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Breaking of Dormancy during After-Ripening of *Triticum durum* DESF.: RNA, poly(A)$^+$RNA and Protein Metabolism in Imbibed Embryos.

By

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With 3 Figures

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Summary

GRILLI I., ANGUILLESI M. C. & FLORIS C. 1994. Breaking of dormancy during after-ripening of *Triticum durum* DESF.: RNA, poly(A)$^+$RNA and protein metabolism in imbibed embryos. – Phyton (Horn, Austria) 34 (1): 119–130, 3 figures. – English with German summary.

Triticum durum DESF. caryopses have a relative dormancy, which is released during a period of after- ripening. Their embryos were studied during seed storage under laboratory conditions at intervals of two months, from harvest to loss of dormancy (six months). The metabolism of total RNA, poly(A)$^+$RNA and proteins was studied on dry, early (40 min), and late imbibed embryos (5 h, 25 h) with or without cordycepin, a polyadenylation inhibitor.

Results showed that the macromolecules studied were synthesized in both non after-ripened (dormant) and after-ripened (non dormant) embryos. However, after 2–4 months of storage, no synthesis was evident.

The results suggest the occurrence, 2–4 months after harvest, of a transition phase from a metabolism typical of seed maturation to a metabolism typical of germination. During after-ripening and imbibition, the embryos showed a degradation of some stored mRNA.

Zusammenfassung

GRILLI I., ANGUILLESI M. C. & FLORIS C. 1994. Das Brechen der Samenruhe während der Nachreifung von *Triticum durum* DESF.: RNA, poly(A)$^+$RNA und Protein-

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stoffwechsel in Embryos nach Wasseraufnahme. – Phyton (Horn, Austria) 34 (1): 119–130, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Karyopsen von *Triticum durum* DESF. besitzen eine relative Samenruhe, welche während einer Periode der Nachreifung gelöst wird. Die Embryos wurden während der Lagerung der Samen unter Laborbedingungen in Abständen von zwei Monaten von der Ernte bis zur Beendigung der Samenruhe (6 Monate) untersucht. Der Stoffwechsel der gesamten RNA, poly(A)$^+$RNA und Proteinen wurde an trockenen, kurz (40 min) und lang (5 h, 25 h) gequollenen Embryos untersucht. Gleichzeitig wurde mit oder ohne Cordycepin, einem Hemmstoff der Polyadenylierung, getestet.

Die Ergebnisse zeigen, daß die untersuchten Makromoleküle in Embryos synthetisiert werden, welche sowohl nicht nachgereift (Samenruhe) als auch nachgereift (Beendigung der Samenruhe) waren. Jedoch nach zwei bis vier Monaten Lagerung konnte keine Synthese mehr festgestellt werden.

Die Ergebnisse lassen das Auftreten einer Übergangsphase (zwei bis vier Monate nach der Ernte) erkennen, in der sich der für die Samenreifung typische Stoffwechsel zu einem für die Keimung typischen ändert. Während der Nachreifung und Quellung zeigen die Embryos einen Abbau einiger gespeicherter mRNAs.

Introduction

Immediately after harvesting, the caryopses of some *Gramineae* have a slower rate of germination at usual temperatures, above about 18° C (BEWLEY & BLACK 1982). This type of dormancy, called relative dormancy, is overcome naturally after the seed has passed some time in a dry state.

Physiological changes in dormant seeds during storage are not well understood and some evidence suggests that the physical state of cell membranes is involved in changes in dormancy (CUMING & OSBORNE 1978 b). Measurable biochemical differences between dormant and non-dormant seeds exist in inhibitors content or in responsiveness to inhibitor (MIYAMOTO & al. 1961; KOORNEEF & al. 1989; MORRIS & al. 1989), in the metabolism of carbohydrates (ANDERSON 1970, ROBERTS & SMITH 1977), and in protein and nucleic acids (JARVIS & SHANNON 1981, SHANNON & JARVIS 1982).

