Eukaryotic initiation factor 3 (eIF3) is a multisubunit complex that is required for binding of mRNA to 40 S ribosomal subunits, stabilization of ternary complex binding to 40 S subunits, and dissociation of 40 and 60 S subunits. These functions and the complex nature of eIF3 suggest multiple interactions with many components of the translational machinery. Recently, the subunits of mammalian and *Saccharomyces cerevisiae* eIF3 were identified, and substantial differences in the subunit composition of mammalian and *A. thaliana* eIF3 were observed. Mammalian eIF3 consists of 11 nonidentical subunits, whereas *S. cerevisiae* eIF3 consists of up to eight nonidentical subunits. Only five of the subunits of mammalian and *S. cerevisiae* are shared in common, and these five subunits comprise a “core” complex in *S. cerevisiae*. eIF3 from wheat consists of at least 10 subunits, but their relationship to either the mammalian or *S. cerevisiae* eIF3 subunits is unknown. Peptide sequences derived from purified wheat eIF3 subunits were used to correlate each subunit with mammalian and/or *S. cerevisiae* subunits. The peptide sequences were also used to identify *Arabidopsis thaliana* cDNAs for each of the eIF3 subunits. We report seven new cDNAs for *A. thaliana* eIF3 subunits. *A. thaliana* eIF3 was purified and characterized to confirm that the subunit composition and activity of wheat and *A. thaliana* eIF3 were similar. We report that plant eIF3 closely resembles the subunit composition of mammalian eIF3, having 10 out of 11 subunits in common. Further, we find a novel subunit in the plant eIF3 complex not present in either mammalian or *S. cerevisiae* eIF3. These results suggest that plant and mammalian eIF3 evolved similarly, whereas *S. cerevisiae* has diverged.

Eukaryotic initiation factor 3 (eIF3) is the most complex and least understood of the protein synthesis initiation factors. eIF3 has been purified from wheat germ (1–3), HeLa cells (4, 5), rabbit reticulocytes (6–12), and *Saccharomyces cerevisiae* (13–16). Depending upon the organism and method of purification, there are 6–11 nonidentical subunits present in functional eIF3 complexes that have been isolated and characterized. Recently, the subunits from the human and *S. cerevisiae* eIF3 complex have all been identified and sequenced. Surprisingly, there are substantial differences in the subunit composition between mammalian and *S. cerevisiae* eIF3 complexes. The mammalian eIF3 complex composition varies depending upon the method of purification (6, 7, 9–12); however, the mammalian eIF3 complex appears to contain 11 subunits, p170 (17), p116 (18), p110 (19), p66 (20), p44 (21, 22), p48 (23), p47 (20), p40 (20), p36 (19), p35 (21) and p28.2 The *S. cerevisiae* eIF3 complex was determined to consist of a core complex of five subunits, Tif32p, Prt1p, Nip1p, Tif35p, and Tif34p (13–15, 24) that correspond to mammalian subunits p170, p116, p110, p44, and p36, respectively (see Table II). There are other proteins associated with the *S. cerevisiae* eIF3 complex, TIF31p (Club1p; Ref. 25), GCD10p (15, 26), eIF5 (15, 22), and Sui1p (eIF1; Ref. 27), that are not present in the mammalian complex (11, 24). TIF31 is not an essential gene in *S. cerevisiae*, and the role of the TIF31 protein in the eIF3 complex is not clear (25). GCD10 has recently been shown to have a role in a nuclear complex required for maturation of initiator methionyl-tRNA (28). eIF5 and eIF1 (Sui1), previously characterized initiation factors, participate in subunit joining and initiation codon recognition, respectively (15, 22, 24).

Several functions have been ascribed to eIF3 including stabilization of ternary complex binding to the 40 S ribosome, binding of mRNA to the 40 S ribosome, and promotion of dissociation of 40 and 60 S ribosomal subunits (29–31); however, the exact mechanisms of these interactions are not understood. It is known that mammalian eIF3, like eIF4A, interacts with the central domain of mammalian eIF4G, but eIF3 appears to have a separate binding site from eIF4A (32–34). The interaction of mammalian eIF3 with eIF4G could play a role in positioning the mRNA and associated initiation factors on the 40 S ribosome at the initiation codon (35). Mammalian eIF4B, another mRNA-associated initiation factor, was shown also to interact with mammalian eIF3 (36). Interestingly, a similar interaction of *S. cerevisiae* eIF4B and *S. cerevisiae* eIF3 could not be demonstrated, suggesting that there may be some fundamental differences in the way eIF3 functions in different organisms (25).

The eIF3 complex isolated from wheat germ contains nine or 10 subunits (2, 3, 37). The expression patterns of some of the subunits of wheat eIF3 indicated differential regulation and expression during seed development and germination and following heat shock (38). Extensive biochemical analysis of the
wheat eIF3 complex showed that certain subunits of the complex were protected from trypsin digestion (39), alkylation (40), or iodination (40). These results suggest that these subunits may be integral to the structure and therefore less solvent-accessible. Furthermore, a group of subunits was found to be resistant to dissociation by mild urea treatment, suggesting that these subunits are more tightly associated with each other within the complex (40). Based on the various studies of the interactions of eIF3 subunits, a model for the interaction of some of the subunits of eIF3 has been proposed (16, 35). This preliminary model suggests that the five subunits shared in common between S. cerevisiae and mammalian eIF3 may have a similar architecture.

