Plant Ecology **151:** 51–54, 2000.

Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland

Zsolt Csintalan[1], Zoltán Takács[1], Michael C. F. Proctor[2], Zoltán Nagy[1] & Zoltán Tuba[1]
[1]*Department of Botany and Plant Physiology, Szent istván University, 2103-Gödöllő, Hungary (E-mail: csintalan@fau.gau.hu);* [2]*Department of Biological Sciences, University of Exeter, Hatherly Laboratories, Exeter, UK*

Key words: Carbon balance, Desiccation tolerance, Rehydration

Abstract

Air temperature and humidity, moss surface temperature, moss water content, and photosynthetically active radiation were measured through a clear dry night and early morning in July 1998; CO_2 gas exchange of the moss was measured by infra-red gas analysis. The measurements showed progressive absorption of water by the moss through much of the night. The moss reached sufficient water content for about 1.5 h of positive net CO_2 uptake immediately after dawn. The cumulative net carbon balance on this occasion was negative, but mornings with heavier dew could give a positive daily carbon balance, and short, early morning periods of photosynthesis during prolonged dry weather may mitigate long-term desiccation damage and allow for regular molecular repair.

Abbreviations: F_v/F_m – maximum photochemical efficiency of PSII; PPFD – photosynthetic photon flux density; PSII – second photochemical system; RFd – fluorescence decrease ratio; RWC –relative water content; WC – water content.

Introduction

Lichen species are widespread and sometimes major components of the vegetation in hot and coastal fog deserts, probably in large part because of the ability of lichens to make use of dew or fog as a source of water (Link & Nash 1984; Büdel & Lange 1991). Desert lichens can achieve positive cumulative net carbon gain over a cycle of rehydration from dew and subsequent desiccation; they can gain about three times more carbon after rehydration from fog (Lange et al. 1990). In coastal zones, sea spray may provide significant moisture for poikilohydric plants, depending on distance from the sea (Bruns-Strenge & Lange 1991).

Extensive temperate continental areas are covered by grassland in which species of cryptogams also play important ecological functions. In this climatic zone, autumn, winter and spring generally have a favourable water supply, but summers are strongly water-limited. For example, the amount of precipitation between June and August is 50–100 mm per month in central and eastern Europe. During this time, only water vapour and dew are available as regular water sources for hydration. The lichen species of temperate grassland have been shown in a number of cases to utilise these water sources, but far less is known about the capabilities of mosses in this respect (Lange 1969).

The most abundant moss species of the calcareous semi-arid sandy grassland, *Festucetum vaginatae danubiale*, in Hungary is the common acrocarpous moss *Tortula ruralis*. In some stands of this community, *T. ruralis* covers wide areas, which appear as ‘black spots’ in summer because of the dark colour of the desiccated moss carpet. In addition, *T. ruralis* has a considerable presence in the spaces between the scattered tufts of dominant grasses, contributing 18–20% to the total cover. This moss undoubtedly has an important role in the function of this community.

On the basis of numerous laboratory experiments, we know a good deal about the photosynthetic behaviour of this moss (e.g., Tuba et al. 1996; Csintalan et al. 1998). During rehydration both the maximal photochemical efficiency of PSII (F_v/F_m) and the fluorescence decrease ratio (RFd) recover rapidly and can reach 95% of fully recovered values in 5–6 min. Chlorophyll and carotenoid contents are substantially unchanged during desiccation and rehydration. These facts indicate that the photosynthetic apparatus remains essentially intact during the desiccation–rehydration cycle. Both F_v/F_m and RFd are relatively constant down to about 0.3 relative water content (RWC, water content expressed as a proportion of content at full turgor but without external water), below which they decline steeply.

Since mosses are poikilohydric plants, water loss is determined mainly by saturation deficit, boundary layer resistance and the radiation environment (Proctor 1979, 1990). As moss that is fully turgid and also covered with external water begins to dry, water loss results in a strong increase in net assimilation. External water greatly increases the resistance to CO_2 diffusion in lichen thalli by completely or partially filling the pore-space for gas exchange (Lange & Tenhunen 1981; Honegger 1991; Cowan et al. 1992) and in ectohydric mosses by filling the external capillary spaces and lengthening the diffusion path to the leaves (Dilks & Proctor 1979). The range of relative water content for optimal photosynthesis in *T. ruralis* is probably about 0.8 to 1.5 RWC. The water content compensation point is about 0.2 RWC. The last phase of drying is always characterised by net CO_2 loss.

In this pilot study, we investigated the capacity of *T. ruralis* in a natural habitat in eastern European semi-arid grassland during the dry summer season to gain sufficient water from humid air or dew-fall for reactivation of photosynthesis, and evaluated the effect of water absorption on carbon balance.

