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Update on Molecular Biology

The Polyadenylation of RNA in Plants[1]

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Poly(A) tracts are a nearly ubiquitous feature of mRNAs in eukaryotes. The poly(A) tail is an important determinant of the function of a eukaryotic mRNA, because it is intimately involved in processes that determine the translatability (Sachs and Wahle, 1993) and lifetime (Jacobson and Peltz, 1996) of mRNAs. From this perspective, the addition of the poly(A) tail to an mRNA is an important, even necessary, step in the expression of eukaryotic genes. However, although the functions of a poly(A) tail are largely manifest in the cytoplasm, the process of polyadenylation itself is an important component of mRNA metabolism. A growing body of evidence indicates that mRNA polyadenylation may be physically linked to the processes of intron removal (e.g. Niwa et al., 1990) and transcription termination (McCracken et al., 1997), and other studies imply an interplay between polyadenylation and transport of mRNA (Huang and Carmichael, 1996). Thus, it may be more appropriate to consider mRNA 3′-end formation as part of a larger series of events that begins with the initiation of transcription by RNA polymerase II and ends with the delivery of a mature, polyadenylated mRNA to the cytoplasm. In this context, the individual components that mediate mRNA polyadenylation may be expected to have an impact on other nuclear processes (splicing, transcription termination, and transport) as well.

Several recent reviews may be consulted for a detailed picture of the process by which mRNAs are polyadenylated in animals and yeast (Wahle, 1995; Proudfoot, 1996; Wahle and Keller, 1996). Briefly, poly(A) tails are nontemplated and are thus added to nuclear mRNA precursors in a posttranscriptional process. Moreover, polyadenylation in the nucleus is usually viewed as an RNA processing event; in other words, the 3′ end of the mRNA to which poly(A) is added is generated, not by termination of transcription by RNA polymerase II, but rather by processing of a larger RNA that is generated by transcription beyond the poly(A) site. In mammals and yeast a finite series of factors (5–6) cooperate to recognize, process, and polyadenylate precursor mRNAs in the nucleus. Several of the mammalian factors contain subunits with amino acid sequence homology to subunits of the yeast apparatus, which suggests a common evolutionary ancestry for parts of this machinery and a common mechanism by which mRNAs are polyadenylated. However, there are important differences between mammals and yeast in terms of the RNA sequences that make up polyadenylation signals as well as the composition and distribution of the subunits of the different polyadenylation factors.

In this *Update* we will summarize our current understanding of mRNA polyadenylation in plants. This will include a review of the nature of plant polyadenylation signals, a discussion of some issues that remain to be resolved, and an overview of a relatively recent development, namely the polyadenylation of chloroplast RNAs.

POLYADENYLATION SIGNALS IN PLANT NUCLEAR mRNA PRECURSORS

The polyadenylation of mRNA is limited to RNAs and regions of RNAs that carry specific sequence signals (or *cis* elements). Thus, an important aspect of mRNA polyadenylation is an understanding of the sequence signals that direct this process. A detailed picture of poly(A) signals has emerged from studies of a number of plant genes. A number of reviews published in the past 3 years provide a comprehensive treatment of this subject and may be consulted for specific information (Hunt, 1994; Wu et al., 1995; Rothnie, 1996).

Briefly, plant polyadenylation signals consist of combinations of three classes of *cis* elements: a FUE, one or more NUEs, and the polyadenylation site (CS) itself (Fig. 1). NUEs are A-rich sequences, between 6 and 10 nts, that are situated between 10 and 40 nts from their associated polyadenylation site. Based on similarities in sequence composition and relative location, it has been suggested that NUEs are functionally analogous to the mammalian polyadenylation signal AAUAAA (Wu et al., 1995). However, the contrasting properties of NUEs and AAUAAA, as revealed by directed mutagenesis studies (Hunt, 1994; Rothnie, 1996), leave open the possibility that NUEs may function in a manner rather different from AAUAAA in mammals. FUEs are distinctive features of plant poly(A)

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Abbreviations: CS, cleavage site; FUE, far-upstream element; nts, nucleotides; NUE, near-upstream element; PAP, poly(A) polymerase.

