Plant Physiol. (1979) 64, 13–17
0032-0889/79/64/0013/05/$00.50/0

Respiration in Relation to Adenosine Triphosphate Content during Desiccation and Rehydration of a Desiccation-tolerant and a Desiccation-intolerant Moss[1]

Received for publication December 21, 1978 and in revised form February 28, 1979

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ABSTRACT

O_2 consumption by the desiccation-tolerant moss *Tortula ruralis* and the desiccation-intolerant *Cratoneuron filicinum* increased markedly during the latter stages of desiccation. ATP content of the mosses during desiccation was not correlated with O_2 consumption, but was influenced by the rate at which the mosses lost water. The more rapid the water loss, the more ATP that was present in the dry mosses. The pattern of O_2 consumption on rehydration also was influenced by the previous rate of desiccation. After rapid desiccation of *T. ruralis* O_2 consumption upon rehydration was considerably elevated, and for up to 24 hours. After very slow desiccation the elevation was small and brief. Normal O_2 consumption did not occur in *C. filicinum* after rapid desiccation, but did so within a few hours of rehydration after slower speeds of drying. ATP levels in *T. ruralis* returned to normal within 5 to 10 minutes of rehydration. In *C. filicinum*, increases in ATP were closely correlated with O_2 consumption. These observations are considered to be related to differential damage caused to mitochondria and to cellular integrity by different speeds of water loss. The desiccation-tolerant moss appears to be able to repair the severe damage imposed by rapid desiccation whereas the desiccation-intolerant moss cannot.

Upon rehydration after desiccation, respiration by desiccation-tolerant lower plants characteristically is stimulated above normal (3, 24). This respiratory burst (or resaturation respiration [23]) has been reported in bryophytes (6, 8, 16, 27), ferns (20, 25), and lichens (10, 21–23). It has been observed that sometimes this burst is more pronounced in species less tolerant of desiccation (8, 23). Also, the magnitude of the burst is related to the severity and duration of the desiccation period (9, 16, 23). For example, in a desiccation-tolerant lichen, a respiratory burst on rehydration occurs only after the thallus has dried below 50% water content (23).

Perhaps more meaningful than measurements of respiration during desiccation and rehydration are measurements of ATP, or of energy charge. However, only two studies have been made of the effects of desiccation and rehydration upon ATP synthesis in tolerant and intolerant lower plants (4, 14). In one (14) it was proposed that the ability of tolerant plants to withstand desiccation depends upon the maintenance of a high level of compounds containing "energy-rich macroerg bonds" (*i.e.* ATP) during drying. In the second study (4), it was suggested that tolerance of desiccation may not depend so much upon the maintenance of high ATP levels during drying, but rather upon the ability to resume ATP synthesis rapidly on rehydration.

Generally there has been a lack of attention to the relationships between respiration and ATP synthesis under any conditions of water stress and upon relief of them. In this paper, results are presented on the correlation between O_2 uptake, CO_2 evolution, and ATP levels during desiccation in a desiccation-tolerant moss, *Tortula ruralis*, and a desiccation-intolerant moss, *Cratoneuron filicinum*. The consequences of different rates of desiccation were tested, since there is evidence that rate of water loss has a profound influence upon the recovery of metabolism and of cellular integrity when these mosses subsequently are rehydrated (5, 7, 13, 19).

MATERIALS AND METHODS

The collection and preparation of the gametophytes of *T. ruralis* ([Hedw.] Gaertn., Meyer, and Scherb.) and *C. filicinum* ([Hedw.] Spruce) (formally misidentified as *Hygrohypnum luridum* [Hedw.] Jenn.) have been described elsewhere (1, 2). Moss pieces were subjected to three different drying regimes: (*a*) rapid drying in Petri dishes over silica gel; (*b*) slow drying in desiccators over a saturated solution of ammonium nitrate (65% RH); or (*c*) very slow drying in Gilson respirometry flasks over 4 ml of 25% (w/v) NaOH or over 20 ml Pardee buffer (19). Air dry weights of 17% original fresh weight were achieved within 1 h, 2 to 3 h, or 8 to 14 h, respectively (*i.e.* 100 mg fresh weight of moss was reduced to 17 mg dry weight in these times). Under any particular drying regime both moss species lost water at similar rates.