Although mammalian and S. cerevisiae eIF3 complexes have some subunits in common, they each have subunits that are unique to their respective complexes. It is important to know whether eIF3 from other eukaryotes will follow a similar pattern of containing a few common subunits but have other subunits that are unique. Higher plants represent a distinct evolutionary path from mammals and fungi. The composition of plant eIF3 should therefore give a good indication of whether eIF3 complexes from eukaryotes will have substantial differences in subunit composition. We report in this paper that the plant eIF3 subunit composition closely resembles that of mammalian eIF3, sharing 10 out of 11 subunits. The plant eIF3 complex contains a unique subunit that is not present in mammalian or S. cerevisiae eIF3. These findings suggest that the eIF3 complexes from most eukaryotes will probably have a subunit composition that is similar to the plant and mammalian complexes and that the subunit composition of the S. cerevisiae complex most likely represents a divergent evolutionary pathway.

**EXPERIMENTAL PROCEDURES**

**Preparation of Wheat eIF3 and Tryptic Peptides—**Wheat germ used for preparation of eIF3 and other initiation factors was purchased from Bob’s Red Mill (Milwaukie, OR). Wheat eIF3 was prepared as described previously (37). eIF3 activity was measured in an in vitro assay system dependent upon the addition of eIF3 as described previously (37). Purified wheat eIF3 was separated on a 10 cm-long, 1.0-mm-thick, 15% Laemmli SDS gel (15% acrylamide, 0.55% bisacrylamide) and blotted onto polyvinylidene difluoride membrane and stained with Ponceau S. The membrane was sent to Dr. John Leszyk (Protein Microsequencing Laboratory, University of Massachusetts Medical School, Worcester, MA) for trypsin digestion and peptide sequence analysis.

**Arabidopsis thaliana Suspension Cell Culture—**Suspension cultures of A. thaliana (Columbia University) were obtained from Dr. A. N. Reddy (Colorado State University) and maintained on Murashige and Skoog (MS) medium containing, per liter, 4.3 g of MS basal salts (Sigma), 30 g of sucrose (Sigma), 1.0 ml of 1000 × MS vitamins (Sigma), and 0.5 mg of 2,4-diphenoxyacetic acid (Sigma). The medium was adjusted with KOH to a pH of 5.7 before autoclaving. Suspension cultures were maintained by transferring every 7 days 1 part of stationary stage culture to 4 parts fresh MS medium in an Erlenmeyer flask that was 2.5–5 times larger than the final volume. The flasks were rotated at 115 rpm on a gyratory shaker at 26 °C in the dark.

**Preparation of A. thaliana Cell Extract—**Cells from 7-day suspension cultures were harvested by pouring cultures through eight layers of cheesecloth. The cells were rinsed with buffer containing 20 mM Hepes-KOH, pH 7.6, 14 mM Mg(OAc)2, 0.1 mM KOAc, and 3% sucrose. Excess liquid was squeezed from the cells by hand and transferred to a 300 ml centrifuge tube. The cells were centrifuged at 21,000 × g for 10 min at 4 °C. The resulting supernatant (S150) was flash frozen in liquid nitrogen and stored at −80 °C.

**Purification of A. thaliana eIF3—**The S150 from ~200 g of cells was made to 40% saturation with solid ammonium sulfate, and the precipitate was collected by centrifugation at 30,000 × g for 15 min at 4 °C. The precipitate pellets were resuspended in 13 ml of buffer N’ (20 mM Hepes, pH 7.6, 10% glycerol, 1 mM dithiothreitol, 0.1 mM EDTA) containing 0.08 M KCl and dialyzed overnight against 2 liters of the same buffer. The dialyzed sample was clarified by centrifugation at 12,000 × g for 10 min at 4 °C.

The dialyzed sample (~200 mg of protein) was made 15% in glycerol and applied to a 20-ml column of Whatman DE-52 cellulose equilibrated in buffer N’ (20 mM Hepes, pH 7.6, 15% glycerol, 1 mM dithiothreitol, 0.1 mM EDTA) containing 0.08 KCl until the A260 was less than 0.1. The protein was eluted with a 5 × linear gradient from 0.08 mM KCl to 0.4 mM KCl in N’ buffer. The resulting fractions were assayed in a wheat germ translation system (37). The eIF3 activity eluted from the column between 0.15 and 0.25 mM KCl.

The pooled DEAE material was adjusted to 0.08 mM KCl with N’ containing no KCl and loaded onto a 0.5-ml column of SP-Sepharose equilibrated in the same buffer. After loading the sample, the column was washed with N’ containing 0.08 KCl, and the eIF3 was eluted with N’ containing 0.2 mM KCl. Fractions with maximum specific activity were pooled.