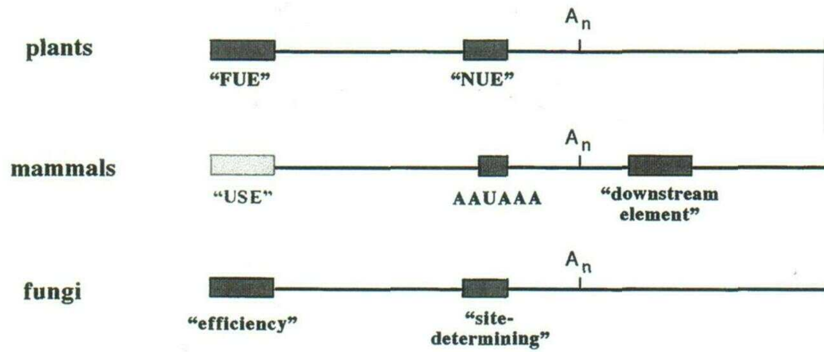

Figure 1. Comparison of polyadenylation signals in different classes of eukaryotes. Elements that function in determining polyadenylation site and efficiency are noted with rectangular boxes. For plant signals, FUEs and NUEs are described in the text. For mammals, AAUAAA and the downstream element are described in detail by Wahle (1995). The upstream stimulatory element ("USE") is defined with a lightly shaded box to indicate that it is not present in all mammalian genes. Terminology for the *cis* elements that define fungal poly(A) signals is that used by Humphrey et al. (1994). Note that for fungal signals, efficiency elements have also been termed as "upstream elements" (Russo et al., 1993) and "far-upstream elements" (Wahle, 1995), and site-determining elements have been termed "downstream elements" (Russo et al., 1993) and "near-upstream elements" (Wahle, 1995). In all cases, the actual poly(A) site is represented with a small vertical tic and noted with the notation A_n.

signals. These elements are situated 5′ to NUEs (hence the term "far-upstream element") and are required for efficient use of their associated poly(A) sites; deletion of an FUE can decrease the apparent efficiency of use of a poly(A) site by more than an order of magnitude. Mutagenesis studies suggest a degree of functional redundancy in FUEs; large deletions involving FUEs can have dramatic effects on polyadenylation, but smaller mutations (point, deletion, or linker-scanning) have more subtle (if any) effects. Moreover, a "complete" FUE may extend for as many as 100 nts. The relative location of FUE is also rather variable, and can be from 13 to 100 nts upstream of the NUE (see the following sections). No highly conserved consensus sequence in FUEs has been defined, although a few sequences that might contribute to FUE function have been suggested (Wu et al., 1995; Rothnie, 1996). Plant CSs are usually situated in a U-rich region of the 3′-untranslated region and contain the dinucleotide Y/(C,A) at the actual site of polyadenylation. The CS may be considered to be an independent *cis* element, since mutation of sequences in the vicinity of the CS nts alters the efficiency or position of poly(A) addition (e.g. Mogen et al., 1992). In this way, plant CSs behave similarly to those in animal and yeast (Wahle, 1995), although in plants, the sequence in front of the CS is not exactly defined. Finally, although there are some indications to the contrary in the literature, sequences downstream from polyadenylation sites do not appear to play a role in the process of mRNA polyadenylation in plants (the controversial aspects of this topic are covered nicely by Rothnie [1996]).

As noted by Dean et al. (1986), most plant transcription units possess several polyadenylation sites, and these are usually situated within a region of 100 to 200 nts in the 3′-untranslated region. This contrasts with the "usual" situation in mammals, the genes of which possess single or widely spaced (alternatively utilized) poly(A) sites (Leff et al., 1986; Wahle, 1995). The presence of multiple polyadenylation sites in plant genes implies the presence of multiple corresponding *cis* elements, a suggestion that has been confirmed in a number of instances. One example of such a situation is illustrated in Figure 2. Each poly(A) site in this gene (the *rbcS*-E9 gene from pea) is controlled by its own respective NUE and CS. However, a single FUE controls three of the four sites, and a second FUE (which overlaps one of the NUEs) controls the remaining site. The ability of a single FUE to control more than one poly(A) site

