Sorghum Biology

Extract with Executive and Extended Summary, non-active content list and literature list related to the book manuscript

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Fig. 1 Oklahoma Farm Bureau, Galleries Grain Sorghum
http://www.okfarmbureau.org/press_pass/galleries/grainSorghum/Sorghum2.jpg

Fig. 2 Schools in West Africa: Students threshing and winnowing sorghum earlier harvested from the school farm. http://wassumbee.blogspot.com/2006/01/schools-in-west-africa-1.html

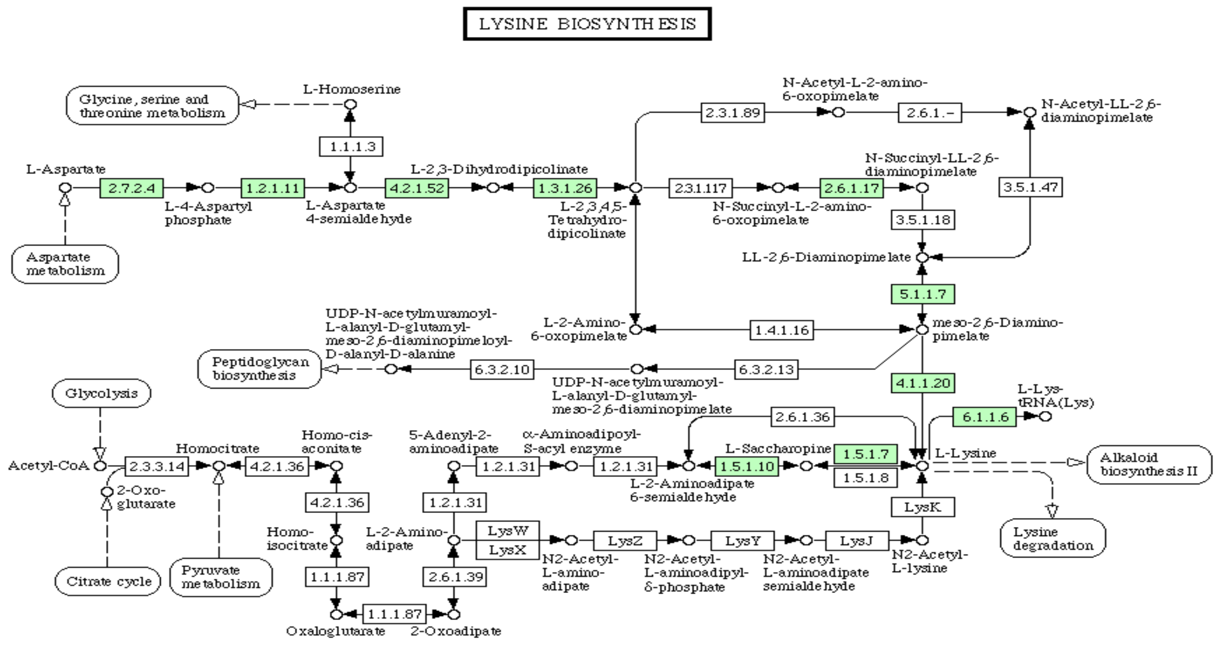

Fig. 3 Lysine Biosynthesis in Sorghum bicolor: GenomeNet Database Service, from KEGG: Kyoto Encyclopedia of Genes and Genomes http://www.genome.jp/dbget-bin/get_pathway?org_name=esbi&mapno=00300

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1. Preface

This text, now grown over some years has its origin in a short report on general Sorghum biology aspects on biodiversity during a brief participation in the Super-Sorghum Project of Africa Harvest in 2005-2006.
The study is in its present scope is restricted to aspects of the *biology* of this fascinating genus, it is dealing with agronomic aspects only in context with its biology in a broad sense and it is not dealing with the Super-Sorghum Project, but will give some basic information on Sorghum in Africa and breeding, specifically also on biofortification activities worldwide.
This work has been encouraged through a contribution of Africa Harvest (for the short 60pp biodiversity report) and with support of the Delft University of Technology, in the framework of a guest professorship 2006-2007.

It is written in a review style, as a result of an extensive literature review with some efficient electronic instruments such as the Web of Science (Knowledge) and the Regensburg Consortium journal retrieval system, the citations are kept in databases built with Endnote Version X2, the document has been written in Word from Office professional for Vista Business.

Some 15000 publications have been screened, over 6000 citations have been transferred to the Sorghum database, the majority on a basis of reading the summary, some 400 papers are inserted in the database with the full original text as a link.

Screening and compiling and the selecting the citations are done by the author alone and he takes full responsibility for the correctness and interpretation of the texts and possible unintentional omissions. It should be mentioned explicitly that this is a compilation text and often authors are fully cited from their abstracts, in order to avoid bias and to give credit to the authors opinion of the original papers. There are only a few cases where the author did not agree with the conclusions of publications in the field of gene flow, which is then explicitly mentioned. The author refrained from making taxonomic decisions in the sense to unify all names under a new system. This is especially blatant with the treatment of two *Sorghum* races *S. arundinaceum* and *S. verticilliflorum*, where various authors follow different taxonomic concepts: Whereas some follow the opinion that both races intergrade so heavily, that distinction is impossible (De Wet et al., 1970), others like (Aldrich & Doebley, 1992; Deu et al., 1995) insist on grounds of genomic analysis that in most populations the two races can be separated properly.

One important source needs to be mentioned explicitly: it's the monograph on Sorghum written by H. Doggett and published in its second edition in 1988, it cannot be replaced by this report in its broad scope. Nevertheless, this report also demonstrates that science has made a lot of progress in the years after 1988, but still - we all stand on the shoulders of this great author. The other major source is the monograph of (Smith & Frederickson, 2000), dealing primarily with agronomic aspects.

The manuscript has been developed over 3 years until September 5, 2007, with a major revision from September 2009 and January 2010.

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2a. Executive Summary

2a.1. General Remarks

To designate *Sorghum* as a "lost" crop, on the face of it, seems like a gross mistake. After all, the plant is Africa's contribution to the world's top crops. It belongs to the elite handful of plants that collectively provide more than 85 percent of all human energy. Globally, it produces approximately 70 million metric tons of grain from about 50 million hectares of land. Today, it is the dietary staple of more than 500 million people in more than 30 countries, let alone in Africa it is an important crop for 300 million people. Only rice, wheat, maize, and potatoes surpass it in its importance for feeding the human race.

More than 11’000 references are listed in the Web of Science, and alone in the last three years 2007-2009 there are nearly a 1000 references registered. The reference figures for wheat: 67’000, rice 48’000, maize 33’000 are strikingly higher of course.

For all that, *Sorghum* now receives merely a fraction of the attention it warrants and produces merely a fraction of what it could. Not only is it inadequately supported for the world's fifth major crop, it is under-estimated considering its vast and untapped potential. Viewed in this light it is indeed a "lost crop" – up to now.

But this situation may not continue much longer. A growing number of researchers in governmental institutions and companies already see that a new and enlightened *Sorghum* era is just around the corner. Accorded research support at a level comparable to that devoted worldwide to wheat or rice or maize, *Sorghum* could contribute a great deal more to food supplies than it does at present. And it would contribute most to those regions and peoples in greatest need. Indeed, if the twentieth century has been the century of wheat, rice, and maize, the twenty-first century could become the century of *Sorghum*. The Bill and Melinda Gates Foundation, in close collaboration with Africa Harvest will make it possible to foster biofortification of this wonderful crop, a crop, which has already proven its big potential for subsistence and commercial farming.

The book presented helps to synthesize the literature and achievements in the research on the biology of *Sorghum* in the wake of the 21st century. May it be of help for future research and development of *Sorghum.*

2a.2. Taxonomy

Sorghum is genetically closely related to other well known crop grasses such as maize, sugar cane and rice, it is obvious from this that transformation among those genera will greatly enhance the agronomic characteristics of those crops. Sorghum bicolor comprise a still not well defined number of cultivars including many landraces and interbreeding wild relatives.