To gain further insight into the biochemical aspects of dormancy in *Triticum durum* Desf. cv. Cappelli, a comparative study of RNA, poly(A)$^+$RNA and protein metabolism in dormant and non dormant seeds (GRILLI & al. 1980, 1986) was made. The breakage of dormancy in the embryos of *durum* wheat, whose caryopses are characterized by a relative dormancy (MELETTI 1964), was accompanied, in dry conditions, by a decline in protein and poly(A)$^+$RNA content and by a reduced capacity of mRNA to codify for proteins (GRILLI & al. 1986).

The present study was carried out on embryos of *durum* seeds in different phases of after-ripening and at different times of seed germination. The influence of cordycepin, an inhibitor of the polyadenylation process, was evaluated in order to identify the synthesis of proteins codified by the new synthesized RNA from the one codified by the stored RNA.

Materials and Methods

The seeds

Experiments were carried out using seeds of *Triticum durum* cv. Cappelli grown in the countryside near Pisa and stored at laboratory temperature (18–20° C) in dry conditions. Batches of size selected seeds were collected at intervals of two months during after-ripening (July, 0 mth.; Sept., 2 mth.; Nov., 4 mth.; Jan., 6 mth.) and then imbibed for 40 min, 5 h, and 25 h before the extractive procedure.

Germination test

Seeds were surface-sterilized for 5 min with 1% Na-hypoclorite, carefully rinsed in sterile distilled water and then germinated in the dark on sterilized filter paper in distilled water alone or containing 0.010 mM gibberellic acid (GA_3) at 23° C.

Germination was evaluated as percentage at 24h intervals over three days. The value shown in the results is the average of three separate experiments (50 seeds each).

Protein content and synthesis

Lots of 50 embryos, hand-isolated from surface sterilized dry seeds, were sown at 23° C in CAERS & al's germination medium (GM) (1979): 10 mM Tris HCl pH 7, 20 mM KCl, 10 mg · mL^{-1} sucrose and 50 μm^{-1} chloramphenicol. Embryos were also sown in GM+Cordycepin (GM + Cor) containing 0.250 mM cordycepin. Both media contained 0.6 MBq · mL^{-1} [4,5–^{3}H] leucine (specific activity: 5.4 TBq · m mol^{-1}).

Soluble proteins were extracted (two replicates) using GRILLI & al. 's method (1986) with 0.05 M acetate pH 5.6 and 0.5% 2-mercaptoethanol. Aliquots of supernatant were used for fluorographic analysis and for the quantitative determination of protein content and synthesis. Protein content was determined using a modified version of the Lowry method (BENSADOUN & WEINSTEIN 1976). The uptake and incorporation of the amino acid were determined using the method of ROBERTS & al. (1973). The filters were treated with Protosol (NEN) and Econofluor (NEN) and then counted. The results are the average of three separate experiments.

Poly(A)$^+$RNA content and synthesis

The RNA extracted by using the phenol-SDS method (LIOI & al. 1984) was dissolved in 10 mM Tris HCl pH 7.4, 0.5 M NaCl, 0.5% SDS and then subjected to oligo(dT)cellulose chromatography (FELICETTI & al. 1975). The poly(A)$^+$RNA was passed twice through an oligo(dT) column and the content was determined by A 260 (22 A 260 = 1 mg · mL^{-1}). In all experiments the values are the means of two replicates.

For the study of the synthesis, poly(A)$^+$RNA was extracted as above from embryos incubated in the medium containing 1.1 MBq.mL [2–^{3}H] adenosine (specific activity: 777 GBq m mol^{-1}, Amity) and then washed in ice-cold sterile distilled water. Uptake and incorporation of extracted RNA were determined before ethanol precipitation. Poly(U)-fiberglass filters (SHELDON & al. 1972) were used for the poly(A)$^+$ synthesis evaluation. Radioactive RNA, obtained by precipitation with ethanol and collected by centrifugation, was dissolved and tested, as in TAKAHASHI & NITTA (1986). The filters were washed with 20 ml ice-cold 5% trichloroacetic acid and treated with Protosol and Econofluor (NEN). The values of the RNA and

poly(A)$^+$RNA uptake and incorporation, reported in the figures are the means of three replicates. All phases of the extraction were carried out at 2–4° C. The glassware was treated at 350° C for 3 h or treated with 0.4% diethylpyrocarbonate and the solutions were autoclaved.

