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REVIEW

Architectural Evolution and its Implications for Domestication in Grasses

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• *Background* The cereal crops domesticated from grasses provide a large percentage of the calories consumed by humans. Domestication and breeding in individual cereals has historically occurred in isolation, although this is rapidly changing with comparative genomics of the sequenced or soon-to-be sequenced genomes of rice, sorghum, maize and *Brachypodium*. Genetic information transferred through genomic comparisons is helping our understanding of genetically less tractable crops such as the hexaploid wheats and polyploid sugarcane, as well as the approx. 10 000 species of wild grasses. In turn, phylogenetic analysis helps put our knowledge of the morphology of cereal crops into an evolutionary context.
• *Grass Architecture* Domestication often involves a change in the pattern and timing of branching, which affects both vegetative and inflorescence architecture, and ultimately yield. Cereal grasses exhibit two main forms of vegetative architecture: the pooid and erhartoid cereals such as wheat and rice have multiple basal tillers, while panicoid cereals such as maize, sorghum and the millets have few tillers or even only a single main stem. These differences are reflected in the differences between the wild species of pooid and some erhartoid grasses, which emphasize basal branching over axillary branching, and the panicoid grasses, where axillary branching is more frequently found. A combination of phylogenetic and genomic analysis is beginning to reveal the similarities and differences between different cereal crops, and relate these to the diversity of wild grasses to which they are related. Recent work on genes controlling branching emphasizes that developmental genetics needs to be viewed in both an evolutionary and ecological framework, if it is to be useful in understanding how morphology evolves. Increasingly, exploring the phylogenetic context of the crop grasses will suggest new ways to identify and create combinations of morphological traits that will best suit our future needs.

Key words: Grass phylogeny, *RAMOSA*, *TEOSINTE BRANCHED1*, tiller, vegetative branching, inflorescence morphology, domestication, evolution, plant architecture.

INTRODUCTION

Grasses are both economically and ecologically important. The 12 or so main domesticated cereals provide a large proportion of the calorific input of humans, and many grasses are important forage for both domesticated and wild animal populations. They are dominant components of the savannah and prairie habitats that cover approx. 20 % of the world (Clayton and Renvoize, 1986). Given their importance it is no surprise that they have been at the forefront of human selection for thousands of years (Harlan, 1973). They have more recently been the focus of intensive breeding efforts, including, over the last few years, the development of molecular markers and the identification of genes responsible for various traits of agronomic interest (Paterson *et al.*, 2005).

Breeding efforts in cereals such as maize, rice, wheat, oats, barley, millets, sorghum, etc. have traditionally proceeded along separate lines, and have produced separate communities of breeders. For example, the USA has a strong and active maize community, Japan a strong rice community and the USA, Europe and Australia strong wheat communities. The lines of research pursued by each of these communities have been influenced by the particular traits of the crop they are concerned with. For example, rice was the first of the cereals to be sequenced because of its small genome, and because it was realized that the genomic sequence from rice would benefit breeding of other cereal crops (Goff *et al.*, 2002; IRGS, 2005). Unlike rice, maize has a very large genome, with extensive regions of genomic repeats that make sequencing difficult (SanMiguel *et al.*, 1996). It also is an ancient tetraploid, but with subsequent losses of one copy of over half of its duplicated genes (Messing *et al.*, 2004). However, maize has an unequalled set of developmental mutants and a complex inflorescence morphology, affording detailed insight into developmental genetic processes underlying morphological change (Neuffer *et al.*, 1997). Modern hexaploid wheat has an even larger genome, although there are related diploid species with smaller genomes such as *Triticum urartu* (Devos and Gale, 2000). Both wheat and maize breeders have been interested in finding closely related species with smaller genomes that may act as models for these important crops – maize breeders look to sorghum and the millets, wheat breeders to a small grass, *Brachypodium distachyon*, whose genome is at present being sequenced (Paterson, 2006).

It is only with the introduction of molecular markers that it has been possible to discern relationships between genomes (Laurie *et al.*, 1983; Gale and Devos, 1998), and

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thus to meaningfully compare traits in different crops. While comparative genetic and genomic efforts between the major crop grasses are now commonplace (Devos, 2005), spurred by the hope that it might be possible to generalize genetic discoveries in one cereal crop to other cereal crops, our increasing understanding of the phylogenetic context of the cereal grasses is not so widely appreciated. In this paper I outline present knowledge of the phylogenetic relationships of the grasses, and explore how phylogenetic comparisons and developmental genetics can help us understand the set of traits that underlie plant architecture.

