GENOME BIOLOGY AND EVOLUTION
SMBE

Transposable Elements: Powerful Contributors to Angiosperm Evolution and Diversity

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Accepted: September 9, 2013

Abstract

Transposable elements (TEs) are a dominant feature of most flowering plant genomes. Together with other accepted facilitators of evolution, accumulating data indicate that TEs can explain much about their rapid evolution and diversification. Genome size in angiosperms is highly correlated with TE content and the overwhelming bulk (>80%) of large genomes can be composed of TEs. Among retro-TEs, long terminal repeats (LTRs) are abundant, whereas DNA-TEs, which are often less abundant than retro-TEs, are more active. Much adaptive or evolutionary potential in angiosperms is due to the activity of TEs (active TE-Thrust), resulting in an extraordinary array of genetic changes, including gene modifications, duplications, altered expression patterns, and exaptation to create novel genes, with occasional gene disruption. TEs implicated in the earliest origins of the angiosperms include the exapted *Mustang*, *Sleeper,* and *Fhy3/Far1* gene families. Passive TE-Thrust can create a high degree of adaptive or evolutionary potential by engendering ectopic recombination events resulting in deletions, duplications, and karyotypic changes. TE activity can also alter epigenetic patterning, including that governing endosperm development, thus promoting reproductive isolation. Continuing evolution of long-lived resprouter angiosperms, together with genetic variation in their multiple meristems, indicates that TEs can facilitate somatic evolution in addition to germ line evolution. Critical to their success, angiosperms have a high frequency of polyploidy and hybridization, with resultant increased TE activity and introgression, and beneficial gene duplication. Together with traditional explanations, the enhanced genomic plasticity facilitated by TE-Thrust, suggests a more complete and satisfactory explanation for Darwin's "abominable mystery": the spectacular success of the angiosperms.

Key words: TE-Thrust, hybridization, polyploidy, adaptation, speciation, domestication.

Introduction

The origin and extremely rapid diversification of flowering plants, which Darwin famously referred to as an "abominable mystery," is one of the most extraordinary, and still not yet fully explained, phenomena in evolutionary history. As the dominant plant taxon, angiosperms are estimated to contain at least 350,000 extant species (Soltis et al. 2008), placing them second only to insects in terms of species richness. This contrasts with their ancient woody competitors, the gymnosperms, which are apparently in stasis and comprise less than 1,000 species. Angiosperms are vastly diverse in form, from the hyphal-like strands of the endoparasitic *Pilostyles* and 1-mm-long single floating leaf of *Wolffia* to the giant banyan trees (*Ficus*) that may cover over a hectare and the >80 m tall eucalypts. Key characteristics of angiosperms are flowers with ovules in an enclosed ovary, double fertilization to produce both a zygote and a (usually) triploid endosperm to nourish the zygote, and the development of fruit-containing seeds. Such evolved reproductive features have been critical to the success of the angiosperms, which occupy a wide range of ecological niches and include all carnivorous and parasitic plants.

Although once said to be "junk," or "parasitic," DNA (Doolittle and Sapienza 1980; Orgel and Crick 1980), a recent large and rapid accumulation of evidence indicates that transposable elements (TEs) have been a significant factor in the evolution of a wide range of eukaryotic taxa (Bennetzen 2000; Kazazian 2004; Biémont and Vieira 2006; Feschotte and Pritham 2007; Böhne et al. 2008; Hua-Van et al. 2011). We have proposed TEs as powerful facilitators of evolution (Oliver and Greene 2009), formalized this proposal into the TE-Thrust hypothesis (Oliver and Greene 2011), and more recently, expanded and strengthened this hypothesis (Oliver and Greene 2012).

The TE-Thrust hypothesis has great explanatory power with regard to adaptation and evolution and was developed from

empirical evidence among the metazoans, principally mammals. It has offered an explanation for the great fecundity of some lineages and the paucity of species in other lineages, for stasis, and for "living fossils" (Oliver and Greene 2009, 2011, 2012). Owing to variable TE activity over time, TE-Thrust also suggests strong support for punctuated equilibrium (Eldredge and Gould 1972; Gould 2002). The TE-Thrust hypothesis posits that the genome-modifying effects of TEs can be either active or passive. Active gene/genome modification is due to transposition of TEs, which often occurs in bursts, whereas passive gene/genome modification is due to ectopic recombination between TEs of similar sequence, scattered throughout the genome (Oliver and Greene 2009, 2011, 2012).

Novel TEs/TE insertions can be acquired in germ lines by endogenous de novo synthesis (e.g., SINEs), de novo modification to resident TEs, de novo formation of chimaeras (e.g., SVAs, SINE-Variable number of tandem repeats-Alus; Wang et al. 2005), endogenization of viral sequences (Feschotte and Gilbert 2012), genomic perturbations such as hybridization or polyploidy (Kawakami et al. 2010; Parisod et al. 2010), and by horizontal transposon transfer, often between completely unrelated taxa (Schaack et al. 2010). Acquisitions of new TEs or reactivation of TEs in germ line genomes can result in intermittent bursts of TE activity, and these have been reported in various lineages, including metazoans (Gerasimova et al. 1985; Marques et al. 2005; Ray et al. 2008) and angiosperms (Naito et al. 2009; Lu et al. 2012; Palmer et al. 2012; El Baidouri and Panaud 2013).

A concept central to the TE-Thrust hypothesis is that either fixed or unfixed TEs in a lineage can facilitate adaptation and evolution by means of their various interactions with the genome that can create realizable intragenomic potential. Intragenomic potential is a continuum that ranges from adaptive potential to evolutionary potential. Adaptive potential, also termed capacitance (Pigliucci 2007), can be realized over periods of tens to hundreds of years, whereas evolutionary potential can be realized over thousands or millions of years (Oliver and Greene 2012).

In angiosperms, genome size and structure is largely determined by TEs because they often constitute the major fraction (up to 84%) of their DNA (table 1). Angiosperm genes in large and TE-rich genomes such as maize have been described as islands surrounded by seas of nested TEs (SanMiguel and Bennetzen 1998). Furthermore, the islands themselves are a moonscape of ancient and recent impacts from TEs. Among the retro-TEs, *Copia*-like and *Gypsy*-like long terminal repeat (LTR) elements are abundant in angiosperms, whereas Long Interspersed Elements (LINEs) and Short Interspersed Elements (SINEs), that are prominent in mammalian genomes, are less common. An important unanswered question for future investigation is the function and significance of the envelope-class LTR retro-TEs found in angiosperms (Vicient et al. 2001) and at least one gymnosperm species (*Pinus pinaster*; Miguel et al. 2008), as these could possibly be the equivalent of the vertebrate endogenous retroviruses, which were prominent in the evolution of mammals (Feschotte and Gilbert 2012; Oliver and Greene, 2012), and are particularly active in the murid rodents (Gibbs et al. 2004; Maksakova et al. 2006). DNA-TEs found in angiosperms belong to several superfamilies and include *CACTA*, *hAT*, *Harbinger*, *Mutator*, *Helitron,* and *Mariner*-like elements (table 1). The generally high TE content of flowering plants, which includes active DNA-TEs and homogeneous LTR retro-TE populations, makes them highly suited for TE-Thrust, both active and passive. Indeed, the relative instability of angiosperm genomes compared with mammals in terms of gene movement and genome rearrangement (Bennetzen 2005; Kejnovsky et al. 2009), implies that TE-Thrust may be especially powerful in flowering plant lineages. We therefore see TE-Thrust as having much explanatory value, in addition to other accepted explanations, for the rapid diversification of the angiosperms, after their mysterious origin, early in the Cretaceous (135–90 Ma) and their rapid rise to dominance among the vascular plants 100–70 Ma.