Results

Germination

The time courses of changes in the percentage germination of seeds, stored for several months, (Tab. 1) show that storage after harvest significantly increases the germination rate. The germination at the first three storage periods was increased by the GA_3 with a higher stimulation in freshly harvested (dormant) seeds.

Table 1

Effect of GA_3 at different times, in the after-ripening seeds. Germination was evaluated in percentage and each value is the mean of three replicates (± S. E.).

Time	Treatment	0*)	2*)	4*)	6*)
24 h	H_2O	8±1	26±2	36±2	86±3
	GA_3	26±3	71±2	82±1	82±2
48 h	H_2O	24±2	54±1	82±1	100
	GA_3	64±0	90±2	100	100
72 h	H_2O	26±2	80±2	84±1	100
	GA_3	94±0	94±1	100	100

*) months after harvest

RNA, poly(A)$^+$RNA and proteins in dry and 40 min imbibed embryos

As in our previous research (Grilli & al. 1986) the dry embryos contain poly(A)$^+$RNA and interestingly this RNA decreases during after-ripening (Fig. 1 b) and the degradation is accompanied by a decline in protein content (Fig. 1 b').

The content of poly(A)$^+$RNA of imbibed embryos during after-ripening is similar to the dry stage, while in dormant seed embryos the content decreases.

In spite of RNA synthesis (Fig. 1 a), in the embryos imbibed for 40 min, it is not possible to prove that [2–^{3}H] adenosine is incorporated into the poly(A)$^+$RNA. The results concur with the absence of an inhibitory effect of cordycepin on the poly(A)$^+$RNA synthesis. By contrast, the incorporation of labelled leucine and the synthesis of proteins, estimated as I/U.100 (Fig. 1a', a"), do in fact occur, to an extent which declines during after-ripening.

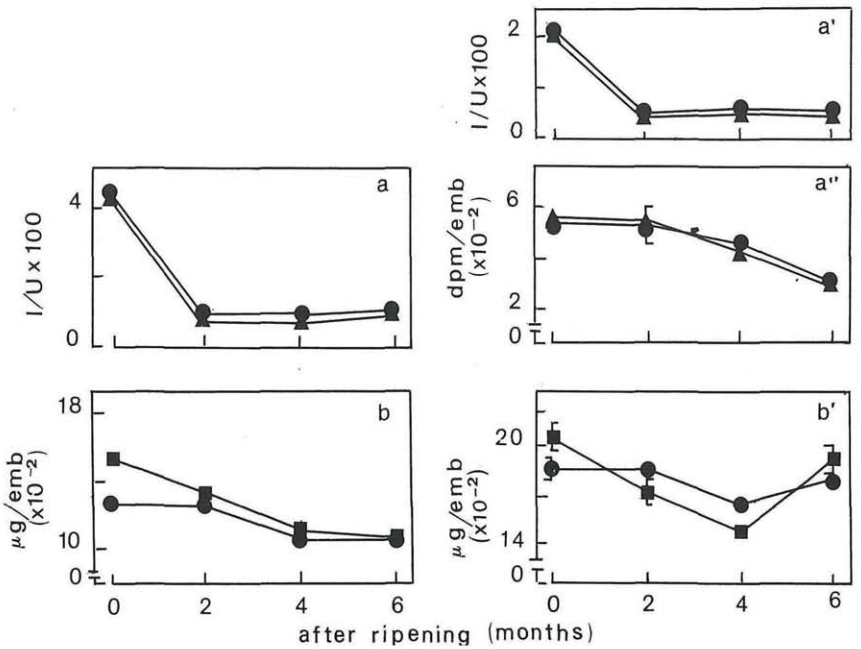

Fig. 1. Effect of after-ripening on the total RNA (a) and proteins (a', a") synthesis; on poly(A)⁺RNA (b) and proteins (b') content. Dry (–■–) and 40 min imbibed embryos in GM (–●–) or GM+Cor (–▲–). Data of synthesis is given as I/U · 100 and dpm/embryo. The values are the means of three replicates. Bars indicate the standard error (S. E.) ; when the S. E. was less than the symbol size, the error bars are not shown.
Data on cordycepin treatments in the poly(A)⁺RNA are not shown because they are similar to the control.

