Integrating Phylogeny into Studies of C_4 Variation in the Grasses

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C_4 photosynthesis consists of morphological and biochemical novelties that create a CO_2 pump that concentrates CO_2 around Rubisco (Kanai and Edwards, 1999), which decreases photorespiration and the resulting energy waste. Consequently, C_4 photosynthesis provides a competitive advantage in all conditions where photorespiration costs become important, especially at high temperatures and in arid and saline conditions (Sage, 2001). Despite being used by only 3% of extant angiosperm species (Sage, 2004), C_4 plants account for one-fifth of global terrestrial primary production (Ehleringer et al., 1997). This is mainly due to the high productivity of C_4 monocots, especially C_4 grasses, which are the most speciose C_4 group (Sage, 2004). The C_4 grasses dominate most open subtropical and tropical habitats, and some, such as maize (*Zea mays*), sorghum (*Sorghum bicolor*), millets (e.g. *Pennisetum glaucum*, *Setaria italica*), and sugarcane (*Saccharum officinarum*), are used as crops and have direct importance for human food consumption and/or as livestock fodder (Table I).

The biochemistry of the C_4 pathway has been an active field of research over the last 40 years and is thus well described (Kanai and Edwards, 1999). However, many issues regarding C_4 photosynthesis are still being investigated. A central problem has to do with the genetic regulation of C_4 photosynthesis. The genetic mechanisms responsible for the transition from C_3 to C_4 remain poorly understood, despite extensive investigation on the part of numerous scientists (e.g. Covshoff et al., 2008; Lara et al., 2008). The evolution of the C_4 pathway was previously thought to have involved relatively few key mutations (Ku et al., 1996), but recent studies showed that the C_4 pathway of maize involves cell-specific expression for 18% of the genes (Sawers et al., 2007) and requires deep synchronization between mesophyll (M) and bundle sheath (BS) cells (Bailey et al., 2007). These transcriptional changes are likely to mediate, at least in part, the variation observed in BS and M plastid proteomes (Majeran et al., 2005, 2008). Rather than extensive changes in cis- and trans-acting regulatory elements, the segregation of enzymes between M and BS cells of C_4 plants could have been acquired through changes in key regulatory elements changing M and BS cellular environments (Covshoff et al., 2008), leading to important differences in their transcriptomes (Sawers et al., 2007). In addition to the C_4 enzymes, C_4 photosynthesis evolution necessitated rearrangements of chloroplast envelope proteins (Bräutigam et al., 2008). Furthermore, transport of C_4 intermediates between M and BS cells is probably not performed through simple diffusion, which suggests that other, unidentified, mechanisms exist (Sowinski et al., 2008), which may be yet another C_4-specific adaptation.

Many of the enzymes that drive the carbon shuttle in C_4 plants are also present in C_3 plants but are involved in other aspects of plant growth and development (Monson, 2003). Tissue-specific regulation of C_4 pathway enzymes appears to have been a crucial step in the evolution of C_4 photosynthesis (Hibberd and Quick, 2002). One aspect of the pathway that remains poorly understood is the genetic components regulating the alteration of leaf anatomy (Kellogg, 1999). The developmental and genetic issues can be addressed with all C_4 species, but the low number of model species used to date limits the generalization of the results.

Grasses have been the focus of much of the recent C_4 research. For example, human-directed improvement of C_3 grass crops, such as rice (*Oryza sativa*), barley (*Hordeum vulgare*), and wheat (*Triticum aestivum*), by introgression of C_4 characteristics is receiving particular attention (Hibberd et al., 2008). Understanding the historical causes of C_4 evolutionary and ecological success is another area of intense research activity (Cerling et al., 1997; Beerling and Osborne, 2006; Osborne and Beerling, 2006; Osborne, 2008). The ecological importance of grasses made this family a natural study system for investigating factors affecting the distribution and success of C_4 plants (Taub, 2000; Carmo-Silva et al., 2007; Cabido et al., 2008; Edwards and Still, 2008). For instance, it has recently been shown that the oldest C_4 origin in grasses is relatively young (approximately 30 million years old), and correlates with a marked decrease of atmospheric CO_2 concentration (Christin et al., 2008; Vicentini et al., 2008). Since atmospheric CO_2 concentration and air

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Table I. *Characteristics of the C_4 grass lineages*

No., Lineage number; *n*, number of C_4 species. PCK, Phospho*enol*pyruvate carboxykinase.