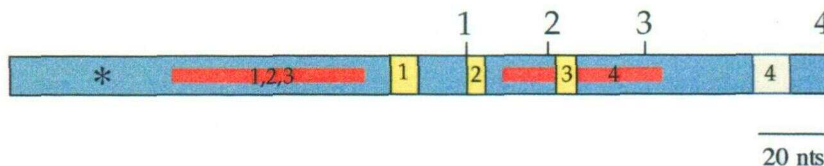

Figure 2. Arrangement of polyadenylation sites and *cis* elements in the 3′-untranslated region of the pea rbcS-E9 gene. This figure is a summary of results of several studies (see Hunt, 1994, and Li and Hunt, 1996). Polyadenylation sites are represented with vertical lines above the bar that defines the RNA itself (blue shaded), and are numbered according to Mogen et al. (1992). NUEs are represented as yellow boxes, with their corresponding sites so noted. The lighter shading of the NUE for site 4 is intended indicate that this NUE has not been formally defined, but rather is so identified based on the occurrence at this position of a characteristic A-rich motif. FUEs are represented with a red line, and the sites controlled by the respective FUE are noted within the element. The translation termination codon in this gene is noted with an asterisk, and the scale (in nts) is noted beneath the representation of the 3′-untranslated region.

has been documented with at least one other plant poly(A) signal (MacDonald et al., 1991), suggesting that the situation depicted in Figure 2 is a general one for plant genes.

It has been reported that monocot polyadenylation signals can be handled differently in dicots (Keith and Chua, 1986), suggesting that there are differences in the composition or functioning of polyadenylation signals in these two general groups of plants. However, two monocot poly(A) signals possess functional maps similar to those seen in dicot signals (Wu et al., 1993, 1994; Ohtsubo and Iwabuchi, 1994), and one set of monocot *cis* elements (from the zein 27-kD gene) functions indistinguishably in monocots and dicots (Wu et al., 1994). These latter results indicate a general commonality in polyadenylation signal structure. Differences in polyadenylation signal usage between different groups of plants may reflect variations in the efficiency of specific sequences (for example, in NUEs), or perhaps more subtle regulatory effects involving particular polyadenylation sites.

At first glance, the arrangement of *cis* elements in plant polyadenylation signals may seem to be dramatically different from their mammalian counterparts, but rather similar to fungal poly(A) signals (Fig. 1). The contrast with mammalian signals is best exemplified by the apparent ubiquity of upstream sequence elements in plant polyadenylation signals and the lack of involvement of downstream sequence elements in polyadenylation in plants. However, a general topological consensus is apparent in plants, animals, and yeast (Fig. 1). Thus, sequences upstream from AAUAAA or their possible functional counterparts can affect polyadenylation efficiency in animals, yeast, and plants. Moreover, sequences within 40 nts of poly(A) sites are required in these different classes of organisms; these sequences include the mammalian polyadenylation signal (AAUAAA) and are related in the sense that they are A rich. The absence of downstream sequence requirements for polyadenylation in plants and yeast might appear to be a departure from this commonality. However, plant FUEs seem to share sequence properties with the downstream elements required for polyadenylation in animal genes, in particular a decided UG/U-richness (Wahle and Keller, 1996). This similarity suggests that an evolutionarily conserved *trans* factor may recognize downstream elements in animals and FUEs in plants. Of course, this must remain speculation until biochemical studies of polyadenylation in plants are undertaken.

OUTSTANDING ISSUES

Although our understanding of plant polyadenylation signals is relatively extensive, a number of questions remain unresolved. Among these is the rationale for the existence of multiple polyadenylation sites in most plant genes. It is possible that there is a degree of "sloppiness" in the plant polyadenylation apparatus, such that processing and polyadenylation would occur in a general region or at any of a number of locations in a given 3′-untranslated region. However, refined mutagenesis studies involving NUEs argue against this scenario, since substitutions of as few as five nts can have dramatic effects on one poly(A) site without affecting neighboring sites (these studies are summarized by Rothnie [1996]). It may be that cooperative interactions between (as yet hypothetical) NUE-recognizing factors are important for efficient 3′-end formation. This would explain the preponderance of poly(A) sites in plant genes, as well as the one-to-one correspondence of NUEs with poly(A) sites. Wu et al. (1993) have suggested such a cooperativity as an explanation for the effects of NUE mutations in the zein 27-kD gene. However, in other genes that carry multiple polyadenylation signals, mutation of one NUE has little discernible effect on the overall functioning of other NUEs (or FUEs; see, e.g. Li and Hunt, 1995). Thus, although cooperativity is a viable explanation for the presence of multiple poly(A) signals in plant genes, more extensive studies are needed to better evaluate this possibility.

