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Update on Plant Mitochondria

The Elusive Plant Mitochondrion as a Genetic System[1]

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MITOCHONDRIAL FUNCTIONS IN HIGHER PLANTS

The mitochondrion, as the site of energy metabolism, plays a fundamental role within the eukaryotic cell. In plants, the function of this important organelle is made more fascinating by the presence of a second energy-generating system in the chloroplast, with which biochemical and genetic activities must be coordinated. The majority of components necessary for mitochondrial and chloroplast functions are supplied by genes encoded within the nucleus. The presence of genetic information within the mitochondrion and chloroplast, as well as within the nucleus, requires that some form of coordinate gene expression must occur. This intracellular cooperation is necessary not only to assure production of essential components for respiratory and photosynthetic processes, but also for the synthesis of transcription, transcript processing, translation, replication, and organellar transmission machinery requisite to organellar maintenance.

Mechanisms regulating the cellular genetic network are poorly understood, as is the evolution of this interorganellar dependence. Mitochondria are currently viewed as integrated endosymbionts, originating from a large group of eubacteria (reviewed by Gray, 1993). The organellar genetic systems are, therefore, somewhat independent of the nucleus insofar as they obey many of their own unique rules of genetics, including uniparental inheritance, somatic recombination, vegetative segregation, gene expression, and genome organization. Many of the nuclear genes required for mitochondrial function are believed to be the result of continuing gene transfer from the mitochondrion during the course of evolution. Within the plant kingdom there can be found a number of presumptive evolutionary intermediates. The legume family, for example, provides convincing evidence that many functions that were originally encoded within the mitochondrion are now gradually being transferred to the nucleus (Covello and Gray, 1992; Nugent and Palmer, 1992). Whereas a particular mitochondrial Cyt oxidase subunit (*coxII*) is encoded and expressed within the mitochondrion in pea, the same subunit is encoded but not expressed within the nucleus. In soybean and common bean, the same gene duplication exists within the mitochondrion and nucleus, but only the nuclear gene is expressed. In mung bean and cowpea, the mitochondrial form of the gene is no longer present and the nuclear gene is the only functional form. This interorganellar transfer has apparently occurred via an RNA intermediate. Other mitochondrial genes are now being identified that have apparently entered this gene-transfer process.

To compound the complexity already inherent in this cellular arrangement, respiratory demands vary greatly among different plant tissues, with the highest respiratory rates occurring during seed germination, pollen development, and fruit ripening. This variation in respiratory activity is presumably reflected in altered regulatory signals at the cell level. It is also apparent that mitochondrial numbers and mitochondrial DNA concentration vary greatly at different stages of plant development, presenting yet another form of regulation required within the cell (Bendich, 1987).

THE UNIQUENESS OF THE PLANT MITOCHONDRIAL GENOME

The plant mitochondrial genome differs from that of other higher eukaryotes in the vast diversity demonstrated in genome size and structure (reviewed by Hanson and Folkerts, 1992). Even within one plant family a 10-fold difference in mitochondrial genome size can be observed. This unusually large size range is not reflective of relative coding capacity, however (Stern and Newton, 1985). The mitochondrial genome encodes only a fraction (estimated at 20–30 proteins) of the gene products required for its function; the vast majority are encoded by the nucleus. The plant mitochondrial genome is known to encode three rRNAs (26S, 18S, and a 5S rRNA unique to plants), several ribosomal proteins, and some of the necessary tRNAs. Those tRNAs necessary for mitochondrial translation that are not encoded by the mitochondrion are located in the nucleus (Dietrich et al., 1992). Among monocots and dicots, the number and identity of the missing mitochondrial tRNA sequences vary. The mechanism of transport of these essential tRNAs to the mitochondrion is not known, which raises interesting questions about nucleic acid transport across cellular membranes.