In putting forward TE-Thrust as an important facilitator of evolution, we do not suggest that it is entirely universal or that other mechanisms of evolution are not significant. In fact, as we have noted previously (Oliver and Greene 2009, 2011, 2012), TE-Thrust, although very important in most extant taxa, is one of many possible facilitators of evolution, which include hybridization (Soltis PS and Soltis DE 2009), polyploidy/whole genome duplication (Van de Peer et al. 2009), recombination (Gaut et al. 2007), and horizontal gene transfer (Keeling and Palmer 2008). In some rare extant species belonging to reasonably fecund genera, TE-Thrust appears to now have little to do with ongoing adaptive potential or evolutionary potential, as such species currently have genomes that are largely devoid of TEs. An example among the angiosperms is the small 80 Mb genome of the recently sequenced bladderwort, *Utricularia gibba*, which is remarkable for having only 3% TE content, yet belonging to a successful genus comprising more than 200 species (Ibarra-Laclette et al. 2013). Significantly, the evolutionary history of this species has been marked by repeated rounds of whole genome duplication (Ibarra-Laclette et al. 2013), whereas the clade to which *U. gibba* belongs exhibits extreme mutation rates that are among the highest within the angiosperms (Müller et al. 2004). These, and possibly other factors, may account for its evolution and also for some current adaptive potential and evolutionary potential.

TE-Thrust Acts in Concert with Other Factors Widely Acknowledged as Promoting Angiosperm Diversity and Dominance

Hybridization and Polyploidy

Frequent tolerance of hybridization and polyploidy (with or without hybridization) are widely acknowledged factors

Table 1
TE Composition (%) of Representative Flowering Plant Genomes

A. Dicotyledons

Family	Rosaceae		Vitaceae	Brassicaceae	Fabaceae		Solanaceae	
Species	***Malus* x *domestica***	***Fragaria vesca***	***Vitus vinifera***	***Arabidopsis thaliana***	***Glycine max***	***Medicago truncatula***	***Solanum lycopersicum***	***Solanum tuberosum***
Genome size (Mbp)	742	240	487	125	1,115	375	900	844
Haploid chromosome number[a]	17	7	19	5	20	8	12	12
Type I: Retro-TEs								
LTR/*Gypsy*	25.2	6.0	14.0	5.2	29.5	1.4	19.7	15.2
LTR/*Copia*	5.5	4.6	4.8	1.4	12.5	2.4	6.3	3.8
LTR/other	0.4	3.8	—	—	—	9.6	35.8	33.2
LINE	6.5	0.2	0.6	0.9	0.25	3.4	0.4	0.7
SINE	—	0.06	—	—	—	0.1	0.2	0.3
Unclassified	—	—	—	—	—	—	—	—
Total Retro-TEs	37.6	14.7	19.4	7.5	42.2	16.9	62.3	53.2
Type II: DNA-TEs								
CACTA	—	2.6	0.2	0.9	10.2	0.1	0.1	0.1
Helitron	—	0.07	—	5.6	0.5	0.2	—	—
hAT	0.3	0.6	0.8	0.3	0.04	0.1	0.1	0.2
PIF/Harbinger	—	0.2	—	0.2	0.3	0.2	—	0.1
Tc1/Mariner	—	—	—	0.3	0.03	—	—	—
Mutator	—	0.2	0.4	3.1	4.5	0.6	—	—
Other		—		0.1	0.09		0.3	0.3
MITE/*Tourist*	0.6[b]	1.6[b]	—	—	0.3	0.1[b]	—	—
MITE/*Stowaway*			—	—	0.5		—	—
Unclassified	—	—	—	0.5	—	0.2	0.2	0.4
Total DNA-TEs	0.9	5.2	1.4	11.0	16.5	1.4	0.9	1.2
Unknown	3.9	0.9	0.7	—		—	—	—
Total TEs	42.4	20.7	21.5	18.5	58.7	18.3	63.2	54.4

B. Monocotyledons

Family	Poaceae							Musaceae
Species	***Triticum aestivum***	***Hordeum vulgare***	***Zea mays***	***Sorghum bicolor***	***Oryza sativa***	***Brachypodium distachyon***	***Setaria italica***	***Musa acuminata***
Genome size (Mbp)	17,000	5,100	2,300	730	389	272	423	523
Haploid chromosome number[a]	7	7	10	10	12	5	9	11
Type I: Retro-TEs								
LTR/*Gypsy*	44.0	18.0	46.4	19.0	12.0	16.0	22.1	11.4
LTR/*Copia*	17.4	8.5	23.7	5.2	2.5	4.9	7.2	25.6
LTR/other	1.5	25.8	—	30.2	9.0	0.5	0.3	—
LINE	0.8	—	1.0	0.04	0.8	1.9	1.8	5.4
SINE	0.004	—	—	—	0.4	—	0.2	—
Unclassified	—	0.5	4.5	0.05	1.1	—	—	—
Total Retro-TEs	63.7	52.7	75.6	54.5	25.8	23.3	31.6	42.4
Type II: DNA-TEs								
CACTA	12.8	3.9	3.2	4.7	3.4	2.2	4.7	—
Helitron	0.2	0.04	2.2	0.8	0.3	0.2	0.2	—
hAT	0.04	0.02	1.1	0.02	0.5	0.2	0.6	1.2
PIF/Harbinger	0.3	0.2	—	0.02	—	0.4	—	0.01
Tc1/Mariner	1.0	0.06	—	—	0.02	0.07	—	—
Mutator	0.4	0.3	1.0	0.06	1.8	0.6	—	0.01
Other	0.01	0.04	—	—	1.3	—	—	0.03
MITE/*Tourist*	—	0.5[b]	1.0	0.9	1.5	0.2	1.4	—
MITE/*Stowaway*	—		0.1	0.2	1.7	0.9	0.6	—
Unclassified	0.06	0.04	—	0.7	3.1	—	1.9	—
Total DNA-TEs	14.9	5.0	8.6	7.5	13.7	4.8	9.4	1.3
Unknown	1.2	0.7	—	—	—	—	5.4	—
Total TEs	79.8	58.4	84.2	62.0	39.5	28.1	46.4	43.7

[a]All are diploids except *S. tuberosum* (tetraploid), *T. aestivum* (hexaploid), and *M. acuminata* (doubled haploid).
[b]Includes all MITEs.

thought to have promoted angiosperm diversification (Baack and Rieseberg 2007; Soltis PS and Soltis DE 2009; Jiao et al. 2011). The emergence of vigorous hybrids can result in gene and TE introgression between species. Such hybrids can sometimes become stabilized into new species, especially if polyploidy also occurs. Significantly, hybridization and polyploidy are often accompanied by extensive transposition of TEs, leading to new genomic modifications and changes in genome size (Liu and Wendel 2000; Shan et al. 2005; Josefsson et al. 2006; Ungerer et al. 2006; Kawakami et al. 2010; Parisod et al. 2010; Piednoël et al. 2013). Potentially deleterious effects on genomes that might result from such bursts of TE activity may be cushioned through gene duplication in polyploids (Matzke MA and Matzke AJ 1998). A good example of a TE burst following hybridization was documented in three diploid sunflower (*Helianthus*) hybrids, where massive TE derepression resulted in genomes at least 50% bigger than either diploid parent (Ungerer et al. 2006; Kawakami et al. 2010). Intriguingly, in contrast to their parent species, each of these hybrids is capable of occupying extreme (arid or saline) habitats.