Alternatively, multiple poly(A) sites may be a consequence of a more general nucleotide preference in 3′-untranslated regions. Specifically, the 3′-untranslated region, like intervening sequences, may be constrained to have a relatively high A+U content; this could be important for 3′-terminal exon definition or transcription termination. A consequence of such a sequence predisposition would be the presence of small domains of high A content (which should be functional as NUEs). In concert with a single FUE (also an element with low sequence conservation, and one likely to occur in regions with elevated U content), multiple poly(A) sites would be expected. This possibility is consistent with observations reported by Luehrsen and Walbot (1994), indicating that AU-rich sequences, not knowingly associated with polyadenylation, were able to serve as poly(A) signals when inserted into a test gene and analyzed in maize.

The model for the structure of plant polyadenylation signals (Figs. 1 and 2) implies the existence of at least three classes of polyadenylation factors in plants—one each for the recognition of the FUE, NUE, and CS. In addition, the existence of a PAP is axiomatic. With the exception of PAPs, the existence of these factors is at the moment largely hypothetical. Wu et al. (1994) observed an increase in polyadenylation efficiency when the spacing between FUE and one particular NUE was decreased. This result is consistent with a model involving the concerted action (and thus interaction) of factors that recognize FUEs and NUEs. There do exist sequences in plant DNA databases with significant homology to mammalian polyadenylation factor subunits (B.J. Elliott, L. Meeks, and A.G. Hunt, unpublished observations), but a correspondence between any such factor and a plant polyadenylation signal *cis* element has yet to be drawn. Preliminary studies suggestive of the presence of an FUE-specific RNA-binding activity in maize nuclear extracts have been described (Wu et al., 1995). However, a role for this factor in any polyadenylation-related process has not been demonstrated.

One polyadenylation factor for which some information is available is the enzyme responsible for poly(A) addition, PAP. PAPs have been reported in a number of plants, and in a range of tissue types or developmental stages: leaf, callus, and germinating seeds in both monocots and dicots (for review, see Rothnie, 1996). In some biochemical re-

spects, such as their nonspecific activities and possible regulation by phosphorylation (Verma and Sachar, 1994), the plant PAPs are similar to their mammalian and yeast counterparts. However, a formal demonstration of a role for any of the enzymes described in the literature in a polyadenylation signal-dependent, nucleus-localized process has yet to be made.

Given the near-universal preponderance of multiple polyadenylation sites in plant genes, one might expect that alternative poly(A) site usage may be important for plant gene expression. Such a mechanism is operative in caulimovirus-infected cells, permitting the production of greater-than-unit-length virus-encoded RNAs that contain a poly(A) signal very near their 5′ terminus (Sanfaçon, 1992). In this case, proximity to the 5′ terminus of the mRNA or to the promoter has been shown to be at least partially responsible for the ineffectiveness of the 5′-proximate poly(A) signal. To date, however, there are no clear cases of an involvement of alternative polyadenylation in the differential expression of cellular genes in plants. Nonetheless, the observation that many different sequences can function as NUEs (indeed, often with different inherent efficiencies [Li and Hunt, 1995]) and FUEs, as well as the differences with which monocots and dicots handle particular polyadenylation signals, leave open the possibility that some poly(A) signals may function in a regulated manner.

It must be noted that much of the preceding makes a fundamental, as yet unconfirmed assumption, which is that the process of mRNA polyadenylation in the nuclei of plants is an unambiguous RNA processing event, as has been shown in mammals and yeast. This would appear to be a reasonable assumption, supported by the general topological similarity of plant poly(A) signals to other such signals (Fig. 1) and the existence of homologs of mammalian polyadenylation factor subunits in plants (B.J. Elliott, L. Meeks, and A.G. Hunt, unpublished observations). However, a direct in vitro demonstration of processing and polyadenylation of a precursor mRNA in a plant-derived extract has yet to be reported. Thus, it remains a formal (and important) possibility that mRNA polyadenylation in plants is fundamentally different from the same process in yeast and mammals, and that a more direct link between transcription termination and polyadenylation may exist. Of course, such a scenario would dramatically change our ideas about the roles of the various *cis* elements in the process of 3′-end formation in plants, as well as the nature of the hypothetical polyadenylation factors postulated above.