The number and identity of plant mitochondrial protein-encoding genes is not yet fully defined. It is known that plant mitochondria encode a number of components of the electron transport complexes, including apocytochrome *b* of the bc_1 complex, three subunits of the Cyt *c* oxidase complex (*coxI*, *coxII*, and *coxIII*), and subunits *nad1* to *nad7* of the NADH-ubiquinone oxidoreductase complex. The organellar genome also encodes at least four subunits of the F_0-F_1 ATPase complex. A variable number of chloroplast sequences, including some tRNA sequences that are apparently functional

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Abbreviation: cms, cytoplasmic male sterility.

(Dietrich et al., 1992), have been transferred to the mitochondrion. These DNA transfers account for part of the variation in relative genome size. New transcribed open reading frames continue to be identified in the plant mitochondrial genome. For example, based on transcription activity, sequence conservation among species, and RNA editing pattern, a Cyt *c* maturation gene was identified in *Oenothera* and carrot (Schuster et al., 1993). It is possible that the functions encoded by some of these open reading frames are unique to plants.

The uniqueness of the plant mitochondrion is not limited to its genome size variability or a few unusual gene products. The mitochondrial genome of plants distinguishes itself from those of other higher eukaryotes in its unusual organization and gene-processing mechanisms. Much of the variability in genome size in plants is accounted for by the surprisingly complex organizations observed among different plant species (see Fig. 1). Mitochondrial DNA recombination events that occur among homologous repeated sequences as well as among apparently nonhomologous sequences result in a highly variable genome configuration in higher plants relative to other eukaryotic systems. These events contribute not only to the complexity of genome structure but to mitochondrial mutation frequency as well. The presence of recombinationally active repeated sequences leads to a multipartite genome structure generated by both intermolecular and intramolecular recombination events (Fauron et al., 1991). The presence of repeats in direct and inverted orientation gives rise to subgenomic DNA molecules and inversions within the genome. Whether these DNA exchanges occur in all cells of the plant or are limited to a particular developmental stage is not known. One clue that homologous recombination events may occur at a high frequency in plant mitochondria comes from the high level of sequence identity maintained among the homologous repeated sequences. Such sequence conservation could result from copy correction during the course of frequent DNA exchange.

Because of the inherent mitochondrial genomic complexity, the identification of a replicative form is not trivial and has not been accomplished for most plant species. Interestingly, recent evidence from genome mapping and pulsed-field gel electrophoresis studies suggests that more than one of the many molecular forms present in the genome may be autonomously replicated (Folkerts and Hanson, 1991; Levy et al., 1991; Janska and Mackenzie, 1993). If this is the case, mitochondrial mutation elimination may involve the selective transmission or elimination of particular mitochondrial chromosomes during plant development (Janska and Mackenzie, 1993). This is possible because much of the mitochondrial genetic information is duplicated on more than one molecular form in the genome. Evidence exists to indicate that some mitochondrial molecules may be maintained at very low copy number relative to others (Small et al., 1987). These substoichiometric forms may become increasingly important to our understanding of the evolutionary processes for maintaining mitochondrial genome integrity. The maintenance of mitochondrial DNA molecules at extremely low copy number may allow the accumulation or retention of mutations with an insignificant phenotypic consequence and, thus, little or no selection pressure for their elimination (Small et al., 1987).

Some of the most poorly understood phenomena in plant mitochondrial biology are the processes that regulate organellar somatic segregation and transmission (Connett, 1987). Based on protoplast-fusion experiments in a number of plant species, it is generally accepted that a condition of heteroplasmy, or a mixture of different mitochondrial types, is unstable and will eventually sort to homogeneity in a random partitioning process. What is not yet clear is whether this process is directed by nuclear genes. In the majority of plant species, mitochondrial transmission to the next generation occurs predominantly through the female gamete, with little or no contribution from the pollen. The molecular basis of this selective cytoplasmic transmission is not understood; the observation in recent years of paternal transmission of mitochondria in some species makes the regulation of this process even more interesting.