PHYLOGENY OF GRASSES

The evolutionary relationships of the approx. 10 000 extant species of grasses have been debated for many years (Clayton and Renvoize, 1986; GPWG, 2001). The most comprehensive overview of grass phylogenetic relationships stems from the successful collaboration of the Grass Phylogeny Working Group (GPWG, 2001), using one morphological and seven molecular data sets (chloroplast: *ndhF*, *rbcL*, *rpoC2*, chloroplast restriction sites; nuclear: *phyB*, *ITS*, *waxy*), and 62 exemplar species. More recent analyses have confirmed the major relationships shown by the GPWG analysis, and have additionally shown that the outgroup family Ecdeiocoleaceae is sister to the Poaceae, and that Joinvilleaceae is sister to the clade of both of these families (Bremer, 2002; Salamin *et al.*, 2002; Michelangeli *et al.*, 2003; Linder and Rudall, 2005). A redrawn and simplified representation of one of the combined analyses of the GPWG, with additional outgroups as indicated by more recent papers, shows that cereal and forage crops have been domesticated from many different grass groups (Fig. 1).

Phylogenetic relationships have been exhaustively discussed in the GPWG paper (GPWG, 2001), but in summary, the earliest diverging lineages of basal grasses have few species and are generally herbaceous plants of tropical forest understoreys. The great radiation of species occurs in the 'crown group' of grasses, whose members diverged from one another approx. 60 million years ago (mya) (Crepet and Feldman, 1991). One large clade (the BEP clade) comprises the basal subfamily Bambusoideae (bamboos) sister to the Ehrhartoideae (including rice and wild rice) and the Pooideae (including wheat, oats, barley, etc.). This large group of approx. 4200 species is sister to another clade (the PACCAD clade) including the Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Aristidoideae and Danthonioideae subfamilies. Within the large subfamily Panicoideae are two tribes, the Paniceae, containing the millets, and Andropogoneae, containing sorghum, maize and sugar cane.

The age of the separation of the BEP and PACCAD clades ('crown group') has been estimated at 55–60 mya, based on fossil pollen (Crepet and Feldman, 1991), but a recent report of grass phytoliths in dinosaur dung may push back the crown group age to 80 mya (Prasad *et al.*, 2005) (Fig. 1). The domesticated cereal grasses span this age range, as the most recent common ancestor of rice and maize is at the base of the crown group (GPWG, 2001) (Fig. 1) (This contrasts with around 20 mya for the split between *Arabidopsis* and *Brassica*; Koch *et al.*, 2001). Molecular phylogenetic dating of the ages of the major grass clades, using the fossil pollen to set a minimum age for the diversification of the crown group of grasses, suggests that the BEP and PACCAD clades had themselves diversified by approx. 35–40 mya (but with wide confidence intervals) (Bremer, 2002). This dating has been corroborated by comprehensive examination of grass phytoliths (silica bodies) preserved from Eocene to late Miocene sediment samples in North America (Stromberg, 2005). These samples also suggest that the rise to ecological dominance of grasslands in North America took place 7–11 million years later than the taxonomic diversification (Stromberg, 2005). The switch between the earlier, C_3 photosynthetic pathway-dominated, grasslands (comprised primarily of pooid grasses) and the later, C_4 photosynthetic pathway-dominated, grasslands (many PACCAD grasses) has been harder to date, primarily because there appear to have been multiple origins of the C_4 pathway, with its major anatomical and physiological changes (Giussani *et al.*, 2001). However, phytolith data suggest that C_4 grasses had evolved by the mid-Miocene (approx. 19 mya) (Stromberg, 2005), well before the rise to ecological dominance of C_4 grassland systems in the late Miocene (7–5 mya) (Sage, 2004), but correlated with a worldwide decrease in the concentration of atmospheric carbon dioxide in the early Miocene (Zachos *et al.*, 2001).

Studies on the phylogeny of grasses have more recently been complemented by genomic analyses of many of the major cereal grasses. These analyses reveal that a genomic duplication pre-dates the divergence of the wild relatives of modern cereal grasses, and that for the first third of the subsequent evolution of these grasses there was little molecular divergence (Paterson *et al.*, 2004). However, marked genomic divergence has occurred in the last two-thirds of the 60–80 million years since the main cereal grass lineages separated (Paterson *et al.*, 2004), resulting in genome size differences that range from rice at 420 Mb to wheat at 16 000 Mb (Goff *et al.*, 2002), compared with arabidopsis with a genome of 125 Mb (AGI, 2000). Given these size differences, and the length of time over which they have evolved, it is remarkable that it is still possible to use heterologous RFLP probes that can hybridize across grasses (Wang *et al.*, 1998), and to discern clear patterns of synteny between grass genomes (Devos and Gale, 2000; Doust *et al.*, 2005). However, genome evolution in grasses has been complex, with a number of rounds of genome duplications followed by gene deletions, making it difficult to positively identify genes which are strictly orthologous (Kellogg, 2003, 2006*b*; Malcomber *et al.*, 2006). Loss of orthologous copies may result in paralogues rather than orthologues being compared in genomic analyses, and may explain why comparative mapping sometimes suggests anomalous synteny relationships across genomes (Paterson *et al.*, 2004). Patterns of differential loss of gene duplicates may also explain the gaps in micro-synteny that have been discovered both within and between species (Bennetzen, 2000; Bowers *et al.*, 2005; Ma *et al.*, 2005). The