Three species of Sorghum are recognized, two are rhizomatous taxa: S. halepense and S. propinquum, and the large and complex S. bicolor to include all annual wild, weedy and cultivated taxa. The latest interpretation about true Sorghums: They originate from Africa and Asia with 2n=20 and 40 chromosomes, and the known progenitor of cultivated S. bicolor is a Sorghum verticilliflorum (arundinaceum) of unknown origin and makeup, most probably of polyploid nature.

2a.3. Evolutionary dynamics and Landraces of Sorghum bicolor

Sorghum bicolor has been cultivated since at least 8000 years, the origins are not yet definitely clarified, but the region between Sudan and Ethiopia seems to harbour many ancestral landraces, although it has to be admitted that early migration between South Africa, Equatorial Africa and the dryer regions of Subsaharian Africa have blurred a clear picture. Strict farming traditions and feeding habits, often related to language and tribes, and an important percentage of inbreeding traits, combined with strictly followed agricultural traditions have maintained clearcut delimitations of landraces over centuries, despite of a proven gene flow from cultivars to wild relatives in Africa.
There are considerable differences in reproduction biology, biogeography and environmental adaptation for many of the landraces. The Africa Harvest project should concentrate on inbreeding Sorghum races in order to reduce considerably gene flow.
According to some authors, the guinea-race is a predominantly inbreeding, diploid cereal crop, but more research is needed.

2a.4. Sorghum Breeding Activities

Encouraged by the results from natural hybridization and selection, attempts at deliberate crossing were made, wherein it was found that crosses between divergent cultivars exhibited high levels of heterosis. The discovery of the cytoplasmic genetic male sterility based on the milo-kafir system was a milestone in Sorghum breeding and research. It is widely used in the commercial exploitation of heterosis. Today, more than 30% of the Sorghum area is under hybrids (in the USA!), which have yields about twice that of any local cultivar.
Species outside the Eu-Sorghum section are sources of important genes for Sorghum improvement, including those for insect and disease resistance, but these have not been used because of the failure of these species to cross with Sorghum.
Most breeding programs consistently select for tolerance to abiotic stresses (such as drought and low temperatures) and biotic stresses (such as Sorghum midge, grain mold, anthracnose, charcoal rot and Striga and bird resistance).
Finally, the integration of molecular genetic technology supports Sorghum improvement by providing a genetic basis for many important traits and through marker-assisted selection.
Biofortification has recently become part of many breeding research and development programmes: Preliminary results suggest that a feasible chain solution consists of breeding for high Fe and moderate phytic acid contents and using soil organic amendments and P fertilization to increase yields but that this needs to be followed by improved food processing to remove phytic acid. Further research on timing of application of phosphate, Fe fertilizer and soil organic amendments is needed to improve phytic acid-Fe molar ratios in the grain. Research on the exact distribution of Fe, phosphate, phytic acid and tannins within the Sorghum grain is needed to enable the development of more effective combinations of food processing methods aiming for more favorable phytic acid-Fe molar ratios in Sorghum-based food.
In another joint project between the university of Ouagadougou and the agricultural research center of Wageningen Sorghum will be better adapted to hard environments and enhancement of starch levels (amylose and amylopectin) and starch depolymerizing enzymes are breeding targets.
Biofortification of Sorghum is achieved in the same partnership by selection of suitable traits, taking into account a holistic implementation approach. Current research activities focus on identifying varieties meeting specific agricultural and food requirements from the great biodiversity of Sorghums to insure food security.

An important effort is now made with the biofortification for a higher lysine content of Sorghum cultivars within the framework of a Africa Harvest research and development project financed mainly by the Bill and Melinda Gates Project (www.SuperSorghum.org), again with the collaboration of ICRISAT.
There is still a lot of work to be done, in all domains of research and development, the maps and statistics on Sorghum yields show this clearly. Yield gain has been achieved in many developed countries on a large scale, in Africa only in Egypt.

2a.5. Gene flow in Sorghum and related species

Gene flow from Sorghum cultivars to wild and feral species is well documented in the United States. In Africa and elsewhere experimental studies are still needed, but gene flow is well documented indirectly with numerous genetic screenings.
Basically, one should distinguish between the high potential of crossability and the low hybridization rate in the reality of agricultural practice.
Situation in the USA: Sorghum halepense is a proven conduit between Sorghum cultivars and the wild and feral populations, gene flow has been studied in field experiments. Although the rates are very low compared to maize as an example, there seems to be persistent establishment possible on a long term, and also seed exchange might play a role.
In Africa, the situation is very different: up to now there are only indirect hints that there is gene flow from wild Sorghums to cultivated ones, and there are only a few reports of spontaneous hybrids between African wild and cultivated Sorghums, which could be due to lack of precise scientific knowledge. Outcrossing rates have been detected, specifically bound to local situations and specific landraces from minimal amounts to 15-nearly 30%. Still, feral complexes of wild and cultivated Sorghums seem to be a reality to such a degree that often harvest is hampered and measures should be taken in order to reduce gene flow in African Sorghum agriculture.
On the other hand, in many countries in-depth genetic analysis has revealed a often striking constance of landraces over centuries, even in cases, where there was no geographical separation. This is normally interpreted by the constancy of agricultural practices and traditional use of the various Sorghum races. There are even examples known in Central Niger and in a village in Cameroon where researchers were able to find all the 5 African Sorghum races ecxept kafir in sympatry without much gene flow and hybridization.

2a.6. Mitigation of Gene Flow in Sorghum and related species

There are a variety of methods available to mitigate the problem of gene flo.
To assess the environmental risk of possible future deployment of transgenic *Sorghum*, more data on the outward flow of genes through *Sorghum* pollen to non-target relatives is needed.

Moreover, available information indicates existence of variation in outcrossing rates among varieties and locations. Knowledge on actual outcrossing rates in selected and specific cases will be essential to come up with recommendations for variety maintenance and on-farm seed production.

This study on *Sorghum* Biology proposes to determine the extent of seed and pollen mediated gene flow in selected experiments using *both* molecular and morphological methods. Present day morphogenetic analysis of landraces, often intricately growing together, shows, that the individuality of the landraces is maintained despite selection and seed exchange activity of the farmers over a long time.

Coexistence rules to be followed

No zero tolerance:

Zero values with intermixing seeds or yield cannot be achieved in most cases (and is not necessary, since the introgressed genes stem from cultivars which have been approved for environmental and food and feed safety anyway). So it is a misleading expression to talk about "contamination", we should use terms like intermixing, and threshold values instead.

Field size influences results

The impact of gene flow and the result of intermixing tracable genes in the yield is depending on the size of the fields involved: Big fields of many hectares usually do not pose a problem, since intermixing will be homogenized to minute traces well below the threshold values fixed by law.

Safety distances:

Coexistence depends on safety distances, which have to be determined in a case by case decision. A multitude of characters of crop reproduction biology will have to be evaluated in order to set up the individual rules of lawful segregation

Biology and production characteristics of seeds: Seed biology, production (and selection practices and exchange) also has to be involved in coexistence ruling

Time scale:

There is, depending on the crop biology, a need to look at several years of crop production because of seed exchange by farmers (which traditionally is low), volunteer plants, tillering and dormant seeds, all these factors depend on the specific characters of a given crop, soil and region.

Traditional knowledge

In the majority of cases, these rules do not have to be invented and developed from scratch, they can be derived from the practices of traditional and modern farming.

Mitigation needs a case to case approach

Mitigation of gene flow and the insurance of coexistence will depend on a variety of methods, which have to be adapted from case to case.

How to avoid gene flow in cultivated Sorghums

In order to avoid gene flow, there are several possibilities open for future development and regulation:

Regulation through establishing safety distances

Working with safety distances is often the easiest strategy of choice, this has been shown with many different crops, the safety distances depending on the field size according to experimental data, see below the table of DEFRA, based on a multitude of field experiments cited in this extensive report. Safety distances have to be assessed in the case of Africa, they will have to be assessed by field experiments with marker genes and with morphometric methods, details see chapters on proposed field experiments of Africa Harvest SuperSorghum project at the end of the study.

