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Plant Desiccation and Protein Synthesis[1]

V. STABILITY OF POLY(A)$^-$ AND POLY(A)$^+$ RNA DURING DESICCATION AND THEIR SYNTHESIS UPON REHYDRATION IN THE DESICCATION-TOLERANT MOSS *TORTULA RURALIS* AND THE INTOLERANT MOSS *CRATONEURON FILICINUM*

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ABSTRACT

Upon desiccation of gametophytes of the desiccation-tolerant moss *Tortula ruralis* preexisting pools of poly(A)$^-$ RNA (rRNA) remain inact, regardless of the speed at which desiccation is achieved. Preexisting poly(A)$^+$ RNA pools (mRNA) are unaffected by slow desiccation but are substantially reduced during rapid desiccation. Poly(A)$^-$ RNA involved in protein synthesis is also unaffected by desiccation, whereas the levels of polysomal poly(A)$^+$ RNA in rapid- and slow-dried moss closely reflect the state of the protein synthetic complex in these dried samples.

Poly(A)$^-$ RNA pools, both total and polysomal, are also stable during the rehydration of both rapid- and slow-dried moss. The total poly(A)$^+$ RNA pool decreases upon rehydration, but this reduction is simply an expression of the normal turnover of poly(A)$^+$ RNA in this moss. Analysis of polysomal fractions during rehydration reveals the continued use of conserved poly(A)$^+$ RNA for protein synthesis. The rate of synthesis of poly(A)$^+$ RNA upon rehydration appears to depend upon the speed at which prior desiccation is administered. Rapidly dried moss synthesizes poly(A)$^+$ RNA at a faster rate, 60 to 120 minutes after the addition of water, than does rehydrated slowly dried moss. Recruitment of this RNA into the protein synthetic complex also follows this pattern. Comparative studies involving the aquatic moss *Cratoneuron filicinum* are used to gain an insight into the relevance of these findings with respect to the cellular mechanisms associated with desiccation tolerance.

In our previous paper (10), we investigated the effect of desiccation and rehydration upon the stability and recruitment of RNA involved in protein synthesis in the desiccation-tolerant moss *Tortula ruralis*. We demonstrated that newly synthesized RNA, *i.e.* that which is synthesized upon rehydration following desiccation, is quickly processed and recruited into ribosomal subunits, ribosomes, and polysomes. However, it takes longer for the new RNA components to be processed and utilized in protein synthesis after rapid-drying than it does after slow-drying. The RNA synthesized in the first hour following the addition of water to dried moss (either rapidly or slowly dried) is preferentially recruited into the polysomal fraction; little enters the ribosome or subunit fractions. Thus the moss selectively recruits newly synthesized mRNA into the protein synthetic complex in response to desiccation.

The RNA components of the protein synthetic complex which are present in the hydrated moss are stable to both rapid and slow desiccation, although more so following the latter drying regime. The moss utilizes the conserved RNAs for protein synthesis immediately upon rehydration and continues to do so for at least 4 h thereafter. Here, we address the relative importance of conserved and newly synthesized RNAs in the establishment of protein synthesis upon rehydration following both slow and rapid desiccation of *T. ruralis*. For comparative purposes we have also investigated the effect of desiccation and rehydration upon the stability and synthesis of ribosomal and mRNA pools in the aquatic moss *Cratoneuron filicinum*, a desiccation-intolerant species (8).

MATERIALS AND METHODS

Plant Material. Gametophytes of *T. ruralis* were collected, stored and prepared for experimentation as described previously (10). *C. filicinum* ([Hedw.] Spruce) was collected from the mouth of a small tributary of Heart Creek, situated between Mount Heart and Mount McGillivray, 2 miles SSE of Exshaw, Alberta where it grows in a semisubmerged state. The clumps were stored in glass containers covered with clear plastic at 5°C and under diffuse lighting. Experimental material was obtained, in this case the apical portions of the gametophyte were 15 to 20 mm in length, in the same fashion as that described for *T. ruralis* (10).

Desiccation Regimes. Slow and rapid desiccation of both species of moss was achieved using the drying conditions described in (10). Desiccation to 20% of original fresh weight was achieved within 1.5 h and 3.4 h, respectively.