The frequent and recurring production of polyploids, both autopolyploids and allopolyploids in angiosperms (Tate et al. 2005), reflects a high rate of production of unreduced gametes, especially in hybrids (Brownfield and Köhler 2011; Leitch AR and Leitch IJ 2012). Although polyploidy often represents a bottleneck due to difficulties with meiosis, nuclear enlargement, and/or epigenetic instability (Comai 2005), it has the potential to promote longer-term evolutionary success (Mayrose et al. 2011). Polyploidy may lead to speciation, as tetraploids for example, are usually reproductively isolated from their parental diploids, and polyploid populations can frequently occupy habitats not available to their parent species. In polyploids, mutations that lead to the formation of bivalents and the elimination of multivalents will be strongly selected. Therefore, genomes with active or many passive TEs (to promote TE-Thrust) may show faster homolog divergence, diploidization, and return to full gamete fertility. All angiosperms are thought to have had at least one polyploidization event in their evolutionary history usually followed by a diploidization process (Jiao et al. 2011), and individual polyploid taxa typically form multiple times (Tate et al. 2005). The widespread prevalence of this phenomenon is reflected in the recent finding that about one third of extant vascular plants are recent polyploids (Wood et al. 2009). Polyploidy has a major impact on genome size in angiosperms; however, the effect of TE amplification (and removal) is even greater (Bennetzen 2005). As new polyploid populations are small and reproductively isolated, they could result in drift to either fixation or extinction of TE families or superfamilies; an example may be the *Gypsy*-like *Gorge* LTR retro-TEs specific to the *Gossypium* genus (Hawkins et al. 2006).

Polyploidy is implicated in the promotion of TE proliferation in a variety of angiosperm species (Parisod et al. 2010; Piednoël et al. 2013), although its effect on TEs appears to be complex and may involve not only transposition but also TE-associated epigenetic changes and DNA recombination events (Parisod et al. 2010). Such events may lead to major genomic restructuring, producing abundant genetic novelty for adaptive evolution. A good example of a successful allopolyploid is the recently emerged and highly invasive dodecaploid species *Spartina anglica* involved in widespread colonizations of salt marshes and estuaries (Thompson 1991). Although no transposition burst was detected in *S. anglica*, major structural and epigenetic changes in the vicinity of TE insertions were observed, supporting a central role for TEs in genome reorganization during allopolyploid speciation (Parisod et al. 2009). Thus, the evolutionary impact of hybridization and/or polyploidy in angiosperms, which are important factors in their own right, would appear to be greatly magnified through the ability to enhance TE-Thrust.

Stress

Cellular TE repression mechanisms are generally sensitive to perturbation. Thus, stress can induce TE activity, which can create intragenomic potential at opportune times to facilitate adaptation in response to environmental challenge (Zeh et al. 2009; Casacuberta and González 2013). In angiosperms, TE mobilization has been reported for a variety of abiotic or biotic stress conditions including high or low temperatures, UV light, wounding, and pathogen attack (Mhiri et al. 1997; Walbot 1999; Grandbastien et al. 2005; Fujino et al. 2011; Matsunaga et al. 2012). Tolerance to one stress factor in particular, fire, has been a major factor in the success of many angiosperms (Keeley et al. 2011), including grasses and resprouting plants that are long lived and rarely reproduce from seed. Bursts of TE activity induced by the heat and damage of fire could result in genetic differences between the multiple apices that regenerate allowing somatic evolution, particularly in very long-lived resprouters and vegetatively reproducing species that rarely reproduce sexually. TEs are known to cause somatic variation in vegetatively propagated plants such as the grapevine, *Vitis vinifera* (Fernandez et al. 2010; Carrier et al. 2012), indicating that TE-Thrust can create intragenomic potential in the soma as well as in the germ line. This is an additional and hitherto undescribed aspect of the TE-Thrust hypothesis.

Genomic Imprinting in Endosperm

A characteristic of speciation is the emergence of pre- or postzygotic barriers to genetic exchange. Maturation of the angiosperm embryo after either intraspecific or interspecific pollination is dependent on normal development of the (usually) triploid endosperm in most taxa, which in turn is dependent on a proper balance in gene imprinting (Kinoshita 2007), consistent with a matching endosperm balance number (EBN) (Johnston et al. 1980). Thus, epigenetic mismatch/differing

EBNs resulting in incorrect gene expression dosage are a frequent cause of failure of crosses and a powerful causal factor of reproductive isolation or incipient speciation. Imprinting in plants is intimately associated with changes to methylation of TEs (Gehring et al. 2009; Wolff et al. 2011), and TE activity is known to alter DNA methylation patterns and gene imprinting in plant genomes (Kashkush et al. 2003; Haun et al. 2009; Parisod et al. 2009). Thus, TEs seemingly have a significant potential to change imprinting patterns in the endosperm, resulting in reproductive isolation, and thereby indirectly promoting speciation and diversity.

Ecological Factors: Horizontal TE Transfers to Angiosperms

Angiosperms have coevolved with pollinators, fruit and seed eaters, browsers, grazers, fungi, prokaryotes, and exogenous and endogenous viruses, and likely with specialized endogenous retroviruses. Specific pollinators, mainly among insects, birds, and bats can seek out and fertilize scattered individuals of a species, allowing high species diversity in populations of angiosperms with biotic compared with wind pollination. Coevolution with metazoans for seed and fruit dispersal is also an important driver of species diversity in many angiosperms. Horizontal transfers of TEs between angiosperm genomes have been documented (Diao et al. 2006; Cheng et al. 2009; Roulin et al. 2009; Woodrow et al. 2012). This is of significance for potentially enabling TEs to prompt genomic variation within new lineages and therefore influence evolutionary trajectories (Schaack et al. 2010). An intriguing possibility worthy of future investigation is the extent to which interactions with metazoans facilitated horizontal transposon transfer to angiosperms, and also possibly, horizontal gene transfer. The same could apply to prokaryotes, fungi, and exogenous viruses.