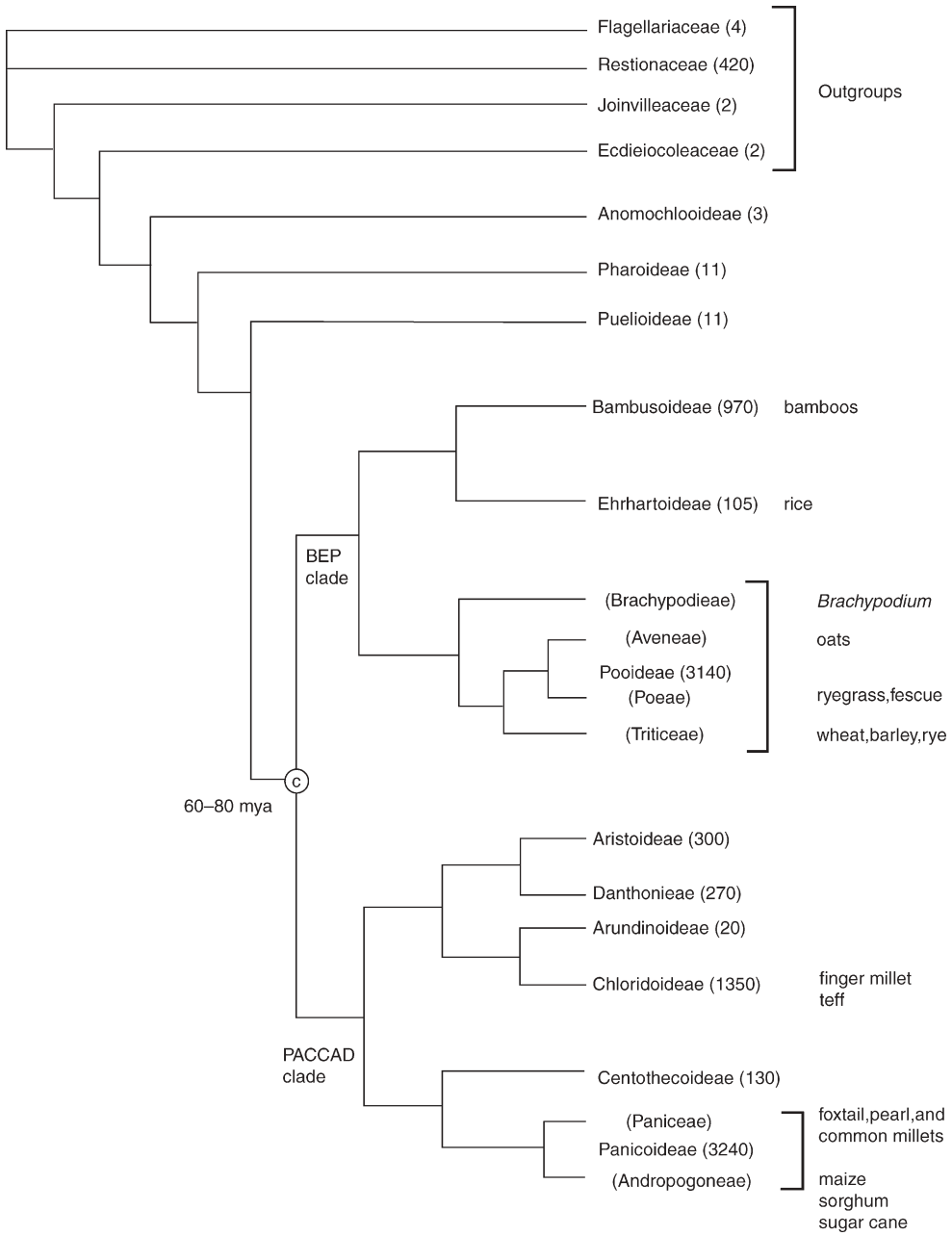

FIG. 1. Grass phylogeny, redrawn from GPWG (2001) and Kellogg (2000), with the addition of the outgroup family Ecdeiocoleaceae (Bremer, 2002; Michelangeli *et al.*, 2003). © denotes crown group of grasses. Taxon terminal names are subfamilies within the grasses (with tribes in parentheses where appropriate). Numbers beside subfamilial labels indicate approximate number of species.

phylogenetic context of gene duplication is of great importance in understanding which gene copies are truly comparable, and how gene copies may have diversified and taken on novel functions during grass evolution (for an excellent review of the complex patterns of gene duplication in a number of key developmental genes across grasses, see Malcomber *et al.*, 2006).

Taxonomic diversification and ecological expansion of grasses set the stage for domestication of cereal crops. In terms of our present-day crops the three most important events were (*a*) the domestication of wheat in south-eastern Turkey near the Tigris and Euphrates rivers approx. 10 500 BP (years before present) (Ozkan *et al.*, 2002), (*b*) the domestication of rice at least twice, once in eastern India and once in southern China approx. 7000–10 000 BP (Londo *et al.*, 2006), and (*c*) a single domestication of maize in the southern highlands of Mexico approx. 9000 BP (Matsuoka *et al.*, 2002). Domestication is likely to have involved selection for seeds to be retained in the seed head, rather than the 'shattering' habit of wild species (Harlan, 1992), but also involved modification of a number of other traits, including selection for annual

habit and modification of plant architecture to increase yield. It is this last trait that I wish to concentrate on, as architectural differentiation in cereal grasses gives an insight into how phylogenetic context can affect domestication potential.