Radioactive Labeling Conditions. Labeling conditions were the same for both species of moss except that incubation and rehydration solutions for *C. filicinum* contained 200 IU/ml penicillin and 250 μg/ml streptomycin to reduce bacterial contamination commonly found with these gametophytes (8). This problem is not encountered with *T. ruralis* (8).

In the investigation into the stability of RNA pools, 24-h hydrated moss (300 mg fresh weight) was incubated in 3 ml water containing 30 μCi [^{3}H]adenosine (Amersham, 25.5 Ci/mmol) for 4 h prior to washing and desiccation. Dried labeled moss was rehydrated in a 33.3 μg/ml solution of unlabeled adenosine for 30, 60, and 120 min. Measurement of RNA synthesis was achieved by rehydrating 60 mg of dried moss in 3 ml water containing 20 μCi of [^{3}H]adenosine for 30, 60, 90, and 120 min. In both stability and synthesis experiments, labeling was stopped by washing the samples with copious amounts of distilled H_2O.

RNA Extraction. Total RNA was obtained using the extraction

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method described earlier (10), except that the final RNA pellet was redissolved in 1 ml binding solution (0.5 M NaCl, 1% w/v sodium lauryl sulfate). Polysomal RNA was obtained by resuspension of a ribosomal pellet, obtained by the method of Oliver and Bewley (10), in 1 ml 0.1 M Tris-acetate buffer, pH 9.0, 0.1 M NaCl, 2 mM EDTA, and 1% w/v sodium lauryl sulfate (11), and RNA was extracted from this resuspended pellet as described for total RNA.

Oligothymidylic Acid-Cellulose Chromatography. Total or polysomal RNA was fractionated into poly(A)$^-$ and poly(A)$^+$ RNAs by oligothymidylic acid-cellulose (Oligo(dT)-cellulose) chromatography, using a modification of the technique described by Dhindsa and Bewley (5). A column of oligo(dT)-cellulose, 1 × 0.5 cm, prewashed with 5 ml 0.1 M KOH followed by 10 ml distilled H_2O (or until the eluant was of neutral pH) was equilibrated with 5 ml binding solution. RNA samples, dissolved in 1 ml binding solution, were applied to the column. The initial eluant was reintroduced onto the column to ensure maximum binding of poly(A)$^+$ RNA. The column was then washed with 3 ml 0.4 M NaCl to remove nonabsorbed RNA, designated poly(A)$^-$ RNA. After passage of a further 10 ml 0.4 M NaCl, bound RNA, designated poly(A)$^+$ RNA, was eluted by the application of 3 ml sterile distilled H_2O. Under these conditions there is some cross-contamination of both fractions, but this was shown (data not presented, [9]) to be negligible. Poly(A)$^+$ RNA collected in this manner could be rebound to oligo(dT)-cellulose with 96% efficiency.

RESULTS AND DISCUSSION

Stability of Cellular RNA Pools during Desiccation and Rehydration. The effect of desiccation and rehydration upon the stability of preexisting total poly(A)$^-$ and poly(A)$^+$ RNA pools is presented in Figure 1. The overall stability of the total RNA pool of the moss (Fig. 1A) appears to be unaffected by either desiccation or rehydration (compare histogram C with 0–120 min rehydration). It is also unaffected by the rate at which desiccation occurs. The poly(A)$^-$ fraction of the total RNA pool exhibits a similar pattern of stability to either speed of drying and to rehydration (Fig. 1B). The similarity in stability between these two pools is not surprising since poly(A)$^-$ RNA constitutes a large proportion of the total RNA.