**Electrophoresis and Mass Spectrometry of A. thaliana eIF3—**About 50 μg of A. thaliana eIF3 or wheat eIF3 from the glycerol gradients and air-dried. The resulting pellets were dissolved in 40 μl of 1 × Laemmlli SDS gel loading buffer and applied to a 10 × 15-cm-long, 1.0-mm-thick, 15% Laemmlli SDS gel containing 14.45% acrylamide and 0.55% bisacylamide (43). The gel was electrophoresed at a constant current of 20 mA until the bromophenol blue tracking dye ran off the bottom. The gel was stained in 45% methanol, 10% acetic acid with 0.25% Coomassie Brilliant Blue R dye and destained. The individual bands of A. thaliana were cut from the gel and digested with trypsin prior to analysis by mass spectroscopy (44). The peptides were separated by HPLC on a Varian 9000 using a 10-cm, 1-mm (inner diameter) C18 column. The mass spectrometry was carried out on a Finnegan MAT LCQ mass spectrometer in the mass spectrometry facility of the Department of Chemistry and Biochemistry, University of Texas at Austin (Dr. Mehdy Omini, Director).

**RESULTS AND DISCUSSION**

**Sequencing and Identification of Tryptic Peptides from Wheat eIF3 Subunits—**To determine which of the wheat eIF3 subunits correlated with the mammalian or S. cerevisiae eIF3 subunits, it was necessary to obtain protein sequence information. Tryptic peptides were prepared from a highly purified preparation of wheat eIF3 separated by SDS-PAGE. The peptide sequences obtained for each subunit of wheat eIF3 are shown in Table I. The peptide sequences were compared with GenBank™ to find potential matches. The p41 subunit of wheat eIF3 gave three peptides that corresponded to two different human eIF3 subunits, indicating that two polypeptides of different sequences migrate with the same mobility on SDS-PAGE. Previous work from this laboratory showed that the wheat p41 subunit separated into two distinct isolectric species of p41 of 5.3 and 7.2 (40). The combination of one p41 from each species and two-dimensional gel data shows that wheat p41 is really two distinct polypeptides with the same SDS-PAGE mobility. Further, quantitation of the band intensities of the wheat eIF3 subunits shown in Fig. 3 suggests that there are two proteins at this position relative to the other subunits. Except for wheat eIF3-p56, matches to mammalian and/or S. cerevisiae eIF3
subunits were found using wheat peptides. The correlation of wheat subunits to mammalian subunits is shown in Table I. A nomenclature is proposed based upon the mammalian eIF3 subunits and gives a letter designation, rather than a molecular weight designation (see Table II). The proposed nomenclature is flexible enough to allow for the differences in subunit composition and to accommodate any additions as more is learned about the subunits and associated proteins from different organisms.

DNA Sequence Analysis of A. thaliana eIF3 Subunits—The plant A. thaliana genome and expressed sequence tag (EST) projects have provided a wealth of easily obtained sequence information. This resource was used to “mine” for cDNA sequences encoding the A. thaliana eIF3 subunits using the wheat peptide sequences shown in Table I. Three A. thaliana full-length cDNAs had already been identified and deposited for eIF3c (AF040102 (45), eIF3f (U54561) (20), and eIF3i (U36765) (46)). For the seven remaining subunits (eIF3a, eIF3c, eIF3d, eIF3e, eIF3g, eIF3h, and eIF3k) ESTs or cDNAs (U36765) (46)). For the seven remaining subunits (eIF3a, eIF3c, eIF3d, eIF3e, eIF3g, eIF3h, and eIF3k) ESTs or cDNAs have not been deposited in the data base. A complete rice gene for eIF3b was obtained by screening a cDNA library with a probe (Ohio State University) and completely sequenced. A cDNA for eIF3c (AF040102 (45), eIF3f (U54561) (20), and eIF3i (U36765) (46)). For the seven remaining subunits (eIF3a, eIF3c, eIF3d, eIF3e, eIF3g, eIF3h, and eIF3k) ESTs or cDNAs were identified. A full-length A. thaliana EST for the p56 subunit (eIF3l) is currently not available. A partial gene sequence is located on a bacterial artificial chromosome derived from A. thaliana chromosome 5, but a bacterial artificial chromosome with the complete gene sequence for this novel subunit has not been deposited in the data base. A complete rice gene was identified using the wheat peptides and used for sequence comparison purposes in this report (see below).

The ESTs for eIF3a, eIF3d, eIF3e, eIF3g, eIF3h, and eIF3k were obtained from the Arabidopsis Biological Resource Center (Ohio State University) and completely sequenced. A cDNA for eIF3b was obtained by screening a cDNA library with a probe from a less than full-length EST for eIF3b. New accession numbers for the complete cDNA sequences were obtained and are indicated in Table II along with the original EST accession numbers.

The complete genes for all of the A. thaliana eIF3 subunits, except eIF3l, were identified in the data base, and accession numbers for the gene(s) are given in Table III. A nomenclature for the genes for the plant eIF3 subunits is proposed that uses the translation initiation factor 3 (TIF3) designation. The species is indicated (e.g. At for A. thaliana), the subunit letter designation is capitalized, and the gene(s) are designated with a number. Subunits eIF3c, eIF3d, and eIF3g each have two genes. The remaining subunits only have one gene, although additional genes may be found when the Arabidopsis genome is completed.

Purification and Analysis of the A. thaliana eIF3 Complex and Comparison with the Wheat eIF3 Complex—Assignments of subunits of A. thaliana eIF3 could be made based on deduced protein sequences, but it is important to show that the proteins predicted to be in the A. thaliana eIF3 complex were in fact in a functional complex. Therefore, A. thaliana eIF3 was purified to homogeneity, and the identity of subunits present in the complex was confirmed by mass spectrometry.