5 h imbibed embryos

Synthesis of RNA, poly(A)⁺RNA and proteins occurs in this pre-growth period. The extent of these syntheses changes during seed post-maturation and shows, two months after harvest, a drop in RNA, poly(A)⁺RNA and protein synthesis (Fig. 2 a, b, c, b', c') in water-imbibed seeds. The drop is followed by a very high increase in both RNA and protein synthesis (Fig. 2a, b', c'). Simultaneously with the drop in the synthesis of proteins, a high value of proteins content occurs showing an accumulation of proteins (Fig. 2d').

The amount of synthesis and the content of poly(A)⁺RNA (Fig. 2 b, d) are very much lower in non-dormant than in dormant seeds as previously shown (GRILLI & al. 1986), in contrast with the amount of protein synthesis, which is similar in dormant and non-dormant embryos.

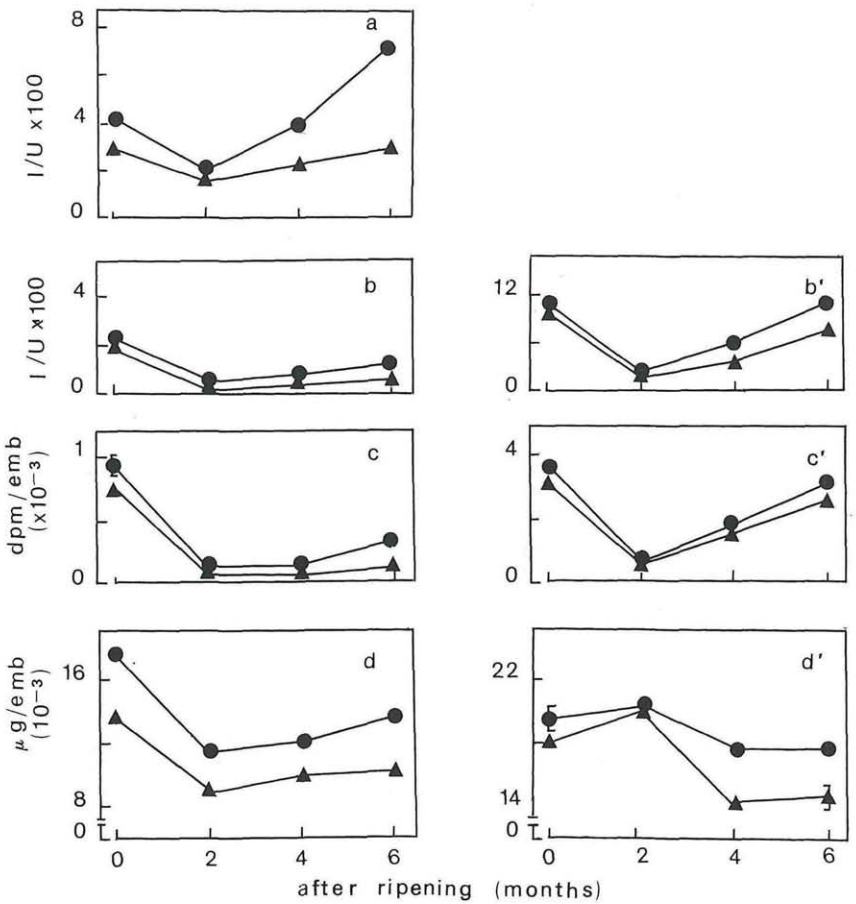

Fig. 2. Changes in total RNA (a), poly(A)$^+$RNA (b,c) and protein (b', c') synthesis, poly(A)$^+$RNA (d) and proteins content (d') in after-ripening embryos. Imbibition in GM (–●–) or GM+Cor (–▲–) for 5h. Synthesis of poly(A)$^+$RNA (b, c) and soluble proteins (b', c') is valuated as I/U · 100 and dpm/embryo.
Vertical bars represent S. E. of the mean of three replicates; when the S. E. was less than the symbol size, the error bars are not shown.