The stability of the cellular poly(A)$^+$ RNA pool to desiccation and rehydration presents a different picture (Fig. 1C). After slow desiccation, the level of radioactivity in the poly(A)$^+$ RNA pool conserved in the dry state is the same as that in the undesiccated control. On the other hand, following rapid desiccation, the level of radioactivity conserved in poly(A)$^+$ RNA is substantially reduced, to approximately 50% of that in the undesiccated control. This loss of radioactivity could be due to destruction of the mRNA itself, or be caused by the cleavage or shortening of the (poly)A tail, thus rendering it incapable of binding to oligo(dT)-cellulose. That the poly(A)$^+$ RNA fraction has the properties of messenger RNA can be accepted on the basis of its capacity to serve as a template in an *in vitro* protein synthesizing system (5, 10). Upon, and during, rehydration there is a further loss of radioactivity from the poly(A)$^+$ RNA fractions, the rate of loss being similar for both rapid- and slow-dried samples. This is taken to indicate that there is a relatively rapid turnover of conserved poly(A)$^+$ RNA during the rehydration phase.

A comparison was then made between the rate of turnover of the various RNA pools upon rehydration and their normal rate of turnover in undesiccated moss. The labeling protocol used for this experiment was identical to that used in the previous experiment (see "Materials and Methods") except that a desiccation event was not included. The turnover of total and poly(A)$^-$ RNA pools of the hydrated moss (Fig. 2A) is similar to that exhibited by the same pools in the rehydrated slow- and rapid-dried moss

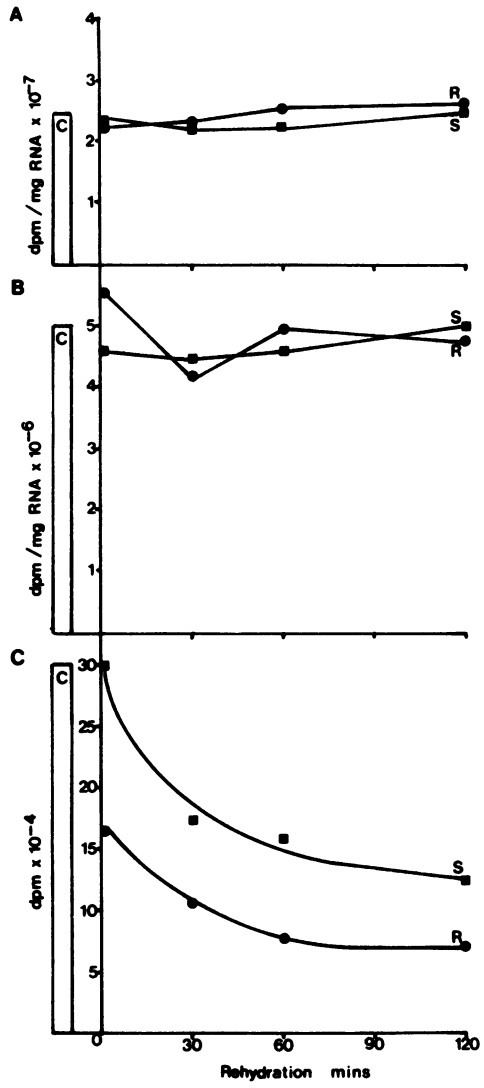

FIG. 1. Stability of cellular RNA pools to desiccation, both rapid (R) and slow (S), and rehydration in gametophytes of *T. ruralis*. A, total RNA; B, poly(A)$^-$ RNA; and C, poly(A)$^+$ RNA. Hydrated moss was incubated for 4 h in the presence of 30 μCi of [^{3}H]adenosine prior to rapid and slow desiccation. Rehydration of duplicate samples, for 30, 60, and 120 min, was achieved by placing dried moss in 3 ml water containing 1 mg of unlabeled adenosine. RNA extraction and fractionation was implemented as described in "Materials and Methods." Levels of radioactivity in RNA pools of undesiccated controls (C) are depicted as histograms to the left of each abscissa.

(Fig. 1, A and B). The stability of the poly(A)$^+$ RNA pool in hydrated moss is shown in Figure 2B. The kinetics of loss of radioactivity from this fraction is comparable to that from the same fraction in rehydrated rapid- and slow-dried moss (Fig. 1C). Hence desiccation, whether it be achieved rapidly or slowly, does not enhance the normal turnover rate of the poly(A)$^+$ RNA pool upon subsequent rehydration.