No.[a]	Name	Age Estimates[f]	*n*	C_3 Sister Group	C_4 Subtype(s)	Crops[m]	Habitat[n]
1[b]	*Stipagrostis*	15.1 (±4.6)–7.5 (±3.1) NA	50	*Sartidia*[a]	NADP-ME	–	Deserts and semideserts
2[b]	*Aristida*	28.8 (±5.2)–14.4 (±4.7) [44.4 (±7.5)–present]	290	*Sartidia*[a]	NADP-ME	–	Large ecological range
3[b]	Core Chloridoideae	32.0 (±4.4)–25.0 (±4.0) [37.6 (±6.6)–22.5 (±5.7)]	1,410	*Merxmuellera rangei*[a,g]	NAD-ME and PCK	Finger millet, teff	Large ecological range
4[b]	*Centropodia*	22.0 (±4.6)–11.3 (±5.5) NA	4	*M. rangei*[a,g]	NAD-ME	–	Dry open habitats (semideserts)
5[c]	*Eriachne*	11.5 (±3.6)–6.6 (±2.8) NA	40	*Isachne*[a,g,h]	NADP-ME	–	Warm open habitats (savannah)
6[b]	Arundinelleae	26.4 (±4.4)–7.9 (±3.4) [31.7 (±5.9)–present]	95	Centotheceae 2[a,g,h]	NADP-ME	–	Large ecological range
7[c,d]	*Panicum*/*Urochloa*/*Setaria* clade	18.5 (±3.7)–16.4 (±3.6) [15.9 (±3.7)–13.1 (±3.2)]	>530	C_3 *Neurachne*[a]	NADP-ME, NAD-ME, and PCK	Foxtail, pearl, and proso millets	Large ecological range
8[c]	*Neurachne munroi*	4.4 (±3.3)–present NA	1	*Neurachne tenuifolia*[a]	NADP-ME	–	Dry open habitats (steppes)
9[c]	*Echinochloa*	13.8 (±3.5)–4.4 (±2.8) [20.6 (±4.5)–2.6 (±1.3)]	30–40	*Parodiophyllochloa*[a,i]	NADP-ME	–	Warm open habitats
10[b]	*Alloteropsis*	15.3 (±3.5)–present NA	4–7	Forest shade clade[a,j]	NADP-ME and PCK	–	Warm open habitats (savannah)
11[c,d]	*Digitaria*	21.2 (±3.9)–8.1 (±3.4) [15.9 (±3.7)–5.4 (±2)]	220	*x* = 9 Paniceae[a]	NADP-ME	Fonio	Various warm open habitats
12[b]	Andropogoneae	21.9 (±3.9)–17.1 (±4.1) [24.3 (±4.9)–19.1 (±4.5)]	1,085	*x* = 10 Paniceae[a,k]	NADP-ME	Maize, sorghum, sugarcane	Large ecological range
13a[b]	*Paspalum* clade	14.1 (±3.4)–8.5 (±3.1) [11.7 (±3.1)–present]	>345	*Streptostachys asperifolia*[a,k]	NADP-ME	Kodo millet	Warm open habitats (savannah)
13b[c]	*Ophiochloa* clade	10.6 (±3.3)–2.8 (±1.9) [13.7 (±3.5)–4.4 (±2.1)]	115	*S. asperifolia*[a]	NADP-ME	–	Large ecological range
14[b]	*Anthaenantia*[e]	14.3 (±3.5)–present [15 (±3.7)–present]	1	*Steinchisma* clade[a,k]	NADP-ME	–	Warm open habitats (savannah)
15[c]	*Streptostachys ramosa*	15.5 (±3.5)–present [16.3 (±3.7)–present]	1	*Cyphonanthus*[l]	NADP-ME	–	Warm open habitats (savannah)
16[b]	*Panicum prionitis* clade	10.4 (±2.9)–6.3 (±2.7) [11.2 (±2.9)–present]	>5	*Arthropogon lanceolatus*[a,k]	NADP-ME	–	Warm open habitats (savannah)
17[c]	*Mesosetum* clade	12.3 (±3.2)–11.3 (±3.0) [14.8 (±3.5)–13.9 (±3.4)]	40	*Homolepis*[a,k]	NADP-ME		Warm open habitats (savannah)

[a]Christin et al. (2008). [b]Independent origin confirmed by PEPC analyses (Christin et al., 2007). [c]Independent origin based on putative species relationships only. [d]Phylogeny from Vicentini et al. (2008) found *Digitaria* and the main *x* = 9 Paniceae C_4 clade clustered together, suggesting a single C_4 origin. [e]Previously named *Leptocoryphium lanatum*. [f]Christin et al. (2008) and Vicentini et al. (2008) into square brackets, ages are given in millions of years. [g]Duvall et al. (2007). [h]Sánchez-Ken et al. (2007). [i]Morrone et al. (2008). [j]C_3 subspecies of *A. semialata* could represent a reversion from C_4 to C_3 (Ibrahim et al., 2009). [k]Vicentini et al. (2008). [l]Morrone et al. (2007). [m]Excluding fodders. [n]Watson and Dallwitz (1992).