O_2 and CO_2 Exchange Measurements. A 20-channel Gilson differential respirometer was used to measure O_2 consumption by 100 mg fresh weight of moss (per cent moisture content on a dry weight basis, about 500). Experiments were carried out at a water bath temperature of 21 ± 1 C. To measure O_2 consumption during desiccation single side-arm Gilson flasks (60-ml capacity) were used and moss pieces were placed on a brass wire shelf supported by the center well over 4 ml 25% (w/v) NaOH. For measurements during rehydration a constant CO_2 concentration (0.2%, v/v) was achieved by placing 20 ml Pardee buffer (19) on the bottom of the flask. The flasks were maintained in darkness during the course of the experiment. O_2 exchange volumes were corrected for standard temperature and pressure, and thermobarometer changes (readings taken from control flasks without moss), and expressed in standard units of time and dry weight.

Evolution of CO_2 from 1 g fresh weight of moss was determined during desiccation and rehydration of the moss using a Beckman 865 infrared gas analyzer (IRGA) (Beckman Instruments, Palo Alto, Calif.). The IRGA was calibrated with nitrogen and with two upscale concentrations of CO_2 (Matheson Gas Co., Canada).

[1] Work supported by National Research Council of Canada Grant A6352 and appropriations from the University of Calgary Research Grants Committee.
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The moss samples were placed upon a wire grid within a glass cuvette, and maintained at 20 ± 1 C in darkness. Then CO_2-free air (scrubbed with Ascarite) was passed into the cuvette, and any enrichment of CO_2 in the air leaving the cuvette was presumed to be due to respiration by the contained moss. Rates of CO_2 exchange were calculated by the standard procedure on the basis of flow rates, calibrated IRGA responses, and the dry weights of the moss samples.

ATP Extraction and Determination. The procedure used was that of Bewley and Gwóźdź (4) with modifications according to Friederich and Mohr (11) and Kimmich *et al.* (18). Batches of moss (100 mg) were ground in 9 ml cold perchloric acid (35%, w/w) and the homogenate was kept on ice for 15 min before centrifugation at 2,000*g* for 35 min. The supernatant was titrated (on ice) to pH 7.0 with 6 N and 0.1 N KOH (both containing 50 mM K_2HPO_4) and left on ice for a further 15 min. The resultant precipitate was cleared at 20,000*g* for 15 min and the supernatant diluted to a constant assayable volume. For ATP assay by the firefly luciferin-luciferinase enzyme technique small borosilicate glass vials were placed inside glass scintillation vials and cooled to 4 C. Into the vials were pipetted 0.9 ml distilled H_2O and 0.1 ml firefly extract (Sigma FLE-250 prepared according to manufacturer's instructions and filtered through Whatman No. 1 filter paper after standing overnight). One-tenth ml of the assay sample was injected from a syringe, with force, into a vial which was lowered immediately into the counting chamber of a Packard 3320 scintillation counter (low energy tritium setting, counting in both A-B channels with the discriminator set at 50–1000, 52% gain and coincidence switch off) for a 6-s counting. Background luminescence values were subtracted and ATP concentration was determined using standard ATP solutions of 1 to 15 pmol/0.1 ml solution.