The Presence of Conserved RNA in Polysomes during Desiccation and Rehydration. Total polysomal RNA (Fig. 3A) appears to be only slightly sensitive, if at all, to desiccation, in that the level of radioactive adenosine found in the ribosomal pellets of dried samples is very similar to that found in the undesiccated control (compare C with time 0). Upon rehydration of either rapid- or slow-dried moss there is only a minor loss of prelabeled RNA showing that, overall, the total polysomal RNA pool is very stable to both desiccation and rehydration. The effect of

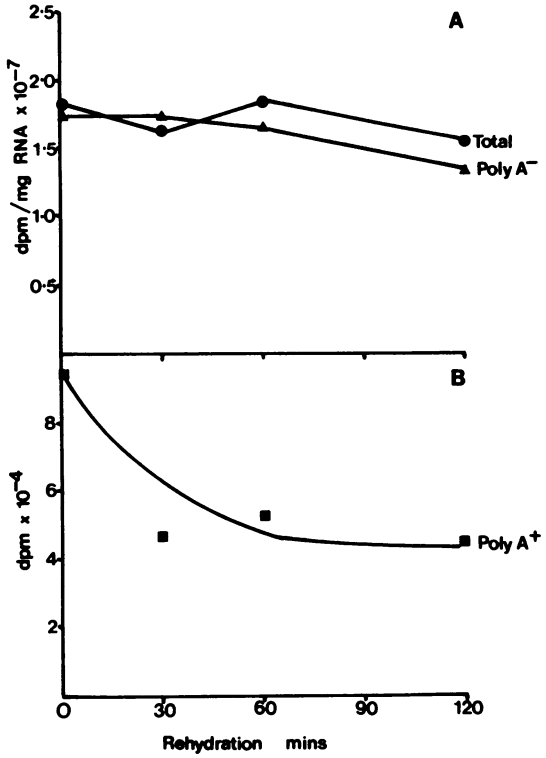

FIG. 2. Turnover of cellular RNA pools in hydrated *T. ruralis* gametophytes. A, total and poly(A)$^-$ RNA; B, poly(A)$^+$ RNA. Hydrated moss was incubated for 4 h in the presence of 30 μCi of [^{3}H]adenosine prior to washing and incubation for 30, 60, 90, and 120 min in a 0.33 mg/ml solution of adenosine. RNA was then extracted and fractionated from duplicate samples as described in "Materials and Methods."

drying and rehydration on the polysomal poly(A)$^-$ RNA pool (Fig. 3B) is similar to that observed for the total polysomal RNA pool, except that the loss during desiccation and rehydration is somewhat amplified. The levels of radioactivity in the polysomal poly(A)$^-$ RNA of both rapid- and slow-dried moss are essentially equal and hence the losses which occur during desiccation are the result of water loss *per se* rather than the speed at which drying occurs. Losses probably represent a movement of RNA from the polysomal pool into the free cellular pool rather than a destruction of RNA.

The effect of desiccation and rehydration on the levels of poly(A)$^+$ RNA in the polysomal fraction is depicted in Figure 3C. Upon desiccation (*i.e.* at time 0), there is a considerable decrease in radioactivity in the poly(A)$^+$ RNA pool when compared to that in the undesiccated control. The loss of poly(A)$^+$ RNA from the protein synthetic complex is greater from samples subjected to slow drying. Since approximately 50% of the polysomes are retained during rapid desiccation and nearly all are lost as a result of slow desiccation (7), the levels of poly(A)$^+$ RNA in this fraction in slow- and rapid-dried moss probably directly reflects the state of the polysomes.

During the first 30 min of rehydration, the level of poly(A)$^+$ RNA in the polysomal fraction of rapid-dried moss declines, but in the slow-dried moss it increases. In slow-dried moss, the increase in the level of conserved poly(A)$^+$ RNA in the polysomal fraction is probably due to the reformation of polysomes upon the addition of water, coupled with an initial recruitment of conserved mRNAs. The decline in conserved poly(A)$^+$ RNA in the polysomes of rapid-dried moss upon rehydration could be due to the complete loss, or limited disruption, of the retained polysomes and their associated messages. At later times of rehydration, the levels of poly(A)$^+$ RNA in the polysomal complex

