07

VIEWPOINT:
MULTIPLE-HARVEST SORGHUMS TOWARD IMPROVED FOOD SECURITY

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ABSTRACT

Perennial crops offer an avenue by which marginal lands might be brought into sustainable production while arresting or even reversing losses of ecological capital. The natural adaptation of sorghum to its native Sahelian region makes it essential to some of the poorest and most food-insecure

human populations, dependent upon some of the world's most degraded soils. Increased demand for limited fresh water, together with rising global temperature and aridity, suggest that the inherent drought tolerance of sorghum will be of growing importance. With some genotypes already known to be suitable for ratoon crop production, and with two sources of perenniality, the *Sorghum* genus has become a model for dissecting the molecular control of ratooning and perenniality. We are pursuing two broad approaches to investigate the efficacy of ratoon/perennial sorghum production and to develop genotypes suitable for these production systems. First, the identification of diploid progeny from crosses between *S. bicolor* and *S. propinquum* offers a starting point for investigation of these traits in conventional sorghums, by crossing to elite sorghums and evaluation of resulting progeny (potentially also employing DNA-marker aided selection to increase the frequency of genotypes that contain known Quantitative trait loci (QTLs) for ratooning and/or perenniality-related traits). Second, crosses between tetraploid forms of *S. bicolor* and their naturally-tetraploid relative *S. halepense*, may offer the possibility to benefit from many traits that differentiate this widespread weedy/invasive plant from its progenitors. While initial efforts have focused on grain production, substantial forage/biomass is also produced by ratoon/perennial sorghums and in principle there appears to be no insurmountable obstacle to also developing perennial 'sweet sorghums' suitable for sugar production. Perennial cropping systems may be especially attractive to smallholder agriculture (particularly benefitting women farmers), in which poor seedling emergence and stand establishment can lead to crop failure and costs of seed, energy, and equipment are limiting factors. However, the benefits of perennials may also apply to intensive agriculture, especially in situations where erosion, nutrient leaching, and declining organic matter levels occur. A fringe benefit of increased knowledge of perenniality may be new tools and approaches by which to control widespread agricultural weeds. Comparative data from sorghum and rice suggest that findings with regard to perenniality may extrapolate broadly to a wide range of taxa, accelerating progress in implementing new production systems (or weed control systems) in other genera.

Keywords: ratoon crop, perennial, *Sorghum propinquum, Sorghum halepense*

INTRODUCTION TO SORGHUM

About 20 million years ago , a population of 20-chromosome grassy plants had a singularly bright future. An early branch diverged from this population ~10-15 million years ago, experiencing genome-wide duplication and genome size expansion accompanied by chromosome number reduction leading to the modern maize genome (Gaut, Clark, *et al.* 1997; Swigonova, Lai, *et al.* 2004). About 8-9 million years ago (Jannoo *et al.* 2007; Sobral *et al.*

1994) another branch diverged, also experiencing genome-wide duplication and leading to the modern genomes of Saccharum. It was perhaps the most important biomass/biofuels crop worldwide, and its close relative *Miscanthus*, which is among the highest-yielding herbaceous temperate biomass crops known (Heaton, Dohleman, et al. 2008). A third branch spawned lineages with a wide range of fates (Spangler *et al.* 1999). One being domesticated into cultivated sorghum, and another experiencing polyploidy to form one of the world's most aggressive weeds (*Sorghum halepense*).

Among these important grasses, all members of the Andropogoneae clade, the genome of *Sorghum bicolor* L. Moench (sorghum) is of central importance both as a botanical model and as a major crop. Sorghum is the most drought-resistant of the world's top five cereal crops, and an important dual-purpose (grain + straw) crop. Its drought resistance is essential in the United States Southern Plains that often receive too little rain for other grains. And in arid countries of northeast and West Africa, sorghum contributes as much as 26-39 percent of calories in the human diet (www.fao.org). Nonetheless, sorghum improvement lags that of maize, wheat and rice, each of which have more than doubled in worldwide average yield in the last 38 years. Sorghum yields only gained 51 percent (www.fao.org). Increased demand for limited fresh water, together with rising global temperature and aridity, suggest that sorghum will be of growing importance.