Recent investigations of mitochondrial gene expression have distinguished the plant kingdom from others in some unexpected ways. Nearly all plant mitochondrial transcripts examined to date show some degree of transcript editing. Generally these changes to the primary transcript involve C $\rightarrow$ U transitions, although a smaller number of U $\rightarrow$ C changes have been observed (reviewed by Wissinger et al., 1992). Editing events are essential for proper gene expression and occur not only within an open reading frame to alter amino acid sequence, but within start and stop codons that define the open reading frame. A number of incomplete processing intermediates are usually present in the transcript population for any one gene. Although the sites of editing are constant for a particular sequence, the order in which these processing events occur appears random. The mechanism of editing is not yet well defined biochemically, although these events appear most likely to involve modification of the incorporated nucleotide (Rajesekhar and Mulligan, 1993). The editing process in plants is distinct from that in trypanosomes, but is possibly similar to editing activities in some mammalian or viral systems (reviewed by Pring et al., 1993).

The mechanism of transcript editing in plants is likely under nuclear control, as suggested by the observation that the extent of transcript editing in the case of *nad3* can be influenced by a single nuclear gene (Lu and Hanson, 1992). This nuclear-mitochondrial interaction apparently serves as one means of posttranscriptional gene regulation. The nuclear genes regulating these mitochondrial transcript-processing events have not yet been characterized or mapped. It should be possible, however, to estimate the degree of genetic complexity associated with this process by determining whether one nuclear locus can influence the editing of more than one mitochondrial gene, or whether different nuclear genes are required for each mitochondrial transcript.

Certain plant mitochondrial genes are encoded by multiple exons that are interrupted by uncommonly large distances. This unusual gene organization is apparently the result of interruption of intron sequences by recombination events. Proper transcript processing for these genes requires the trans-splicing of the interrupted intron sequences to derive a mature transcript. All interrupted introns observed to date have been group II introns, requiring appropriate intron secondary structure to allow the association of the separated,