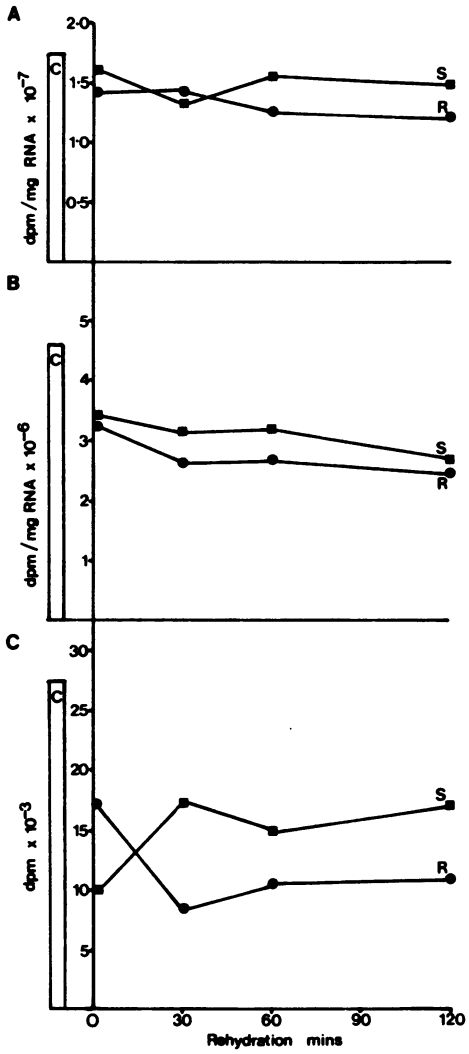

FIG. 3. Stability of polysomal RNA pools to desiccation, both rapid (R) and slow (S), and rehydration in gametophytes of *T. ruralis*. A, total polysomal RNA; B, polysomal poly(A)$^-$ RNA; and C, polysomal poly(A)$^+$ RNA. Hydrated moss was incubated for 4 h in 3 ml water containing 30 μCi [^{3}H]adenosine prior to desiccation. Rehydration was achieved by placing dried moss in a 0.33 mg/ml solution of adenosine. RNA was extracted from ribosomal pellets obtained from duplicate samples as detailed in "Materials and Methods." Levels of radioactivity in RNA pools of undesiccated controls (C) are depicted as histograms to the left of the abscissae.

of both rehydrated rapid- and slow-dried moss remain constant (or possibly increase slightly), which is indicative of the continued use of conserved messages. It is also indicative of the ability of *T. ruralis* to conserve mRNA in a potentially active form upon desiccation (4).

Synthesis of RNA in the Total Cellular Pools upon Rehydration of Dried Moss. The effect of desiccation upon the rate of recovery of RNA synthesis upon rehydration, using [^{3}H]uridine as precursor, has been documented (2, 3, 10). Essentially, RNA synthesis starts almost immediately upon rehydration, and at a faster rate following slow desiccation than after rapid desiccation. Identical results were obtained when [^{3}H]adenosine was used as precursor (9), and synthesis of poly(A)$^-$ RNA upon rehydration is also faster after slow than after rapid desiccation (9). The resumption of poly(A)$^+$ RNA synthesis upon rehydration does not follow this trend, however (Fig. 4). The rate of [^{3}H]adenosine incorporation into poly(A)$^+$ RNA is identical during the first 60

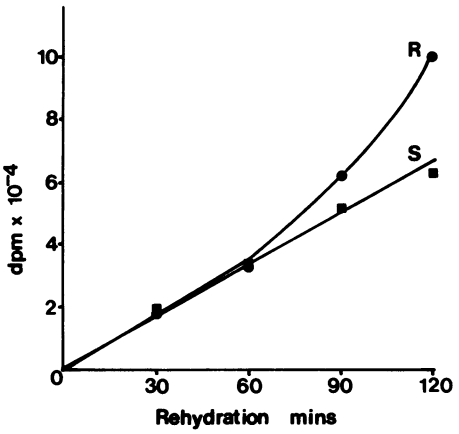

FIG. 4. Synthesis of poly(A)$^+$ RNA upon rehydration of both rapid- (R) and slow- (S) dried *T. ruralis*. Duplicate samples of dried moss were rehydrated in 3 ml water containing 20 μCi [^{3}H]adenosine for 30, 60, 90, and 120 min. RNA extraction and fractionation was implemented as described in "Materials and Methods."

