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Key words: Cyperaceae, dauciform root, nonmycorrhizal root, nutrient-impoverished soils, root adaptations.

Ancient duplication of cereal genomes

The discovery of multiple ancient polyploidization events in *Arabidopsis* (Vision *et al.* 2000; Simillion *et al.*, 2002; Bowers *et al.*, 2003) foreshadowed the finding that *Oryza* (rice), too, had undergone extensive ancient duplication of its chromatin. Although the possibility of duplication in the rice genome had been suggested long ago, early studies of the sequence raised questions about whether rice was an 'ancient aneuploid' (Vandepoele *et al.*, 2003) or paleo-polyploid across its entire genome (Paterson *et al.*, 2003). In this issue, Wang *et al.* (pp. 937–946), contribute to a resolution of this question by using an independent assembly of a divergent rice subspecies, generally supporting the occurrence of a whole-genome duplication – although some questions still remain unanswered. Using independent dating approaches, Wang *et al.* also support prior estimates (Paterson *et al.*, 2004) that this event occurred about 70 million yr ago, suggesting

that it has affected the genome organization of virtually all of the world's cereal crops.

'Many more, if not all, higher plant species, considered as diploids because of their genetic and cytogenetic behaviour, are actually ancient polyploids'

Polyploidy and the angiosperms

Polyploidy, the merger of multiple chromosome sets in a common nucleus, ranks among the most important of evolutionary mechanisms affecting angiosperm genomes. It has long been suspected that many angiosperms were ancient polyploids (Stebbins, 1966). By contrast, the relative scarcity of polyploidy in dioecious organisms (such as most animals, but few plants) is thought to be related to a need for balanced gene dosage between autosomal loci and the nondegenerated members of heteromorphic sex chromosome sets (Orr, 1990). The discovery that one polyploidization event predates the monocot–eudicot divergence arguably suggests that all angiosperms may be ancient polyploids (Bowers *et al.*, 2003). The discovery of several additional events in the same lineage (Bowers *et al.*, 2003) raises the as yet unanswered question of whether polyploidy might truly be cyclical, with distinct advantages that are gradually eroded by 'diploidization' and divergence of suites of duplicated genes.

The controversy about rice, and why it is important

As the first representative of the Poaceae (cereals), a plant family that provides the majority of calories consumed by humans together with a growing share of our fuel and also many other 'ecosystem services' such as erosion control, duplication analysis of the *Oryza* (rice) sequence was of special importance. It had long been known that rice chromosomes occasionally paired with seemingly incorrect partners (Lawrence, 1931), and had been shown by restriction fragment length polymorphism (RFLP) mapping that rice chromosomes 1–5 (Kishimoto *et al.*, 1994) and 11–12 (Nagamura *et al.*, 1995) each contained duplicated gene pairs in what appeared to be collinear orders. Initial analysis of genomic shotgun sequence suggested a widespread propensity for gene duplication that was consistent with a large-scale event perhaps 40–50 million yr ago (Goff *et al.*, 2002).

In view of this background, it was no surprise that two early investigations of partial assemblies for *Oryza sativa* (L.) ssp. *japonica* each suggested ancient duplication of rice chromosomes. However, the findings of the two groups differed in key ways, with one reporting duplication over only about 15% of the genome ('ancient aneuploidy'; Vandepoele *et al.*, 2003), and the other suggesting a probable whole-genome event based on duplication over about 62% of the genome (Paterson *et al.*, 2003). The importance of resolving this difference was highlighted by the finding that this event predated the divergence of the major cereals from one another (Paterson *et al.*, 2004), and thus it is a common factor affecting the genome structure of many of the world's leading crops.

Perspective from a second subspecies

In this issue, Wang *et al.* describe analysis of an independent and advanced sequence assembly from *O. sativa* ssp. *indica*, a close relative of ssp. *japonica* that has been the target of a whole-genome shotgun effort (Yu *et al.*, 2002). Across 370 Mb assembled into 12 chromosomes, Wang *et al.* find 10 duplicated blocks that contain 47% of the predicted transcriptome. While the largest of these, between chromosomes 2 and 4, was found in both earlier studies (Paterson *et al.*, 2003; Vandepoele *et al.*, 2003), smaller ones such as between chromosomes 1 and 5 escaped detection by Vandepoele *et al.* (2003). Wang *et al.* corroborated the estimate of 70 million yr ago for the antiquity of the rice event (Vandepoele *et al.*, 2003; Paterson *et al.*, 2004) based on analysis of rice/maize homologs, and suggested that the extent of gene loss has been somewhat less (32–65%) than found in the earlier studies (~80%). Finally, Wang *et al.* tentatively assigned a date of about 5 million yr ago to a duplication of chromosomes 11 and 12, chromosomes that had not yet been adequately sequenced for Vandepoele *et al.* (2003) to address, and which Paterson *et al.* (2003, 2004) identified as more recently duplicated than the remainder of the genome but did not estimate a date.

Admirably, while Wang *et al.* was in review, concerns about the diversity of findings had motivated reanalysis of more advanced rice assemblies (TIGR v1.0) using less stringent thresholds for inferring significance. These analyses made it clear that the fraction of the rice genome found in duplicated blocks is indeed appreciably larger than the 15% reported in Vandepoele *et al.* (2003) and agrees more closely with Wang *et al.* and Paterson *et al.* (2004). Yet another independent analysis of the *japonica* sequence arrived at a similar conclusion (Guyot & Keller, 2004). These re-analyses also support the finding that, apart from a continuous mode of (tandem) duplication, both a recent small-scale (i.e. chromosome 11–12) and an older large-scale duplication event shaped the rice genome. The observation that approximately 7% of the rice genome is located in overlapping block duplications suggests that older, perhaps cryptic cycles of polyploidy (such as the γ event thought to be shared by all angiosperms (Bowers *et al.*, 2003) may also have shaped the genome.