RESULTS

O_2 Consumption and CO_2 Evolution during Desiccation of *T. ruralis* and *C. filicinum*. The rates of O_2 consumption and CO_2 evolution in darkness by unstressed *T. ruralis* and *C. filicinum* were very similar: about 1 μl (mg dry weight)$^{-1}$ h^{-1} (compare Figs. 1 and 2 with Figs. 3 and 6). During desiccation of both mosses in Gilson flasks over 25% NaOH O_2 consumption did not increase substantially until some 30 to 40% of the original fresh weight was attained. This occurred if this level of dryness was achieved within 4 to 5 h (Fig. 1, ○) or 7 to 8 h (Fig. 1, ●) for *T. ruralis*, and within 8 to 9 h for *C. filicinum* (Fig. 2). Thereafter O_2 consumption increased markedly until the mosses were almost dry (20 to 25% of original fresh weight), and as they finally dried out (to 17% of original fresh weight) O_2 consumption was reduced to zero. In a subsequent experiment, for which the data are not presented, the O_2 consumption by six samples of each moss was followed during desiccation. These samples of *T. ruralis* and *C. filicinum* took between 7 and 10 h, and 8 and 12 h, respectively, to dry out. All of them exhibited a burst of similar magnitude and at the same stage of drying as those shown in Figures 1 and 2. Complete drying in less than 7 or 8 h was not possible over 25% NaOH. More rapid desiccation techniques did not yield satisfactory results, either because drying was too rapid to allow for equilibration of the Gilson flasks in the respirometer, or because the desiccant itself (*e.g.* silica gel) adsorbed gases.

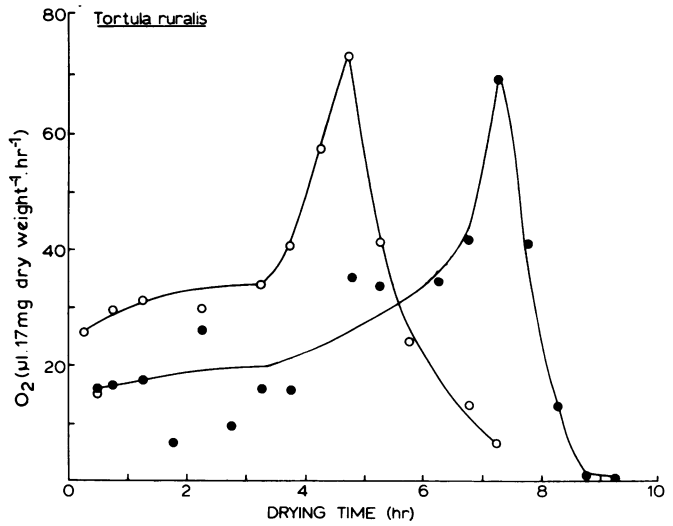

FIG. 1. O_2 consumption during desiccation of two batches of *T. ruralis* which lost water at different rates over 25% NaOH in Gilson flasks. The 17-mg dry weight is equivalent to 100 mg fresh weight. Each point represents a single measurement.

The evolution of CO_2 in darkness during desiccation in a dry or a partially water-saturated atmosphere was followed (Fig. 3). Undesiccated samples of *T. ruralis* and *C. filicinum* placed in a darkened chamber evolved CO_2 at a rate of about 0.75 μl (mg dry weight)$^{-1}$h^{-1}. During desiccation at very slow rates, CO_2 evolution declined steadily to zero evolution by the dry moss (Fig. 3). No increase in evolution occurred at any stage during water loss. A similar steady decline in CO_2 evolution was observed in both mosses during rapid desiccation (data not presented). No gaseous exchange was carried out by the dried moss following all three rates of desiccation.

Changes in ATP Content during Desiccation at Different Speeds. During very slow desiccation of both *T. ruralis* and *C. filicinum* their ATP content declined steadily. In the dried mosses, after 12 h, ATP content was some 33 to 40% of that of undesiccated controls (Fig. 4). With increasing time in the dry state, during which there was imperceptible loss in fresh weight, ATP content declined further, until after 24 h very little remained. Mosses which had been dried rapidly, and stored for 24 h still maintained a high content of ATP, and those dried slowly and stored maintained about 30% of control levels. Both moss species behaved similarly at all three rates of drying.

O_2 Consumption and CO_2 Evolution on Rehydration. The pattern of O_2 consumption by rehydrated *T. ruralis* was influenced by the previous rate of desiccation. Following rapid desiccation there was a pronounced increase in O_2 consumption to 80 to 100% above that by hydrated control moss (Fig. 5). Control rates were regained within 9 to 12 h. After very slow desiccation the increase was barely significant and lasted, at most, for only a few hours (Fig. 5).