min of rehydration for both rapid- and slow-dried *T. ruralis*. After this initial period of equality, the rate of adenosine incorporation into poly(A)$^+$ RNA in samples that were rapidly dried substantially increases above that exhibited by the moss that had undergone slow desiccation. In fact, between 90 and 120 min post hydration, the rate of adenosine incorporation into poly(A)$^+$ RNA of rehydrated rapid-dried moss is three times that into poly(A)$^+$ RNA of rehydrated slow-dried moss (1312.5 dpm/min rehydration and 416.7 dpm/min rehydration, respectively). Since total RNA synthesis occurs at a faster rate in moss rehydrated from the slow-dried state (2, 3, 10), it appears that in rapidly desiccated moss there is some preference for poly(A)$^+$ RNA synthesis upon rehydration. This may reflect a response of the moss, which is rapidly dried, to replace mRNA damaged during desiccation (Fig. 1C).

Recruitment of RNA Types into Protein Synthesis upon Rehydration. The recruitment into the protein synthetic complex of the total and poly(A)$^-$ RNA synthesized upon rehydration of both rapid- and slow-dried samples (Fig. 5, A and B) closely resembles the rate of synthesis of total RNA described previously (10). Moreover, as with the synthesis of total poly(A)$^+$ RNA upon rehydration (Fig. 4), its rate of recruitment into protein synthesis is the same for both slow- and rapid-dried moss during the first 60 min of rehydration (Fig. 5C). Following this period, the rate of recruitment of poly(A)$^+$ RNA for protein synthesis of rehydrated rapid-dried moss increases appreciably above that of the rehydrated slow-dried moss. The kinetics of poly(A)$^+$ RNA recruitment into protein synthesis for both samples is somewhat sigmoidal in nature—more so for the recovered rapid-dried moss. The point of exponentiality for the recruitment of poly(A)$^+$ RNA in this sample corresponds to the point at which the synthesis of poly(A)$^+$ RNA increases (Fig. 4). The enhanced recruitment of poly(A)$^+$ RNA, coupled with the increase in synthetic rate, in rehydrated rapid-dried moss may reflect the greater requirement for proteins essential for repair of cellular damage incurred during rapid desiccation (compared to the lesser damage resulting from slow-drying), as suggested by Bewley (1).

RNA Stability and Synthesis in the Aquatic Moss *C. filicinum*. For comparison, the stability of the RNA pools to desiccation and rehydration were analyzed for the aquatic moss *C. filicinum*, a nondesiccation-tolerant moss (8), as was its ability to synthesize RNA upon rehydration.

The total RNA pool (Fig. 6A) is unaffected by desiccation, irrespective of the speed at which it occurs (compare undesiccated control C to time 0). Upon rehydration, however, there is a rapid