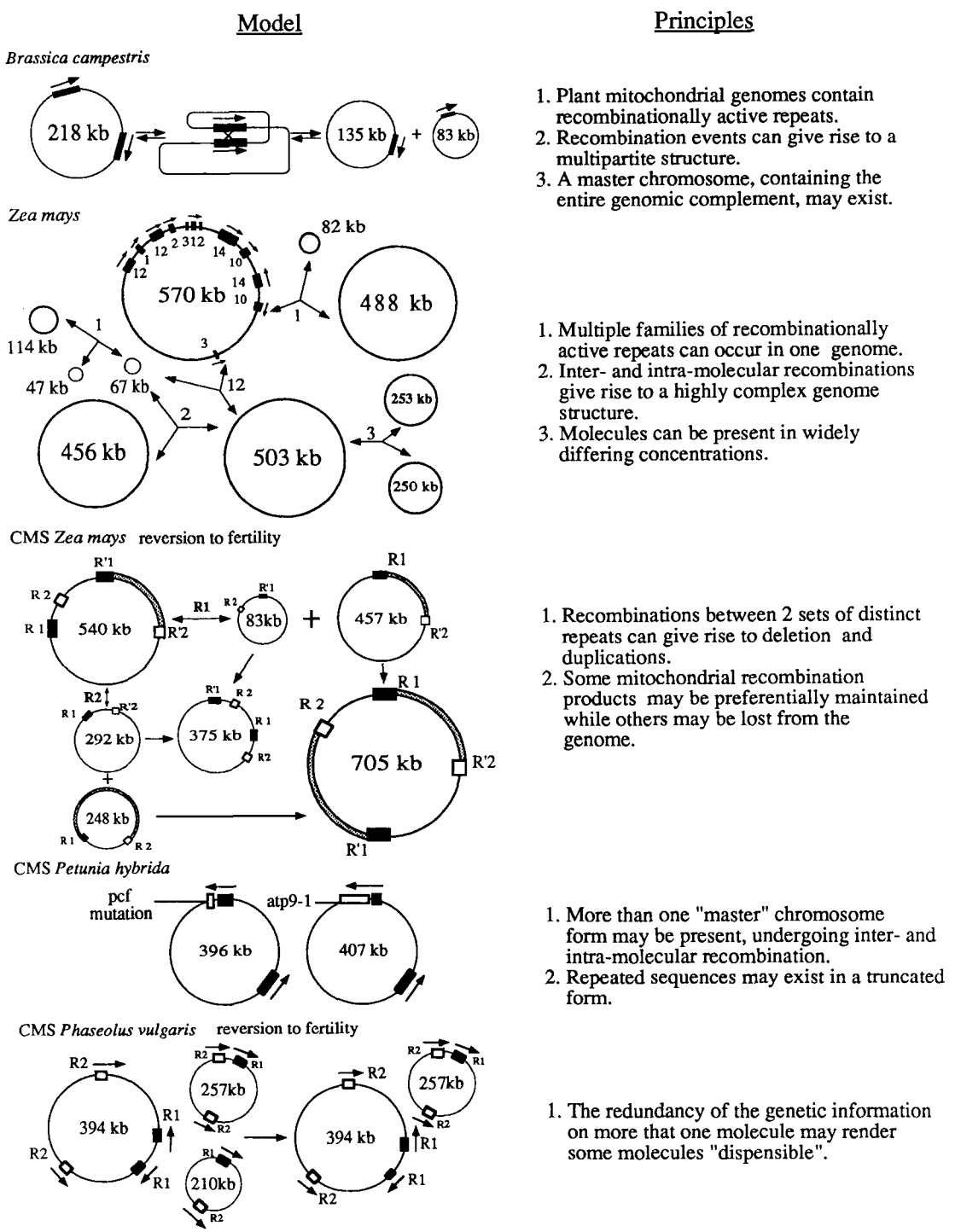

Figure 1. Examples of the structural diversity observed among plant mitochondrial genomes. Based on genome-mapping data, a number of models have been developed to account for the array of genomic configurations. Many of these models have been based on certain underlying principles that may be unique to the plant kingdom, including a propensity to undergo multiple recombinations, a multipartite genome structure, and the retention of mutations derived by various aberrant genomic reorganizations. Many of these mutations are associated with the common phenotype of cms. Small boxes indicate repeated sequences and arrows indicate relative repeat orientation. Mitochondrial molecules are presented in circular form based on physical mapping data. There is, however, no definitive physical evidence that they exist in the genome as circles. Models were taken from Palmer and Shields (1984), Lonsdale et al. (1984), Fauron et al. (1990), Folkerts and Hanson (1992), and Janska and Mackenzie (1993).

transcribed intron segments for splicing to proceed (see Wissinger et al., 1992). The biochemical processes involved in trans-splicing have yet to be defined. Although the intron splicing may be an autocatalytic event, cellular factors may be important to this process. RNA editing, for example, constitutes a trans-acting factor that is essential for defining the splicing-competent primary and secondary structure required for at least some group II introns.

These unique features of the plant mitochondrial genome have made this organelle and its interactions with the nuclear genome particularly interesting. Thus, the identification of mitochondrial mutations as well as those nuclear genes that can correct the mutant phenotypes has been an essential focus of the research in plant mitochondrial biology for some years.

STUDY OF MITOCHONDRIAL GENETICS

Many of the most important lessons regarding mitochondrial function have been learned through investigations in fungal systems, most notably yeast (*Saccharomyces cerevisiae*). This is primarily because the indispensable nature of mitochondrial functions to the higher eukaryotic cell makes mutational analysis in studies of mitochondrial genetics generally infeasible. In those yeasts that are able to survive without a functional mitochondrion via fermentation, a large collection of important mutations in mitochondrial genes as well as nuclear genes involved in mitochondrial functions is available. This collection, together with the availability of nuclear gene disruption and replacement technologies and DNA-mediated mitochondrial transformation systems, has allowed the elucidation of a number of important mitochondrial processes in biogenesis and gene expression (Bolotin-Fukuhara and Grivell, 1992). It has, as well, facilitated the identification of both mitochondrial and nuclear genes involved in mitochondrial function in higher eukaryotes, including plants.