Interestingly, cordycepin inhibits RNA and poly(A)$^+$RNA synthesis at a different rate during after-ripening (Tab. 2). The inhibitory effect is much higher on non dormant than on dormant embryos and this event also occurs in the protein synthesis. This different inhibitory effect is not due to a variation in the uptake of the labelled precursors. In fact, differences are not recorded in the uptake during postmaturation between the controls and the cordycepin treated embryos (our data, not shown here).

Table 2

Percentage of inhibition by cordycepin on the poly(A)$^+$RNA and protein synthesis at 5 h and 25 h of imbibition.

Months after harvest	Poly(A)$^+$RNA		Proteins	
	5 h	25 h	5 h	25 h
0	17	24	11	38
2	57	40	2	0
4	38	54	12	49
6	49	63	18	54

25 h imbibed embryos

After a more prolonged imbibition RNA, poly(A)$^+$RNA and protein synthesis in the embryos follow a similar pattern to that at 5 h. The labelled leucine and adenosine are taken up and incorporated into proteins and poly(A)$^+$RNA, with nearly the same intensity, in both the fresh embryos in the dormant stage and the after-ripened embryos (Fig. 3). As with 5 h imbibition, there is a drop after two months of storage for protein synthesis and after two and four months for poly(A)$^+$RNA.

Discussion

Freshly harvested seeds of *Poaceae* such as *Avena fatua* (CORBINEAU & al. 1991), *Oryza sativa* (SESHU & DADLANI 1991) may be dormant, in the case of *Triticum durum* cv. Cappelli the dormancy is relative (MELETTI 1964): dormant caryopses placed in water germinate very slowly even though environmental conditions are optimum for the germination of non dormant seeds.

Dry storage (six months) progressively breaks dormancy (Tab.1) and the storage was also overcome by germinating the seeds in GA_3 as in *Avena fatua* (ADKINS & al. 1984). In Tab.1 there is the evidence that GA_3 plays an important role in the regulation of dormancy in wheat grains. The extent of stimulatory effects decreases during storage in parallel with the breakage of dormancy. For some months, the seeds maintained relative dormancy to varying degrees: maximum in freshly harvested seeds (dormant), minimum after four months, and absent after six months storage (non dormant).

The metabolic activity in cereal seeds during after-ripening is still not well understood: changes in germination, growth, respiration and glucose metabolism of partially dormant wheat seeds were reported (ANDERSON 1970); in *Avena fatua,* in particular, the content of fatty acid and the degree of dormancy have been correlated (BERRIE 1979). In *Oryza sativa* LEOPOLD