Transgenic mitigation (TM), Tandem constructs,

where a desired primary gene is tandemly coupled with mitigating genes that are positive or neutral to the crop but deleterious to hybrids and their progeny.

propose tandem constructs, which would avoid or at least reduce considerably the spread of transgenes, the concept has been proven to produce stable gene constructs and sustainable mitigation: Transgenic mitigation (TM), where a desired primary gene is tandemly coupled with mitigating genes that are positive or neutral to the crop but deleterious to hybrids and their progeny.

The linked unfitness through TM would be continuously manifested in future generations, keeping the transgene at a low frequency.

Male sterility and apomixis in Sorghum, the prevention of gene flow

Several studies demonstrate the effects of cytoplasmatic pollen sterility with Sorghum, a valid method to mitigate gene flow. Gene flow through pollen can be severely restricted in Sorghum by adaptation of this technique aiming at A3 cytoplasmic male sterility. The low levels of seed set on selfed A3 F2 individuals (0.04%) as compared with A1 F2 individuals (74%) is a clear indication of greatly reduced amounts of viable pollen production from volunteer progeny of seed that escapes harvest in the cropping year. In field scale research and crop production, it is unlikely that all risks associated with new technologies can be completely eliminated.

Apomixis has been studied for years in other crops, and it could be promising to develop such outcrossing prevention also for Sorghum.

Application of gene switching technologies, a method to avoid gene flow

Gene switching might develop in a real opportunity, first studies for other purposes show, that mechanisms could be developed for a crop protection technology. A Chinese study claims that chemical regulation of transgene expression presents a powerful tool for basic research in plant biology and biotechnological applications. Various chemical-inducible systems based on de-repression, activation and inactivation of the target gene have been described. The utility of inducible promoters has been successfully demonstrated by the development of a marker-free transformation system and large scale gene profiling. In addition, field applications appear to be promising through the use of registered agrochemicals (e.g. RH5992) as inducers. most of the systems reported thus far are unsuitable for field applications because of the chemical nature of the inducers. Further work should focus on systems suitable for applications with transgenic crop plants, with particular emphasis on agricultural chemicals (e.g. insecticides and safeners; the latter chemicals are used in agriculture to render crops tolerate to herbicides) that have already been registered for field usage. An additional interest would be to develop multiple-inducible systems to independently regulate several target genes.

2b. Extended summary Report Sorghum Biology

2b.1. General Remarks

To designate *Sorghum* as a "lost" crop, on the face of it, seems like a gross mistake. After all, the plant is Africa's contribution to the world's top crops. Indeed, according to the numerous authors contributing in the last decades it belongs to the elite handful of plants that collectively provide more than 85 percent of all human energy. Globally, it produces approximately 70 million metric tons of grain from about 50 million hectares of land. Today, it is the dietary staple crop of more than 500 million people in more than 30 countries, let alone in Africa it is an important crop for 300 million people. Only rice, wheat, maize, and potatoes surpass it in feeding the human race.
For all that, however, *Sorghum* now receives merely a fraction of the attention it warrants and produces merely a fraction of what it could. Not only is it inadequately supported for the world's fifth major crop, it is under-supported considering its vast and untapped potential. Viewed in this light it is indeed a "lost crop".
But this situation may not continue much longer. A growing number of researchers in governmental institutions and companies already see that a new and enlightened *Sorghum* era is just around the corner. Accorded research support at a level comparable to that devoted worldwide to wheat or rice or maize, *Sorghum* could contribute a great deal more to food supplies than it does at present. And it would contribute most to those regions and peoples in greatest need. Indeed, if the twentieth century has been the century of wheat, rice, and maize, the twenty-first could become the century of *Sorghum*. The Bill and Melinda Gates Foundation, in close collaboration with Africa Harvest will make it possible to foster biofortification of this wonderful crop, a crop, which has already proven its big potential for subsistence and commercial farming. Research on *Sorghum* has received a big boost, let alone the Web of Science reveals some 700 publications for the year 2010.

The book presented should help to synthesize the literature and achievements in the research on the biology of *Sorghum* in the wake of the 21st century.
May it be of help for future research and development of *Sorghum.*

2b.2. Taxonomy of Sorghum, the wider picture

Sorghum Moench is a heterogeneous genus. In the taxonomic literature, usually the following sections of the genus are recognized (Section = defined group of species within one genus): *Stiposorghum*, *Parasorghum*, *Sorghum*, *Heterosorghum* and *Chaetosorghum*. *Stiposorghums* are characterized by distinct rings of hairs at each culm node, with the awns over 65mm long. those of *Parasorghums* are substantially shorter.

Maize and even more so Sugarcane are both genetically closely related to Sorghum, opening breeding prospects both ways with modern molecular tools.

It is important to know why interspecific hybridization does not occur within the genus Sorghum: The growth of alien pollen tubes is inhibited in Sorghum pistils. For three species where limited fertilization and embryo formation occurred, the endosperm in immature seed aborted and no viable seed were produced.

Conclusions from DNA sequence studies about the phylogeny split Sorghum into two lineages, one comprising the 2n = 10 species with large genomes and their polyploid relatives, and the other with the 2n = 20, 40 species with relatively small genomes. An apparent phylogenetic reduction in genome size has occurred in the 2n = 10 lineage. Genome size evolution in the genus Sorghum apparently did not involve a one way ticket to genomic obesity as has been proposed for the grasses.

2b.3. Sorghum species

Three species of Sorghum are recognized, two are rhizomatous taxa: S. halepense and S. propinquum, and the large and complex S. bicolor to include all annual wild, weedy and cultivated taxa. The latest interpretation about Eu-Sorghum: They originate from Africa and Asia with 2n=20 and 40 chromosomes, and the known progenitor of cultivated S. bicolor is a Sorghum verticilliflorum (arundinaceum) of unknown origin and makeup, most probably of polyploid nature.

2b.4. Sorghum halepense, Johnsongrass

Sorghum (x) halepense (Johnsongrass) is derived from a doubling of the chromosomes in a natural cross between S. verticilliflorum (arundinaceum) and S. propinquum. Still, and rightly so, Sorghum halepense is recognized as a species due to its worldwide establishment, originating from the temperate regions of the Mediterranean region eastwards.

Sorghum x drummondii originated from a natural cross between S. bicolor and S. arundinaceum and Sorghum x almum is the natural cross between S. bicolor and S. halepense.

The close genetic relationship and inter-crossability between the Eu-Sorghum species is well documented. Although S. bicolor (2n = 2x = 20) and S. halepense (2n = 4x = 40 and higher) differ in ploidy, numerous artificial crossing studies have demonstrated that S. bicolor can serve as the pollen parent of triploid and tetraploid hybrids.

Naturalized populations of S. halepense occur in many regions where Sorghum is cultivated. In the United States, S. halepense is a very common roadside weed. It also invades cultivated fields of many warm season crops and can reduce agricultural productivity by as much as 45%. The two species frequently grow in close physical proximity have overlapping flowering periods. Hybridization with cultivated (non-transgenic) S. bicolor has been proposed as a potential cause of increased aggressiveness in the weed. Based on morphological evidence, it has been suggested that 'Johnsongrass' in North America may actually be an S. halepense × S. bicolor hybrid similar to S. almum (Columbus grass) (2n = 4x = 40) of South America. A relatively high frequency of occurrence of cultivar-specific alleles in S. halepense populations far from Sorghum fields and outside the region of the United States where S. bicolor is cultivated has been found. Sorghum halepense has only recently invaded the more northerly portions of its introduced range in the United States and Canada and it is possible that alleles have been maintained in populations that experienced previous introgressive hybridization.

The existence of intermediary forms in most Sorghum growing areas of the warm temperate zones in the Americas offers an empirical evidence for weedy forms arising from continued introgression (exo-ferality) among different Sorghum types.

2b.5. Sorghum propinquum

S. propinquum is a species related to S. bicolor in the broad sense. It belongs to the six Eu-Sorghum species and it is reputedly a perennial rhizomatous relative of S. bicolor.
Molecular data have shown that there is good transferability from Sorghum propinquum for interesting genetic sites to the cultigens, and breeders will use these new insights.
The natural distribution of Sorghum bicolor, however, is strictly African, and since Sorghum propinquum is spatially isolated from the annual S. bicolor, there are no spontaneous African hybrids between S. propinquum and African wild S. bicolor reported.