TE-Thrust and the Evolutionary Success of Angiosperms Compared with Gymnosperms

Among plants, the angiosperms have undergone tremendous evolutionary innovations and radiations when compared with their sister clade, the gymnosperms. Apparent explanations for the lower genomic plasticity, morphological diversity, and rates of speciation in gymnosperms include lack of hybridization, polyploidy, and genetic imprinting, as well as decreased base substitution rate (Ahuja 2005; Buschiazzo et al. 2012). Significantly, despite having an abundance of TEs, TE-Thrust also appears to have been much less effective in gymnosperms. Since the angiosperm divergence, gymnosperms have experienced low TE activity with a very slow and steady accumulation of a diverse set of TEs, mainly LTR retro-TEs (Kovach et al. 2010; Nystedt et al. 2013). Thus, TEs in extant gymnosperms appear to be ancient and nonviable, whereas those in extant angiosperms are much younger and show evidence of repeated bursts of activity within the relatively recent past (Stuart-Rogers and Flavell 2001; Naito et al. 2009; Kovach et al. 2010; Lu et al. 2012; Palmer et al. 2012; El Baidouri and Panaud 2013). Moreover, in contrast to the relatively few TE subfamilies that were expanded in angiosperms (Nystedt et al. 2013), the diversity of TEs in gymnosperms makes their genomes relatively poorly suited for passive TE-Thrust. In keeping with this, gymnosperm TEs appear to be removed less frequently by unequal recombination than those in angiosperm genomes (Nystedt et al. 2013), a key outcome being the development of very large genomes that are characteristic of this lineage (Bennett and Leitch 2005). This one-way road to genomic obesity in gymnosperms may be a compounding factor in their relative lack of evolutionary diversity, as smaller angiosperm genomes offer advantages in terms of rapid seedling establishment, short generation times, and the costs and rates of reproduction (Bennett 1987). However, some angiosperm genomes are very large, as they have a much greater variety in size due to dynamism in terms of their TE amplification and TE-mediated recombination processes (Devos et al. 2002). Thus, ongoing and large amplifications, and removals, of both retro-TEs and DNA-TEs confined to the angiosperms, offer a plausible additional explanation for the lack of evolutionary innovation and speciation in the gymnosperm lineages as compared to the remarkable success of angiosperms.

Mechanisms by Which Plant Genomes Are Modified by TEs

Active TE-Thrust

TEs can powerfully facilitate genetic changes to angiosperm genomes and create intragenomic potential (standing variation), as they do in metazoans, in a large variety of ways, both active and passive. In their active role, TEs can be exapted to create new genes or functional sequences (also referred to as molecular domestication). Although not particularly common, exaptation can nevertheless have enormous impacts, such as the generation of adaptive immune system in jawed vertebrates (Schatz 2004) and of the mammalian placenta (Rawn and Cross 2008; Oliver and Greene 2012). A significant number of genes whose sequences are largely TE derived have now been reported in angiosperms (He et al. 2000; Bundock and Hooykaas 2005; Cowan et al. 2005; Muehlbauer et al. 2006; Lin et al. 2007; Roccaro et al. 2007; Duan et al. 2008; Joly-Lopez et al. 2012; Knip et al. 2012), but not in examined gymnosperms, indicating that TEs have made beneficial contributions specifically to the angiosperm gene repertoire. It is likely that further examples will be identified as more genomes are analyzed. Through exaptation, TEs can blur the distinction between themselves and their host genomes by becoming entwined with normal

host cell biology. For instance, most of the matrix attachment regions (MARs) in rice and sorghum were found to colocalize with miniature inverted-repeat TEs (MITEs), suggesting that these DNA-TEs can actually serve as MARs (Avramova et al. 1998). Similarly, TEs have been found to act as source DNA for long tandem arrays at some centromeres in a variety of plant species including the potato (*Solanum tuberosum*) (Macas et al. 2009; Gong et al. 2012).

In addition to donating entire genes, TEs can contribute partially to individual genes, for instance, through the creation of introns, exons, or chimeric genes. These are not rare events, and a substantial proportion of genes in angiosperms harbor TEs, as for example rice, where more than 10% of transcripts are reported to contain TEs (Sakai et al. 2007). Significantly, this includes a contribution to about 2% of rice protein coding regions (Sakai et al. 2007). In the model plant *Arabidopsis thaliana*, 7.8% of expressed genes were found to contain a region with close similarity to a known TE sequence (Lockton and Gaut 2009). Brassicaceae lineage-specific genes in *Arabidopsis* showed an even greater percentage (about 10%) that were partly derived from TEs (Donoghue et al. 2011), which lends support for our proposal that TEs can be an important factor in lineage divergence (Oliver and Greene 2009, 2011, 2012).

Changes to gene regulation play a critical role in evolution (Carroll 2008) and a major way that TEs act to functionally modify genomes is by inserting novel regulatory elements adjacent to genes to alter or expand their expression patterns (Rebollo et al. 2012). Indeed, it was the very ability of TEs to affect gene activity in plants (specifically maize) that prompted their discoverer McClintock (1984) to refer to them as "controlling elements." A growing body of evidence now indicates that TE-derived regulatory elements can act conventionally as binding sites for transcription factors. Alternatively, they may cause epigenetic gene silencing by being targets for DNA methylation, as in the case of *Arabidopisis FLC* and *FWA* loci, and maize *B1* locus (Selinger and Chandler 2001; Fujimoto et al. 2008; Zhai et al. 2008).

Beyond their effect on the expression of individual genes, TEs can impact on gene regulation on a genomewide scale by acting as modular carriers of readymade promoters and/or enhancers via their ability to transpose throughout the genome (Britten and Davidson 1969; Feschotte 2008). This enables the widespread dissemination of discrete regulatory elements with those that confer benefit likely to be retained. A striking case is a subset of MITE DNA-TE insertions that have generated regulatory networks in rice that render adjacent gene stress inducible (Naito et al. 2009). Also striking is the presence of GC (guanine/cytosine)-rich Pack-MULE (mutator-like element) DNA-TEs at the 5′-end of many grass genes, which may act to epigenetically control gene expression (Jiang et al. 2011). Similarly, LTR retro-TEs of the recently amplified *Dasheng* family have been implicated in the methylation and tissue-specific expression of adjacent rice genes (Kashkush and Khasdan 2007). Bursts of TE activity may thus be crucial for rapidly generating the large-scale genetic diversity required by angiosperms in the face of environmental and ecological challenges. They also provide a plausible mechanism by which entire sets of genes can become coregulated to fashion new cellular pathways or build on existing ones, thus potentially enhancing the extraordinary diversification of angiosperms.

The capacity of TEs to partake in the regulation of host genes is particularly supported by data from the rice genome. One sixth of rice genes are associated with retro-TEs, with insertions either in the gene itself or within putative promoter regions (Krom et al. 2008), whereas 58% are associated with a MITE (Lu et al. 2012). Thus, a large proportion of rice gene promoters appear to contain a TE. Recent evidence also indicates that many exapted plant TE sequences may actually be transcribed to function as microRNAs (miRNAs) that regulate gene expression posttranscriptionally. Now acknowledged as an important class of regulatory genes in eukaryotes, many regulatory miRNA genes found in rice are derived from TEs that have the potential to regulate thousands of genes (Li et al. 2011; Ou-Yang et al. 2013). Moreover, MITEs generate nearly a quarter of all small RNAs identified in rice (Lu et al. 2012). Thus TEs, which provide a mechanism to account for the origin of miRNAs (Buchon and Vaury 2006), appear to fulfill essential functions in plants by serving as master regulators with widespread regulatory influence.