GRASS ARCHITECTURE

Plant architecture is primarily determined by patterns of branching. Vegetative branching patterns play a major role in determining overall biomass of the plant as well as the number of inflorescences produced, while inflorescence branching patterns influence the number of seeds that each inflorescence will bear (Zhao *et al.*, 2006). Of these, vegetative branching is much more variable, responding quickly to changes in environmental conditions, while inflorescence branching is less variable, and is often used as a source of taxonomic characters for separating both species and genera (Clayton and Renvoize, 1986). Much work has been done in major cereal crops such as maize, rice and wheat to elucidate the environmental conditions that contribute to variation in branching, and to identify genome regions and genes that control branching (Poncet *et al.*, 1998; Lafarge *et al.*, 2002; Li *et al.*, 2003; Doust *et al.*, 2004; Duggan *et al.*, 2005; Ishikawa *et al.*, 2005; Doust and Kellogg, 2006). Less work has been done on integrating environmental and gene-based approaches (but see Lukens and Doebley, 1999), or appreciating the phylogenetic context of morphological differences (Kellogg, 2000). Such an understanding may lead to new insights into the direction of future breeding efforts as well as outlining the lineage-specific constraints that may limit such efforts.

VEGETATIVE BRANCHING

In most cases, a grass will produce more branch meristems than the plant will use, the unused meristems being available for quick regrowth after damage such as grazing or fire. The degree of vegetative branching affects both leaf biomass and numbers of inflorescences, as an inflorescence usually terminates the main axis, and any future growth must come from axillary meristems (Lafarge *et al.*, 2002; Dingkuhn *et al.*, 2005). Domesticated crops have decreased levels of vegetative branching compared with their wild relatives.

Branching patterns

Amongst the species of grasses that gave rise to domesticated cereal crops there are two distinct types of vegetative branching (Fig. 2). In the first type, the axillary meristems at the first few nodes of the grass culm (main stem) elongate to become tillers that are similar in shape and height to the primary culm. The basal internodes on the primary culm do not expand, so that all of the tillers emerge more or less at ground level. This enables the tillers to produce their own adventitious roots and so achieve at least a partial independence from the primary shoot. The second type of branching is when axillary branches arise from axillary buds in the axils of leaves higher up the culms, where stem internodes have expanded. The growth of these branches is often suppressed at the bud stage, under genetic and hormonal control (Leyser, 2003, 2006; McSteen and Leyser, 2005).

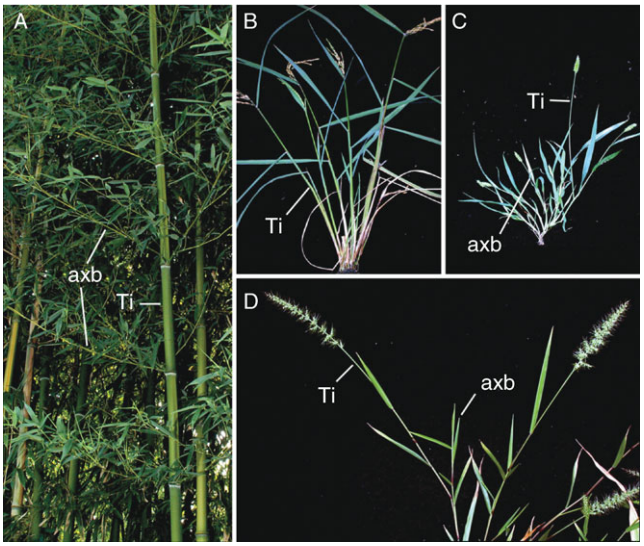

FIG. 2. Grass architecture, showing tillers and axillary branches (Ti = tiller; axb = axillary branch): (A) bamboo (*Phyllostachys aureosulcata*); (B) rice (*Oryza sativa*); (C) green millet (*Setaria viridis*); (D) *Setaria grisebachii*.

Tillers can either grow erect, resulting in an upright, tufted caespitose growth habit, or can be variously decumbent, resulting in a stoloniferous or rhizomatous growth habit. All cereals are caespitose, although studies in maize, sorghum and rice have shown that relatively few genes control the shift from an upright to a rhizomatous perennating habit (Paterson *et al.*, 1995*b*; Hu *et al.*, 2003; Westerbergh and Doebley, 2004). In almost all cases domesticated cereal crops have been derived from ancestors with annual growth habits, although the ancestor of rice, *Oryza rufipogon*, has both annual and perennial forms (Londo *et al.*, 2006).