Materials and methods

The ectohydric, highly desiccation-tolerant moss *Tortula ruralis* (Hedw.) Gaertn. ssp. *ruralis* was investigated *in situ* in a sandy grassland near Fülöpháza in Kiskunság National Park, Hungary (19°14′ E; 47°30′ N), at 130 m above sea level through the night and early morning of 13–14 July, 1998. The water content at full turgor (RWC = 1) of *T. ruralis* collected at the time of our measurements was about 1.60 g water g^{-1} dry mass. As also found by Proctor et al. (1998), the relative water content at turgor loss was about 0.75. Measurements on three representative 2 × 2 cm samples of moss carpet gave a mean shoot density of 16.4 (s.d. 0.63) shoots cm^{-2}, and a mean water content at full turgor of about 0.023 g cm^{-2} (equivalent to 0.23 mm of precipitation). Mean dry mass of the current year's green shoots was about 0.014 g cm^{-2}

CO_2 exchange was measured with a LI-6400 porometer (LI-COR, Lincoln, Nebraska, USA). Water content was recorded simultaneously on a separate moss cushion using a digital precision balance (PAG OERLIKON 300-99438/A, Zürich). Measurements of zenith sky temperature and the surface temperature of the moss carpet with a RAYNGER II infrared thermometer (Raytek Co.) at 15 to 30 min intervals gave an approximate indication of net radiation balance. Air temperature and relative humidity were measured at 1 m and at ground level (0.1 m) with 50Y sensors (Campbell Scientific) and recorded at 5-min intervals by a CR10 data logger (Campbell Scientific).

Results

The field measurements were carried out on a clear night following a warm day without precipitation, which had brought the moss to a metabolically inactive, desiccated state. As the air temperature fell, relative humidity and moss water content increased gradually (Figures 1 and 2). A dip in RWC during 00:00–02:00 h was probably due to an increase in wind speed. The water content of the moss peaked at dawn (Figure 2). Total water absorption during the night was equivalent to about 0.13 mm of precipitation, or about one-third of the theoretical maximum dew-fall. This water content and the mild temperatures enabled the moss to respire during the night at up to 50% of the maximal rate seen during the cycle (Figure 2). Moss water content declined sharply after sunrise (Figures 1 and 2). The light compensation point was around 50 μmol m^{-2} s^{-1}. Net assimilation did not start to decline at the same time as water content, since the increasing PPFD counterbalanced the effect of decreasing water content on CO_2 gas exchange until the water content fell below 0.26–0.30 RWC.

Discussion

Our measurements showed that a relatively light dew-fall rehydrated *T. ruralis* to about 0.6 RWC and sup-

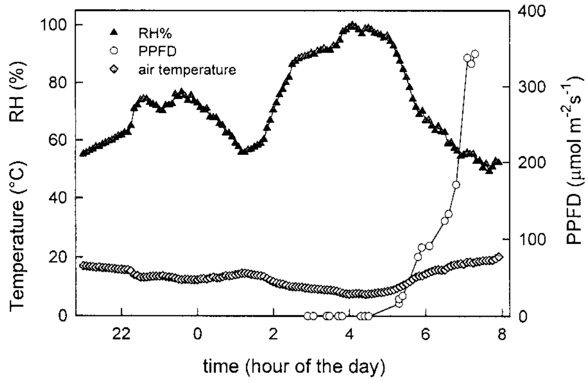

Figure 1. Changes in air temperature, photosynthetic photon flux density (PPFD) and relativ humidity (RH) during the night and early morning of 13–14 July 1998.

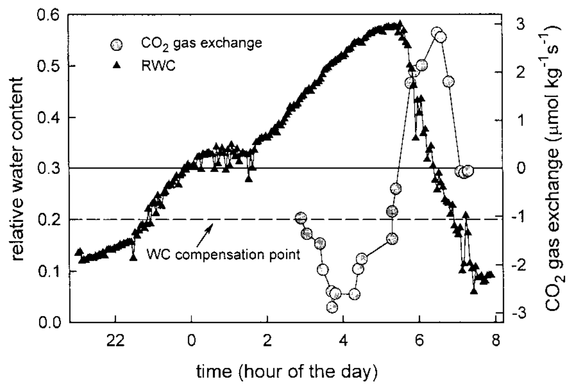

Figure 2. Changes in relative water content and CO_2 gas exchange of *Tortula ruralis* during the night and early morning of 13–14 July 1998. Values are individual measurements.

ported positive net photosynthesis. Although we did not separate the effects of water vapour from those of dew, it is possible that absorption of water vapor alone might have rehydrated the moss to its water compensation point for photosynthesis. Lange (1969) showed this to be possible in some mosses exposed to air of 98% relative humidity under laboratory conditions.