We determined at which stage during desiccation of *T. ruralis* the rate of water loss most greatly affected the induction of elevated O_2 consumption on subsequent rehydration. This was achieved by rapidly drying separate 100-mg samples of the moss to various water contents, rehydrating them, and comparing sub-

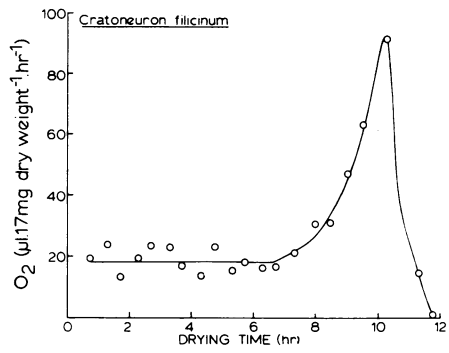

FIG. 2. O_2 consumption during desiccation of *C. filicinum* over 25% NaOH in Gilson flasks. Each point represents a single measurement.

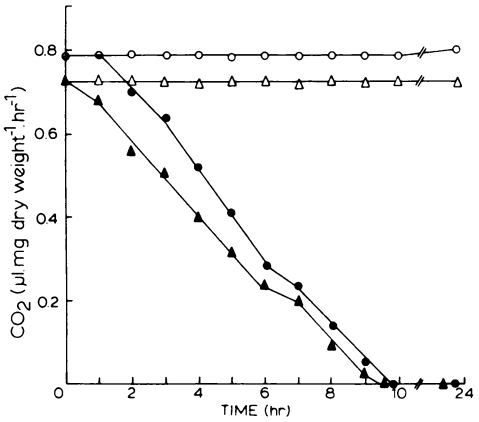

FIG. 3. Evolution of CO_2 by *T. ruralis* (○, ●) and *C. filicinum* (△, ▲) during very slow desiccation (●, ▲) or in the unstressed state (○, △). Each point is the mean value obtained from duplicate experiments and the range at any point is smaller than the size of the symbol.

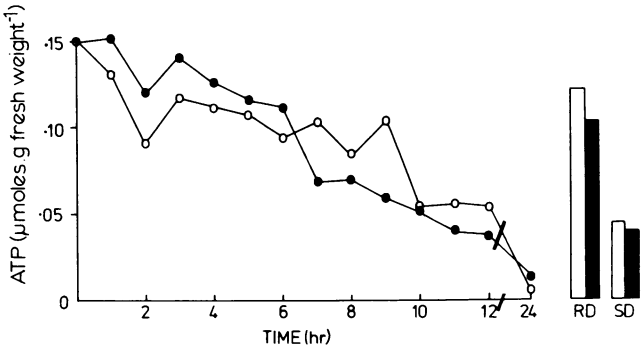

FIG. 4. ATP content during very slow desiccation of *T. ruralis* (●) and *C. filicinum* (○). Histograms show ATP levels after 24 h in rapidly dried (RD) and slowly dried (SD) *T. ruralis* (■) and *C. filicinum* (□).

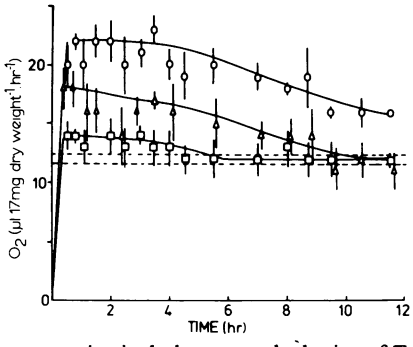

FIG. 5. O_2 consumption in darkness on rehydration of *T. ruralis* following rapid desiccation (○), slow desiccation (△), and very slow desiccation (□). O_2 consumption by hydrated control moss is shown by the dashed lines (± SE, N = at least 50). Data points are the means of at least three replicates ± SE which are shown by bars when they exceed the symbol size.

sequent rates of O_2 consumption with that by the undesiccated moss, and by that dried rapidly to air dry weight (Table I). No increase in O_2 consumption occurred on subsequent rehydration until the moss had lost water down to 26 to 30% of its original fresh weight. With further desiccation the increase was greater and more prolonged.