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temperature both affect C_4 plant success, the current changes in global climate will potentially trigger important perturbations in major ecosystems, and could affect the performance of extensively cultivated tropical cereals. Therefore, a complete understanding of C_4 ecology and physiology is necessary for conservation biology and agriculture to face future climate changes (Sage and Kubien, 2003; Ainsworth et al., 2008).

Comparative analyses offer an attractive approach for both the study of genetic determinants of C_4 photosynthesis (Christin et al., 2007) and the identification of attributes associated with it (Edwards et al., 2007; Edwards and Still, 2008). Such an approach requires comparing several independent origins of C_4 plants to determine characteristics that are shared among them. Indeed, if two C_4 species inherited the C_4 trait from their common ancestor, they do not represent independent replicates. Ideally, comparative studies should consist of distinct C_4 clades, known to represent distinct origins of the C_4 pathway, as well as C_3 sister groups to each of the C_4 lineages. For this approach to work, species relationships have to be assessed by phylogenetic analyses, rendering the phylogenetic framework of systematic botany useful to evolutionary and physiological investigations.

C_4 EVOLUTIONARY LINEAGES IN GRASSES

The grass family is composed of approximately 10,000 species, of which about 45% are C_4 (Sage, 2004). Grass taxonomy recognizes between 12 and 13 main subfamilies but all C_4 grasses belong to the PACMAD clade (Fig. 1; Duvall et al., 2007; or PACCMAD, Sánchez-Ken et al., 2007). Both the distribution of C_4 grasses in distinct taxonomic groups and the high variability of their C_4 syndrome led to the inference of multiple origins of the C_4 pathway in this family (Sinha and Kellogg, 1996; Kellogg, 2001). Phylogenetic analyses of the subfamily Panicoideae further suggested that C_4 photosynthesis appeared several times independently, although a single appearance followed by multiple reversions could not be excluded (Giussani et al., 2001; Duvall et al., 2003; Vicentini et al., 2008). The ancestral state reconstructions adopted in these studies are strongly dependent on species sampling and rely on statistical methods whose assumptions can produce different results. In addition, the transition rate from C_3 to C_4 could also change through time (Vicentini et al., 2008), for instance as a function of atmospheric CO_2 levels (Christin et al., 2008) or after the acquisition of preadaptations to C_4 photosynthesis (Sage, 2001). Finally, inferences of characters that affect the rates of speciation or extinction can yield erroneous conclusions if not carefully considered (Goldberg and Igić, 2008).

Some studies have thus focused on the evolutionary dynamics of specific key enzymes involved in the C_4 pathway, in particular phospho*enol*pyruvate carboxylase (PEPC). The use of PEPC for the atmospheric CO_2 fixation is one of the rare characteristics common to all C_4 plants (Sinha and Kellogg, 1996; Sage, 2004), and its recruitment is an important step in the integration and optimization of C_4 biochemistry (Svensson et al., 2003) and can be considered as a critical event in the evolution into a C_4 plant. The presence of a Ser at position 780 of PEPC (numbered based on the maize sequence) is required for C_4 function (Svensson et al., 2003) and was accompanied by many other recurrent adaptive amino acid changes (Christin et al., 2007) that left reliable C_4-specific genetic signatures. Because changes along a DNA sequence are amenable to statistical modeling, they can easily be traced on a PEPC phylogenetic tree. This technique was used to identify the grass lineages that likely evolved the C_4 trait independently (Table I; Christin et al., 2007, 2008).

C_4 MODEL SPECIES IN GRASSES

The grasses contain few examples of closely related C_3/C_4 pairs, and those that exist are not easily accessible. *Alloteropsis semialata* contains a C_3 and a C_4 subspecies, which are closely related (Ibrahim et al., 2009) but differ in chromosome number (Liebenberg and Fossey, 2001) and so are presumably intersterile. A recent phylogenetic study suggested that C_3 subspecies of *A. semialata* could represent an evolutionary reversion from C_4 to C_3 photosynthesis (Ibrahim et al., 2009). The genus *Neurachne* includes both C_3 and C_4 species (Moore and Edwards, 1989); these are native to Australia and grow in relatively inaccessible parts of the continent and have not, to our knowledge, been cultivated. The C_3/C_4 intermediate *Steinchisma hians* (formerly *Panicum milioides*) is sister to a group of C_3 species, and has been crossed with them (Brown et al., 1985). *Steinchisma* as currently circumscribed is mainly South American.