2b.6. Sorghum bicolor (L.) Moench

The species S. bicolor (L.) Moench includes all annual taxa of the section Sorghum as recognized by early authors. It comprises an extremely variable complex of cultivated taxa, including a widely distributed and ecologically variable wild African complex, and also stabilized weedy derivatives (a complex of feral taxa) originating from introgression between domesticated grain Sorghums and their closest wild relatives.

There are three complexes recognized as subspecies:
Sorghum bicolor subsp. bicolor see 3.6.1.
Sorghum bicolor subsp. drummondii see 3.6.2.
Sorghum bicolor subsp. verticilliflorum see 3.6.3.

2b.6.1 Sorghum bicolor subsp. bicolor: the cultivated grain Sorghums

The variation of cultivated African Sorghum is discontinuous and justifies the above designation of five major races with some varieties included, the definite number of races and varieties will have to be decided for in a new comprehensive monograph of the whole genus.
Cultivated grain Sorghums were earlier divided into the Guineensia, Nervosa, Bicoloria, Caffra and Durra complexes. A modern monograph, based on sturdy molecular analysis is still lacking, but it will be a major undertaking involving many laboratories and scientists.
The variability in cultivated Sorghums can be described in terms of four roughly geographic races (guinea, durra, kafir and caudatum) and one widely distributed morphologically primitive race bicolor.

3b.6.1. Race bicolor

Race bicolor is morphologically seen the most primitive. It has small, ellipsoidal grains which are tightly enclosed by the glumes. This race occurs widely but is not grown much for grain. Most bicolors are now grown for their sweet stalks or for production of beer or dye. The primitive morphology of bicolor Sorghums and wide geographic distribution suggest that a bicolor type was the progenitor of the more highly derived races.

2b.6.1.1. Race guinea

Race guinea is distinguished by long glumes that gape at maturity and discoid grains that twist up to go degrees at maturity. Guineas are adapted to areas with a long rainy season, areas too wet for other Sorghums and most other cereals and do not yield as much grain as some other Sorghums, but many varieties are highly prized because they yield a superior nonbitter white flour.
According to recent studies, the guinea-race is a predominantly inbreeding, diploid cereal crop. For more details about inbreeding guinea races see chapter on gene flow avoidance. It originated from

West Africa and appears to have spread throughout Africa and South Asia, where it is now the dominant Sorghum race, via ancient trade routes.

2b.6.1.1.1. Race guinea variety margaritiferum

Margaritiferum varieties of the race guinea are characterized through very small, hard grains (3-5mm) eaten like rice, grown in parts of West Africa, receiving up to 120 inches of rain during the growing season.

2b.6.1.1.2. Race guinea variety conspicuum

Conspicuum varieties are characterized through very large grains (5-8mm), grown in the fog belt of Mozambique, Malawi, and Swaziland.

2b.6.1.1.3. Race guinea variety roxburghii

Roxburghii Sorghums are distinguished from gambicum varieties by glumes larger than the grain, and have intermediate grains in size (between margaritiferum and conspicuum varieties) and are grown in East and South Africa.

2b.6.1.1.4. Race guinea variety gambicum

Gambicum Sorghums are distinguished from variety roxburghii by glumes subequalling the grains, they have also intermediate grains in size and grown in tropical West Africa.

2b.6.1.2. Race durra

Sorghums of race durra have glumes which are usually creased horizontally. The grains are very broad and blunt at the top and taper to a relatively small, wedge-shaped base. Some mature in as little as three months and thus can be grown in areas with a very short rainy season. Durras are grown in India and south-west Asia as well as the northern fringe of the African savanna. The pattern of distribution strongly suggests that durras were brought into Africa under Islamic influences.

2b.6.1.3. Race kafir

Sorghums of race kafir have grains that are broadly ellipsoid. The part of the grain which extends beyond the clasping glumes is symmetrical and round. Kafir Sorghums are found in parts of Africa south of the equator, mainly in areas with one well-defined rainy season such as Natal, Transvaal, and Orange Free State.

2b.6.1.4. Race caudatum

The caudatums are distinguished by its very asymmetrical grain. The embryo side of the grain bulges; the opposite side is flat or may even be concave; and the tip of the grain often comes to a point. This combination of characters gives race caudatum a very distinctive appearance. Caudatum Sorghums are grown in Hyparrhenia and Andropogon dominated regions of north-central Africa receiving 15 to 50 inches of rain per year. They are the staff of life in much of Sudan and Chad, and parts of Cameroon and Uganda. Caudatums have not, however, been widely accepted as human food by peoples outside traditionally caudatum-growing areas possibly because most caudatum varieties contain polyphenolic compounds often called 'tannins' that make caudatum flour bitter and dark in color. This biochemical characteristic makes caudatum inferior in a culinary sense to most guinea, kafir, and durra Sorghums. Though caudatum is not very popular as food for humans outside the areas listed, caudatum varieties such as 'feterita' and 'hegari' or hybrid derivatives of these varieties are important in sub-humid to semi-arid regions of the world where they are grown for use as stock feed.

It is typical for caudatum Sorghums that its more difficult to define them clearly on morphological grounds. Caudatum, more than any other indigenous African crop, can be counted on to produce a crop despite high water, drought, parasites such as witch weed, and every other kind of hazard, a considerable overall contribution to African food safety.

2b.6.2. Sorghum bicolor subsp. drummondii, (Nees ex. Steud.) de Wet & Harlan or ex Davidse,

Sudangrass

Its an annual weed thought to be a natural hybrid between subsp. bicolor and verticilliflorum, grouped mainly with a subset of the cultivated subsp. bicolor (namely, race bicolor).

Subspecies drummondii occurs as a weed in Africa wherever cultivated grain Sorghums and their closest wild relatives are sympatric. All races of subspecies Sorghum and all wild kinds of S. bicolor hybridize to produce weedy derivatives. Morphologically stabilized derivatives often accompany grain Sorghums as weeds beyond the natural range of S. bicolor.

2b.6.3. Sorghum bicolor subsp. verticilliflorum, Wild Sorghum bicolors

This subspecies includes also Sorghum arundinaceum and is defined as the wild subspecies of Sorghum bicolor.

The following ‘races’ intergrade heavily, but are still often distinguished and named and also found with typical morphology:

2b.6.3.1. Race verticilliflorum

can be distinguished from other wild Sorghums by its large and open inflorescences with spreading, but not pendulous branches. This race grades into race arundinaceum which is distributed across tropical Africa as a forest grass. In the broad leaf savannah race arundinaceum is often difficult to distinguish from race verticilliflorum except by inflorescences in which the branches become pendulous at maturity.

3.6.3.2. Race virgatum

resembles race verticilliflorum except that the inflorescence branches are more erect, and the leaf blades are narrowly linear. Race virgatum occurs along stream banks and irrigation ditches in arid northeastern Africa. It is mentioned in various studies on genetic diversity and agronomic characterization.

2b.6.3.3. Race aethiopicum

is a desert grass, and is easily recognized by its large ovate-lanceolate, densely tomentose sessile spikelets. It occurs across the Sahel from Mauritania to the Sudan. It is mentioned as a possible source for Striga resistance.

The close relationships identified between S. bicolor and several wild species caused gene flow over centuries, but they have also exciting prospects in utilizing this diverse gene pool for improving Sorghum production.

2b.7. Numerical taxonomy of Sorghum

If characters known for their moderate variability, excluding leaf and inflorescence sizes and plant height, are used exclusively from certified type specimens, numerical taxonomy shows reasonable clustering and fits well with the view of earlier taxonomists.

2b.8. Molecular taxonomy of Sorghum

There are some 750 papers published on molecular analysis of Sorghum. Progress in molecular knowledge is considerable, and growing rapidly in the last few years, helping to understand taxonomic relationships, but also providing basic knowledge on useful details for future breeding efforts.

2b.9. Distribution of Sorghum

The genus Sorghum is strictly Old-World in its original distribution, extending almost continuously from Southern Africa to subtropical Australia. The cultivated-weed complex of Sorghum reached Australia and the New World only after the colonization of the Europeans. The cultivated Sorghums are even more variable than the feral complexes through continuous selection and extensive exchange of germplasm, including hybrid plants. Still it is possible to distinguish geographically between four distinct cultivated complexes. Centers of Biodiversity and Crop Biodiversity are not the same, although sometimes they overlap.