A. thaliana eIF3 was purified from a suspension cell culture as described under “Experimental Procedures.” The final step of purification was centrifugation through a glycerol gradient. A. thaliana eIF3 migrated in the glycerol gradient similarly to wheat eIF3 (see Fig. 1). The ability of A. thaliana eIF3 to support polypeptide synthesis was compared with purified wheat eIF3 in an in vitro translation assay. Wheat and A. thaliana eIF3 were found to have a similar specific activity (see Fig. 2). A. thaliana and wheat eIF3 were compared by SDS-PAGE as shown in Fig. 3. A. thaliana eIF3 has a similar number of subunits compared with wheat eIF3, although a few subunits differ in apparent molecular weight. The relative intensities of the subunits in this gel (see the legend to Fig. 3) suggest that the subunits are present in close to stoichiometric amounts; however, those subunits that appear to be present in less than stoichiometric amounts are in regions of overlap, and quantitation is not as accurate. The relative intensity of the p41 subunit supports the presence of two polypeptides migrating at this position. It should be noted that the protein migrating between subunits eIF3h and eIF3i in the A. thaliana eIF3 preparation (indicated by an asterisk in Fig. 3) and the doublet (also indicated by an asterisk) migrating between subunits eIF3e and eIF3h,i in the wheat eIF3 preparation appear to be the same protein. The proteins in the wheat doublet give the same tryptic digest pattern, suggesting that they are the same protein, the smaller one presumably a degradation product. The wheat peptides and the mass spectrometry of the A. thaliana protein (asterisk) both identify the same A. thaliana unidentified open reading frame. Data base analysis did not yield any similar proteins from other organisms. The appearance of the protein doublet in wheat eIF3 preparations is variable. This protein, therefore, may be another plant-specific subunit of eIF3 or a loosely associated protein of unknown function. Further analysis will be necessary to distinguish between these two possibilities.

To identify the subunits of A. thaliana eIF3 in the SDS-PAGE gel and to correlate them to the wheat eIF3 subunits, the protein bands were excised from the SDS-PAGE and treated with trypsin. Each subunit digest was subjected to HPLC, and the masses of the tryptic peptides were obtained by mass spectrometry. The masses of the tryptic peptides were compared with the predicted peptide masses based on deduced A. thali-
Eukaryotic eIF3 subunits

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<th>Subunit</th>
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<th>S. cerevisiae</th>
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- Determined from SDS-PAGE mobility of wheat eIF3 subunits.
- Calculated from protein sequence.
- Defined as an EST identified in the database and sequenced in this report. The accession number for the complete cDNA sequence is noted in the next column.
- Calculated from protein sequence.
- This subunit is not part of the core S. cerevisiae eIF3 complex.
- This is a gene sequence for an analogous protein from rice.

A. thaliana ESTs, cDNAs, and genes for the subunits of eIF3

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<th>Gene name</th>
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</table>

- Proposed nomenclature and mammalian subunit designation.
- Indicates an EST identified in the database and sequenced in this report. The accession number for the complete cDNA sequence is noted in the next column.
- AF255680 is a full-length cDNA identified and sequenced in this report; AF255699 was recently deposited in GenBank™ (70).
- Only the cDNA for the AtTIF3F1 gene was determined. ESTs do exist for the AtTIF3F2 gene but were not sequenced. Evidence for peptides from both genes was found in the eIF3 complex.
- This is a gene sequence for an analogous protein from rice.

Protein Sequence Comparisons of eIF3 Subunits—The deduced A. thaliana protein sequences for eIF3 subunits were used to search the Caenorhabditis elegans, Schizosaccharomyces pombe, and Drosophila melanogaster genomes for corresponding genes. The proteins were aligned using MACAW (47), and a graphical representation is shown in Fig. 4. The substantial similarity among the subunits (see Table IV) suggests that many aspects of the structure and function of eIF3 are conserved throughout eukaryotes. It should be noted that the C. elegans, S. pombe, and D. melanogaster sequences are included based solely on similarity to proteins present in the mammalian and/or A. thaliana eIF3 complexes. eIF3 complexes from C. elegans, S. pombe, and D. melanogaster have not been purified and characterized for subunit composition.

- eIF3a (p170, TIF32p, or RPG1p)—The A. thaliana eIF3a cDNA sequence in this report encodes a protein that appears to be highly conserved, particularly at the N terminus of the protein. The A. thaliana eIF3a is 74% similar to maize and tobacco eIF3a, respectively, compared with 45–51% with other eukaryotes (Table IV). Like other eIF3a subunits, the A. thaliana eIF3a contains a PCI or PINT motif. The PCI (proteasome, COP9, initiation factor) (48) or PINT (proteasome, int-6, Nip-1, Trip-15) (49) motif is conserved in the middle portion of all eIF3a subunits as well as in the C termini of two other eIF3 subunits, eIF3c and eIF3e (48–50). The PCI motif is also found...
The activity of the eIF3 preparations obtained from the glyceral gradients shown in Fig. 1 was measured as described under "Experimental Procedures." After centrifugation, fractions of 0.3 ml were collected. The protein concentration (C) and eIF3 activity (A) were determined. Sedimentation is from left to right.