A major distinction between the architectural form selected for in both pooid (wheat, oats, barley, etc.) and ehrhartoid (rice) cereals, versus the cereals in the PACCAD clade (millets, maize, sorghum) is in the type of vegetative branching they possess. The pooid and ehrhartoid cereal grasses characteristically have many tillers but no axillary branches. This is despite there being, in at least some cases, axillary meristems initiated in the leaf axils (Fig. 3A). These cereals, and the wild grasses that are related to them, appear to strongly favour production of tillers over axillary branches, with each tiller terminating in an inflorescence. The strong tendency to tiller in pooid and ehrhartoid grasses may be related to grazing pressures or other ecological factors. Panicoid cereal grasses, such as maize, sorghum, pearl millet and foxtail millet, produce tillers, but in most cases they also produce axillary meristems, that can grow out into axillary branches, given non-limiting space and light (Fig. 3B). In maize, it is, in fact, an axillary branch that bears the ear (female inflorescence). During domestication of panicoid cereal grasses the outgrowth of multiple axillary branches appears to

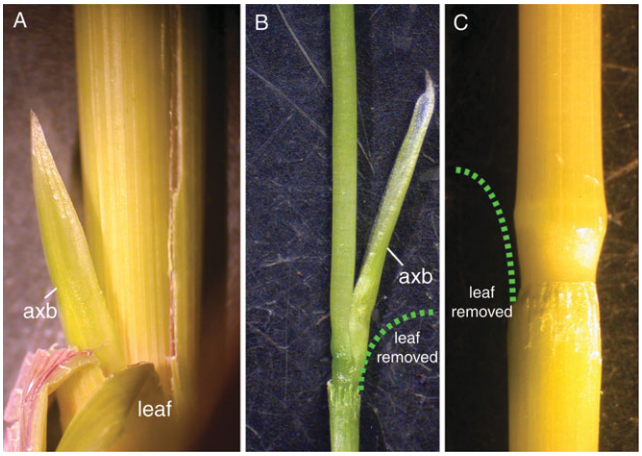

FIG. 3. Axillary shoots: (A) rice; (B) green millet (*Setaria viridis*); (C) foxtail millet (*S. italica*) (without axillary branch meristem). axb = axillary branch, green dashed line indicates position of leaf attachment.

have been selected against, with the result that the plant puts all its photosynthetic capital into a single large inflorescence (or into a separate male and female inflorescence in maize). However, in the wild ancestors of these crops, and in other related wild grasses, axillary branching is a common occurrence, usually occurring after the apical meristem of the main stem has transformed into an inflorescence meristem (Doust *et al.*, 2004). These evolutionary differences in preferred mode of branching between pooid and ehrhartoid grasses, on the one hand, and panicoid grasses on the other, strongly affect the different architecture of domesticated cereal crops derived from them.

There have been attempts to engineer rice vegetative architecture in a way which more resembles that of the panicoid cereals. Traditionally, breeders have achieved high yield in *indica* varieties by breeding plants that produce more productive tillers (tillers which bear an inflorescence) (Sheehy *et al.*, 2001). However, the size of the inflorescence terminating each tiller is relatively small. A new plant type was bred, using tropical *japonica* germplasm, that had low tiller numbers and large panicles (Sheehy *et al.*, 2001). This produced more spikelets per tiller than an elite *indica* variety, but the increase was offset by the greater number of tillers produced by the *indica* variety. Interestingly, the results from growing the two varieties at both normal and widely spaced densities, without nitrogen limitations, showed that in each case only about half of the juvenile spikelets produced actually filled to produce mature grain. Thus, the authors concluded that there was a limit to increasing production by traditional breeding, and that further major increases could only come about through increasing photosynthetic input (Sheehy *et al.*, 2001). One way to do this would be to engineer the C_4 pathway of photosynthesis characteristic of panicoid grasses into rice (which is a C_3 grass), a goal that is being actively pursued (Mitchell and Sheehy, 2006).

Tillering in rice has consistently been shown to be important in weed suppression, and tiller density and the ability of the rice crop to quickly produce an unbroken canopy are highly correlated (Haefele *et al.*, 2004). This is especially important in aerobic rice production, where rice is grown as an upland crop and is subject to severe weed infestation (Zhao *et al.*, 2006). Zhao (2006) found that the tillering ability of a cultivar when grown at low density was predictive of vegetative crop biomass when planted more densely. This trait was highly heritable and correlated with yield under both weed-free and weedy conditions. In these trials, selection under meaningful conditions of seed infestation is especially important, as plant characteristics measured in monocultures had no explanatory value for the competitive ability of tested lines under heavy weed infestation (Haefele *et al.*, 2004).

Maize and other panicoid crop grasses have been selected for a decrease in both tillering and axillary branching, but even elite maize varieties will show vegetative branching under ideal growing conditions without competition (Moulia *et al.*, 1999). However, teosinte, the wild progenitor of maize, shows higher levels of branching than maize, whether grown with or without competition, and maize appears to be less sensitive than teosinte to variations in planting density (Lukens and Doebley, 1999). Green millet (*Setaria viridis*), the wild progenitor of foxtail millet (*S. italica*), also shows great variation in both tiller and axillary branch number under differing planting densities, whereas the differences in tiller branching between low and high densities for the domesticated foxtail millet were much reduced (Doust and Kellogg, 2006). Axillary branching in some varieties of foxtail millet is abolished entirely, as no axillary meristems can be observed (Fig. 3C).