Rather than directly contributing functional sequences to angiosperm genomes, another major way that TEs can actively generate genetic novelty is by using their transpositional (or retrotranspositional) mechanisms to delete, rearrange, or partially or fully duplicate genes or chromosomal segments. Gene duplication, in particular, is a crucial aspect of evolution and constitutes the principal means by which organisms evolve new genes (Ohno 1970). Both DNA-TEs and retro-TEs have a propensity to capture and transpose genes or gene fragments, which can result in gene duplication, exon shuffling, or regulatory element seeding, depending on the nature of the sequence involved. For example, in the rice genome, there are reportedly more than 1,200 retrogenes (Wang et al. 2006). Many of these are conserved, which implies that they have been advantageous. This includes the huge pentatricopeptide repeat gene family that likely expanded in angiosperms as a consequence of one or more waves of retrotransposition by retro-TEs (O'Toole et al. 2008). The rice genome also harbors thousands of *Mutator* superfamily (Pack-MULE) DNA-TEs containing fragments derived from more than 1,000 genes (Jiang et al. 2004; Juretic et al. 2005). The unparalleled ability of TEs to generate genetic novelties is reflected in the fact that many of the Pack-MULEs contain sequences from multiple chromosomal loci that are fused to form new open reading frames, some of which are expressed as chimeric transcripts. Importantly, many have undergone purifying selection (Hanada et al. 2009), indicating that they have acquired highly beneficial functions. In maize,

there is a similar situation with a very high rate of gene capture and exon shuffling by *Helitron* DNA-TEs that replicate via a rolling circle mechanism (Gupta et al. 2005; Lai et al. 2005; Morgante et al. 2005; Yang and Bennetzen 2009). The number of novel transcripts expressed by *Helitrons* is at least 11,000 or 25% of the total number of genes in the maize genome (Du et al. 2009; Barbaglia et al. 2012). Other DNA-TEs implicated in the capture and integration of gene fragments in angiosperm species include the *CACTA* and *Harbinger* DNA-TE superfamilies (Paterson et al. 2009; Vogel et al. 2010). Thus, TEs seemingly have a vast ability to concoct new coding regions and combinations of coding regions as an indispensable form of realizable intragenomic potential (standing variation) for possible future selection, whether by natural or human means.

Besides duplication, TEs are adept at moving genes, both protein and RNA coding, to new locations within a genome. Such movement has the potential to reprogram gene expression through a change in regulatory elements. An illustrative example can be found in grasses where a substantial number of miRNA genes appear to have been relocated by TEs (Abrouk et al. 2012). TEs can also induce DNA deletions through their transpositional activity, as has been observed by *hAT* elements in maize (Zhang and Peterson, 2005). Beyond molecular-scale changes, active TE transposition can mediate large-scale chromosomal rearrangements leading to karyotypic variation, which is a factor in the formation of reproductive barriers and speciation (Rieseberg 2001; Levin 2002). This is best documented in maize, where alternative *hAT* element transposition reactions can cause major changes to chromosomal architecture, including deletions, inversions, and translocations (McClintock 1950; Zhang et al. 2009). Karyotypic variability is common in angiosperms and can even occur within species. Although many TE-mediated karyotypic differences may be incidental to speciation, they represent an important potential contributory mechanism to reproductive isolation, angiosperm diversification, and species radiations.

Passive TE-Thrust

The presence of large numbers of similar TEs in genomes can separately play a passive role in plant evolution by promoting gene or segmental duplications (or deletions) through homology-driven ectopic recombination of DNA (Oliver and Greene 2009, 2011, 2012). Duplication events are particularly important because they create functional redundancy and the potential for gain of function.

TE-induced recombination events are often difficult to detect, especially those from the distant evolutionary past, which may now be untraceable. Thus, compared with active TE-Thrust, the passive effects of TEs have been less well documented. Nevertheless, passive TE-Thrust has been in evidence in *Arabidopsis* where *Copia*-like LTR retro-TEs, and *CACTA* and *Mutator* DNA-TEs, apparently generated segmental duplications that occurred after the monocot-dicot divergence and probably after the Rosales and Brassicales divergence (Hughes et al. 2003). On the whole, and as we outline in further detail below, the evidence points to both the active and passive effects of retro-TEs (mainly LTRs) and DNA-TEs as having greatly facilitated and influenced the trajectory of flowering plant evolution.

Evidence for Intragenomic Potential Derived from TEs in Angiosperms: Specific Examples of Traits Generated by TEs

Most data on the genomic impact of TEs are presently derived from mammals and angiosperms. In this context, realizable intragenomic potential due to TE-Thrust previously demonstrated in mammals (Oliver and Greene 2011, 2012) is also demonstrable in angiosperms, with numerous studies reporting genotypic changes due to TEs being correlated with the generation of specific flowering plant phenotypes (tables 2 and 3). Although these examples are biased toward traits of domesticated plant species, they nevertheless provide a good illustration of the power of TEs to uniquely create diverse and elaborate intragenomic potential, which can be realized by selection. Human selection in plant domestication and improvement has foresight and strategy, but is a selective force that, unless using induced mutation, must rely on the same generators of change as blind natural selection.

Tables 2 and 3 list 65 known instances in which TEs have altered or created individual plant genes and thus were directly implicated at a genomic level in the origin of various traits, both domesticated and wild. Notably, DNA-TEs were the major contributors to these traits, accounting for nearly two thirds of the total (fig. 1*A*). The autonomous *hAT* and *CACTA* elements and nonautonomous MITE DNA-TEs were particularly prevalent contributors, whereas LTR retro-TEs were responsible for the remaining one third of traits. This suggests that DNA-TEs may be particularly effective at facilitating evolution, at least via active TE-Thrust (Oliver and Greene 2011), which accords with findings in disparate lineages, including the vespertilionid bats (Ray et al. 2008; Pagán et al. 2012; Mitra et al. 2013). Traits associated with cultivated plants were most commonly a consequence of gene disruption (50%; fig. 1*B* and table 2) rather than due to the creative effects of TEs. Although gene disruptions by TEs occur in natural populations, they generally result in a reduction of fitness and were therefore expected to be relatively uncommon. However, gene disruption features prominently in domesticated plant traits due to humans having selected for desirable null phenotypes. By contrast, traits facilitated by TEs that could be of value in wild populations were more diverse in origin and most commonly were the result of regulatory changes to plant

Table 2

Specific Examples of TEs Implicated in Flowering Plant Domestication and Diversification