**FIG. 1.** Glycerol gradient analysis of wheat and *A. thaliana* eIF3. Wheat eIF3 (0.75 mg in 0.4 ml) (A) or *A. thaliana* eIF3 (1.3 mg in 0.4 ml) (B) was each applied to a 34 ml 15–40% linear glycerol gradient as described under "Experimental Procedures." After centrifugation, the samples were applied to a 15% acrylamide gel and electrophoresed at 20 mA. The gel was stained with Coomassie Brilliant Blue R and destained. The protein bands were removed from the gel, treated with trypsin, separated by HPLC, and analyzed by mass spectrometry as described under "Experimental Procedures." The subunits are marked according to the nomenclature proposed in Table II. The relative intensities of the subunits in this gel were measured using ImageJ (available on the World Wide Web). The eIF3 subunit intensity was chosen arbitrarily to be 1. The wheat eIF3 subunit intensities relative to the wheat eIF3l band are as follows: 1.0 (a), 0.96 (b), 0.5 (c), 0.93 (d), 1.2 (e), 1.0 (f), 0.93 (g), 1.7 (h, i), 0.84 (k), and 1.1 (*; both bands). The *A. thaliana* eIF3 subunit intensities relative to the *A. thaliana* eIF3l band are as follows: 0.6 (a), 0.9 (b), 1.2 (c; both bands), 1.3 (d; both bands), 1.1 (e), 0.96 (f), 1.1 (g), 1.6 (h), 1.3 (i), 0.6 (k), and 0.9 (*).

**FIG. 2.** Comparison of purified wheat and *A. thaliana* eIF3 activity. The activity of the eIF3 preparations obtained from the glycerol gradients shown in Fig. 1 was measured as described previously (37). A fractionated assay dependent upon the addition of eIF3 was programmed with 5 pmol of satellite tobacco necrosis virus RNA; 8 pmol (37). A fractionated assay dependent upon the addition of eIF3 was measured as described previously (37). After centrifugation, fractions of 0.3 ml were collected. The protein concentration (C) and eIF3 activity (A) were determined. Sedimentation is from left to right.

**FIG. 3.** SDS-PAGE analysis of wheat and *A. thaliana* eIF3. The wheat and *A. thaliana* eIF3 preparations obtained from the glycerol gradients shown in Fig. 1 were analyzed by SDS-PAGE. About 50 μg of purified wheat or *A. thaliana* eIF3 were precipitated with methanol/chloroform as described under “Experimental Procedures” and resuspended in 40 μl of 1× SDS gel loading buffer. The samples were applied to a 15% acrylamide gel and electrophoresed at 20 mA. The gel was stained with Coomassie Brilliant Blue R and destained. The stained bands were removed from the gel, treated with trypsin, separated by HPLC, and analyzed by mass spectrometry as described under “Experimental Procedures.” The subunits are marked according to the nomenclature proposed in Table II. The relative intensities of the subunits in this gel were measured using ImageJ (available on the World Wide Web). The eIF3 subunit intensity was chosen arbitrarily to be 1. The wheat eIF3 subunit intensities relative to the wheat eIF3l band are as follows: 1.0 (a), 0.96 (b), 0.5 (c), 0.93 (d), 1.2 (e), 1.0 (f), 0.93 (g), 1.7 (h, i), 0.84 (k), and 1.1 (*; both bands). The *A. thaliana* eIF3 subunit intensities relative to the *A. thaliana* eIF3l band are as follows: 0.6 (a), 0.9 (b), 1.2 (c; both bands), 1.3 (d; both bands), 1.1 (e), 0.96 (f), 1.1 (g), 1.6 (h), 1.3 (i), 0.6 (k), and 0.9 (*).

These results suggest that eIF3 and protein synthesis are central to progression of the cell cycle.

*eIF3c (p110, NIP1p)—* *S. cerevisiae* eIF3c, was originally identified as a protein that copurifies with the nuclear COP9 complex; however, eIF3c is not part of the core COP9 complex (45). The COP9 complex plays a role in light signal transduction and structurally resembles the 26 S proteosome, suggesting a common evolutionary ancestry (59). Complexes similar to COP9 have been identified in other eukaryotes, suggesting a conserved role in development regulation (59, 60). It is intriguing that plant in subunits of the proteosome and COP9, both of which are large multisubunit complexes like eIF3 (48, 49). Although the function of the PCI motif is not known, it is speculated to have a role in the assembly of large multisubunit complexes (48, 50).

Interestingly, there is a conserved nuclear localization signal sequence identified by PSORT (available on the World Wide Web) in the C-terminal region of the *A. thaliana* eIF3a and other eukaryotic eIF3a protein sequences. The significance, if any, of this nuclear localization signal sequence has not been determined.

*eIF3b (p116, PRT1p)—* *A. thaliana* eIF3b contains a conserved RNA recognition motif (RRM) located near the N terminus that is similar to the RRM found in other eIF3b subunits. The *A. thaliana* eIF3b is 80% similar to tobacco eIF3b (51), compared with 45–56% similar to nonplant eIF3c subunits. The *S. cerevisiae* eIF3c gene, *PRT1*, was originally isolated as a conditional lethal mutation that reduced the stability of ternary complex binding to 40 S subunits (54, 55) and DNA synthesis (56). The tobacco eIF3b transcript expression was shown to accumulate in tissues with high mitotic activity and to be cell cycle-regulated (51). These results suggest that eIF3 and protein synthesis are central to progression of the cell cycle.