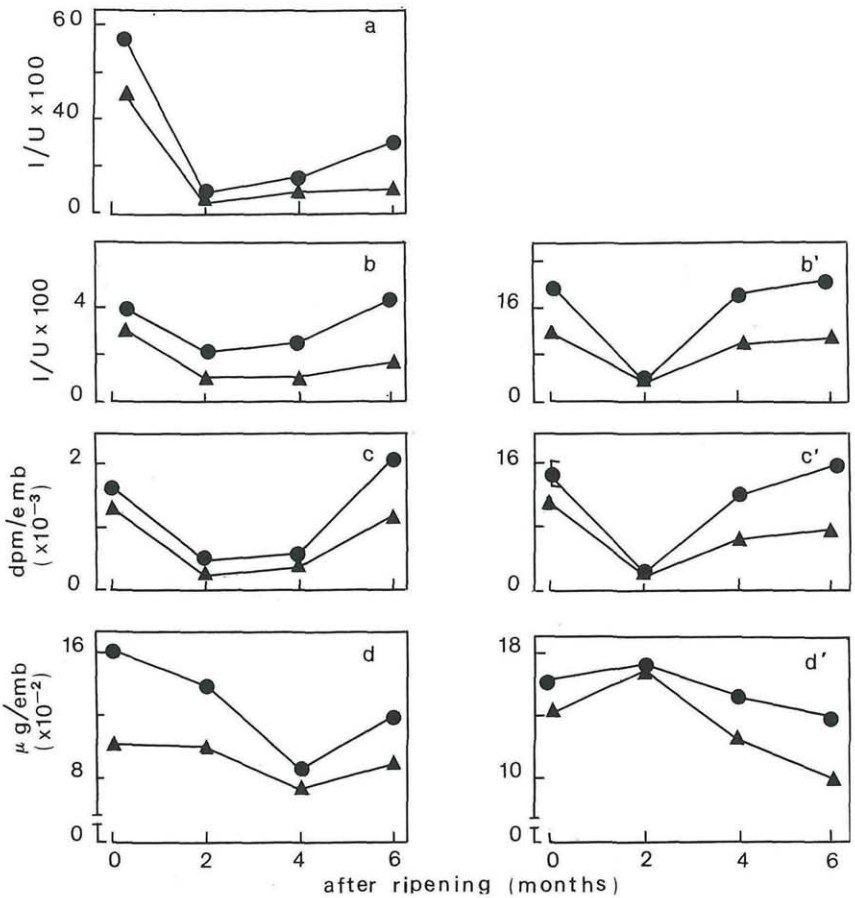

Fig. 3. Changes in total RNA (a), poly(A)⁺RNA (b, c) and proteins (b', c') synthesis, poly(A)⁺RNA(d) and proteins (d') content in after-ripening embryos. Imbibition in GM (–●–) or GM+Cor (–▲–) for 25 h. Synthesis of poly(A)⁺RNA (b, c) and soluble proteins (b', c') is valuated as I/U · 100 and dpm/embryo.
Vertical bars represent S. E. of the mean (when the S.E. was less than the symbol size, the error bars are not shown).

& al. 1988 suggested that after-ripening may involve changes related to some oxidative reactions which would be limited on the high moisture.

Our results shows as in a previous research (GRILLI & al. 1986) the presence of residual poly(A)⁺RNA in dry dormant and non dormant embryos. Interestingly this residual poly(A)⁺RNA during the after-ripening (Fig. 1b) suggests a degradation of RNA not used in the metabolic processes occurring during imbibition of non dormant embryos.

As in SPIEGEL & MARCUS 1975 the imbibition of 40' is not sufficient to allow a synthesis of poly(A)$^+$RNA differently to the protein synthesis. This result suggests that the protein synthesis established during this period may be dependent on the stored mRNAs.

Studies on imbibed embryos of a number of species, including *Avena fatua* (CUMING & OSBORNE 1978 a), *Vaccaria pyramidata,* (HECKER & KOHLER 1979), buds of *Solanum* (MACDONALD & OSBORNE 1988) have demonstrated that dormancy is not characterized by a total lack of metabolic and synthetic activity. Our results confirm that dormant as well as after-ripened embryos are characterized by a high level of [4,5-^{3}H] leucine incorporation into proteins and also by the high levels of [2-^{3}H] adenosine into RNA. This agrees with a previous work (GRILLI & al. 1986), since any substantial differences in the amount of proteins and poly(A)$^+$RNA synthesis were not observed between imbibed (25 h) dormant and non dormant embryos, as it has been demonstrated for wild oat (CUMING & OSBORNE 1978 a). In studies on *Avena fatua* (OSBORNE & al. 1984) no differences were observed between imbibed dormant and non dormant tissues until the onset of DNA replication and cytokinesis. In the non dormant *T. durum* embryos imbibed at 25 h, the DNA replication probably begins: in fact, DNA synthesis in non dormant germinating wheat becomes appreciable after 9 to 15 h of imbibition (TAYLORSON & HENDRICKS 1977). Therefore, the differences we observed in the studied macromolecules would have taken place before the initiation of DNA replication in non dormant embryos.