2b.10. Centers of crop origin

These centers have changed in concept and are still in debate, since in many cases reliable archaeobotanical data still lack. The best solution is to divide in *centers* and *non-centers*.
There is no real proof of any genuine place or country of origin of Sorghum. But clearly, the region of Sudan and partly Ethiopia harbor a series of ancestral landraces, show a high biodiversity and certainly can be taken as the centers of Sorghum landrace biodiversity of the present time. Present day understanding is based on a center of origin as a wide zone in the broad-leaved savanna belt that stretches from about lake Chad to eastern central Sudan. Vast amounts of wild Sorghum are found along the Sudan-Ethiopia border, but there is no indication that the area was ever farmed before government settlement projects were established. Variations in Sorghum do not suggest that its homeland is Ethiopia; by far the bulk of Ethiopian Sorghums are durras, which are the most specialized traits with a narrow genome and certainly derived from cultivated Sorghum.

2b.11. Earliest evidence of Sorghum cultivation in Africa 8000 years ago

Early domestication in Africa and India is often cited, but the data on which these conclusions were until recently at best circumstantial.
Although not generally known, in the early nineties, a discovery pushed back the origin of Sorghum domestication for many thousand years, this opens new perspectives for the history of domestication: Archeobotanical results allow to trace back Sorghum grains to much earlier times than assumed before: Excavations at an early Holocene archaeological site in southernmost Egypt, 100 km west of Abu Simbel, have yielded hundreds of carbonized seeds of Sorghum and millets, with consistent radiocarbon dates of 8,000 years before present (BP), thus providing the earliest evidence for the use of these plants. They are morphologically wild, but the lipid fraction of the Sorghum grains shows a closer relationship to domestication than to wild varieties. Whatever their domestication status is, the use of these plants 8,000 years BP suggests that the African plant-food complex developed independently of the Levantine wheat and barley complex. This ancient history, going back maybe even to the old Saharan population which existed before the dramatic desertification of huge regions, would also explain the high degree of biodiversity of landraces which does not follow the rules of their present day distribution properly.

2b.12. Centers of biodiversity generally more robust against alien invasions

Centers of crop biodiversity usually are rich in plant species. Although it is clear, that centers of biodiversity in general suffer from species loss due to many different factors, there are enough data in population ecology to show that plant communities with a rich set of species are less susceptible to alien species invasions, except in cases where those species have a considerable advantage in competitiveness. The rule is that in heavily disturbed areas one finds the most dramatic invasion impacts of alien species.

2b.13. Preservation of landraces through participative breeding programs

Landraces cannot be preserved with a conservative system, since they are dynamic populations, having been subject of spontaneous breeding and seed interchange for centuries. In consequence, it will be important to establish participative breeding programs in order to preserve landraces, since landraces have only a chance of survival, if there is still a market for the products.

An important consequence of environmental and human selection is that each race of Sorghum has become ecologically and culturally specialized. A race of Sorghum resulting from generations of selection in one climate will not do well in another. And a race of Sorghum selected by one group of people is usually considered undesirable by another group of people. Predilections of Africans of the present in favor of their own

Sorghums and against Sorghums of other peoples are so strong as to suggest that traditional African farmers do not and have not casually borrowed and adopted unfamiliar Sorghums raised by unrelated peoples. The usual reaction to an unfamiliar kind of Sorghum is that it is unfit for human consumption. And in fact very little exchange of Sorghum varieties of different races has been observed among unrelated groups of people. But this should not be mistaken for an appeal of an inconsiderate traditional approach, since history of agriculture has shown major shifts of cultivation tradition, especially in the face of threatening malnutrition situations.

Limitations in ecological amplitude of the staple crop must have imposed limitations on the direction and extent of migration of peoples who depended on Sorghum for their food. Looking at this more positively, we might say that the ability of a group of Sorghum-growing peoples to occupy an area or to expand into new areas has probably been determined in part by the productivity, genetic potential, and ecological amplitude of the Sorghum cultivars they created and depended on for food. This all can be taken as a serious caveat when new Sorghum with definitely better agronomic characteristics should be introduced in Africa. If the African farmers should benefit from new Sorghum breeding, the new traits will have to be carefully adapted to the local needs of the population. Nevertheless, (Deu et al., 2006) state, that the genetic distinctness of rnargaritiferums from other guinea Sorghums from western Africa is remarkable, all the more both are interfertile and cultivated in sympatry in the same season by the same farmers. This can also be taken as a hint that we do not yet understand Sorghum cultivation in Africa in all important population genetics aspects.

2b.14. Development of Sorghum breeding

Sorghum breeding general remarks

Depending on the region of production, the type of Sorghum and the purpose for its production varies widely. Whether they are breeding varieties or hybrids, the primary focus of Sorghum breeders throughout the world are yield, adaptation and quality. In addition to breeding for these factors, reducing losses due to stress is equally important. Most breeding programs consistently

select for tolerance to abiotic stresses (such as drought and low temperatures) and biotic stresses (such as Sorghum midge, grain mold, anthracnose, charcoal rot and Striga and bird resistance). Finally, the integration of molecular genetic technology is enhancing Sorghum improvement by providing a genetic basis for many important traits and through marker-assisted selection.
Species outside the Eu-Sorghum section are sources of important genes for Sorghum improvement, including those for insect and disease resistance, but these have not been used because of the failure of these species to cross with Sorghum.
An understanding of the biological nature of the incompatibility system(s) that prevent hybridization and/or seed development is necessary for the successful hybridization and introgression between Sorghum and divergent Sorghum species.
Studies of S. bicolor (L.) Moench are beginning to link physiological behavior to specific genes and hormone-based regulatory systems in ways that suggest specific strategies for improvement. Findings from several other grasses like maize and sugarcane are adding to the pool of information being derived from Sorghum. This information relates to flowering and floral development, maturity and senescence, temperature effects via the biological clock, shade avoidance behavior, apical dominance, shoot elongation, and root development including constitutive aerenchyma formation. These studies, along with others, offer a number of options for conventional plant breeding and genetic transformations to improve grass-based crops and satisfy part of the projected human food needs of coming decades. The global economic importance of Sorghum makes it a prime candidate for genetic transformation.

2b.14.1. The various breeding programs

Encouraged by the results from natural hybridization and selection, attempts at deliberate crossing were made, wherein it was found that crosses between divergent cultivars exhibited high levels of heterosis. The discovery of the cytoplasmic genetic male sterility based on the milo-kafir system was a milestone in Sorghum breeding and research. It is widely used in the commercial exploitation of heterosis. Today, more than 30% of the Sorghum area is under hybrids (in the USA!), which have yields about twice that of any local cultivar.

2b.14.2. Biofortification is now belonging to several breeding programs

Preliminary results suggest that a feasible chain solution consists of breeding for high Fe and moderate phytic acid contents and using soil organic amendments and P fertilization to increase yields but that this needs to be followed by improved food processing to remove phytic acid. Further research on timing of application of phosphate, Fe fertilizer and soil organic amendments is needed to improve phytic acid-Fe molar ratios in the grain. Research on the exact distribution of Fe, phosphate, phytic acid and tannins within the Sorghum grain is needed to enable the development of more effective combinations of food processing methods aiming for more favorable phytic acid-Fe molar ratios in Sorghum-based food.
In another joint project between the university of Ouagadougou and the agricultural research center of Wageningen Sorghum will be better adapted to hard environments and enhancement of starch levels (amylose and amylopectin) and starch depolymerizing enzymes are breeding targets. Biofortification of Sorghum is achieved in the same partnership by selection of suitable traits, taking into account a holistic approach. Current research activities focus on identifying varieties meeting specific agricultural and food requirements from the great biodiversity of Sorghums to insure food security.

An important effort is now made with the biofortification for a higher lysine content of Sorghum cultivars within the framework of a Africa Harvest research and development project financed mainly by the Bill and Melinda Gates Project (www.SuperSorghum.org), again with the collaboration of ICRISAT.