*eIF3e (p110, NIP1p)—* *S. cerevisiae* eIF3c, was originally isolated as an essential gene involved in nuclear import (57). *S. cerevisiae* eIF3c interacts with eIF5 and eIF1 (Sui1p) both in vivo and in vitro, suggesting a key role in the process of initiation (15). *A. thaliana* eIF3c is 78% similar to a cDNA isolated from *Medicago truncatula* (58), compared with 42–55% similar to nonplant eIF3c subunits. The eIF3c subunit from *A. thaliana* was originally identified as a protein that copurifies with the nuclear COP9 complex; however, eIF3c is not part of the core COP9 complex (45). The COP9 complex plays a role in light signal transduction and structurally resembles the 26 S proteosome, suggesting a common evolutionary ancestry (59). Complexes similar to COP9 have been identified in other eukaryotes, suggesting a conserved role in development regulation (59, 60). It is intriguing that plant...
eIF3c copurifies with COP9 and also shares the PCI domain in common with some of the COP9 subunits. A regulatory role for eIF3c has been suggested (70), but the significance of the COP9 and eIF3c interaction in the cell has yet to be determined. The eIF3c in wheat eIF3 is specifically phosphorylated by a wheat kinase incorporating up to 6 pmol of phosphate/pmol of eIF3 complex (61). This suggests the potential for regulation by phosphorylation, although no effect \textit{in vitro} on protein synthesis by phosphorylation was observed (61); however, the phosphorylation may affect some other process, such as an interaction with other protein complexes (e.g. COP9).

The \textit{A. thaliana} eIF3c gene is induced during photomorphogenesis and shows differential tissue accumulation (45). The eIF3c subunit from \textit{M. truncatula} was identified in a screen for genes induced during symbiosis with a plant fungal agent (58). These observations suggest that the eIF3c mRNA and its translation are developmentally regulated or are altered in response to changes in the environment.

There are two genes for \textit{A. thaliana} eIF3c, both on chromosome 3; however, only AtTIF3C1 appears to be transcriptionally active, since no ESTs corresponding to AtTIF3C2 are present at this time in the data base. This suggests that AtTIF3C2 is either a pseudogene, is expressed at very low levels, or is expressed in a tissue- or time-specific manner.

eIF3d (p66)—The eIF3d subunit in mammalian eIF3 does not appear to have an equivalent in the \textit{S. cerevisiae} eIF3 complex; nor does there appear to be similar protein encoded in the \textit{S. cerevisiae} genome. The \textit{A. thaliana} cDNA sequenced in this report is not full-length. The missing amino-terminal sequence was derived from gene AtTIF3D1 (see Table IV). The \textit{A. thaliana} eIF3d subunit contains a basic region in the N terminus similar to that of mammalian eIF3d. Although the amino acids flanking this region are conserved, the sequence of the RNA binding region itself is not conserved among eukaryotes; however, the overall character of the region being rich in basic amino acids is maintained. The amino acids comprising this RNA binding region in eIF3d are over 20% basic and have predicted pIs greater than 9.

There are two genes for \textit{A. thaliana} eIF3d, and both appear to be transcriptionally active, since ESTs are present for both genes in the data bases. Furthermore, peptides from both gene products are present and are represented in the eIF3 complex isolated from \textit{A. thaliana} (see Fig. 3, d1 and d2), suggesting that either gene product may function in eIF3.

eIF3e (p48)—The \textit{A. thaliana} eIF3e subunit, like eIF3a and eIF3c, contains a PCI motif in the C terminus of the protein. However, epitope-tagged \textit{S. pombe} eIF3e was shown to coimmunoprecipitate with \textit{S. pombe} eIF3b, suggesting that it is part of the \textit{S. pombe} eIF3 complex (71, 72). Interestingly, \textit{A. thaliana} eIF3e, like eIF3c, is suggested to be associated with the COP9 complex (70). Antibodies to \textit{A. thaliana} eIF3e show both nuclear and cytoplasmic staining, and green fluorescent protein fused to eIF3e also showed both nuclear and cytoplasmic localization.
eIF3 from Plants Resembles Mammalian eIF3

Comparisons were made using the Gap function of Genetics Computer Group software with a blossom 62 scoring matrix. % I, percentage identity; % S, percentage similarity.

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* Accession numbers for S. pombe subunits: eIF3a, O74760; eIF3b, Q10425; eIF3c, O14164; eIF3d, O43060; eIF3g, 78795; eIF3h, CAB57439; eIF3i, P79083.

* Accession numbers for S. pombe subunits: eIF3a, P34339; eIF3b, CAA21681; eIF3c, O61820; eIF3d, CAA87773; eIF3g, O19706; eIF3i, AC24867; eIF3k, CAB57439; eIF3l, AAB66128.

* Accession numbers for D. melanogaster subunits: eIF3a, AAF52196; eIF3b, AAF57842; eIF3e, AAF57818; eIF3d, AAF52190; eIF3f, AAF52190; eIF3g, AAF52190; eIF3h, AAF52190; eIF3i, AAF52190; eIF3j, AAF52190; eIF3k, AAF52190; eIF3l, AAF52190.

* ND, a subunit with appropriate similarity could not be found in the database.

Table IV

Comparison of A. thaliana eIF3 subunits with other eukaryotes

The eIF3 complex has not been determined.