While grain is of special importance, the value of other sorghum products should not be underestimated. Sweet sorghum for stock feed (indirectly sustaining protein production) is a large and growing market, and the possibility of production systems based on perenniality combined with low/no-till farming are very attractive. Further, bioenergy sorghums are a promising source of cellulosic ethanol (Rooney *et al.* 2007). They are even better suited to tropical regions (such as much of Africa) than temperate regions, because a more continuous supply of feedstock is possible in the tropics.

The sequenced ~740 Mb sorghum genome (Paterson *et al.* 2009) is a logical complement to that of *Oryza* (rice) for grass functional genomics. It is a representative of tropical grasses in which biochemical and morphological specializations ('C4' photosynthesis) improve carbon assimilation at high temperatures. The sorghum karyotype is suggested by parsimony to have been shared by the Andropogoneae common ancestor, with only ~3 percent differential sorghum-rice gene loss and less sorghum-rice structural rearrangement in 50 million years than sorghum-maize rearrangement in about 15 million years (Bowers *et al.* 2003). With 70 million years of 'abstinence' from genome duplication, functions of *S. bicolor* genes also may still resemble those of the common cereal ancestor.

Sorghum evolution and improvement have yielded a remarkable diversity of morphologies. Differences in inflorescence and seed morphology are used to classify *S. bicolor* races. Also they have been embellished by divergent selection applied to forms cultivated for purposes ranging from 'broomcorn' to the compact inflorescences and large seed of grain types. Divergent selection

has also affected plant stature, with stalks of up to 6 metres being a key building material in Africa, but less than 1 metre favoured for mechanized harvest. Selection for carbohydrate rich seed/grain has increased harvest index (carbon partition to grain) in grain types, while selection for sugar-rich stalks and/or total biomass has reduced seed size and output in others to an extreme exemplified by *S. propinquum* (Figure 1). Human selection has been superimposed on rich natural variation in plant architecture and carbon allocation, for example ranging from one to 100+ tillers per crown, and branching along a tiller ranging from none to secondary, tertiary, and even quaternary. Its morphological and biochemical diversity makes sorghum the only crop that is compatible with fuel production from each of three routes, including starch (seed), cellulose (stalks), and sugar ('sweet' sorghums have sugar yields comparable to those of sugarcane).

FIGURE 1. COMPARISON OF ANNUAL *SORGHUM BICOLOR* AND PERENNIAL *S. PROPINQUUM*

(A) Crowns – including extensive rhizomes of *S. propinquum*.
(B) Seeds – those of *S. bicolor* grain types are large and carbohydrate rich, while those of *S. propinquum* are very small.

FIGURE 2. (A) SAHEL PRECIPITATION, 1900-2007; (B) SAHEL CROPPING AREA, 1960-2010
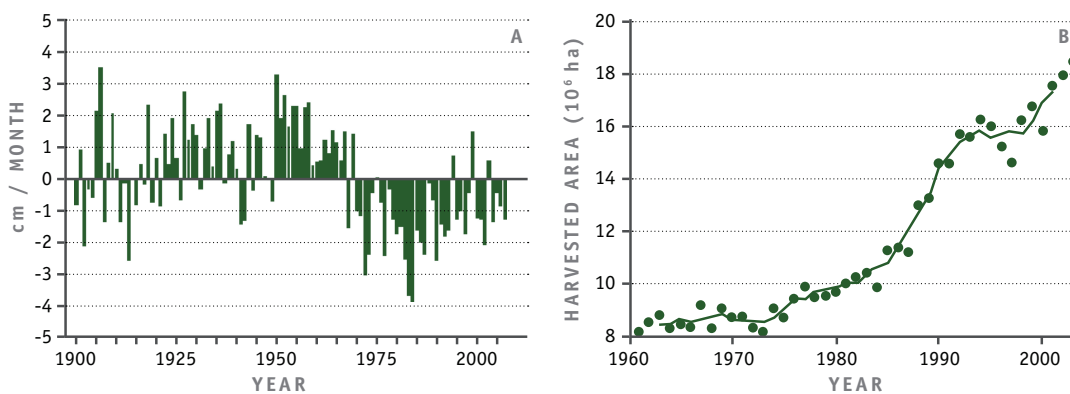
A: modified from Haywood *et al.,* 2013
B: *source*: Kandji *et al.,* 2006

Rich resources are in place to link sorghum phenotypic diversity to its molecular basis. More than 30 sorghum genomes and 40 transcriptomes, sampling all botanical races of cultivated sorghum, wild *S. bicolor*, and appropriate outgroups, have now been sequenced by the United States Department of Energy Joint Genome Institute. GBS has been performed on several reference collections (Morris *et al.* 2013), including two developed by the International Crops Research Institute for the Semi-Arid-Tropics (ICRISAT) that have been focal points of phenotyping for morphological variation, yield components, and drought responses (Upadhyaya *et al.* 2009).