CO_2 evolution by *T. ruralis* on rehydration after rapid desiccation was monitored (Fig. 6). During the time of peak O_2 consumption (*i.e.* after 1–3 h from the start of rewetting) CO_2 evolution in darkness was constant at 0.68 µl (mg dry weight)$^{-1}$ h^{-1} which was not appreciably lower than the amount of evolution by undesiccated moss, 0.78 µl (mg dry weight)$^{-1}$ h^{-1} (Fig. 3).

Table I. Development of "resaturation respiration" in *Tortula ruralis* following partial desiccation at a rapid rate over activated silica gel.

The rate of oxygen consumption by treated moss was determined during the intervals 3 to 6 hours and 20 to 24 hours following rehydration and expressed as a percentage of fresh moss respiration over the same time periods. Values are a compilation of four separate experiments.

WATER CONTENT		RESPIRATION (% CONTROL)	
% original fresh weight	g(g dry weight)$^{-1}$	3-6 hr	20-24 hr
100	5.06	100	100
80	3.61	94	94
57	2.37	93	97
46	1.94	74	90
38	1.30	95	104
30	0.89	100	106
26	0.63	132	122
25	0.57	122	114
21	0.29	219	114
20	0.21	162	126
17	0.06	162	139
16	0	211	167

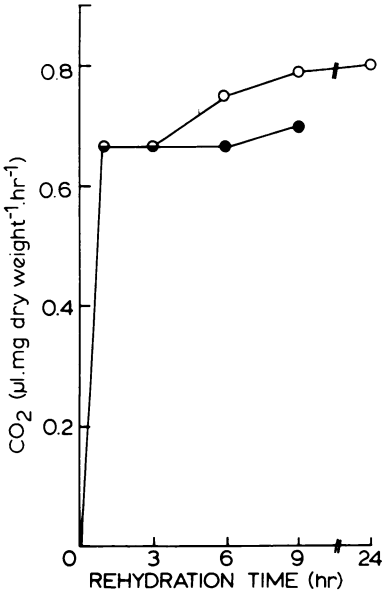

FIG. 6. Evolution of CO_2 by *T. ruralis* on rehydration following rapid desiccation (○) or very slow desiccation (●). Each point is the mean value obtained from duplicate experiments and the range at any point is smaller than the size of the symbol.

After rapid desiccation *C. filicinum* failed to recover its capacity to consume O_2, and only low levels were recorded for the first 10 h after rehydration (Fig. 7). Similarly, CO_2 evolution on rehydration was less than 10% of that of undesiccated controls (data not presented). Following both slow and very slow desiccation O_2 consumption was elevated above undesiccated control levels, but not greatly, nor for longer than 6 h.

It has been suggested (12) that contaminating microorganisms could account for some, or all, of the apparent O_2 consumption by rehydrated mosses, particularly after longer times. We have not found this to be so for *T. ruralis*. Thorough washing of the cut moss pieces with sterile distilled H_2O prior to use in experiments removed most contaminants, as determined by plating and counting colonies grown on bovine heart infusion (bacteria) or potato dextrose agar (fungi). O_2 uptake by control mosses, and by that

rehydrated for 24 h after rapid desiccation (the harshest drying regime which causes most leakage of solutes from the cells [7]) was measured in the presence or absence of antibiotics (50–500 IU ml^{-1} penicillin-streptomycin). Although these eliminated all residual contamination they had no effect upon O_2 exchange by *T. ruralis*. In *C. filicinum*, particularly following rapid drying, antibiotics were necessary to distinguish between plant respiration and that of an ever-expanding population of microorganisms (19).

Changes in ATP Content during Rehydration. Within 30 min of rewetting of *T. ruralis* after rapid, slow, or very slow desiccation, control levels of ATP were regained (Fig. 8A). In fact, after slow and very slow desiccation they were regained within 5 min. In some experiments, we have found that after rapid desiccation control ATP levels also may be regained within 5 min. After all rates of desiccation, high ATP levels were maintained over a 24-h period, with some fluctuations.