TE-Generated or Modified Trait	Gene Affected	Gene Function	TE Responsible	Taxon	Type of Event	Effect	Type of TE-Thrust	Reference
Spring growth habit	*Vrn1*	Transcriptional regulator	LTR (gypsy-like)	*Triticum turgidum*	Regulatory	Positive regulation	Active	Chu et al. 2011
Purple coloration	*BoMyb2*	Transcriptional regulator	Harbinger	*Brassica oleracea*	Regulatory	Positive regulation	Active	Chiu et al. 2010
Floral branching	*Apo1*	F-box protein	hAT	*Oryza sativa*	Regulatory	Positive regulation	Active	Ikeda-Kawakatsu et al. 2009
Fruit cluster morphology	*VvTFL1A*	Plant development	hAT	*Vitis vinifera*	Regulatory	Positive regulation	Active	Fernandez et al. 2010
Blood orange	*Ruby*	Transcriptional regulator	LTR (copia-like)	*Citrus sinensis*	Regulatory	Stress responsiveness	Active	Butelli et al. 2012
Chinese blood orange (Jingxian)	*Ruby*	Transcriptional regulator	LTR	*Citrus sinensis*	Regulatory	Stress responsiveness	Active	Butelli et al. 2012
Apical dominance	*Tb1*	Transcriptional regulator	LTR (copia-like)	*Zea mays*	Regulatory	Enhancer	Active	Studer et al. 2011
Plant pigmentation	*B1*	Transcriptional regulator	LTR	*Zea mays*	Regulatory	Epigenetic silencing	Active	Selinger and Chandler 2001
Waxy kernels	*Wx*	Granule-bound starch synthase	hAT	*Zea mays*	Transposition	Altered protein	Active	Wessler et al. 1986
Flower color pattern	*niv*	Anthocyanin pigmentation	hAT	*Antirrhinum majus*	Transposition	Altered expression	Active	Lister et al. 1993
Orange kernels and cob glume	*P-oo*	Transcriptional regulator	hAT	*Zea mays*	Transposition	Novel fusion gene	Active	Zhang et al. 2006
Double flowers	*DP*	Transcriptional regulator	CACTA	*Ipomoea nil*	Transposition	Gene loss	Active	Nitasaka 2003
Elongated fruit	*Sun*	Auxin transport	LTR (copia-like)	*Solanum lycopersicum*	Retrotransposition	Duplicated gene	Active	Xiao et al. 2008
High-latitude cultivation	*GmphyA2*	Photoperiod sensitivity	LTR (copia-like)	*Glycine max*	Gene disruption	Gene inactivation	Active	Kanazawa et al. 2009
Bread-making quality	*Glu-1*	Glutenin seed storage protein	LTR (copia-like)	*Triticum aestivum*	Gene disruption	Gene inactivation	Active	Harberd et al. 1987
Parthenocarpic fruit production	*MdPI*	Transcriptional regulator	LTR	*Malus domestica*	Gene disruption	Gene inactivation	Active	Yao et al. 2001
Golden hull coloration	*osCHI*	Flavonoid biosynthesis	LTR	*Oryza sativa*	Gene disruption	Gene inactivation	Active	Hong et al. 2012
Wrinkled seed	*SbeI*	Starch-branching enzyme	hAT	*Pisum sativum*	Gene disruption	Gene inactivation	Active	Bhattacharyya et al. 1990
White flowers	*Dfr-B*	Anthocyanin pigmentation	Helitron	*Ipomoea tricolor*	Gene disruption	Gene inactivation	Active	Choi et al. 2007
White/variegated flowers	*Chs-D*	Anthocyanin pigmentation	hAT	*Ipomoea purpurea*	Gene disruption	Gene inactivation	Active	Habu et al. 1998
Pale flowers/Ivory seed	*bHlh2*	Anthocyanin pigmentation	hAT	*Ipomoea purpurea*	Gene disruption	Gene inactivation	Active	Park et al. 2007
Yellow seed	*BrTT8*	Transcriptional regulator	Helitron	*Brassica rapa*	Gene disruption	Gene inactivation	Active	Li et al. 2012
High oleate seeds	*ahFAD2B*	Microsomal oleoyl-phospatidyl choline desaturase	MITE	*Arachis hypogaea*	Gene disruption	Gene inactivation	Active	Patel et al. 2004
Waxy millet	*Gbss1*	Granule-bound starch synthase	Multiple	*Setaria italica*	Gene disruption	Gene inactivation	Active	Kawase et al. 2005
Glutinous rice	*Wx*	Granule-bound starch synthase	LTR	*Oryza sativa*	Gene disruption	Truncated transcript	Active	Hori et al. 2007
Variegated pigmentation	*Y*	Phlobaphene pigmentation	CACTA	*Sorghum bicolor*	Gene disruption	Aberrant splicing	Active	Chopra et al. 1999
Pink flowers, lighter color, and higher protein content of seeds	*Wp*	Flavonoid biosynthesis	CACTA	*Glycine max*	Gene disruption	Aberrant splicing	Active	Zabala and Vodkin 2005
White fruit	*VvMyba1*	Transcriptional regulator	LTR (gypsy-like)	*Vitis vinifera*	Gene disruption	Low expression	Active	Walker et al. 2007
Waxy kernels	*Wx*	Granule-bound starch synthase	LTR	*Zea mays*	Gene disruption	Low expression	Active	Varagona et al. 1992
Higher kernel oil content	*ZmGE2*	Cytochrome P450 enzyme	Mutator	*Zea mays*	Gene disruption	Low expression	Active	Zhang et al. 2012
Plant pigmentation	*S1*	Transcriptional regulator	CACTA	*Zea mays*	Duplication	Novel gene	Passive	Walker et al. 1995
Red fruit	*VvMyba1*	Transcriptional regulator	LTR (gypsy-like)	*Vitis vinifera*	Deletion	Regained expression	Passive	Kobayashi et al. 2004
Grain hardness	*Pina, Pinb*	Lipid-binding proteins	Various	*Triticum aestivum*	Deletion	Gene loss	Passive	Chantret et al. 2005

Table 3

Specific Examples of TEs Implicated in Flowering Plant Physiology, Development, or Stress Resistance

TE-Generated or Modified Trait	Gene Affected	Gene Function	TE Responsible	Taxon	Type of Event	Effect	Type of TE-Thrust	Reference
Growth and flowering	*Mustang 1-8*	Transcriptional regulator	Mutator	Angiosperms	Domestication	Novel gene	Active	Cowan et al. 2005; Joly-Lopez et al. 2012
Development	*Sleeper*	Transcriptional regulator of plant development	hAT	Angiosperms	Domestication	Novel gene	Active	Bundock and Hooykaas 2005; Knip et al. 2012
Light-induced responses	*Fhy3*	Transcriptional regulator of light signaling	Mutator	Angiosperms	Domestication	Novel gene	Active	Lin et al. 2007
Light-induced responses	*Far1*	Transcriptional regulator of light signaling	Mutator	Angiosperms	Domestication	Novel gene	Active	Lin et al. 2007
	Gary	Unknown	hAT	Cereal grasses	Domestication	Novel gene	Active	Muehlbauer et al. 2006
Fungal resistance	*Rim2*	Unknown	CACTA	*Oryza sativa*	Domestication	Novel gene	Active	He et al. 2000
	AtCopeg1	Hormone and nutrient stress signaling	LTR (copia-like)	*Arabidopsis thaliana*	Domestication	Novel gene	Active	Duan et al. 2008
Flower development	*TamRSI*	Transcriptional regulator	CACTA	*Antirrhinum majus*	Domestication and transposition	Novel gene	Active	Roccaro et al. 2007
Virus resistance	*N*	Disease resistance	MITE	*Nicotiana glutinosa*	Exonization	Novel isoform	Active	Kuang et al. 2009
	OsRp16-1	Ribosomal protein	Harbinger	*Oryza sativa*	Exonization	Enhanced expression	Active	Kubo et al. 2008
Plant stress response	*ALP-A3*	Acireductone dioxygenase-like	CACTA	Triticeae (diploid)	Regulatory	Major promoter	Active	Akhunov et al. 2007
Fungal resistance	*Pit*	Disease resistance	LTR (copia-like)	*Oryza sativa*	Regulatory	Positive regulation	Active	Hayashi and Yoshida 2009
	Hsp70	Heat shock protein	MITE	*Oryza sativa*	Regulatory	Positive regulation	Active	Zhang et al. 2012
Growth and development	*Abp1*	Auxin-binding protein	MITE (Tourist)	*Zea mays*	Regulatory	Positive regulation	Active	Elrouby and Bureau 2000
Aluminium resistance	*AltSB*	Efflux transporter	MITE (Tourist)	*Sorghum bicolor*	Regulatory	Positive regulation	Active	Magalhaes et al. 2007
Stress response	*OsGSTL2*	Detoxification enzyme	hAT/MITE (Stowaway)	*Oryza sativa*	Regulatory	Herbicide/hormone responsiveness	Active	Hu et al. 2011
Light-induced responses	*TCS*	Ribosome-inactivating protein	MITE	*Trichosanthes kirilowii*	Regulatory	Light responsiveness	Active	Xu et al. 2007
Flowering behavior	*FLC*	Transcriptional regulator	hAT	*Arabidopsis thaliana*	Regulatory	Epigenetic silencing	Active	Zhai et al. 2008
Flowering behavior	*FWA*	Transcriptional regulator	SINE	*Arabidopsis thaliana*	Regulatory	Epigenetic silencing	Active	Kinoshita et al. 2007; Fujimoto et al. 2008
Dessication tolerance	*CDT-1*	siRNA	Unknown retro-TE	*Craterostigma plantagineum*	Regulatory	siRNA silencing	Active	Hilbricht et al. 2008
Stress response	*siRNA854*	siRNA	LTR (gypsy-like)	*Arabidopsis thaliana*	Regulatory	siRNA silencing	Active	McCue et al. 2012
	Adh1	Alcohol dehydrogenase	hAT	*Zea mays*	Transposition	Enhanced expression in pollen	Active	Dawe et al. 1993
Biosynthesis	*Cyp72A27*	Cytochrome P450 monooxygenase	Helitron	*Zea mays*	Transposition	Novel gene	Active	Jameson et al. 2008
	ZmCda3	Cytidine deaminase	Helitron	*Zea mays*	Transposition	Novel gene	Active	Xu and Messing 2006
Stress response	*ALP-A3*	Acireductone dioxygenase-like	Unknown	Triticeae (diploid)	Transposition	Novel gene	Active	Akhunov et al. 2007
Reproductive development	*Bs1*	Unknown	LTR (copia-like)	*Zea mays*	Retrotransposition	Novel gene	Active	Elrouby and Bureau 2010
Sexual reproduction	*N17*	Unknown	LTR	*Paspalum notatum*	Retrotransposition	Novel gene	Active	Ochogavía et al. 2011
Sexual reproduction	*N22*	Unknown	LTR (gypsy-like)	*Paspalum notatum*	Retrotransposition	Novel gene	Active	Ochogavía et al. 2011
	PPRs	Gene expression	Unknown	Angiosperms	Retrotransposition	Novel genes	Active	O'Toole et al. 2008
Flowering behavior	*FLC*	Transcriptional regulator	MITE	*Arabidopsis thaliana*	Gene disruption	Low expression	Active	Michaels et al. 2003
Flowering behavior	*FLC*	Transcriptional regulator	LTR (copia-like)	*Arabidopsis thaliana*	Gene disruption	Low expression	Active	Michaels et al. 2003
Seed development	*z1C cluster*	Seed storage proteins	Unknown	*Zea mays*	Duplication	Novel genes	Passive	Song et al. 2001