The eIF3 complex will have to be isolated to determine whether eIF3a and eIF3b are present in the S. pombe complex. However, epitope-tagged S. pombe eIF3f was shown to interact with other eIF3 subunits but not with eIF3i (21). The strongest interactions of eIF3 subunits a, b, c, and h and with itself in a yeast two-hybrid analysis but not with eIF3i (21). The strongest interactions of human eIF3f were with eIF3a and with eIF3b (21). It was also shown that human eIF3f was not able to complement a S. cerevisiae eIF3f knockout (21). Interestingly, the only monoclonal antibody to wheat eIF3 subunits that specifically inhibits its translation initiation and the binding of mRNA to 40 S ribosomal subunits was to eIF3g, suggesting a key role for this subunit in the binding of mRNA to 40 S ribosomes (66).

There are two A. thaliana genes for eIF3g that encode proteins that show 79% similarity and 73% identity to each other. Both AtTIF3G1 and AtTIF3G2 gene products are expressed, since ESTs for these genes are found in the data base; however, only peptides corresponding to the gene product of AtTIF3G1 were found in the A. thaliana eIF3 complex.

eIF3h (p40)—A. thaliana eIF3h is also a member of the MOV34 family of proteins (11, 20). There is a gene for a similar protein in the S. pombe genome; however, the presence of this subunit in the S. pombe complex has not been determined.

Interestingly, a gene with sufficient similarity to eIF3h from C. elegans could not be identified in the data base. The C. elegans eIF3 complex will have to be isolated to determine whether there is an eIF3h-like subunit.

eIF3i (p36, TIF35p)—eIF3i contains 5–7 WD repeat elements, depending upon the criteria of the motif search program used (16, 19, 46). WD elements fold into a circular structure termed a "β-propeller" (67). This circular structure is thought to provide a scaffold that is important in protein-protein interactions and formation of complexes (67). The presence of the
WD repeats in eIF3i suggests that the function of eIF3i may be central to the structural integrity of the complex (16, 68). This idea is supported by the fact that S. cerevisiae temperature-sensitive eIF3i mutants have lower levels of all of the eIF3 subunits, and the eIF3i-depleted eIF3 complex no longer binds to 40 S subunits (68). Temperature-sensitive S. cerevisiae mutants with amino acid substitutions in certain WD repeats were more severely affected than mutants in other regions, suggesting that these WD repeats are important for subunit interactions and complex stability (16). The human eIF3i is identical to the TRIP-1 protein (19). The TRIP-1 protein was found in a yeast two-hybrid screen to associate with TGF-β type II receptors (46). The A. thaliana eIF3i was originally reported as a protein similar to the mouse TRIP-1 gene product (46). Another EST for eIF3i was identified and sequenced in this report. It is identical to the previously reported A. thaliana eIF3l.

eIF3k (p28)—Both the A. thaliana and wheat eIF3 complexes contain a subunit of ~28,000 Da. The presence of a 28,000-Da subunit in the mammalian eIF3 complex has been confirmed2; however, a subunit of this molecular weight is not present in the S. cerevisiae complex.

An A. thaliana EST for eIF3k was identified based on similarity to peptides obtained from wheat eIF3k and completely sequenced. The deduced protein sequence is shown in Fig. 5 and compared with the protein sequences of eIF3k from human2 and with deduced protein sequences from C. elegans and D. melanogaster genomes. The A. thaliana sequence is 43, 42, and 45% similar to putative human, C. elegans, and D. melanogaster eIF3k, respectively. No sequence similar to eIF3k was found for S. pombe, suggesting that this subunit may be unique to higher eukaryotes. The presence of eIF3k in eIF3 complexes from other higher eukaryotes will have to be confirmed by purification of the protein complex.

There are numerous ESTs for the A. thaliana eIF3k subunit, suggesting that it is highly expressed. Examination of the eIF3k sequences using protein domain search programs, ProDom (available on the World Wide Web) or InterPro (available on the World Wide Web), did not yield any similarity to other proteins of known function or protein motifs. The predicted secondary structure from Jpred (available on the World Wide Web) indicates that overall the protein is α-helical with a small region of β-sheet near the N terminus. Since there are no obvious motifs for eIF3k, it is difficult to speculate on its function at this time. Biochemical analysis of the wheat eIF3 complex suggests that this subunit is protected from the solvent, since it was not alkylated (40), was not iodinated appreciably (40), and was resistant to trypsin digestion (39), and since no monoclonal antibodies were obtained to this subunit (40).

eIF3k (Wheat eIF3-p56)—A subunit of ~56,000 Da is present in the wheat eIF3 complex. It was previously thought that the 56,000 Da subunit might correspond to the S. cerevisiae GCD10 subunit based on protein mobility; however, the sequence analysis presented in this paper shows that this is a novel protein. Peptides from wheat eIF3l were used to search the database for a corresponding protein in A. thaliana. A full-length A. thaliana cDNA or gene is currently not available. However, a rice gene was found that encodes a protein with a sequence that is similar to both of the wheat eIF3l peptides (see Fig. 3). Blast searches with rice eIF3l yielded numerous matches to other plant ESTs, suggesting that it is a highly expressed transcript. The mRNA for maize eIF3k appears to be particularly abundant in a maize root cDNA library.