Many more difficulties arise in the direct identification of genetic components of the nuclear-mitochondrial communication network in higher-plant systems. Gene mutations that interfere with normal mitochondrial function are likely to be lethal and can be maintained only in a heteroplasmic (mixed mitochondrial) population. The nonchromosomal stripe mutants of maize represent mutations within essential mitochondrial genes maintained via heteroplasmy and observed as sectoring within the plant (Gu et al., 1993). Mitochondrial genomic alterations have been associated with enhanced disease susceptibility (Levings, 1993), altered chloroplast function (Roussell et al., 1991; Martinez-Zapater et al., 1992), severe growth abnormalities (Newton et al., 1989), reduced plant vigor (Jan, 1992), and aberrant floral developmental patterns (Kofer et al., 1991; Gourret et al., 1992). Additionally, a large collection of plant mitochondrial mutations that result in abnormal pollen development, known as cms, has accumulated over the past 20 years. The phenomenon of cms, reported in over 150 plant species, has provided an important focus for studies of mitochondrial genomic alteration, gene expression, and nuclear-mitochondrial genetic interactions.

CYTOPLASMIC MALE STERILITY AND MALE STERILE MUTANTS

Plant mitochondrial dysfunction can occur for at least two reasons: spontaneously arising mutation/genomic rearrangements and nuclear-cytoplasmic incompatibilities. Nuclear-cytoplasmic incompatibilities generally arise when the cytoplasm from one species is combined with the nucleus of a different species. This is effected most readily either by interspecific protoplast fusion or by wide hybridization followed by subsequent recurrent backcrossing to the nuclear donor (pollen parent in the original cross). In most cases of mitochondrial mutation or nuclear-cytoplasmic incompatibility the observed phenotype is that of cms. The cms phenotype is characterized by the inability of the plant to produce and/or shed viable pollen. The phenomenon demonstrates maternal inheritance and is generally not accompanied by changes in female fertility.

The apparent association of plant mitochondrial genome alterations with aberrant pollen development remains an enigma. It is not clear why this particular plant developmental stage would be most vulnerable to alterations in mitochondrial function when, for most of the identified mitochondrial mutations, expression of the sterility-associated mitochondrial product is detected at all plant developmental stages. The processes of microsporogenesis and microgametogenesis are affected differently in many cases of cms. For example, in at least two cases, only the individual developing microspores (gametophytic stage) are affected by the mitochondrial lesion (Lee et al., 1980; Johns et al., 1992), whereas in many other cases the abnormality is most pronounced as premature or aberrant breakdown of the tapetum (sporophytic tissue surrounding the developing microspores). In certain cases, male sterility is the result of abnormal development or feminization of the male reproductive structures (Kofer et al., 1991; Gourret et al., 1992). Consequently, the precise points in the pollen development process most profoundly affected by mitochondrial dysfunction are not known. It is generally assumed, however, that the development of the male gametophyte in plants is accompanied by a pronounced increase in respiratory activity, because mitochondrial numbers increase markedly following meiosis. A commensurate increase in mitochondrial DNA replication accompanies these processes (reviewed by Dickinson, 1987).