During the cycle of wetting and drying observed, the brief period of net photosynthesis in the morning was insufficient to compensate for the more prolonged period of respiration during the night, making the cumulative daily net carbon balance negative (< -1.5 nmol g^{-1}). On mornings with heavier dew-fall, which is likely during late summer and early autumn, the water content of *T. ruralis* should regularly reach the level needed for maximal photosynthetic activity. In fact, the full-turgor water content estimated on whole green shoots probably overestimates the water required for photosynthesis, because water vapour or dew will first moisten the apical leaves, and these may photosynthesise actively while the lower parts of the shoots are still at a lower water content. Low water content requirement and rapid recovery of the photosynthetic system from dehydration allow *T. ruralis* to react rapidly to short, intermittent wet periods and survive during the hot and dry summer. During the summer drought stress periods, the moss contributes significantly (7–8% of total production) to the daily net primary production of the community; the dominant grasses may have a negative carbon balance during this time (Tuba et al. 1998).

The present results suggest that heavier dew depositions, those sufficient to be obvious to the eye, could enable *T. ruralis* to achieve a positive cumulative daily carbon balance. Perhaps of at least equal importance, dew provides brief periods of hydration during the long summer drought, which may mitigate long-term desiccation damage and allow a degree of molecular repair. Further field measurements and experiments are needed to establish the frequency and durations of periods of activity of *T. ruralis* during the water-limited summer season and to elucidate their ecophysiological effects.

Acknowledgement

This work was supported by grants from the USA-Hungarian TeT (W/28/99), MEGARICH R&D (EU), OTKA 032568 (Budapest) to Z. Tuba and Bolgai Jànos Research Scholarship

References

Bruns-Strenge, S & Lange, O. L. 1991. Photosynthetic primary production of the lichen *Cladonia portentosa* in a dune habitat at the Island Baltrum in the North Sea. I. Field measurements of microclimate, water relations and CO_2-exchange. Flora 185: 73–97.

Büdel, H. & Lange, O. L. 1991. Water status of green and blue-green phycobionts in lichen thalli after rehydration by water vapour uptake: Do they become turgid? Bot. Acta 104: 361–366.

Cowan I. R., Lange O. L. & Green, T. G. A. 1992. Carbon-dioxide exchange in lichens: determination of transport and carboxylation characteristics. Planta 187: 282–294.

Csintalan, Z., Takács, Z., Proctor, M. C. F., Lichtenthaler, H. K . & Tuba, Z. 1998. Desiccation and rehydration responses of desiccation tolerant moss and lichen species from a temperate semidesert grassland. J. Hattori Bot. Lab. 84: 71–80.

Dilks, T. J. K. & Proctor, M. C. F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol. 82: 97–114.

Honegger, R. 1991. Functional aspects of the lichen symbiosis. Annu. Rev. Plant Physiol. Plant Molec. Biol. 42: 533–578.

Lange, O. L. 1969. CO_2-Gaswechsel von Moosen nach Wasserdamnfaufnahme aus dem Luftraum. Planta 89: 90–94.

Lange, O. L., Meyer, A., Zellner, H., Ullmann, I. & Wessels, D. C. J. 1990. Eight days in the life of a desert lichen: water relations and photosynthesis of *Teloschistes capensis* in the coastal fog zone in the Namib desert. Madoqua 17: 17–30.

Lange, O. L. & Tenhunen, J. D. 1981. Moisture content and CO_2 exchange in lichens. II. Depression of net photosynthesis in *Ramalina maciformis* at high water content is caused by increased thallus carbon dioxide diffusion resistance. Oecologia 51: 426–429.

Link, S. O. & Nash, T. H. 1984. The influence of water on CO_2 exchange in the lichen *Parmelia praesignis*. Oecologia 64: 204–210.

Proctor, M. C. F. 1979. Structure and eco-physiological adaptation in bryophytes. Pp. 479–509. In: Clarke, G. C. S. & Duckett, J. D. (eds), Bryophyte systematics. The Systematics Association Special Volume No. 14. Academic Press, London.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. Bot. J. Linnean Soc. 104: 61–77.

Proctor, M. C. F., Nagy, Z., Csintalan, Z. & Takács, Z. 1998. Water-content components in bryophytes: analysis of pressure-volume relationships. J. Exp. Bot. 49: 1845–1854.

Tuba, Z., Csintalan, Zs. & Proctor, M. C. F. 1996. Photosynthetic responses of a moss, *Tortula ruralis*, ssp. *ruralis*, and the lichens *Cladonia convoluta* and *C. furcata* to water deficit and short periods of desiccation, and their ecophysiological significance: a baseline study at present-day CO_2 concentration. New Phytol. 133: 353–361.

Tuba, Z., Csintalan, Z., Nagy, Z., Szente, K., Kemény, G., Takács, Z., Koch, J., Badacsonyi, A., Murakeözy, P., Palicz, G., Kóbor, S., Ötvös, E. & Bartha, S. 1998. Szünfiziológia: alapozó gondolatok és exploratív vizsgálatok egy születő Növényökológiai tudományterülethez. (Synphysiology: Principles and explorative studies in a newly developing branch of plant ecology). Pp. 171–196. In: Fekete, G. (ed.), A közösségi ökológia frontvonalai (Trends in community ecology) Scientia Kiadó, Budapest.