The future of Sorghum breeding

There is still a lot of work to be done, in all domains of research and development, the maps and statistics on Sorghum yields show this clearly. Yield gain has been achieved in many developed countries on a large scale, in Africa only in Egypt. In all other African countries there is still a lot of work to be done.

2b.15. Evolutionary dynamics of cultivated Sorghums

Molecular data support previous concepts of Sorghum evolution; namely, that multiple origins, diverse environments and human involvement have contributed to

the existence of different types of wild and cultivated Sorghum. Outcrossing has led to gene introgression and gene flow among the natural populations. Then polymorphic subpopulations develop, and disruptive selection started. Intermediate types may have existed for a period, but differentiation continued until a number of distinct, separate and adaptive populations are subsequently formed. In summary, the population structure of modern Sorghums seems to fit well into Wright's "shifting balance" theory of adaptation.

2b.16. Gene flow from Sorghum cultivars to wild and feral species

Gene flow from Sorghum cultivars to wild and feral species is well documented in the United States. In Africa and elsewhere experimental studies are still needed, but gene flow is well documented indirectly with numerous genetic screenings.

Basically, one should distinguish between the high potential of crossability and the low hybridization rate in the reality of agricultural practice.

Situation in the USA: Sorghum halepense is a proven conduit between Sorghum cultivars and the wild and feral populations, gene flow has been studied in field experiments. Although the rates are very low compared to maize as an example, there seems to be persistent establishment possible on a long term, and also seed exchange might play a role.

In Africa, up to now there are only indirect hints that there is gene flow from wild Sorghums to cultivated ones, and there are only a few reports of spontaneous hybrids between African wild and cultivated Sorghums, which could be due to lack of precise scientific knowledge. Still, feral complexes of wild and cultivated Sorghums seem to be a reality to such a degree that harvest is hampered and measures should be taken in order to reduce gene flow in African Sorghum agriculture.

2b.17. Gene flow in Sorghum from crop to crop

Gene flow between different varieties of the same crop is almost as old as agriculture itself. Native plant genes as well as genes from transgenics can be dispersed either in seed or pollen, but in the case of the partially autogamous crop Sorghum the outbreeding effects remain low, the result is that landraces of Sorghum in Africa were maintaining their individual genomes over centuries. There are even examples known in Central Niger and in a village in Cameroon where Monique Deu and her team were able to find all the 5 African Sorghum races exept kafir in sympatry without much gene flow and hybridization (personal communication).

Pollen mediated gene flow and the separation distances employed to minimize it typically generate more public interest than that for seed dispersal. For the most part, gene flow takes place within a few meters of the plant, *but the up to now published data sets cannot be taken for reality:*
The cases documented for gene flow with Sorghum cultivars and Johnsongrass from the US cannot be compared to African situations. The existing studies from the US, although very detailed, are of a more theoretical interest, since the receiving fields has been planted with pollen sterile traits, in order to get a maximum rate of outcrossing. In reality it is possible to choose traits with a very high degree of autogamy (self-pollination), a similar situation as in wheat, which has no real outcrossing problems from crop to crop. From Africa, a few studies demonstrate highly variable outcrossing rates from minimal to 16 until nearly 30%, verified with genomic analysis methods.
Distance from a pollen source and cross-pollination frequency with neighboring crops has been identified for major crops and employed in the production of certified seeds. In the case of Sorghum, certified seed production fields are isolated by at least 100 meters from other Sorghum fields, sufficient to maintain genetic purity of at least 99 per cent over many years of production. However, restricting gene flow between GM and non-GM varieties needs to be still better understood, and several methods already developed should be put in practice. These will efficiently help to maintain co-existence as it was practiced for many decades in modern agriculture without transgenic crops.
There are a variety of methods available to mitigate the problem of gene flow, this will be dealt with in a separate chapter on the consequences and mitigation of gene flow and hybridization, and the SuperSorghum project will be able to take care of it.
To assess the environmental risk of possible future deployment of transgenic Sorghum, more data on the outward flow of genes through Sorghum pollen to non-target relatives is needed.
Moreover, available information indicates existence of considerable *variation in outcrossing rates* among varieties and locations. Knowledge on actual outcrossing rates in selected and specific cases will be essential to come up with recommendations for variety maintenance and on-farm seed production.

2b.18. Gene flow from weedy to cultivated Sorghums

Only a few studies have been undertaken on assessing weed to crop gene flow in Sorghum, all refer to weed-to-crop gene flow only in an indirect manner. There are no field studies which aim at the direct assessment of weed to crop gene flow. Therefore, we still have insufficient information on the rate and the extent of genetic exchange in situ. It is probable, based on the potential of cross pollination and the overlap in natural habitats, that there is a continual transfer of an array of fitness and other genes from weedy types to cultivated Sorghum. Allele exchange has been shown in numerous cases in Africa. However, this is the result of century old neighborhood of wild and cultivated Sorghum.

2b.19. Assessment of gene flow of cultivated Sorghums in Africa

2b.19.1. Distribution of Landraces

Race bicolor, most widely distributed and least different in morphology from wild Sorghum, is presumed to be the primitive cultivated type from which the more highly differentiated races were selected. It is not known whether cultivated bicolor Sorghums arose in one or several places in Africa. The four remaining other races of Africa, which are centered in different regions and different climates, differ from each other in morphology and some aspects of physiology. These races appear to be the products of two kinds of selection:

2b.19.2. Segregation and persistence of Sorghum landraces

Natural (environmental) selection in various regions has resulted in different physiological characteristics such as photoperiodic responses, maturity cycles, moisture requirements, and some spikelet and inflorescence characters.

Human selection is undoubtedly responsible for environmentally neutral aspects of the size, shape, and color of the grain and some culinary qualities. Thus, natural and human selection have simultaneously acted to produce cultivars which are physiologically suited to perform well in the environment where selection has occurred and culturally suited to the needs, expectations, and aesthetics of the people who have raised the Sorghum for countless generations.

An important consequence of environmental and human selection is that each Sorghum race has become ecologically and culturally specialized. A race resulting from generations of selection in one climate will not do well in another. And a race selected by one group of people is usually considered undesirable by another group of people.

Present day predilections of Africans in favor of their own Sorghums and against Sorghums of other people are so strong as to suggest that traditional African farmers do not and have not casually borrowed and adopted unfamiliar Sorghums raised by unrelated peoples. The usual reaction to an unfamiliar kind of Sorghum is that it is unfit for human consumption.

In fact very little exchange of Sorghum varieties of different races has been observed among unrelated groups of people. One would guess that ecological and cultural specialization of races of Sorghum has had profound historical implications for Sorghum-growing peoples. It seems clear that the fate of Sorghum-growing people has been inextricably linked to the Sorghum cultivars created by their forefathers.

2b.19.3. Case studies from Somalia and Ethiopia

Sudan has the largest land area in Africa, yet the population base in low, only a third of the population in Ethiopia. Per-capita holdings of arable land are higher in the Sudan than all other African countries. In northern Sudan, where human settlement has been historically very light, the genetic identity of wild Sorghums may have been further protected by their isolation from human disturbance. Thorough genetic studies indicate the strong differentiation among the Sorghum materials. In the central clay plains of Somalia where Sorghum farming is practiced under irrigation and in rotation with other crops, wild Sorghums have also survived as weed in cotton and wheat fields and along the irrigation ditches.

Studies in those regions give insight to Sorghum landrace management regarding biodiversity and distribution of S. bicolor: The problems of vanishing landraces and their invaluable characteristics are addressed, having adapted to harsh conditions over centuries.

Today this traditional inter-dependence is at risk with catastrophic consequences for local poor resources farmers and maintenance of genetic diversity within Sorghum. Traditional landraces are being relegated to marginal and risk prone areas as they are replaced by improved varieties. This can lead to the loss of local knowledge of traditional landraces and to an erosion of genetic diversity. This should be taken into account by all breeding programs, including those on biofortification within humanitarian projects.