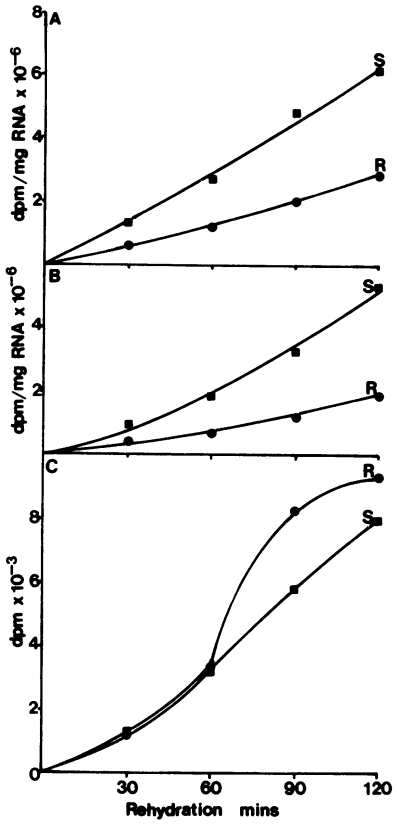

FIG. 5. Recruitment of newly synthesized RNA types into the protein synthetic complex upon rehydration of both rapid- (R) and slow- (S) dried *T. ruralis*. A, total polysomal RNA; B, polysomal poly(A)$^-$ RNA; and C, polysomal poly(A)$^+$ RNA. Duplicate samples of dried moss were rehydrated in 3 ml water containing 20 μCi [^{3}H]adenosine for 30, 60, 90, and 120 min. Ribosomal pellets were isolated and subjected to RNA extraction and fractionation as described in "Materials and Methods."

decline in the level of total RNA such that after 30 min post-hydration only about 40% of the original RNA remains. For the remainder of the 2 h rehydration period, there is no further reduction in total RNA levels. This situation is mirrored in the stability profile of the poly(A)$^-$ RNA pool (Fig. 6B). Thus, we suggest that for these RNA pools it is rehydration, and not desiccation *per se*, that causes a loss of RNA integrity. This suggestion is consistent with earlier studies involving protein synthesis and other metabolic processes (1).

The effect of desiccation and rehydration on the levels of poly(A)$^+$ RNA is somewhat different (Fig. 6C). Desiccation, at either slow or rapid speeds, results in a small decline in poly(A)$^+$ RNA levels, with approximately 80% of the poly(A)$^+$ RNA pool remaining in the desiccated state. As with the total and poly(A)$^-$ RNA pools, poly(A)$^+$ RNA declines rapidly during the first hour of rehydration, after which the levels are stable. This decline in stability upon rehydration is independent of the speed at which desiccation is achieved. Although the stability of poly(A)$^+$ RNA in undesiccated *C. filicinum* was not measured, the decline in poly(A)$^+$ RNA upon rehydration of this moss is remarkably similar to that exhibited by poly(A)$^+$ RNA of *T. ruralis* (Figs. 1C and 2B). The recruitment of conserved RNA into protein synthesis was not investigated in this moss since upon rehydration of *C. filicinum* there is complete inactivation of both retained polysomes (following rapid-drying) and of single ribosomes (6).

The extent of RNA synthesis upon rehydration of both rapid- and slow-dried gametophytes of *C. filicinum* is presented in Table I. Although there is some incorporation of [^{3}H]adenosine into

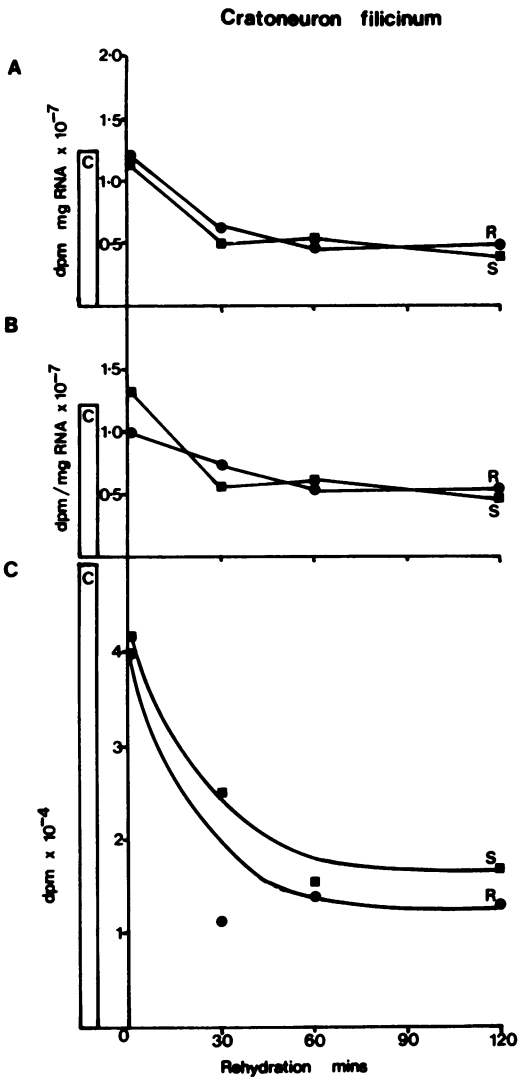

FIG. 6. Stability of cellular RNA pools to desiccation, both rapid (R) and slow (S), and rehydration in gametophytes of *C. filicinum*. A, total RNA; B, poly(A)$^-$ RNA; and C, poly(A)$^+$ RNA. Gametophytes of *C. filicinum* were labeled and analyzed as described for *T. ruralis* (Fig. 1). Levels of radioactivity in RNA pools of undesiccated controls (C) are depicted as histograms to the left of the abscissae.