OVERVIEW OF RESEARCH ON PERENNIALITY IN SORGHUM

The natural adaptation of sorghum to its native Sahelian region makes it essential to some of the poorest and most food-insecure human populations and dependent upon some of the world's most degraded soils. Years of above average rainfall were followed by drought in the Sahel starting in the late 1960s (Figure 2A). A dramatic increase in the Sahelian area devoted to crops began at that time, with falling yields necessitating greater effort to cultivate ever-more fragile lands to feed growing populations (Figure 2B). These considerations are thought to contribute greatly to the fact that the Sahel now includes some of the most degraded lands on the planet.

Recently, the potential benefits of perennial grain crops have gained wider recognition (Glover *et al.* 2010). Perennial crops are essential to bringing marginal lands into sustainable production (Cox *et al.* 2002; Scheinost, 2001; Wagoner, 1990), maximizing ecosystem productivity (Field, 2001) and minimizing losses of topsoil (Pimentel *et al.* 1995), water, and nutrients. Perennial cover is >50 times more effective than annual crops in maintaining topsoil (Gantzer *et al.* 1990), and 30-50 times more effective than annuals at preventing nitrogen losses (Randall and Mulla, 2001). Perennial cropping systems (Cox *et al.* 2006; Jackson and Jackson, 1999; Piper, 1998) may be especially attractive to smallholder agriculture, in which poor seedling emergence and stand establishment can lead to crop failure, and costs of seed, energy, and equipment are limiting factors. It also may benefit mechanized agriculture in situations where erosion, nitrate (and other nutrient) leaching, and declining organic matter levels occur.

The *Sorghum* genus has become a model for dissecting the molecular control of ratooning and perenniality largely due to the availability of the diploid perennial *S. propinquum* which is abundantly tillering and has rhizomes that contribute to perenniality (Hu *et al.* 2003; Jang *et al.* 2006; Jang *et al.* 2008; Paterson *et al.* 1995). Tillers and rhizomes both develop from axillary buds at the lowermost nodes of the erect leafy shoot of the plant, with acropetally increasing tendency to develop into tillers (Gizmawy *et al.* 1985). There is appreciable correspondence in the locations of QTLs determining tillering and rhizomatousness (Paterson *et al.* 1995),

thought to be related to the number of buds available. The commitment of a bud to rhizome development, tiller development, or quiescence is genetically-determined (Paterson *et al.* 1995), and is associated with marked differences in gene expression (Jang *et al.* 2006). Finally, a high level of correspondence of rhizome QTLs between sorghum and rice (Hu *et al.* 2003), thought to have diverged from common ancestry about 50 million years ago, suggests that key genes conferring perenniality-related traits may be shared by many Poaceae cereals. In other words, fundamental information about these traits in one cereal may extrapolate broadly to many other cereals.

While no members of the cultivated species, *Sorghum bicolor,* are rhizomatous, there is variation among cultivars for ratoon crop productivity (Duncan *et al.* 1980; Duncan and Moss, 1987), and close relatives sugarcane and *Miscanthus* are usually grown as ratoon crops. Ratooning (regrowth) is a complex trait, showing quantitative inheritance (Duncan *et al.* 1980). Likewise, QTL mapping in an F2 population of a cross between an elite grain sorghum inbred BTx623 (later used for the reference sequence) and *S. propinquum*, showed regrowth to be closely related to both rhizomatousness and tillering, but was only able to account for 14-30 percent of phenotypic variance in these traits (Paterson *et al.* 1995). A recombinant inbred line population for this cross (Kong *et al.* 2013), now provides for replicated genetic analysis of productivity, and includes genotypes with a range of 'degrees' of ratoon cropping from near-zero to fully perennial. The recombinant inbred line population has been genetically mapped with both the population itself and map publicly available (Kong *et al.* 2013), and with three years of phenotyping for tillering, rhizomatousness, and basic metrics related to grain production (yield components) presently being analysed for peer-reviewed publication.