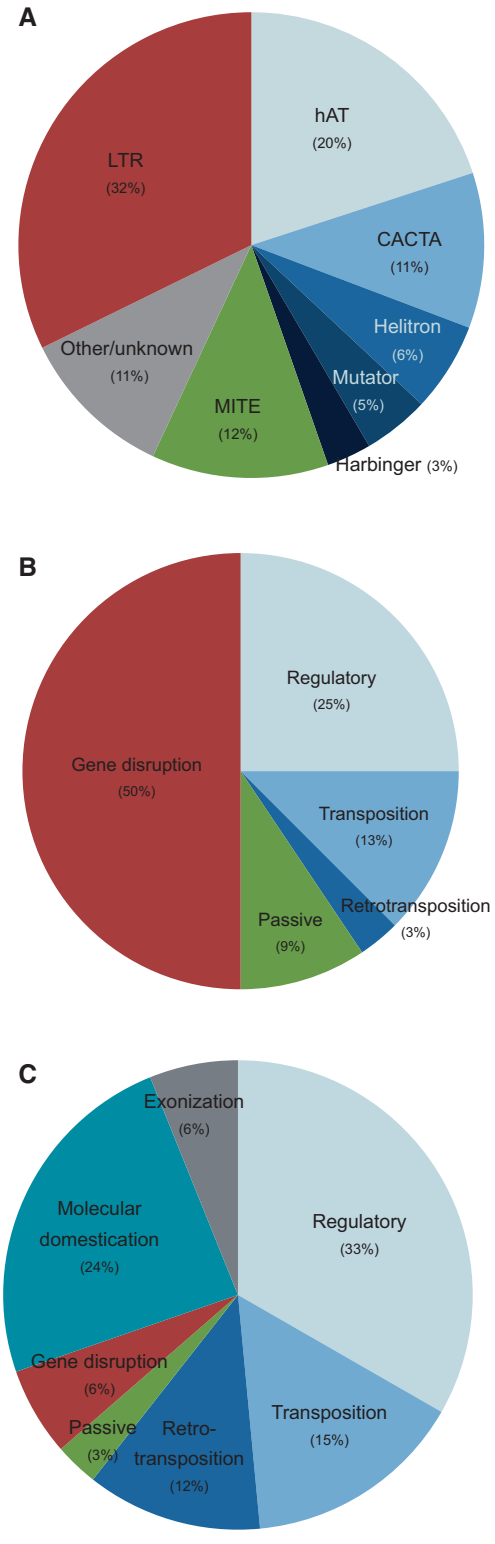

Fig. 1.—Summary of the effect of TEs on angiosperm adaptation and evolution. (*A*) Types of TEs implicated in the generation of traits in flowering plants. (*B*) Types of events mediated by TEs underlying flowering plant domestication and diversification. (*C*) Types of events mediated by TEs underlying wild traits in flowering plants. Based on the published data shown in tables 2 and 3.

genes (33%; fig. 1*C* and table 3). As outlined below, TE-generated traits in angiosperms could be classified into one of the four phenotypic groups, which are not necessarily mutually exclusive.

Domestication and Diversification of Crops and Ornamentals

Cultivated plants possess artificially selected characteristics that often greatly distinguish them from their wild progenitors. TEs have substantially contributed to plant domestication, in particular through gene disruption, to generate null alleles and by reprogramming gene expression (fig. 1*B* and table 2). The domestication of various angiosperm species provides a model to observe recent and ongoing adaptive potential due to TE-Thrust, a prominent example of which is cultivated maize. The morphology of maize, which underwent a very marked transformation from a highly branched wild progenitor (teosinte) to its modern apically dominant form, is explained in large part by the insertion of a *Copia*-like LTR retro-TE into a regulatory region of the *teosinte branched 1* (*tb1*) gene to create an enhancer element (Studer et al. 2011). The resultant TE-modified (TEm) allele has increased expression of *tb1*, which encodes a transcriptional regulator that represses branching. The timing of the *tb1* retro-TE insertion predates maize domestication by at least 10,000 years (Studer et al. 2011), indicating that human selection realized adaptive potential (standing variation) due to TE-Thrust. This closely parallels the recent realization of adaptive potential due to TE-Thrust observed in *Drosophila melanogaster*, where preexisting TEm alleles were adaptive for insecticide resistance and colonization of temperate climates (González et al. 2010; Schmidt et al. 2010).