After rapid desiccation of *C. filicinum* ATP content of the rehydrated moss declined to a low, constant level (Fig. 8B). In contrast, the ATP levels of rehydrated moss, previously slowly and very slowly desiccated, gradually increased to those of controls over the first 2 h from initial imbibition, and remained there for 24 h.

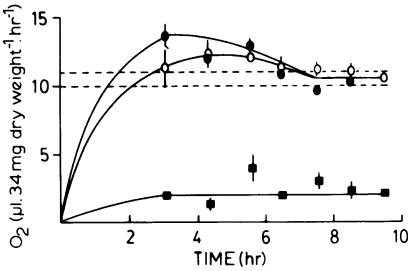

FIG. 7. O_2 consumption in the dark on rehydration of *C. filicinum* after rapid desiccation (■), slow desiccation (●), and very slow desiccation (○). Samples were treated with penicillin-streptomycin, 200 IU ml^{-1}. O_2 consumption by hydrated control moss shown by dashed lines (± SE, N = at least 21). Variability around data points as in Figure 5.

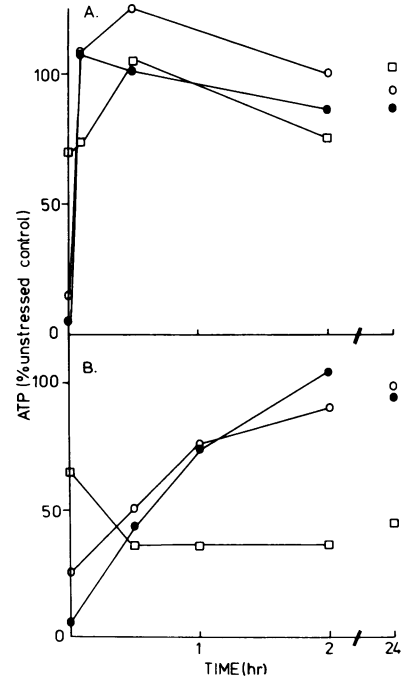

FIG. 8. Changes in ATP content during rehydration of *T. ruralis* (A) and *C. filicinum* (B) following rapid desiccation (□), slow desiccation (○), and very slow desiccation (●).

DISCUSSION

In drought-sensitive vegetative tissues of higher plants mild to moderate water stresses may induce an increase, a decrease, or have no effect upon respiration (17). At moderate to severe levels of water stress, respiration in sensitive and tolerant tissues generally declines, although it may be more persistent in more tolerant tissues. O_2 consumption declines steadily with increasing desiccation stress in desiccation-tolerant *Polypodium polypodioides* (25), *Myrothamnus flabellifolia* (15), *Neckera crispa* (14), and *Stratonostoc commune* (14). The large increase in O_2 consumption observed during the late stages of desiccation of both *T. ruralis* and *C. filicinum* (*i.e.* after 75–80% loss of fresh weight) has not been reported elsewhere. An increase has been reported to occur during the early stages of water loss from the desiccation-sensitive moss *Atrichum undulatum* and *Plagiochasma asplenioides* (14), but in the same study no increase was detected in O_2 consumption by a desiccation-tolerant moss and a tolerant blue-green alga during drying. The reasons for the differences in patterns of O_2 consumption by the different species are not readily apparent. They may be inherent, but in some cases differences in techniques used to measure O_2 exchange could be responsible. For example, a decline in O_2 consumption during late desiccation was reported previously for *T. ruralis* (16). There, though, the moss was dried in desiccators at high RH before being transferred to Gilson flasks for O_2 exchange measurements over brief time periods after known amounts of water had been lost. In the experiments reported here O_2 consumption was monitored continuously and the increase was detected. It has been suggested (14) that a steady decline in O_2 consumption during desiccation is characteristic of desiccation-tolerant species, and that an increase is indicative of disturbed metabolism during desiccation, which occurs only in desiccation-intolerant species. Clearly this suggestion is not supported by the present study.

