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R paramutation primer (*R* paramutation made simple): How transposable elements (TEs) may explain *R paramutation*

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TEs have occupied genomes for millions of years (Fedoroff, PNAS 97:7002-7007, 2000; Feschotte and Pritham, Rev. Genet. 41:331-368, 2007).

Silencing machinery was required to maintain TE silencing (Slotkin et al., Nature Rev. Genet. 8:272-285, 2007).

TEs have increased gene redundancies throughout the genome - gene duplications like TEs had to be silenced.

Haplotypes of *R1* and *R1-st* contain *R* duplications (Kermicle, in Russo et al., eds., Epigenetic Mechanisms of Gene Regulation, Cold Spring Harbor Press, 1996; Walker et al., EMBO J. 14:2350-2363, 1995).

R duplications are attributable to TEs. The inverted repeat duplications of *R* are weakly silenced by *doppia* in S2 promoter.

Weakly silenced *R* was known as *R* "mottle" (Brink, Genetics 41:872-889, 1956; Brink, Quart. Rev. Biol. 35:120-137, 1960). The silencing of *R* mottle was amplified by the *R1-st* haplotype, and amplified silencing of *R* "mottle" was recognized as paramutation.

Paramutation engages the silencing machinery of TEs (Sidorenko and Chandler, Genetics 180:1983-1993, 2008; Chandler and Stam, Genetics 5 :534-543, 2004).

The silencing machinery is photo thermally sensitive (Hashida et al., Plant Cell 18:104-118, 2006; Szittya et al., EMBO J. 22:633-640, 2003; Mikula, Genetics 65:733-742, 1967; Mikula, Genetics 1140:1379-1387, 1995).

Photo thermal conditions also induce transition to flowering (Lin et al., Science 318:1302-1305, 2007).

These same photo thermal conditions modulate paramutation.

Transition to flowering is induced by phytochrome, and phytochromes are photo thermally sensitive (Lin et al., 2007).

Phytochrome is dependent on transposases from MULE TEs (Mu-like elements).

TEs have provided R duplications, silencing machinery, and photo thermal modulation of epigenetic change, i.e. paramutation!

Paramutation results in heritable chromatin marks, and heritable chromatin marks provide an epigenetically heritable system (Jablonka and Lamb, Epigenetic Inheritance and Evolution, Oxford Univ. Press, 1995).