Further to plant domestication per se, there is a clear link between TEs and crop improvement and/or varietal diversification. TE-generated null mutations have been particularly useful in this regard, leading to a range of agronomically useful traits (table 2), as well as Mendel's wrinkled peas (Bhattacharyya et al. 1990). Remarkably, the generation of TE-destroyed (TEd) alleles of the granule-bound starch synthase (*GBSS1*) gene have been repeatedly observed to underlie low amylose/sticky and waxy traits in a number of grass species including rice, maize, and millet (Varagona et al. 1992; Kawase et al. 2005; Hori et al. 2007). In the case of foxtail millet, multiple low amylose and waxy alleles of *GBSS1* have been created via independent insertions of *Copia*- and *Gypsy*-like LTR and non-LTR retro-TEs, as well as autonomous (*Mutator*) and nonautonomous/MITE (*Tourist*) DNA-TEs (Kawase et al. 2005). These findings seemingly implicate TEs as a major source of new mutations, at least in some angiosperm lineages. They also suggest that the destructive power of TEs may be a significant factor in regressive evolution, a phenomenon where certain species lose features (e.g., floating aquatic plants with no roots). However, with the

occasional exception, gene disruption by TEs would be unlikely to have much value in nature as an adaptation or contribute to the evolution of a lineage.

Resistance to Stress and Disease

Plants are not mobile and must adapt to many adverse stresses such as drought, soil conditions, and temperature. TEs are known to be intimately associated with plant stress responses, both biotic and abiotic, and undergo transposition and transcription in response to stress (Grandbastien 1998). Moreover, recent findings suggest that TE-Thrust has directly made genomic contributions to the molecular and physiological responses that underlie the ability of plants to cope with stresses (table 3). Examples discovered in *A. thaliana* are the *Copia evolved gene 1* (*AtCopeg1*), which is implicated in hormone and nutrient stress signaling, apparently having been domesticated from a *Copia*-like LTR retro-TE (Duan et al. 2008), and a *Gypsy*-like LTR retro-TE, which when epigenetically activated, produces a siRNA (siRNA854) that regulates expression of the *UBP1b* gene involved in responding to and regulating cellular stress (McCue et al. 2012). TEs have also been found to underlie stress responses in cultivated plants, for example, in sorghum, where the insertion of a MITE (*Tourist*) element upstream of an organic acid efflux transporter locus (*AltSB*) is implicated in enhanced root apex expression of the *AltSB* gene to confer tolerance to aluminum in soil (Magalhaes et al. 2007). Attesting to the ability of TEs to cause genetic change above and beyond traditional mutagens (Oliver and Greene 2012) is the evolution of the *ALP-A3* gene (encoding an acireductone dioxygenase-like protein) in some Triticaceae species, including diploid wheat. Remarkably, TEs facilitated both the creation of this gene through DNA transposition and its subsequent expression by virtue of a promoter sequence derived from a *CACTA* DNA-TE (Akhunov et al. 2007). TEs have also enhanced the ability of plants to defend against disease. The *Rim2* gene implicated in defense against fungal infection appears to have been directly exapted from part of a *CACTA* DNA-TE element (He et al. 2000), whereas an inactive rice blast disease resistance gene, *Pit*, was refunctionalized by the recruitment of a *Copia*-like LTR element as a promoter (Hayashi and Yoshida 2009).

Growth and Development

Growth, reproduction, and development are key fitness determining factors that have been influenced by TEs (table 3). Two particularly striking examples of fitness benefits brought about by TEs in flowering plants are the *Mustang* and *Sleeper* gene families, whose sequences derive from exapted transposases from *Mutator*-like DNA-TEs and *hAT* DNA-TEs, respectively (Bundock and Hooykaas 2005; Cowan et al. 2005; Joly-Lopez et al. 2012; Knip et al. 2012). *Mustang* genes are present only in the angiosperm lineage and encode putative transcriptional regulators that play important roles in growth, flower development, and reproduction. They are important for fitness because plants harboring mutated *Mustang* genes show major defects in floral organ development, fecundity, and reproductive timing (Joly-Lopez et al. 2012). Similar findings have been reported for *Sleeper* genes (Bundock and Hooykaas 2005; Knip et al. 2012). Because *Mustang* and *Sleeper* genes are found in all examined angiosperms, they appear to have been important factors in the phyletic differentiation of the angiosperms and seemingly represent key instances of realized evolutionary potential due to TE-Thrust.

Physiological and Metabolic Adaptations

TEs underlie a variety of adaptations associated with plant physiology and metabolism (table 3), including responses to light, which plants not only harness as a source of energy but also monitor constantly in order to grow and respond to seasonal changes. Most processes regulated by light involve alterations in gene expression. TEs can impart light responsiveness on genes via insertion into gene regulatory regions, as in the Chinese cucumber (*Trichosanthes kirilowii*) *TCS* gene, which has a MITE DNA-TE in its promoter (Xu et al. 2007). Two genes identified in *Arabidopsis* associated with light-induced responses, *Fhy3* and *Far1,* represent further prime examples of exaptation. These genes were co-opted from an ancient transposase belonging to a *Mutator*-like DNA-TE (Hudson et al. 2003; Lin et al. 2007) and encode transcriptional regulators that jointly act downstream of the photoreceptor phytochrome A to specifically modulate far-red light-responsive gene expression. This is crucially required for various processes such as chlorophyll biosynthesis, circadian rhythm, shade tolerance, seed germination, and flowering (Nagy et al. 2000; Allen et al. 2006; Tang et al. 2012). Such key light-sensing mechanisms have been suggested to be a critical development in angiosperm evolution, conferring upon this lineage an adaptive advantage as well as promoting their extraordinary diversification (Mathews 2006).

Conclusion

By assessing the available evidence, we conclude that TE-Thrust operates in, and has been crucial to, the evolution of flowering plants. The additional involvement of TEs in the artificial arena of plant domestication provides direct and relatively recent evidence for the importance of TEs in the generation of selectable variation in angiosperms. TE-Thrust is therefore potentially a general phenomenon that may have very widespread significance to many lineages of life on earth. Nevertheless, TE-Thrust is only one of the many facilitators of evolution, and its relative importance may vary from lineage to lineage and from age to age. A comprehension of the full magnitude of the contributions that TEs have made to angiosperm evolution will require complete genome sequencing and detailed trait characterization in a wide range of plant

species, including nondomesticated species of angiosperms and species from other plant phyla. However, any measure of TE impact will likely be an underestimate owing to important contributions having been made by ancient TEs that have been lost or are no longer recognizable.

Accepted explanations for angiosperm diversity are valid and persuasive, but still cannot fully account for the extreme diversity of angiosperms. We add to this explanation by proposing that there is good evidence that the TE-Thrust hypothesis, in addition to the accepted explanations, gives a fuller and more complete explanation for the extraordinary angiosperm diversification. The same realizable intragenomic potential due to TE-Thrust shown in metazoans, particularly mammals, is affirmed here in angiosperms. Thus, the remarkable advancement and radiation of the angiosperms appears to have been significantly aided by TE-Thrust powered by the prominent presence of LTR elements in partnership with active DNA-TE families. However, due to a paucity of data regarding the deeper evolutionary history of angiosperms and the short timescale of human selection, adaptive potential, rather than evolutionary potential, is more readily apparent at present. Nonetheless, exceptional examples of evolutionary potential appear to include the TE-derived *Mustang* and *Sleeper* genes, which may have underpinned the development of floral organs, a key morphological divergence of the angiosperms. All things considered, current evidence points to TEs being a highly significant facilitator of evolution in the angiosperms, as we have previously proposed them to be in other lineages (Oliver and Greene 2009, 2011, 2012), and this significantly broadens the applicability of, and base of support for, the TE-Thrust hypothesis.

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Associate editor: Ellen Pritham