Historically much of the work on C_4 grasses focused on the genus *Panicum* because it appeared to have species with all possible photosynthetic pathways. Unfortunately, this genus was an assemblage of unrelated species (Aliscioni et al., 2003) whose taxonomy is being completely redefined (Morrone et al., 2007, 2008; Sede et al., 2008). The name *Panicum* should be restricted to a set of species that are all C_4 with the subtype using the NAD-malic enzyme (NAD-ME), including switchgrass (*Panicum virgatum*). C_3 species of *Panicum* are not closely related to true *Panicum* (Aliscioni et al., 2003).

Future C_4 research should consider additional C_4 species systems since including other independent lineages would increase the power of comparative analyses. In particular, *Aristida* and *Stipagrostis*, as well as the subfamily Chloridoideae, represent interesting C_4 lineages. These groups are ecologically important (Table I) and strongly differ from the Panicoideae C_4 species in terms of ecological attributes, such as aridity tolerance (Taub, 2000; Sato and Kubota, 2004; Carmo-Silva et al., 2007). They are species rich and widely

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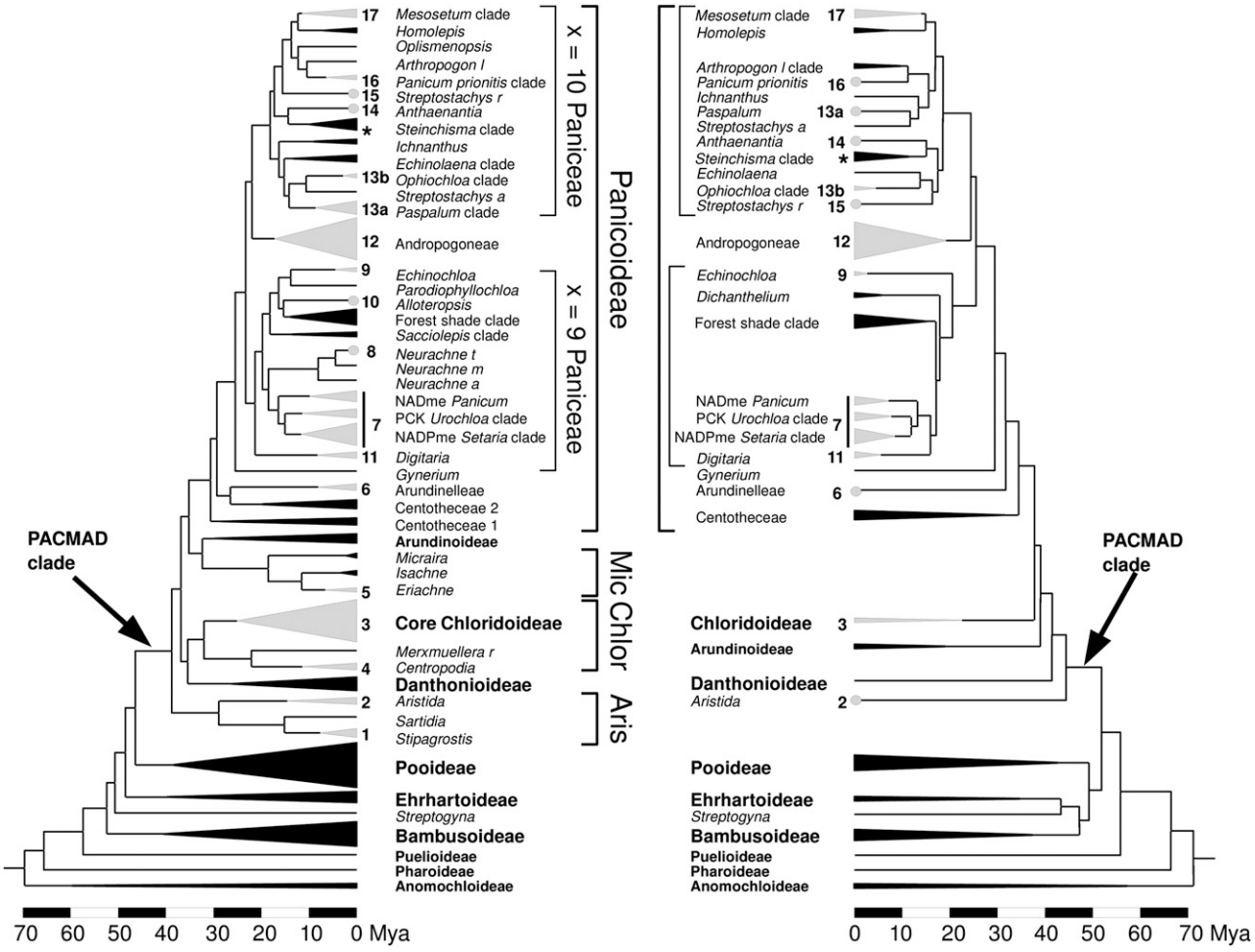

