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The spaceflight environment can induce transpositional activation of multiple endogenous transposable elements in a genotype-dependent manner in rice

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Summary

Spaceflight represents a unique environmental condition whereby dysregulated gene expression and genomic instability can be provoked. However, detailed molecular characterization of the nature of genetic changes induced by spaceflight is yet to be documented in a higher eukaryote. Transposable elements (TEs) are ubiquitous and have played a significant role in genome evolution. Mounting evidence indicates that TEs constitute the genomic fraction that is susceptible and responsive to environmental perturbations, and hence, most likely manifesting genetic instabilities in times of stress. A predominant means for TEs to cause genetic instability is via their transpositional activation. Here we show that spaceflight has induced transposition of several endogenous TEs in rice, which belong to distinct classes including the miniature inverted terminal repeat TEs (MITEs) and long-terminal repeat (LTR) retrotransposons. Of three rice lines studied, transposition of TEs were detected in the plants germinated from space-flown dry seeds of two lines (RZ1 and

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Abbreviations: AFLP, amplified fragment polymorphism; LTR, long-terminal repeat; MITE, miniature inverted terminal repeat transposable element; ORF, open-reading frame; RILs, recombinant inbred lines; TEs, transposable elements; TPase, transposase.

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RZ35), which are genetically homogeneous and stabilized recombinant inbred lines (RILs) derived from a pure-line rice cultivar, Matsumae. In contrast, the TEs remained immobile in plants derived from space-flown seeds of Matsumae itself, indicating a genotype-dependent manner of TE transposition under the spaceflight environment. Further examination showed that at least in some cases transposition of TEs was associated with cytosine demethylation within the elements. Moreover, the spaceflight-induced TE activity was heritable to organismal progenies. Thus, our results implicate that the spaceflight environment represents a potent mutagenic environment that can cause genetic instabilities by eliciting transposition of otherwise totally quiescent endogenous TEs in a higher eukaryote.

Introduction

The spaceflight environment is unique in that multiple factors, including cosmic irradiation, micrograviy, space magnetic fields, etc., are involved, which are conceivably interacting and cause alterations in gene expression and jeopardize genomic stability (Mashinsky and Nechitailo, 2001). Indeed, numerous studies have reported that spaceflight is mutagenic and induces various types of phenotypic mutations and molecular changes (Krikorian and O'Connor, 1984; Kuang et al., 1996; Mei et al., 1998; Nechitailo et al., 2005; Li et al., 2007). However, except in a case of microorganism where enhanced mutation rate of both point mutations and larger insertion/deletion events were documented at the nucleotide sequence level (Yatagai et al., 2000), nature of the phenotypic mutants in eukaryotes (mainly in plants) have not been molecularly characterized. Furthermore, some other studies have found no evidence for genetic variability in plants subjected to a long-term (a complete organismal generation) space-flight (Sychev et al., 2007). Thus, the extent to which the spaceflight environment is mutagenic and the underlying mechanism are issues that remain to be determined.

Transposable elements (TEs) are major and ubiquitous components of both prokaryotic and eukaryotic genomes and have played a significant role in their structure, function and evolution (Bennetzen, 2000; Kidwell and Lisch, 2000; Hirochika et al., 2000; Casacuberta and Santiago, 2003; Feschotte and Pritham, 2007). Depending on their mode of transposition, TEs are divided into two major classes: Class I elements or retrotransposons transpose by reverse transcription of an RNA intermediate, and hence, via a "copy-and-paste" mode, while class II elements or DNA transposons transpose directly from DNA to DNA via a "cut-and-paste" or a replicative mechanism (Bennetzen 2000; Feschotte et al., 2002). Although most TEs are transcriptionally inert and transpositionally quiescent under normal conditions, recent studies have provided compelling evidence indicating that activity of at least a fraction of TEs are responsive to various induction conditions including both mutagenic and genetically non-mutagenic factors (Wessler, 1996; Capy et al., 2000; Feschotte and Pritham, 2007). For example, plant TEs are almost always quiescent during normal growth and development but some of which can be activated at the transcriptional or transpositional levels by various biotic and abiotic stresses like wounding, pathogen attacks, cell culture, extreme environmental conditions (e.g., low temperature), and inter-specific hybridizations (Hirochika et al., 1996; Wessler, 1996; Grandbastien 1998; Labrador et al., 1999; Hashida et al., 2003; Shan et al., 2005; Michalak, 2009). In addition, it has been well-established that ionizing radiation may cause transpositional activation of normally dormant TEs (Walbot, 1999). It was further established that a major reason for inducibility of TE activity is their normally repressive control by epigenetic mechanisms like cytosine DNA methylation which are sensitive to perturbations (Finnegan, 2002; Kato et al., 2003; Kovalchuk et al., 2004; Boyko and Kovalchuk, 2008).

Taken together the characteristics of the spaceflight environment (described above) and the epigenetically controlled inducibility of TEs, we assumed that if spaceflight represents a mutagenic condition, then activities of certain TEs might be preferentially induced. Therefore, the aim of this study was to investigate effect of the spaceflight environment on transpositional activity of a selected set of TEs that are known or suspected as prone to induction by various stress conditions. We have chosen to study the issue in rice because of its prominence both as a model higher plant and as a staple food crop. In addition, several cases on spaceflight-induced phenotypic mutants have been reported in rice, though the