Knowledge of the genetic control of vegetative branching in grasses is increasing rapidly (Wang and Li, 2005, 2006), and can be considered in terms of three developmental decisions: (1) whether to initiate, (2) once initiated, whether to remain viable, and (3) when viable, whether to elongate into an axillary shoot. It is not yet possible, in the vast majority of cases, to determine whether the genes that have been shown to be important in controlling development will also be found to underlie evolutionary diversification, although this is a major assumption of evolutionary-developmental (evo-devo) studies.

Axillary meristem initiation

One of the genetic pathways involved in axillary meristem initiation in grasses involves *monoculm1* (*Os-moc1*), a gene characterized from a rice mutant that had almost no branching (Li *et al.*, 2003). This gene is a member of the GRAS transcription factor family, and is necessary for axillary meristem initiation. It shares similarities with the *LATERAL SUPPRESSOR* gene (*At-las*, *Le-ls*) from arabidopsis and tomato that controls aspects of branching in these model dicot plant systems. In rice, *Os-moc1* affects all branch meristems so that both vegetative and inflorescence branching are severely curtailed (Li *et al.*, 2003).

Another gene that similarly affects both vegetative and inflorescence axillary meristem initiation in maize is *barren stalk1* (*Zm-ba1*) (Ritter *et al.*, 2002; Gallavotti *et al.*, 2004). This is a basic helix-loop-helix transcription

factor that shares similarities with *LAX PANICLE1* (*Os-lax1*) in rice, but does not appear to have a related gene in any dicot system. *Os-lax1* differs from *Zm-ba1* in only affecting inflorescence branching (Komatsu *et al.*, 2003), although, when a double mutant is made between *Os-lax1* and another gene that only affects inflorescence branching, *small panicle1* (*Os-spa1*), a mutant plant that lacks both vegetative and inflorescence branching is produced. This implies that these two genes show redundancy for vegetative but not inflorescence branching (Komatsu *et al.*, 2003), and suggests that control of the elaborate inflorescence structures in grasses has been built on top of more general controls for plant branching.

Once initiated, meristems usually either remain dormant or grow out as branches. However, a third possibility is shown by the *uniculm2* (*Hs-cul2*) mutant in barley. Here, meristems are initiated as bulges in the axils of leaves, in a similar manner to wild-type plants (Babb and Muehlbauer, 2003), yet these axillary meristems do not initiate leaves, and the cells quickly become enlarged and appear to lose their meristematic potential. During further development the meristem disappears and is incorporated into the internode above it. Double mutants made between *Hs-cul2* and a range of other mutants with a variety of tillering phenotypes led almost without exception to single-stemmed plants, indicating that *Hs-cul2* is epistatic to these mutants. Interestingly, inflorescence morphology was also affected in both the *Hs-cul2* single mutant and in double mutants, with very few viable spikelets being produced. Similar mutant phenotypes in other grasses are yet to be reported.

Axillary meristem outgrowth

In most grasses, every leaf will subtend an axillary meristem, but in general not all of these meristems will ever grow out as branches. The ability to selectively suppress meristem growth in response to both internal and external cues is an important strategy that allows the plant to be able to control its shape and to respond to environmental variation. Hormones, such as the balance between auxin and cytokinin, play a major part in regulating meristem growth, but much remains to be discovered about how hormone levels and gene activation are related (Beveridge, 2006; Leyser, 2006; Veit, 2006). John Doebley's group has spent many years unravelling the function and evolution of the TCP transcription factor, *teosinte branched1* (*Zm-tb1*), the best characterized gene in maize known to control vegetative axillary meristem outgrowth (Doebley and Stec, 1991; Doebley *et al.*, 1997; Hubbard *et al.*, 2002; Clark *et al.*, 2006). This gene has orthologues in other grasses but is not known from arabidopsis or other model dicot systems. *Zm-tb1* is closely related to *Os-tb1* in rice, which also suppresses meristem outgrowth, and corresponds to a classical many-tillered mutant, *fine culm1* (*Os-fc1*) (Takeda *et al.*, 2003). *Zm-tb1* and *Os-tb1* act to suppress axillary meristem outgrowth, but *Os-tb1* in rice appears to have less effect than *Zm-tb1* does in maize. This may be because both mutant and wild-type rice plants have more than one tiller (Luo *et al.*, 2001; Goto *et al.*, 2005). In contrast modern maize usually only has a single main stem, while the mutant has many tillers and axillary branches (Doebley *et al.*, 1997; Hubbard *et al.*, 2002). In QTL studies of foxtail millet (*Setaria italica*) (Doust *et al.*, 2004) and pearl millet (*Pennisetum glaucum*) (Poncet *et al.*, 2000), QTL for tiller number co-localize with the map position of the *Zm-tb1* orthologue, whereas QTL for axillary branch number do not, suggesting that tillering and axillary branching may be under separate genetic control.