Looking back at ancient duplications from the future

While the evidence for a large-scale, if not genome-wide, duplication event in a common ancestor of the cereals is growing stronger, many questions remain. Although the large-scale duplication event (i.e. duplicated blocks with 0.95 > Ks > 0.78) accounts for the majority of all duplicated blocks (~62% of all anchor points) in the rice genome, these blocks cover less than half of the physical rice genome. Consequently, it appears that these blocks may *not* actually be 'uniformly over 10 of all 12 chromosomes' as suggested (Wang *et al.*). It will be of much interest to shed light on whether there exists differential preservation of ancient gene orders in different regions of the genome, and what factors might contribute to it.

Furthermore, diploidization processes appear to vary widely in different taxa. By many measures, rice and *Arabidopsis* are thought to have experienced genome duplications at similar times (although even this remains controversial, with different authors supporting estimates of from 30 to 100 million yr). However, age distributions of duplicated genes are considerably different in the two taxa (fig. 5 in Vandepoele *et al.*, 2003). In fact, one recent study of age distributions fails to detect evidence of duplication in rice (Blanc & Wolfe, 2004). One possible explanation may be that the rate of gene loss is much higher in rice than in *Arabidopsis* (but the rates of gene loss and the fraction of genes in tandem duplications in *Arabidopsis* and rice do not seem to be significantly different at first sight; Simillion *et al.*, 2004; Wang *et al.*). Finally, Wang *et al.* are among the first to try to mitigate the effect of the negative correlation of Ks with guanine+cytosine (GC) content, an issue that is of special importance in high-GC lineages such as the rice. In any case, these additional incongruities need to be resolved before we can conclude with certainty that rice underwent a truly whole-genome duplication event.

The archaeology of plant genome duplication is only just emerging from infancy. While there naturally remains room for improvement of methodology associated with detecting paleopolyploidy, a more seminal need is better understanding of the fates of individual genes and interacting sets of genes following polyploidy. While many new data from microbes such as yeast are shedding valuable light on the roles and consequences of gene duplication, population genetic theory predicts that these consequences should be very different in organisms with larger body size and associated smaller effective population sizes (Lynch & Conery, 2003). The propensity of the angiosperms for polyploidy, together with rapidly growing genomic data and tools, makes them an especially attractive system in which to explore consequences of polyploidy that may be more likely to extend to most crown eukaryotes.

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Key words: ancient duplication, *Arabidopsis*, cereal crops, *Oryza* (rice), polyploidization.

Meetings

A pioneer perspective on adaptation

Functional genomics of environmental adaptation in *Populus*: the 12th *New Phytologist* Symposium, Gatlinburg, TN, USA, October 2004

In its natural habitat, the black cottonwood tree (*Populus trichocarpa* Hooker) is a pioneer species that thrives in the dynamic, resource-rich environments created by massive flooding (Fig. 1; Braatne *et al.*, 1996). With the recent public release of the complete genome sequence of *P. trichocarpa* (http://genome.jgi-psf.org/Poptr1/Poptr1.home.html), an analogous flood of data is creating unprecedented opportunities in basic and applied research on this model tree (Strauss & Martin, 2004; Tuskan *et al.*, 2004). This is a landmark event for ecological research in particular, because unlike herbaceous model plants like *Arabidopsis*, corn, and rice, *Populus* is a wild, perennial plant that constitutes a dominant component of many ecosystems throughout the northern hemisphere (Braatne *et al.*, 1996). The genome sequence provides a cryptic blueprint of the molecular underpinnings of adaptation in natural populations, raising the possibility of linking molecular polymorphisms to adaptively significant phenotypic variation, a feat that has been accomplished only rarely in plant research until recently (Remington *et al.*, 2001; Jackson *et al.*, 2002). Breakthroughs in the understanding of ecologically significant molecular variation will require continued technological advancement and investment in genomic resources for additional ecologically important species, as well as cross-disciplinary collaboration in ecology, population genetics and molecular biology (Feder & Mitchell-Olds, 2003). To facilitate this collaboration, the 12th *New Phytologist* symposium brought together a diverse group of ecologists, geneticists and molecular biologists to explore the prospects for determining molecular determinants of adaptive variation in *Populus* and other species. Rapid progress is likely in the understanding of molecular underpinnings of adaptation in *Populus* due to a rapidly expanding molecular toolbox, an energized and growing research community, and ecological assets that are unparalleled among sequenced model plants.

Adaptation research in forest trees

Adaptation research in forest trees has a long history, driven in part by the commercial importance of producing well-adapted and improved seed stocks for reforestation, and in part by the ecological importance of forest trees (Howe *et al.*, 2003). Initially, studies focused exclusively on adaptive traits, and usually involved planting diverse provenances in a common garden and performing a battery of measurements over a long time span. Such studies continue to be important because they provide the most direct means for determining the distribution of adaptive variation on the landscape, the degree of genetic and environmental control of a wide range of complex traits, and the extent of genotype by environment interactions (Zobel & Talbert, 1984). However, such studies provide little insight into the underlying genetic architecture of complex traits (i.e. the number and strength of genes involved, and the degrees of additivity and dominance of individual genetic loci).