A relative of sorghum, *S. halepense*, is a wild perennial polyploid resulting from natural hybridization between *S. bicolor* (2n = 20) and *S. propinquum* (2n = 20), a wild perennial diploid native to Southeast Asia and estimated to have diverged from *S. bicolor* ~1-2 million years ago. *S. halepense* finds occasional use as forage and even food (seed/flour), but is most noted as one of the world's most noxious weeds, having spread from its west Asian centre of diversity across much of Asia, Africa, Europe, North and South America, and Australia. Its establishment in the United States of America is probably typical of its spread to other continents, including intentional introduction as a prospective forage and/or unintentional introduction as a contaminant of sorghum seedlots (McWhorter, 1971). However, while *S. bicolor* has remained largely confined to cultivation, *S. halepense* has readily naturalized – revealing genetic potential for adaptation that goes well beyond that of sorghum. *S. halepense* crosses readily with *S. bicolor* (Arriola and Ellstrand, 1996) –more than 90 percent of plants in naturalized *S. halepense* populations growing adjacent to long-term sorghum production fields contain alleles introgressed from sorghum (Morrell *et al.* 2005).

RESEARCH AGENDA

We are pursuing two broad approaches to investigate the efficacy of ratoon/perennial sorghum production, and to develop genotypes suitable for these production systems.

First, the identification of diploid progeny from crosses between *S. bicolor* and *S. propinquum* (Kong *et al.* 2013) offers a starting point for investigation of these traits in conventional sorghums, by crossing to elite sorghums and evaluation of resulting progeny (potentially also employing DNA-marker aided selection to increase the frequency of genotypes that contain known QTLs for ratooning and/or perenniality-related traits).

Second, crosses between tetraploid forms of *S. bicolor* and their naturally-tetraploid relative *S. halepense*, may offer the possibility to benefit from many traits that differentiate this widespread plant from its progenitors. While *S. halepense* is generally under selection for weediness-related attributes that are undesirable in annual row-crop production, some selection pressures may favour *S. halepense* alleles that are of potential value in sorghum, for example conferring rapid vegetative development and early flowering. An attractive but unproven hypothesis, which the ability of *S. halepense* to naturalize in a much wider range of environments than sorghum is cultivated may have been accompanied by selection for alleles associated with valuable attributes such as cold tolerance (for example in the northern United States of America and Russia), drought tolerance (Africa, Arabia, United States of America in the southwest), disease resistance (many) or other traits. Moreover, a host of data now show that unpredictable, presumably epistatic, effects of allele introgressions from seemingly undesirable sources can confer valuable traits to crops (Bernacchi *et al.* 1998a; Bernacchi *et al.* 1998b; Chee *et al.* 2005; Eshed and Zamir, 1995; Fridman *et al.* 2004; Fulton *et al.* 1997; Gur and Zamir, 2004; Schauer *et al.* 2006; Tanksley *et al.* 1996; Xiao *et al.* 1996; Zamir, 2001).

At present, we are phenotyping and analysing F2 populations, their F3 progeny and the progeny of backcrosses to *S. bicolor* for perenniality, plant architecture, yield components and domestication traits. While we find some of these tetraploids to have fecundity comparable to diploid sorghums and are potentially directly usable, another attractive route for their utilization would be to extract diploids with selected properties of *S. halepense* either by backcrossing or by the development of haploids.

IMPLICATIONS

The benefits of perenniality as a cropping system are receiving renewed interest. Perennial plants have four advantages over annuals: a longer growing season; better access to water and nutrients; more conservative use of nutrients and better adaptation to marginal lands (Cox *et al.* 2006). The first three of those characteristics are expressed on all landscapes, from prime farmland to poor or sloping soils unsuitable for annual cropping. The expansion of agriculture

to provide plant biomass for production of fuels or chemical feedstocks with little or no carbon release (Fargione *et al.* 2008) will require greater utilization of marginal land (Tilman *et al.* 2009), maximizing ecosystem productivity (Field, 2001) and minimizing losses of topsoil (Pimentel *et al.* 1995), water, and nutrients.