The mitochondrial mutations associated with cms in several plant species have been identified and characterized. In each case the alteration is distinct, although particular regions of the mitochondrial genome, such as the 3′ end of the *atpA* gene, appear to be more highly susceptible to rearrangement. cms-associated alterations may involve DNA deletion (e.g. Chetrit et al., 1992), insertion of sequences of unknown origin (e.g. Laver et al., 1991; Johns et al., 1992), multiple intragenic recombination events generating chimeric gene arrangements (e.g. Young and Hanson, 1987; Levings, 1993), often producing polycistronic messages and, in one case, unusual virus-like particles (Grill and Garger, 1981). This diversity of mutations initially made it difficult to identify those features linking each system to a similar aberrant phenotype. One feature that appears to link many of the sterility-associated mitochondrial sequences is that they generate novel open

reading frames. Perhaps the most important feature of the predicted gene products of these open reading frames is the presence of a hydrophobic stretch of amino acids, often at the amino terminus of the predicted polypeptide. This observation suggests that, although each sterility-associated sequence appears distinct, the mechanism for inducing mitochondrial dysfunction may involve a common phenomenon, namely the anchoring to, or complete insertion within (Levings, 1993), the inner mitochondrial membrane of an aberrant mitochondrial peptide. It is conceivable that such unusual peptide insertions may have relatively minor consequences to mitochondrial function during most stages in plant development, but may cause phenotypic changes when respiratory demand is sharply increased. This hypothesis, although often suggested, has not yet been tested for any cms system. Alternatively, cms mutations may invoke tissue-specific or stage-specific changes in gene expression, as has been suggested in the case of cms petunia by Conley and Hanson (1994).

NUCLEAR GENE REGULATION OF MITOCHONDRIAL FUNCTION

The vast diversity of potential mitochondrial mutations obtained with the selection for cms has provided an important opportunity for the investigation of nuclear-mitochondrial genetic interactions in higher plants. The cms phenotype provides the most efficient available genetic screen for the identification of nuclear genes that regulate plant mitochondrial function. These nuclear genes, identified by their ability to restore normal pollen development to a cms line, are referred to as fertility-restorer genes. Fertility restorers have been identified in nearly every cms system. Restorer systems vary in their gene number, with most restorers consisting of a single dominant gene. No fertility-restorer genes have yet been cloned, although at least three laboratories are currently pursuing this endeavor. The apparent mechanisms of fertility restoration vary and provide opportunity for the identification of nuclear factors involved in many levels of mitochondrial regulation.

The best-characterized fertility restorers involve nuclear factors apparently acting in mitochondrial transcript processing, alteration of relative transcript levels, or possibly mitochondrial translation (Brown, 1993). Some restorers appear to limit their effects to tissues involved in pollen development (Young and Hanson, 1987). One unusual fertility restorer system involves a single nuclear gene that directs the complete loss of the mitochondrial sterility-associated sequence from the genome (Mackenzie and Chase, 1990). In some cms systems only one fertility-restoration system has been identified, although multiple fertility restorers are available for a number of cases of cms (e.g. petunia, bean, rice, wheat, rape). The availability of multiple fertility restorers in a single cms system is important and has not, to date, been fully exploited. These systems suggest that a cms-inducing mutation can serve as an excellent genetic target for identifying a variety of nuclear mechanisms to modify mitochondrial gene expression (nuclear-encoded mitochondrial transcription, transcript processing, and translation factors) or to eliminate mitochondrial mutations (nuclear-encoded factors involved in mitochondrial DNA replication, recombination, and/or mitochondrial segregation). Some of these nuclear regulatory factors could perhaps be obtained in a more amenable genetic system like yeast. However, the essential features distinguishing plant mitochondrial biology, such as tissue specificity of mitochondrial functions, unique genome organization and expression, and the implicit complexity that a multicellular structure imposes on mitochondrial segregation, have added intrigue to the investigations in plant systems and promise to provide essential information about intracellular regulation clearly unique to plants.

A plant mitochondrial transformation system is not yet available and will be an essential component of more definitive future studies in the area of nuclear-mitochondrial interaction. With the development of high-density maps (and transposon tagging systems) in most of the crop plants for which well-characterized cms systems exist, the opportunity is now available to localize these nuclear factors involved in plant mitochondrial control. The many different functions represented by the available collection of restorers assures the opportunity to identify at least some of the factors in the elaborate regulation of plant mitochondrial transmission, gene expression, and genome organization.

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