outside rather than inside the plant (Proctor *et al.,* 1998) and the intercellular water is an essential functional component in the physiology of many bryophytes (Dilks and Proctor, 1979).

Becket (1997) studied the PV isotherm of several poikilohydric plants including lichen *Roccella hypomecha* (Ach.) Bory. and moss *Plagiomnium rhynchophorum* (Hook.) Kop, and also provided explanation for varied values of PV isotherms. Similar to the current study the lichen *R. hypomecha* consisted low OP (estimated from PV curve), low RWC at turgor loss, low elasticity modulus and low solute concentration. The intercellular water content was more in *R. hypomecha* while apoplastic water content was almost same as moss *P. rhynchophorum*. Proctor *et al.,* (1998) studied the water contents of several bryophytes including a lichen *Cladonia convoluta* (Lam.) Cout. using PV relationship, where the lichen contained low OP, low RWC at TLC and low bulk elasticity modulus.

It is clear from the study that physiological behaviour of *S. foliolosum* and *R. subsecundum* in several occasions are similar. However, lichen shows its superiority over moss in its desiccation tolerance and fulfills all the characteristics of an ideal desiccation tolerant species by having low OP at full turgor, low apoplastic water content, low RWC at turgor loss and low elasticity modulus. The maximal photochemical quantum yield, Fv/Fm of lichen decrease gradually during dehydration and recovers fully during rehydration, where in moss Fv/Fm decreases at a faster rate and do not recover fully. Oxidation and re-reduction at the reaction centre was continued in lichen at rehydration stage, while in moss re-reduction slowed down. The lichen reflects more light than moss both in natural (fresh) conditions as well during desiccation than moss as a mechanism to avoid accepting more light. Singh *et al.,* (2013) studied in detail the reflectance properties, light utilization capacity and the desiccation tolerance of *S. foliolosum* under laboratory conditions. Their study showed that desiccation does not have a severe or long term impact on the lichen and all the observed changes show a rapid recovery on rewetting the lichen.

Conclusion

The water and light are two important environmental factor needed for survival of a species. In a diurnal cycle light intensity gradually increases from morning, attains maximum in noon and decreases during evening. Nayaka *et al.,* (2009) studied the vitality of lichens of the same study site during early summer and observed that most of the lichens were experiencing stress. The stress in the studied area was related to the availability of water in addition to high intensity light and to some extent anthropogenic interference. Though lichen and moss need light for the photosynthesis its high intensity causes desiccation and the species undergo an inactive phase. The occurrence of moss along with lichen may be

a chance rather than an association. In the locality from where the lichen and moss are collected it is observed that they grow very closely with inter-mingling. In such condition physiological difference in lichens and moss would be helpful to each other for better survival. During desiccation slow water loosing ability of lichen is useful to moss which looses water a little faster. The moisture in the lichen may help moss to be active for an extended period due to their physical contact. Similarly, during rehydration faster water absorbing ability of moss may influence lichens. Moss starts absorbing the water immediately when provided. Due to the physical contact lichens may start absorbing water a much earlier along and start its metabolic activity. In a mixed population high reflectance of lichen may be advantageous to moss in reflecting maximum amount of total light incident on the population. As said earlier most of the times it is observed that twigs of mosses are found beneath the lichen. The possible advantage of co-occurrence of lichen and moss discussed here are highly speculative and in-depth physiological studies are required to understand same, which is beyond the scope of present study.

ACKNOWLEDGEMENT
We are thankful to Director, CSIR-NBRI for providing laboratory facilities, to Drs. D.K. Upreti and U.V. Pathre for their encouragement, to CSIR for financial assistance under project SIP-009, to Dr. Vinay Sahu for identifying the moss sample and to members of Plant Physiology and Lichenology laboratory for their cooperation during the study.

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