The benefits of perenniality apply to food, as well as biomass, crops. Annual food crops have dominated the agricultural landscape since the time of the earliest farmers. In the last few decades alone, one-third of the planet's arable land has been lost to soil erosion (Pimentel *et al.* 1995). No-till production of annual crops, designed to control soil loss, has so far required increased use of herbicides. Direct-seeded annual cropping systems produce as high or higher nitrate emissions as tillage systems (Mummey *et al.* 1998). 'Natural systems agriculture', based on developing a "domestic prairie" with herbaceous, perennial grain-producing crops grown in polyculture (Jackson and Jackson, 1999; Piper, 1998), has been proposed as a means to produce food on otherwise marginal lands while arresting or even reversing losses of ecological capital.

In smallholder production systems that are widespread in regions where sorghum is a staple in the human diet, conservation-agriculture approaches may particularly benefit women farmers, by reducing dependence on duties generally performed by men (ploughing) and mitigating the need for duties performed by women and children (uprooting grass, de-stumping) (Milder *et al.* 2011). Moreover, women frequently are given marginal fields that should be left fallow (Kevane, 2011), for example those which will be the greatest beneficiaries of multi-cropping approaches. Male farmers, with access to generally higher levels of land, labour, and cash, have a somewhat greater tendency to grow cash crops (Gilbert *et al.* 2005) – further indicating that early adopters of reduced-cost, reduced-labour multi-cropping sorghum production systems may tend to be female. A reduced requirement for seed selection in multi-cropping production systems (which propagate vegetatively), may also reduce male investment as seed selection is largely male-dominated (Freeman and Boateng, 2012).

Perenniality plays two contrasting roles in agriculture, being: (i) a valuable asset in establishment and persistence of dense, productive stands of plants suitable for multiple harvests, and (ii) an essential component of "weediness" of many of our most noxious weeds. Better understanding of the biology of *S. halepense* itself, one of the most noxious weeds affecting world agriculture (Holm *et al.* 1977), may also be of high value. *S. halepense* is a major contaminant in sorghum seed production, an alternate host and means of over-wintering for pests and pathogens of both monocot and dicot crops. It is also a highly-effective competitor for sunlight and other resources, causing reductions in economic yield of 45 percent or greater in crops as diverse as monocots such as sugarcane (Millhollen, 1970) and dicots such as soybean (McWhorter and Hartwig, 1972). The first United States federal appropriation for weed control research targeted Johnsongrass (House Bill #121, 1900), yet it remains largely unchecked today.

The *S. halepense* problem constrains improvement of sorghum through biotechnology. *S. halepense* is a particular problem in and around sorghum fields because no known herbicide

can selectively eliminate it without damaging the sorghum. Transformation of sorghum was first accomplished in 1993 (Casas *et al.* 1993), and introduction of transgenes for resistance to insects, diseases, or herbicides could have a major impact on sorghum productivity. However, the risk of transgene escape constrains the ability of regulatory agencies to approve the release of sorghum cultivars with transgenes that could enhance agricultural productivity.

Better understanding of the biology of *S. halepense* and associated new functional genomics tools might aid greatly in identification of genes, regulatory elements, and biochemical functions that are important to its weediness, particularly its rhizomes, but dispensable to other plant processes (Jang *et al.* 2006). Identification of such genes would provide the foundation to search for plant growth regulators that specifically target rhizomes, perhaps providing for control of rhizomatous weeds even in closely related crops such as *S. halepense* in sorghum. Moreover, better understanding of rhizome development may also benefit development of plant genotypes optimal for biomass/biofeedstock production on marginal lands, as well as improvement of a host of forage and turf grasses.

Our demonstration that most QTLs responsible for rhizomatousness in *Sorghum* and *Oryza* respectively, map to corresponding locations (Hu *et al.* 2003), suggests that *information about rhizomatousness from a few models (that are also major crops) may extrapolate broadly to a wide range of taxa*. Successes in clarifying the genetics of perenniality in this genus, may accelerate progress in implementing new production systems in other genera, and also to controlling a wide range of related agricultural weeds.

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