total RNA, the level of incorporation as a percentage of uptake is low compared to control values, and hence the RNA synthetic capacity of *C. filicinum* is disrupted severely by desiccation. The low level of incorporation is probably an indication that only a few cells of the gametophyte survive this treatment.

CONCLUSIONS

The total RNA pool, and the poly(A)$^-$ RNA subpool of *T. ruralis* are highly stable to desiccation, regardless of the speed of drying, and to rehydration. In comparison, the same RNA pools of the aquatic moss *C. filicinum* are only stable to desiccation and are partially lost during the initial phases of rehydration. That poly(A)$^-$ RNA in *C. filicinum* is not damaged during desiccation can be inferred from the observation that ribosomes extracted from dried moss are active in an *in vitro* protein synthesizing system (Malek and Bewley, unpublished). From this we suggest that it is during the rehydration process that irreversible cellular damage occurs. Moreover, the ability of a moss to conserve RNA when in the dry state, and protect it during the influx of water, is an important factor in conferring desiccation tolerance. In *T. ruralis* the stable, conserved total cellular poly(A)$^-$ RNA (predominantly rRNA) pool is utilized in protein synthesis during rehydration to an extent which is determined by the prior speed of drying. In contrast, rRNA in *C. filicinum* loses its ability to participate in protein synthesis upon rehydration (6). *T. ruralis* is capable of synthesizing and utilizing rRNA upon rehydration, whereas this does not occur in *C. filicinum*. Thus the ability to retain the capability of RNA synthesis upon rehydration following desiccation is also an important factor involved in desiccation tolerance.

Table I. *Recovery of RNA Synthesis during the First 2 Hours of Rehydration of C. filicinum following Rapid or Slow Desiccation*

Samples rehydrated in 3 ml distilled water containing 20 μCi [^{3}H] adenosine, 200 IU/ml penicillin, and 250 μg/ml streptomycin.

	Incorporation during Recovery from Desiccation for		
	30 Min	60 Min	120 Min
	dpm/mg RNA × 10^{-6}		
Control	5.7 (22.3)[a]	9.24 (21.3)	11.65 (22.5)
Slow-dried	0.11 (1.0)	0.09 (0.7)	0.15 (1.3)
Rapid-dried	0.04 (0.3)	0.06 (0.5)	0.08 (0.5)

[a] Numbers in parentheses indicate incorporation as a per cent of uptake.

Surprisingly, the stability of mRNA to desiccation and rehydration does not appear to be a factor in conferring desiccation tolerance on a moss. The cytoplasmic pool of mRNA in the *C. filicinum* gametophytes is largely stable to desiccation, and its decline upon rehydration appears to be similar to that in *T. ruralis* (compare Fig. 1C with 6C). In fact, it seems that the cellular mRNA pool of *C. filicinum* is more stable to desiccation, when the desiccation is rapid, since only 20% is lost during desiccation of this moss, compared to approximately 50% in *T. ruralis*. There is no apparent explanation for this phenomenon. Nevertheless, it is the ability of *T. ruralis* to utilize conserved mRNA for protein synthesis, and its capacity for new mRNA synthesis upon rehydration that is an important aspect of its ability to withstand desiccation. The failure of *C. filicinum* to synthesize RNA upon rehydration is consistent with previous findings that this species also fails to recover protein synthesis upon the readdition of water (8), probably as a consequence of the complete inactivation of both retained polysomes and ribosomes (6). The results presented here also give support to the hypothesis that it is the influx of water into the dry moss, rather than drying *per se*, that is the major disruptive force in this system (1).

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