The effect of both *Zm-tb1* and *Os-tb1* is responsive to the level of shading experienced by the plants, with high planting densities reducing the number of tillers that develop, without affecting the number of axillary meristems that are produced (Lukens and Doebley, 1999; Takeda *et al.*, 2003). Thus, *Zm-tb1* may be involved in the shade response (Schmitt *et al.*, 2003; Kebrom *et al.*, 2006), which involves elongation of plant internodes and suppression of branching when a plant is overshaded by other plants. This response is triggered by the plant's perception via the phytochrome pathway of a decreased red : far red ratio, the result of red light being absorbed by the chlorophyll of surrounding plants (Sawers *et al.*, 2005). The expression of the sorghum orthologue of *Zm-tb1*, *Sb-tb1*, was shown to be correlated with bud suppression in *Sb-phyB-1* sorghum mutants that constitutively expressed a shade response, as well as with plants that were grown with supplemental far-red light. This suggests that the phytochrome pathway is in some way involved in the control of *Sb-tb1* and axillary meristem outgrowth (Kebrom *et al.*, 2006). This result provides a link between environmental variation and gene action controlling branching, and agrees well with other observations that grass tillering is strongly affected by planting density (Doust and Kellogg, 2006).

Phytochromes are implicated in other responses to changing light environments. There are members of three subfamilies of phytochromes in grasses (*PhyA*, *PhyB*, *PhyC*) (Sawers *et al.*, 2005). In maize, each of these genes is duplicated to make six in all (Sawers *et al.*, 2005). Even more can be present in genomes such as wheat, where, for example, there are three copies of *PhyC* that are all expressed (Devos *et al.*, 2005). There has been much interest in manipulating phytochromes to change the perceived environment of a plant, by changing how it perceives light quality. Over-expression of an arabidopsis *phyA* gene under the rice *rbcS* promoter in an *indica* variety of rice resulted in shorter plants with more tillers (Garg *et al.*, 2006), while a similar construct under the same promoter in a *japonica* variety resulted in fewer tillers (Kong *et al.*, 2004), suggesting that different cultivars may respond in different ways to similar genetic manipulations. This may be related to differences in allocation of resources in *indica* and *japonica* varieties (whether to more tillers and smaller inflorescences, or the reverse).

A gene family controlling axillary meristem outgrowth that does appear to be present in both monocots and dicots is the *more axillary branching/decreased apical dominance/ramosus* (*max/dad/rms*) gene pathway, found in arabidopsis, petunia and pea (Stirnberg *et al.*, 2002; Sorefan *et al.*, 2003; Booker *et al.*, 2005; Snowden *et al.*,

2005; Bennett *et al.*, 2006; Simons *et al.*, 2006), and now in rice (Ishikawa *et al.*, 2005; Zou *et al.*, 2005). *At-max* mutants are bushier than wild-type plants, due to outgrowth of axillary meristems that are usually suppressed. There are four components of this pathway that have been described to date, and recently the many-tillered rice mutants *dwarf3* (*Os-d3*) and *high tillering dwarf1* (*Os-htd1*) have been positionally cloned and identified as closely related to *max2* and *max3* (Ishikawa *et al.*, 2005; Zou *et al.*, 2005). Moreover, the rice genome contains genes that are closely related to the other two *max* genes, strongly implicating a conserved *max* pathway in both monocots and dicots for axillary meristem suppression.

INFLORESCENCE BRANCHING

All grasses have inflorescences that terminate the main axes of growth (Linder and Rudall, 2005), and inflorescence branching is much less susceptible to environmental influences than vegetative branching. Grass inflorescences have complex branching patterns, and contain more distinguishable types of branch meristems than do arabidopsis or other model dicot inflorescences (Bommert *et al.*, 2005). Careful comparative developmental morphology establishes that much of the inflorescence variation we see in groups of related grasses is due to changes in the number of branches, the numbers of orders of branches, and the amount of axis elongation (Doust and Kellogg, 2002). However, it has been difficult to relate the major changes wrought by mutations of developmentally essential genes to the quantitative changes seen amongst natural groups of grasses. One set of genes characterized from maize holds promise for explaining some of the natural variation observed. These are the *ramosa1*, *2* and *3* (*Zm-ra1*, *Zm-ra2*, *Zm-ra3*) mutants, which control the transition between the production of long and short branches in the maize inflorescence (Vollbrecht *et al.*, 2005; Bortiri *et al.*, 2006; Satoh-Nagasawa *et al.*, 2006). In *ramosa* mutants, branches are produced that are intermediate between long and short branches, defining the normal function of *ramosa* gene products as controlling inflorescence branch outgrowth (Kellogg, 2006*a*).