Although the empirical evidence described from Somalia and Ethiopia is still in many places circumstantial and only based on genomic analysis, gene flow ultimately needs to be assessed experimentally, which needs to be done in the framework of the differential effects of gene flow in contrast to ecological and demographical factors and to farming practices.
Sudan and Ethiopia are the presumed birth places of the crop and have witnessed the evolution of wild and primitive forms of Sorghum, although empirical data from Ethiopia show that Sorghum durra is the predominant race with a rather narrow genome. Another example on why the risk assessment approaches must be carried out in a case by case manner is demonstrated from studies in Somalia, where the situation is different from Ethiopia:
In both the rainfed and irrigated Sudanese agriculture, genetic exchange between Sorghum and its wild relatives has resulted in formation of two widely recognized forms of crop-wild hybrids: Aggressive forms of weedy Sorghum bicolor have evolved that are readily identified and recognized by most farmers as feral weeds, and known under a local name of "adar". This is a form of shattercane that is widely distributed and almost accepted as unavoidable. In spite of continual weeding and selective roguing this weedy S. bicolor has not been easy to eradicate in Sudan.
The second form of intermediate is equally feral, but appears to be more similar to cultivated Sorghum and produces grains that only slowly shatter. Continued introgression of cultivated Sorghum genes into wild forms has resulted in this hybrid form called "kerketita". Farmers selectively harvest these types and encourage their continued existence, for they rely on them as feed and food depending on the harvest prospect: In bad years, these fast growing intermediates provide the only harvest possible, particularly for fodder.
So in conclusion gene flow between wild and cultivated Sorghums in Africa cannot be a really serious problem: over centuries obviously wild Sorghums and cultivated species maintained their identity well, although there are regional differences, as discussed in the chapter on the origin of Sorghum. They are manifested some genetic studies. Some geographic portions of the wild gene pool are genetically more similar to the cultivars than others. Collections of wild Sorghum from Uganda, Sudan, and the Ivory Coast exhibit the highest genetic similarity with the cultivars. Although this latter collection from the Ivory Coast is quite similar to the cultivars, the other 4 wild collections from northwest Africa (Ivory Coast and Nigeria) do not share this relationship and are isolated in the principal component plot at the end opposite the cultivars. Similarly, wild Sorghum from southern Africa is quite distinct from the cultivars. In contrast, the majority of wild collections from northeast Africa (Egypt, Ethiopia, and Sudan) and central Africa (Kenya and Uganda) are fairly similar to the cultivars.

Thus, the majority of wild Sorghum from both southern and northwest Africa share less resemblance with the cultivars of the same region than does Sorghum of central and northeast Africa. Therefore, most of the cultivated Sorghum was probably domesticated from wild progenitors of the northeast and central African regions.

In chapter on molecular taxonomy the results of genomic analysis have been summed up, it is now fact that the races caudatum and kafir are not uniform and need to be studied further on.

2b.20. The agricultural reality

A picture close to agricultural reality of outcrossing rates of landraces has been developed in Morocco, building on population genetic data analysis in the field. The outcrossing rate of Sorghum

landraces was assessed by sampling in situ from two fields under traditional cultivation in north-western Morocco using genotypic data from five micro satellite loci. Assuming a mixed mating model, they outcrossing parameters were estimated by two methods based on progeny analyses, which demonstrated, that Sorghum landraces in this region are predominantly autogamous but still show measurable outcrossing rates.
An other study presents molecular taxonomic data which demonstrate gene flow among landraces: Outcrossing has led to gene introgression and gene flow among the natural populations. Then polymorphic subpopulations develop, and disruptive selection starts. Intermediate types may exist for a period, but differentiation continues until a number of distinct, separate and adaptive populations are formed. In summary, the population structure of modern Sorghums seems to fit well into Wright's "shifting balance" theory of adaptation, which assumes that genetic drift and selection operating on subpopulations leads to a number of genotypes occupying different adaptive peaks, even though gene flow can occur between the subpopulations.
A study from Burkina Faso gives real time and geography based data on the genetic relationship among Sahelian Sorghum bicolor landraces. It showed that in this Sahelian region there is a high level of diversity between Sorghum landraces and a low rate of outcrossing.

2b.21. A summary of gene flow in Sorghum cultivars and its wild relatives

Gene flow between different varieties of the same crop is almost as old as agriculture itself. Native plant genes as well as genes from transgenics can be dispersed either in seed or pollen, but in the case of the partially autogamous crop *Sorghum* the outbreeding effects remain low, the result is that landraces of *Sorghum* in Africa were maintaining their individual genomes over centuries.
Several papers deal in all detail with the gene flow from crop to crop, and gene flow has been documented on a morphological and genetic basis, its so minimal, that it should not pose any problem with the introduction of new traits in Africa, provided some mitigation measures are taken, see chapter on consequences and prevention of gene flow.

It has to be stated very clearly, that gene flow with most Sorghum species and cultivars did always happen in the last centuries, but there are many data available to show that landraces have been remained stable, despite of free breeding and selection activity by the farmers. To erect absolute gene flow barriers would mean the genetic stabilization of the landraces and in this way ultimately lead to the end of their existence. This has been shown in the case of the Mexican landraces of maize.

Pollen mediated gene flow and the separation distances employed to minimize it typically generate more public interest than that for seed dispersal. For the most part, gene flow takes place within a few meters of the plant, but the up to now published data sets cannot be taken for reality:
The case of gene flow with Sorghum cultivars and Johnsongrass cannot be compared to African situations, it is restricted to the Americas.
The now often cited results of Schmidt et al. do not apply to agricultural reality: They are of a more theoretical interest, since the receiving field has been planted with pollen sterile traits, in order to get a maximum rate of outcrossing. In reality it is possible to choose traits with a very high degree of autogamy (self-pollination), a similar situation as in wheat, which has no real outcrossing problems from crop to crop.

Distance from a pollen source and cross-pollination frequency with neighboring crops has been identified for major crops and employed in the production of certified seeds. In the case of Sorghum, certified seed production fields are isolated by at least 100 meters from other Sorghum fields, sufficient to maintain genetic purity of at least 99 per cent over many years of production. However, restricting gene flow between GM and non-GM varieties needs to be still better understood, and several methods already developed should be put in practice. These will efficiently help to maintain co-existence as it was practiced for many decades in modern agriculture without transgenic crops.

However, intermediate forms such as the Shattercanes appear also in the agro-ecosystems of Africa where Sorghum cultivation is practiced without sufficient isolation from wild forms and in sympatry with weedy relatives. It has to be stressed that this is not a new situation, and it will be interesting to see and learn how African farmers have coped up with such phenomena over centuries. But we have no reason to romanticize the situation: Up to now, this was often accompanied by considerable yield losses. At the end of the day it is not the introgression itself, it's the *consequences* of gene flow which counts. There is some experience from several studies existing about the importance of taking in farmers knowledge on various levels of screening landrace diversity and studying farmers management methods and their influence on agricultural ecology:
African landraces are according to many authors threatened through the shift in agriculture and not through gene flow. The modern world is placing a range of pressures on wild areas and on traditional agricultural communities, and external interests (often dominated by economic or political issues) strongly impinge. The major external forces relevant to this discussion advocate the introduction of high-yield varieties, accompanied by mechanization and major chemical inputs, as the means to increase total production and economic return. These forces change the nature of the decision-making process dramatically; the farmer is encouraged to grow high-yield varieties in monoculture using inputs of fertilizer and pesticides.

Consequences of recurrent gene flow between cultivated Sorghum and its wild relatives should therefore not be generalized in the case of Africa: Sorghum biodiversity, mating characteristics and diversity of farmers management methods of the many landraces are just too diverse: Many of the African Sorghum varieties are strong inbreeders (especially som of the true Guineas growing in wet tropical Africa). (For more details see chapter on gene flow avoidance). And for sure we should not make the mistake of copying the concerns of the American Sorghum breeders with their problems with Sorghum halepense. Sorghum gene flow should always be considered on a case by case basis and in individual countries where the crop is grown.

2b.22. Consequences and mitigation of gene flow in African Sorghum

There are a variety of methods available to mitigate the problem of gene flow, this is dealt with in a separate chapter on the consequences and mitigation of gene flow and hybridization, and the SuperSorghum project will be able to take care of it.

To assess the environmental risk of possible future deployment of transgenic *Sorghum*, more data on the outward flow of genes through *Sorghum* pollen to non-target relatives is needed.