Comparisons with protein data bases were used to identify a human cDNA and to identify D. melanogaster and C. elegans genes encoding proteins that are similar to eIF3l (Fig. 6). The human and D. melanogaster are more similar to the rice eIF3l, with 54 and 53% similarity respectively, whereas the C. elegans is only 35% similar. Overall, the C. elegans protein was less similar to the other eIF3l-like proteins, indicating that it may be more distantly related. There was no S. pombe or S. cerevisiae equivalent for eIF3l, suggesting that this subunit may be unique to higher eukaryotes. There were no obvious motifs or related proteins for eIF3l using ProDom or Interpro database searches. The overall secondary structure predicted by Jpred appears to be α-helical with a small portion of β-sheet near the C terminus. Biochemical analysis of the wheat eIF3 complex indicated that eIF3l was iodinated to the highest extent of all the subunits and was moderately alkylated, and monoclonal antibodies were obtained (40). These observations would suggest that eIF3l is surface-exposed in the complex; however, wheat eIF3l was resistant to trypsin treatment (39) despite a composition of over 10% basic amino acids.

There is no equivalent of eIF3l in the mammalian eIF3 complex; however, the presence of a mammalian cDNA that
encodes a similar protein suggests that whatever the role of eIF3l, it has been retained in the evolution of higher eukaryotes. Further analysis will be necessary to determine the function of the eIF3l subunit and whether it is present in other eukaryotic eIF3 complexes or is a plant-specific subunit.

CONCLUSIONS

In this report, we find that the subunit composition of plant eIF3 is more similar to mammalian eIF3 than to S. cerevisiae eIF3. In plant eIF3, 10 out of 11 subunits are equivalent to mammalian eIF3 subunits based on amino acid sequence similarity. Wheat, a monocot, and A. thaliana, a dicot, have a similar subunit composition, suggesting that eIF3 complexes from all higher plants share a similar composition.

The plant eIF3 complex does not appear to contain a protein similar to mammalian eIF3j (p35); nor is there a similar protein encoded in the genomes of S. pombe or C. elegans. A gene containing a short region of similarity was found in the D. melanogaster genome, but this may not be a genuine eIF3j subunit. Consequently, further analysis is necessary to determine whether eIF3j is specific to mammalian eIF3 complexes. Similarly, the eIF3l subunit of plant eIF3 may be specific to the plant eIF3 complex, since it is present in both the wheat and A. thaliana eIF3 but not in mammalian eIF3. However, proteins that are similar to plant eIF3l are present in other eukaryotes including mammals. Further analysis of eIF3 complexes isolated from other eukaryotes will be necessary to determine whether other species have an eIF3j-like or an eIF3l-like subunit, or other unique subunit(s).

Fig. 6. Sequence alignment of eIF3l (wheat eIF3-p56). The protein sequences were aligned using GCG Pile-Up (Genetics Computer Group, Inc.) and enhanced with Boxshade (available on the World Wide Web). The peptide sequences similar to those obtained from wheat eIF3l (see Table I) are overlined.

Rice eIF3l

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<th>Rice eIF3l</th>
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</tr>
</tbody>
</table>

Similar amino acid sequences are indicated by dashes (-).

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The analysis of deduced protein sequences from the genomes of *S. pombe*, *D. melanogaster*, and *C. elegans* indicate that other eukaryotes will have an eIF3 subunit composition more similar to mammals and plants than to *S. cerevisiae*. The *S. cerevisiae* eIF3 complex appears to have retained five subunits in common with other eukaryotes, but its evolution has diverged independently of other eukaryotes. Other *S. cerevisiae* initiation factors, with the exception of eIF4B (69), show significant sequence conservation (e.g. eIF4A, eIF1A, eIF5) and similar subunit composition (e.g. eIF2 and eIF4F) with other eukaryotes. The differences in subunit composition of eIF3 between *S. cerevisiae* and mammalian or plant eIF3 are the most dramatic noted in the translational machinery so far. It is therefore not surprising that mammalian or plant eIF3 subunits shared in common with *S. cerevisiae* have lost the ability to complement *S. cerevisiae* eIF3 mutants in those subunits. It is apparent that the analysis of eIF3 function in higher eukaryotes will require another genetic model system in addition to *S. cerevisiae*.

Now that a clearer picture of the subunit composition and role of the different subunits of eIF3 is beginning to emerge, further biochemical and genetic analyses will be possible to unravel the mysteries of this complicated initiation factor in eukaryotes.

Acknowledgments—We thank Dr. Arlen Johnson for critical reading of the manuscript. Dr. Farida Safadi-Chamberlain for advice on the growth of the *A. thaliana* suspension culture, and Daniel Mchugh for assistance in preparation of the MACAW alignments.

Note added in proof—The complete gene sequence for *A. thaliana* eIF3A was located on recently deposited bacterial artificial chromosome (AC008432). The gene encodes a 60,189 Da polypeptide with 77% similarity to the rice eIF3A described in this report. The similarity to human, *D. melanogaster*, and *C. elegans* eIF3A was 60%, 59%, and 39%, respectively. The mass spectrometry analysis of *A. thaliana* eIF3A matched 13 peptides predicted from the gene sequence.

REFERENCES

Plant Initiation Factor 3 Subunit Composition Resembles Mammalian Initiation Factor 3 and Has a Novel Subunit
Elizabeth A. Burks, Paula P. Bezerra, Hahn Le, Daniel R. Gallie and Karen S. Browning

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