POLYADENYLATION OF CHLOROPLAST mRNA

Although usually considered to be a modification of importance in eukaryotic cells, RNA polyadenylation is also a process that occurs in bacteria (Sarkar, 1996). It should thus come as no surprise that RNA polyadenylation occurs in chloroplasts as well. PAP were reported in chloroplast extracts some 24 years ago (Burkard and Keller, 1974). More recently, polyadenylated chloroplast RNAs have been identified and characterized (Kudla et al., 1996; Lisitsky et al., 1996). It is interesting that the poly(A)-rich tracts on these RNAs are not exclusively adenosine, but can contain other bases (primarily guanosine; Lisitsky et al., 1996). This property is consistent with the reported existence in chloroplast extracts of enzymes that can add oligoadenylate or oligoguanylic tracts to RNAs (Burkard and Keller, 1974).

In chloroplasts poly(A) tracts are found at the 3′ ends of presumed degradation intermediates (RNAs that have been cleaved by endonucleases, or on which an exonuclease has stalled; Kudla et al., 1996; Lisitsky et al., 1996). Moreover, polyadenylated RNAs are degraded much more rapidly than are nonpolyadenylated RNAs in chloroplast extracts (Kudla et al., 1996; Lisitsky et al., 1996), and polyadenylated chloroplast RNAs are more prevalent in vivo under some conditions that also promote chloroplast RNA degradation (Kudla et al., 1996). These observations suggest that polyadenylation may promote RNA turnover in chloroplasts in vivo. This hypothesis is analogous to recent models in bacteria that postulate a role for polyadenylation in accelerated RNA turnover (e.g. Ingle and Kushner, 1996). Given the importance of posttranscriptional events, including mRNA turnover, in chloroplast gene expression (Mayfield et al., 1995), the potential link between RNA polyadenylation and turnover is very interesting.

The subject of polyadenylation in chloroplasts is, in a chronological sense, a rather mature one. It is, nonetheless, a very new area in most senses. Little or nothing is known about the specificity (if any) of polyadenylation in chloroplasts, as well as any control of poly(A) addition that might exist. Although the first reports of chloroplast PAPs, and/or poly(G) polymerases, date to more than 20 years ago, little is known about the enzymes that add poly(A) to chloroplast RNAs. However, chloroplast RNA processing and metabolism are amenable to direct in vitro analysis, and it is reasonable to expect that rapid progress should be made in answering these and other questions regarding polyadenylation in chloroplasts.

CONCLUSIONS AND PROSPECTS

Currently, our understanding of the nature of plant polyadenylation signals is relatively clear, so much so that models proposed 5 years ago continue to be of excellent predictive value. However, much remains to be learned regarding the biochemistry of mRNA polyadenylation in plants. Indeed, those studies that have been so informative in mammalian and yeast systems (in vitro dissection of the process of processing and polyadenylation of pre-mRNAs) have not proven feasible with plant systems, for reasons that are not entirely clear. With the advent of various plant genome initiatives and the discovery of plant homologs of mammalian polyadenylation factor subunits, there is much promise for a new era of discovery with regard to the means by which a plant polyadenylation signal functions. Likewise, the isolation of clones encoding plant PAPs (a reasonable expectation, given the availability of relatively pure preparations of this enzyme [e.g. Kapoor et al., 1993]) should be informative.

This promise should extend to other fields as well. As stated above, insight into polyadenylation may be expected to lead to a greater understanding of the workings of RNA polymerase II in plants. It is to be expected (or at least anticipated) that plant polyadenylation factors should be important players in cytoplasmic polyadenylation, as has been shown in animals (Bilger et al., 1994). Finally, the (re)discovery of polyadenylated RNAs in chloroplasts provides yet another parallel between these organelles and bacteria in terms of mRNA metabolism. It also offers an additional stage at which posttranscriptional control of chloroplast gene expression might be affected.

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