Moreover, available information indicates existence of variation in outcrossing rates among varieties and locations. Knowledge on actual outcrossing rates in selected and specific cases will be essential to come up with recommendations for variety maintenance and on-farm seed production.

This study on *Sorghum* Biology proposes to determine the extent of seed and pollen mediated gene flow in selected experiments using *both* molecular and morphological methods. Present day morphogenetic analysis of landraces, often intricately growing together, shows, that the individuality of the landraces is maintained despite selection and seed exchange activity of the farmers over a long time.

2b.23. Coexistence rules to be followed

2b.23.1. No zero tolerance:

Zero values with intermixing seeds or yield cannot be achieved in most cases (and is not necessary, since the introgressed genes stem from cultivars which have been approved for environmental and food and feed safety anyway). So it is a misleading expression to talk about "contamination", we should use terms like intermixing, and threshold values instead.

2b.23.2. Field size influences results:

The impact of gene flow and the result of intermixing tracable genes in the yield is depending on the size of the fields involved: Big fields of many hectares usually do not pose a problem, since intermixing will be homogenized to minute traces well below the threshold values fixed by law.

2b.23.3. Safety distances:

Coexistence depends on safety distances, which have to be determined in a case by case decision. A multitude of characters of crop reproduction biology will have to be evaluated in order to set up the individual rules of lawful segregation

2b.23.4. Biology and production characteristics of seeds:

Seed biology, production (and selection practices and exchange) also has to be involved in coexistence ruling

2b.23.5. Time scale:

There is, depending on the crop biology, a need to look at several years of crop production because of seed exchange by farmers, volunteer plants, tillering and dormant seeds, all these factors depend on the specific characters of a given crop, soil and regional factors.

2b.23.6. Traditional knowledge

In the majority of cases, these rules do not have to be invented and developed from scratch, they can be derived from the practices of traditional and modern farming.

3.23.7. Mitigation needs a case to case approach

Mitigation of gene flow and the insurance of coexistence will depend on a variety of methods, which have to be adapted from case to case.

2b.24. How to avoid gene flow in cultivated Sorghums

In order to avoid gene flow, there are several possibilities open for future development and regulation:

2b.24.1. Regulation through establishing safety distances

Working with safety distances is often the easiest strategy of choice, this has been shown with many different crops, the safety distances depending on the field size according to experimental data, see below the table of DEFRA, based on a multitude of field experiments cited in this extensive report. Safety distances have to be assessed in the case of Africa, they will have to be assessed by field experiments with marker genes and with morphometric methods, details see chapters on proposed field experiments of Africa Harvest Super*Sorghum* project at the end of the study.

2b.24.1.1. Transgenic mitigation (TM), Tandem constructs,

where a desired primary gene is tandemly coupled with mitigating genes that are positive or neutral to the crop but deleterious to hybrids and their progeny.

propose tandem constructs, which would avoid or at least reduce considerably the spread of transgenes, the concept has been proven to produce stable gene constructs and sustainable mitigation: Transgenic mitigation (TM), where a desired primary gene is tandemly coupled with mitigating genes that are positive or neutral to the crop but deleterious to hybrids and their progeny. This was tested experimentally by the team of Gressel from Rehovot in Israel as a mechanism to mitigate transgene introgression. Dwarfism, which typically increases crop yield while decreasing the ability to compete, was used as a mitigator. A construct of a dominant ahasR (acetohydroxy acid synthase) gene conferring herbicide resistance in tandem with the semidominant mitigator dwarfing Δ gai (gibberellic acid-insensitive) gene was transformed into tobacco (Nicotiana tabacchum). The highest reproductive TM fitness relative to the wild type was 17%. The results demonstrate the suppression of crop–weed hybrids when competing with wild type weeds, or such crops as volunteer weeds, in seasons when the selector (herbicide) is not used. The linked unfitness would be continuously manifested in future generations, keeping the transgene at a low frequency.

2b.24.1.2. Male sterility and apomixis in Sorghum, the prevention of gene flow

Several studies demonstrate the effects of cytoplasmatic pollen sterility with Sorghum, a valid method to mitigate gene flow. Gene flow through pollen can be severely restricted in Sorghum by adaptation of this technique aiming at A3 cytoplasmic male sterility. The low levels of seed set on selfed A3 F2 individuals (0.04%) as compared with A1 F2 individuals (74%) is a clear indication of greatly reduced amounts of viable pollen production from volunteer progeny of seed that escapes harvest in the cropping year. In field scale research and crop production, it is unlikely that all risks associated with new technologies can be completely eliminated.

In the event that transgenic Sorghum is developed to the stage that field testing becomes appropriate, utilization of this technique should be considered in combination with cultural controls including spatial isolation, crop rotation or fallowing in subsequent cropping seasons, and herbicides active against Sorghum hybrids to reduce risk of gene flow to weedy relatives. Related to yield, the experiments from the ETH in Zurich Switzerland indicate that such associations can bring about grain production as high or even higher than those produced by pure male-fertile maize crops, especially when the male-sterile component is pollinated non-isogenically. The grain yield benefits from cytoplasmic male sterility and xenia as well as the fact that seed of male-sterile varieties can be produced cheaply and reliably in large quantities. This would facilitate the implementation of the proposed system in agricultural practice. Exploiting this technique has proven successful for the production of high oil maize and high grain quality maize and may be used to restrict gene flow in genetically modified Sorghum as well.

2b.24.1.3. Application of gene switching technologies, a method to avoid gene flow

Gene switching might develop in a real opportunity, first studies for other purposes show, that mechanisms could be developed for a crop protection technology. A Chinese study claims that chemical regulation of transgene expression presents a powerful tool for basic research in plant biology and biotechnological applications. Various chemical-inducible systems based on de-repression, activation and inactivation of the target gene have been described. The utility of inducible promoters has been successfully demonstrated by the development of a marker-free transformation system and large scale gene profiling. In addition, field applications appear to be promising through the use of registered agrochemicals (e.g. RH5992) as inducers. most of the systems reported thus far are unsuitable for field applications because of the chemical nature of the inducers. Further work should focus on systems suitable for applications with transgenic crop plants, with particular emphasis on agricultural chemicals (e.g. insecticides and safeners; the latter chemicals are used in agriculture to render crops tolerate to herbicides) that have already been registered for field usage. An additional interest would be to develop multiple-inducible systems to independently regulate several target genes.

2b.24.2. Proposed gene flow studies

The study on Sorghum Biology proposes to determine the extent of seed and pollen mediated gene flow in selected experiments using both molecular and morphological methods. Present day morphogenetic analysis of landraces, often intricately growing together, shows, that the individuality of the landraces is maintained despite selection and seed exchange activity of the farmers over a long time.

The situation in the USA and Africa is different regarding gene flow:
In the Americas Sorghum halepense and Sorghum almum pose problems with some gene flow and their weedy character, causing also problems in cultures like maize and soya.
In Africa a steady but slow gene flow is indirectly documented through genomic analysis. Wild Sorghums are widespread and cause problems for the local farmers, weeding is often not enough and in some years yield reduction is considerable. It will be crucial to learn from the local farmers about their specific problems with wild Sorghums.

A case by case view needs to be applied, it will also include local agricultural management tradition. S. bicolor offers an excellent example of the sympatric association and interaction of a crop-wild-weed complex of a species in an agro-ecosystem. The nature of genetic interaction among forms of the taxa and the consequences of these exchanges depend not only on the power of the genes involved but also on several other associated factors. Many of the African landraces are autogamous. Prevalence of wild relatives naturally varies from region to region based on extent of inherent genetic diversity, existence of selective pressures, and the farming systems in the region.

2b.24.3. Assessment projects for gene flow summary

Two methods are proposed for the assessment of gene flow for the AHBFI-Project:

Marker gene based assessment with field data
Marker genes will be selected and tested in field experiments in order to quantify gene flow in real time and real field situations.

Morphometric assessment of hybridization dynamics with field data
In gradients of gene flow in the field morphometric data allow to trace down gene flow which produced hybrid progeny, a data set relevant to agricultural reality.

For the chapters of the full document, see the interactive contents index
and the interactive list of figures at the beginning of the document

A chapter with several Sorghum bibliographies is appended

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