ATP changes during water loss do not parallel those of O_2 consumption. During very slow desiccation of both *T. ruralis* and *C. filicinum* there is a gradual decline in ATP content of the mosses, with no increases at the time of elevated O_2 consumption. If O_2 uptake during desiccation is indicative of respiratory activity of the mitochondria, then it appears that ATP synthesis becomes more uncoupled as drying proceeds. Presumably, during very slow desiccation, available ATP is utilized in metabolic reactions and is not replenished because mitochondrial activity is restricted by increasing water stress. During more desiccation, where ATP levels are maintained closer to those of undesiccated moss, both ATP-producing and ATP-utilizing systems presumably are affected equally.

Whereas both desiccation-tolerant *T. ruralis* and desiccation-intolerant *C. filicinum* behave similarly during water loss at all three rates, their responses to subsequent rehydration are quite different in several respects. Recovery of respiration by *T. ruralis* occurs after all rates of desiccation, although the respiratory burst is greater upon rehydration after faster rates of desiccation. There appears to be little correlation between O_2 uptake and ATP content at early times after rehydration, for the amounts of O_2 consumed after rapid and very slow desiccation are very different, and for many hours, and yet ATP levels are very similar. It is possible that after rapid desiccation ATP synthesis is largely uncoupled from O_2 consumption but still is sufficient to maintain a constant pool size. Indeed, electron microscopy observations on mitochondria in rehydrated moss show that they are considerably swollen and lacking in internal structure (5, 26). Alternatively, both ATP production and utilization could be higher (and equally so) after rapid desiccation.

The changes in O_2 consumption during desiccation and rehydration of *T. ruralis* may be related to the amount of damage that this moss sustains during these stresses. It is plausible to suggest that the metabolism of this moss on rehydration is more deleteriously affected by prior rapid desiccation than by desiccation at

slower rates. Recovery of protein synthesis is, for example, slower after rapid desiccation than after slow desiccation (13) and leakage of solutes from cells is greater (7). It is interesting to note that loss of water in the latter stages of drying most greatly influences the extent to which O_2 consumption occurs on subsequent rehydration. It may be that slow removal of water in these latter stages allows for more controlled adjustment to drying of membranes, *e.g.* mitochondrial membranes and their associated enzyme complexes, whereas rapid water loss does not. Thus, on rehydration, rapidly desiccated mitochondria are more damaged, they take longer to repair (electron microscope studies have shown that damaged mitochondria regain their integrity within 24 h of rehydration [5, 26]), and hence consume O_2, in an uncoupled manner, for longer.

A better correlation between O_2 consumption, ATP accumulation, and cellular damage is exhibited by the desiccation-intolerant *C. filicinum*. Extensive cellular damage occurs to this moss on rehydration after rapid desiccation (5, 19). This is reflected in the low level of O_2 consumption, and failure of the moss to regain control ATP levels. Following very slow desiccation about 50% of the cells recover their normal appearance within 24 h of rehydration, whereas the others are severely disrupted (5, 19). O_2 consumption and ATP levels return to those of controls after slow rates of desiccation, in fact to a higher level than might be expected since the integrity of all cells is not retained. There is no ready explanation for this. Nevertheless the return to control levels is not as rapid as in *T. ruralis*, which is a reflection of the poorer adaptation of *C. filicinum* to desiccation.

There appears to be little correlation between O_2 consumption and ATP conservation during desiccation of either *T. ruralis* or *C. filicinum*, nor during rehydration of *T. ruralis*. Only when O_2 consumption is impaired, *e.g.* during rehydration of rapidly dried *C. filicinum*, or in *T. ruralis* in the presence of respiratory inhibitors (4), is ATP content reduced. It has been proposed (14) that survival of desiccation-tolerant plants depends upon their capacity to maintain control levels of ATP during drying, so that their energy can be transferred to appropriate organelle/membrane structures to facilitate maintenance of their structural integrity. Since very slow dried *T. ruralis* maintains almost no ATP and yet survives desiccation (perhaps even better than that brought on by rapid desiccation when ATP levels remain high) our observations here, and those made earlier (4), do not support this proposal. It appears that ATP depletion during drying at slow speeds is inconsequential if high levels can be resynthesized during rehydration and, presumably, if mitochondria can retain enough activity and/or be repaired rapidly enough to maintain a large pool of ATP for metabolism.

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