has been proposed for the appearance of Rubisco. For example, the *Chlamydomonas reinhardtii* ac 20 mutant lacks detectable Rubisco (80,209) yet possesses wild-type levels of pSSU mRNA and at least part of this mRNA is associated with the translational machinery of the cell (144). The lack of Rubisco accumulation would appear to be a consequence of the failure of plastids to synthesize LSU essential for Rubisco assembly. In addition, the report of Silverthorne and Ellis (184) and the research conducted on a nuclear gene mutant of *Petunia hybrida* (50) which employed a cDNA probe to measure levels of LSU mRNA both suggest that changes in the synthesis of LSU reflect fluctuations in the level of translatable mRNA for this subunit.

Taking both of these observations into consideration, it is not surprising that in the case of this M, pSSU can be readily detected and immunoprecipitated from the *in vitro* translation products directed by either poly(A) RNA or polysomal mRNA using either wheat germ (Fig. 19 and 20) or reticulocyte lysate (Fig. 21) as the cell-free protein synthesis system. The very low levels of Rubisco reported earlier (12,106), particularly in 4 d M seedlings, can be explained by the failure of plastids to synthesize wild-type levels of LSU. This assessment is supported by the evidence that little LSU mRNA appears to be associated with polysomes at 4 d of development (Fig. 21, lane 5). Any pSSU synthesized in excess of LSU available would, presumably, be proteolytically degraded.

The failure to observe wild-type levels of LSU produced by *in vitro* translation of polysomal RNA could arise either because the LSU mRNA is transcribed at very low levels in M plastids or, alternatively, because 70S ribosomes make only a negligible contribution towards M polysomal profiles at 4 d of development. Unfortunately, neither possibility is mutually exclusive. That is, transcriptional difficulties within the plastid may not only affect the population of mRNA (including LSU mRNA) but might very well affect the levels of tRNA and rRNA available for organellar protein synthesis. Reduced levels of rRNA would lead to an inevitable reduction in 70S ribosomes available for polysome assembly. Even if rRNA were singularly affected, unless LSU mRNA could become associated with 70S polysomes the accumulation of this subunit would most certainly be reduced.

As coupling of the synthesis of pSSU and LSU have been proposed, a slightly reduced amount of translatable pSSU mRNA in the M is not unexpected. This somewhat reduced quantity of pSSU represented among 4 d M *in vitro* translation products is suggested by poly(A) RNA directed products of wheat germ (Fig. 19 and 20, lanes 3) and reticulocyte lysate (Fig. 21, lanes 3 and 7). Furthermore, immunoprecipitation of pSSU synthesized by a reticulocyte lysate cell-free system shown in Figure 21 supports this observation. However, Figure 21 also provides evidence that M polysomes synthesize pSSU despite the poor translation of LSU, suggesting that the synthesis of these two subunits is not tightly coupled in the M. A disadvantage realized by *in vitro* translation and subsequent immunoprecipitation is that quantification of messages is not possible nor is this approach as sensitive or as conclusive as results provided by RNA-DNA hybridization studies. While a cDNA probe for pSSU mRNA would be useful in measuring the magnitude of the difference in quantities of this message present in the N and M, the question of whether or not transcription of rbcL proceeds at wild-type levels would best be addressed using a suitable cDNA probe for LSU mRNA.

Although the very distinct pale-green phenotype of light-grown M seedlings provides a striking contrast to the N, the mutation is expressed even in dark-grown plants which are phenotypically very similar. Distinct features of etiolated M seedlings include reduced levels of protochlorophyllide (127), abnormal etioplast ultrastructure (106) and a quantitative difference found between polysomal profiles of etiolated N and M tissue shown in Figures 10 and 11. Polysomal profiles of 4 d etiolated M seedlings are distinguished by the lack of a peak found in comparable N profiles. This peak, as described in "Results and Discussion", is very likely to be identified with 70S ribosomes.

Unfortunately, a number of possibilities could be entertained in attempting to explain the apparent reduction in 70S ribosomes. Research published by Mets and Bogorad (139) demonstrated that mutations can arise in either the cytoplasmic or organellar-synthesized components of ribosomes. Conceivably, such mutations could lead to 70S ribosome assembly problems. Low carotenoid levels have been implicated in causing the premature photo-destruction of newly formed 70S ribosomes in the *tigrina o*^{14} barley mutant (99). Another possibility that has been explored is that the activity of chloroplast DNA dependent RNA polymerase may be a primary cause in reducing 70S ribosomes by preventing the transcription of plastid rRNA. However, results using heat-treated 70S ribosome-less seedlings (33) and the plastid ribosome deficient *albostrians* mutant of barley (183) show that RNA polymerase activity is not markedly affected in either of these plants. These results do serve to substantiate the nuclear location of synthesis for this enzyme as originally proposed, using inhibitor studies (65). Due to the complicated interdependence between the activities of the nuclear and plastid genomes, as seen even in rates of plastid transcription, the actual cause of the absence 70S ribosomes, either by physiological heat-treatment or by mutation remains an enigma.