Zm-ra1 orthologues have been characterized from maize, sorghum and *Miscanthus*, all members of the tribe Andropogoneae, within the panicoid grasses (Vollbrecht *et al.*, 2005). It has not, however, been isolated from rice or arabidopsis, despite repeated attempts. It encodes for a zinc-finger transcription factor of the EPF class, and is primarily expressed at the base of the short branches that will become the spikelet pair (Vollbrecht *et al.*, 2005; McSteen, 2006). As such it appears to confer determinacy on the short branch, such that its removal allows these branches to grow out and produce additional spikelets. *Zm-ra2* encodes for a LOB domain protein, a transcription factor that appears to be expressed earlier, and epistatic to *Zm-ra1* (Vollbrecht *et al.*, 2005; Bortiri *et al.*, 2006). *Zm-ra3* encodes for a trehalose phosphate phosphatase, a metabolic protein that is expressed later than *Zm-ra2* and may be downstream of it (Satoh-Nagasawa *et al.*, 2006). Unlike *Zm-ra1*, *Zm-ra2* is also found in rice and barley, and is very conserved in its pattern of expression just outside the meristems of both long and short branches and of spikelet meristems (Bortiri *et al.*, 2006). Interestingly, unlike *Zm-ra1*, which was cloned by transposon tagging, *Zm-ra2* was positionally cloned using colinearity with the rice genome (Bortiri *et al.*, 2006), making it the second gene, after, *teosinte glume architecture1* (Wang *et al.*, 2005), to be cloned directly from its position on a linkage map (McSteen, 2006).

The diversity of grass inflorescences represented by maize, sorghum and *Miscanthus*, represent some of the critical specific differences seen amongst grasses as a whole. *Ra1* expression patterns are correlated with these differences, so that in *Miscanthus*, which only has long branches with spikelet pairs, there is a delay in the start of *ra1* expression. However, in sorghum, *ra1* expression is delayed substantially while the inflorescence undergoes a number of rounds of branching before producing spikelet pairs. This does not fully explain the condensed inflorescence head of sorghum as compared with maize or *Miscanthus*, but certainly implicates *ra1* in morphological change. Differences within species also suggest the actions of the *ramosa* genes. Recently, a study comparing open and closed inflorescence forms in sorghum found a QTL corresponding to *Zm-ra2* (Brown *et al.*, 2006), while in maize, QTL for tassel branch number were found in a position that corresponded to *Zm-ra1* (Upadyayula *et al.*, 2006).

CONCLUSIONS

Cereal grasses are important sources of food for both humans and the animals we farm. They are also ecologically significant, especially in prairie and savannah habitats. The history of domestication of each of the cereal grasses has been more or less independent from one another, until the advent of molecular techniques allowed common markers to be used in different crop species, establishing the high level of synteny between grass genomes. This colinearity of genomes has been used to predict genes for marker associations, and has given rise to the idea that domestication in different grass species may select on the same genes or gene pathways (Paterson *et al.*, 1995*a*), and that grasses could be considered a single genetic system (Bennetzen and Freeling, 1993).

The promise of comparative mapping suffered a blow with the increasing availability of genomic sequence, as it became clear that there were many small regions of the genome which did not show conserved synteny. This is true both within and among species, and is likely to be the result of multiple rounds of gene and genome duplications, followed by differential gene loss. Detailed phylogenetic analysis with adequate sampling is needed in order to understand which genes might be truly comparable (orthologues) versus those that are related but do not show a unique common ancestor (paralogues). Adequate sampling in this case requires sampling of crop and non-crop grasses, in order to understand the phylogenetic context in which the cereals are found. The advent of significant genomic sequence data for a large number of

species is greatly increasing our ability to perform such analyses and to elucidate orthologous and paralogous gene relationships. The complete sequencing of the two rice genomes (*indica* and *japonica*), and the promise of complete sequences for *Brachypodium*, sorghum and maize, is also improving the success of positional cloning approaches to gene discovery. This will enable gene candidates to be established for QTLs from many different species.

However, in the face of the torrent of genetic information that is now being generated, it is good to remember the need to relate developmental genetics to the behaviour of the crop plant in its environment. The elucidation of signalling pathways, and the continuing work on the physiological and morphological responses of grass crops to environmental variation (especially in light quality), will be critical in relating genetic and genomic variation to real-world crop behaviours. Establishing the evolutionary basis of differences in behaviour may also be important in understanding how best to direct breeding efforts to take advantage of these differences. The evolution of C_4 grasses from C_3 ancestors multiple times (Giussani *et al.*, 2001) provides evidence that complex anatomical and physiological changes can be labile in evolutionary time, suggesting that even the task of producing a C_4 rice plant is possible. Understanding patterns of relationships is essential for inferring gene function in non-model grasses from known genetic phenomena in model grasses like rice and maize. Ultimately, it is the leveraging of genetic information from model to non-model grasses that will tell us most about evolution and give us the deepest insights into the spectrum of possibilities for future breeding efforts. Continued work in phylogenetics and genomics, coupled with physiological and ecological experimentation, is the surest way to understand the process of domestication and to support the on-going plant breeding efforts necessary for our long-term food survival.

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