In the course of after-ripening at room temperature, the seeds of *T. durum* lose dormancy and their metabolism and synthetic activity are particularly interesting. This work shows that the typical change displayed by seeds in the gradual loss of dormancy is the drop in the metabolism of RNA, poly(A)$^+$RNA and proteins after two months of after-ripening. The decline in protein synthesis at two months of after-ripening (Fig. 2 b', c'; Fig. 3 b',c') may be due to a decline in the translable long lived mRNAs, after this period of dry storage a high synthesis of new mRNAs typical of non dormant seeds is probably present. The inhibitory effect of cordycepin (Tab.2) changes during storage and the increased action of this drug is in accordance to a new synthesis of poly(A)$^+$RNAs during the later after-ripening. The metabolic changes at two months of storage are probably responsible of overcoming dormancy. There seems to be a period of transition from a metabolism that correlates with maturation to a metabolism that correlates with the processes involved in seed germination. Moreover, not only a degradation of a probably residual poly(A)$^+$RNA during dry storage is evident but, during imbibition, there is an inactivation or a degradation of some of the stored poly(A)$^+$RNA, probably mRNA, which codified for proteins characteristic of fresh dormant embryos. The inactivation, or de-

gradation, may well be connected to a new synthesis of mRNA. Therefore the genome would not remain repressed, but probably the classes of RNA and proteins synthesized differ between dormant and non dormant embryos. This investigation should now be followed by a detailed study of the transcription and turnover of mRNA, and by studies of the comparison of in vitro translation products of different messengers during after-ripening.

Acknowledgements

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Recensiones

BAYER Clemens 1994. Zur Infloreszenzmorphologie der *Malvales*. - Dissertationes botanicae, Band 212. – 8°, VI + 280 Seiten, 90 Abb. im Text, 2 Tafeln; kart. – J.Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart.

Die Blütenstände von zahlreichen Arten aus 96 Gattungen aus den Familien *Sterculiaceae, Elaeocarpaceae, Tiliaceae, Bombacaceae* und *Malvaceae* sind untersucht worden. Die Ergebnisse sind nach Familien, Tribus und Gattungen gereiht, auf p. 19–162 dargestellt und durch zahlreiche Abbildungen (Strichzeichnungen, Grund- und Aufrisse, 13 REM-Photos von frühen Entwicklungsstadien) dargestellt. Daran schließt sich eine sehr ausführliche Diskussion der Ergebnisse (p. 163–262). Als charakteristisch für *Sterculiaceae-Byttnerioideae* und *Tiliaceae* wird eine nach *Theobroma bicolor* als „Bicolor-Endverzweigung" benannte Gestaltung der Partialinfloreszenzen angesehen: Einer Endblüte gehen eine sterile Braktee und zwei zumindest potentiell fertile Brakteen voraus. Auf dieser Basis können auch zweiblütige Partialinfloreszenzen mancher *Sterculiaceae* und das Zustandekommen von Außenkelchen interpretiert werden. Das Verhältnis monoteler zu polytelen Synfloreszenzen wird ebenso diskutiert, wie ontogenetische, phylogenetische und systematische Fragen.

H. TEPPNER

COCQUYT C., VYVERMAN W. & COMPÈRE P. 1993. A Check-List of the Algal Flora of the East African Great Lakes (Malawi, Tanganyika and Victoria). – Scripta botanica belgica, Volume 8. – Gr. 8°, 55 Seiten; Karton geheftet. – National Botanic Garden of Belgium, B-1860 Meise. – BeF 280,–. – ISBN 90-72619-15-3.

Gemessen an den Schwierigkeiten, die der Versuch bereiten würde, zu einer kommentierten Liste, etwa der Algen in den Seen Österreichs, zu kommen, hat es den Rezensenten überrascht, eine solche Liste für die Algen (inkl. *Cyanophyta*) der drei großen ostafrikanischen Seen mit insgesamt 1472 infragenerischen Taxa aus 228 Gattungen in die Hand zu bekommen! Die Autoren sind Limnologen bzw. Algologen aus den Niederlanden bzw. aus Belgien. Außer der eigentlichen Check-List (p. 7–33) enthält das Heft noch eine Synonymaliste, gegebenenfalls mit taxonomischen oder nomenklatorischen Anmerkungen (p. 35–47) und ein Schriftenverzeichnis (inkl. Bestimmungsliteratur über 100 Titel). Die Geschichte der algologischen Erforschung der drei Seen ist in der kurzen Einleitung dargestellt.

H. TEPPNER