In the case of this *virescens* mutant, it is difficult to resolve whether or not the reduced quantity of 70S ribosomes is an additional symptom of the nuclear mutation or a direct consequence of the lesion. Furthermore, as 70S ribosomes are required for the synthesis of many of their ribosomal proteins, a reduced protein-synthesizing capacity of plastids would be accentuated if the demand for more plastid products arose, which might very well occur during early stages of chloroplast biogenesis.

A previous study analyzing ribosomal components of the N and M barley (113) led to the suggestion that the M may not be as competent as the N in terms of cytoplasmic translational capacity. However, comparison of 4 d N and M polysomal profiles (Fig. 8) suggests that polyribosome formation in the M is apparently unaffected. However, it is not advisable to extrapolate *in vivo* rates of protein synthesis from such profiles without considering estimates of *in vivo* rates of translation initiation, elongation and termination (55). These estimates are not accounted for by the simple rates or percentages expressing polysomal aggregation presented in Table IV. Perhaps one of the very few detailed reports with respect to estimates of *in vivo* protein synthesis was published by Baumgartel and Howell (15) using *Chlamydomonas reinhardtii*. These authors were able to estimate rates of translation initiation and elongation by pulse labelling the nascent polypeptide chains associated with polysomes. In this manner the authors were able to obtain more reliable estimates of the *in vivo* rate of protein synthesis than those determined by measuring the uptake and incorporation of a radioactive amino acid. This report showed that polysome aggregation in this organism is largely a function of rates of polypeptide initiation. While initiation is a primary regulator of translation, rates of elongation were found to play only a minor role. However, as *Chlamydomonas reinhardtii* provides a rather advantageous organism to conduct pulse-labelling experiments, it is not surprising that few studies of this nature have been attempted for higher plants.

Mösinger and Schopfer (148) were able to show that exposure of dark-grown seedlings to light resulted in a considerable aggregation of polysomes accompanied by the concomittant recruitment of newly transcribed mRNA. By comparing the profiles of 4 d etiolated seedlings (Fig. 10) to those of light grown material (Fig. 8), it is evident that the response of the N to light, as seen by the aggregation of polysomes, is also featured in M profiles. Furthermore, extraction and *in vitro* translation of polysomal RNA demonstrates that translatable mRNA is indeed associated with ribosomes in the M and the N. However, there is no unequivocable evidence to contend that the actual rates of *in vivo* protein synthesis are equal or, in fact, different between N and M seedlings. Perhaps the most judicious interpretation of the polysomal profiles depicted in Figures 8 to 11 and the ratios tabulated in Table IV is that the M responds to light by enhanced polysome aggregation and it would appear that the M is well-equipped to conduct cytoplasmic protein synthesis. However, the protein synthesizing capacity appears to be reduced in young, M seedlings by a decreased complement of 70S ribosomes.

A possibility that should be raised is that the import of metabolites across the M plastid membranes may be impaired. Metabolites that are transported across the chloroplast membrane include amino acids, sugars and polypeptides. The recent report of two mitochondrial protein transport mutants of yeast (236) suggests that conditional mutants of this nature could also give rise to pleiotropic effects. The temporal recovery made by this mutant would be construed as a "funneling" effect with the accumulation of building materials within the chloroplast being instrumental towards the eventual recovery of chloroplast function. However, there is no specific evidence presented by this study that would support or, indeed, exclude this explanation. Evaluation of plastid envelope transport functions is complicated by the difficulties encountered in purifying intact barley plastids.

An observation raised in the earlier part of this discussion is that *in vitro* translation of N and M poly(A) RNA did not reveal any qualitative differences between the products synthesized. However, concerns have already been addressed in the "Results and Discussion" regarding the reliability of *in vitro* systems in responding to exogenously added messages. The preferential initiation of certain messages such as LHCP mRNA (151) serves to underscore the caution that should be exercised in making quantitative judgements from wheat germ generated polypeptide profiles. However, it is hoped that any factors which would have affected *in vitro* translation of N products would have similarly affected those of the M. Furthermore, for the wheat germ assay system, comparisons made for any particular product across lanes might be safer than quantitative evaluations made for different polypeptides within any given lane.

The selective nature of the wheat germ system is shown by the apparent inability of this system to synthesize LSU as shown by comparing lanes 4 and 5 in Figure 19. Also, while LSU may be readily identified and immunoprecipitated from among reticulocyte lysate products (Fig. 21, lane 2) no comparable immunoprecipitate is detected from wheat germ products directed by a similar source of RNA (Fig. 19, lane 6). The fact that both systems are eukaryotic in nature excludes the argument of difficulties engendered by prokaryotic-eukaryotic translation barriers as originally proposed by Bottomley *et al.* (26). More recently, Lerbs *et al.* (123) provide evidence that some batches of wheat germ can be used to successfully translate chloroplast mRNA from spinach, *Nicotiana* and *Euglena* but only in the absence of cytoplasmic mRNA. They report that even minor levels of cytoplasmic mRNA appear to suppress the synthesis of chloroplast mRNA-encoded products. These observations help to reconcile the differing and rather contradictory opinions expressed about the value of wheat germ for chloroplast and cytoplasmic mRNA studies (48,162).

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