Figure 1. Calibrated phylogenetic trees of the grass family. Phylogenetic trees are from independent studies by Christin et al. (2008; on the left; based on plastid markers) and Vicentini et al. (2008; on the right; based on one plastid and one nuclear marker). Branch lengths are proportional to elapsed time, in million years (Mya). All clades containing only C_3 species are compressed (in black). Similarly, homogeneously C_4 lineages are also compressed but in gray. C_4 lineages represented by a single species are highlighted by a gray circle at the tip. C_4 lineages are numbered according to Christin et al. (2008). Clade names and subfamilies are indicated between the two topologies. Asterisks indicate the position of the C_3/C_4 intermediate species *S. hians*. Mic, Micrairoideae; Chlor, Chloridoideae; Aris, Aristidoideae; PACMAD clade, subfamilies Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae. x = 9 and x = 10 Paniceae identify two distinct groups of this tribe that differ according to their basic chromosome number (9 and 10, respectively; Giussani et al., 2001).

distributed, facilitating sampling for more detailed study.

INTEGRATING PHYSIOLOGICAL STUDIES IN A PHYLOGENETIC CONTEXT

Understanding C_4-specific growth, survival, and reproductive success, as well as the environmental conditions that influence these traits, is of prime ecological, agricultural, and evolutionary importance. Assessment of plant physiological traits, such as photosynthetic activity and efficiency, is time consuming, especially when performed under a range of environmental conditions. Therefore, physiological studies typically consider only a limited number of species. Unfortunately, due to the strong variations of the C_4 pathway (Sinha and Kellogg, 1996), all C_4 plants are far from being equivalent. Species sampling for physiological investigations is crucial to ensure the generalization of conclusions. As noted above, taxa that inherited their C_4 trait from a common ancestor do not represent independent replicates. Their common ancestry can potentially lead to spurious correlations, which in turn can entangle characteristics due to the C_4 trait and those resulting from a close phylogenetic relationship (Taub, 2000). A sound phylogenetic framework showed that a low carbonic anhydrase activity, previously attributed to C_4 grasses (Gillon and Yakir, 2001), characterizes the whole PACMAD clade

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and is not linked to the C_4 trait (Edwards et al., 2007). Thanks to its highly convergent nature, the C_4 trait is present in numerous natural replicates. Species sampling for C_4 physiological studies can take advantage of this by comparing species from independent C_4 lineages, as well as each C_4 clade with its C_3 sister group (Table I). Therefore, species relationships deduced from molecular markers should serve as a guide for species sampling.

As a C_4 study system, the grass family allows combining physiological, ecological, genomic, and evolutionary approaches, which are all necessary for a complete understanding of C_4 photosynthesis. Integration of the wide knowledge we are gaining about C_4 grasses to reach a full picture requires incorporation of evolutionary history by using phylogenetic information. Important efforts have led to a reasonably well-resolved phylogenetic tree for the grass family (e.g. Grass Phylogeny Working Group, 2001; Aliscioni et al., 2003; Duvall et al., 2007; Christin et al., 2008; Vicentini et al., 2008) but conflicts between plastid and nuclear markers (Fig. 1) still need to be resolved. Recent analyses of C_4 genes have identified grass lineages that evolved the C_4 pathway independently (Christin et al., 2007, 2008). These correspond to more than 15 independent replicates (Fig. 1), enabling wide-scale comparative studies to sort general attributes of C_4 plants as well as particular ones. By taking advantage of the convergent nature of C_4 photosynthesis, multidisciplinary studies in the grasses could bring a complete view of the selective pressures and genetic mechanisms responsible for the evolution of C_4 photosynthesis and the factors that control the current distribution and success of C_4 plants. C_4 photosynthesis in grasses could become a model of macroevolution process when completely elucidated, from the selective pressures to the genetic mechanisms that led to its appearances.

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