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Fondation pour l'agriculture
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RECONNUE D'UTILITE PUBLIQUE

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Sommaire

FARM

What are the prospects for genetic improvement in drought-tolerant crops?

This study seeks to answer the following question: "What are the prospects for genetic improvement in drought-tolerant plants?". The objective is to yield an update of the strategies, in research and development, in order to provide farmers with plants showing a better drought tolerance potential compare to the current varieties.

The approach is based on facts and is also prospective. Based on facts, for the authors are intent on making as precise an account as possible of the information they have gathered. It is prospective, because drought-tolerance research is still in its infancy. At the time this study was launched, no new variety primarily claiming such an advantage was being commercialised. However, this issue itself attracts considerable scientific investment in both public and private research.

Introduction

The topic of drought tolerance was selected because of how crucial it is to farming. There is a chance that drought will be one of the major consequences of climate change for a significant part of the planet, whether it is the tropics or the temperate zones in Europe and North America. Drought is also the constraint with the most severe repercussions which most farmers worldwide are being subjected to year after year. Ever since the inception of farming, Man has learned just how precious water is for plant growth and for agricultural production as whole. There are several ways of overcoming drought. This study will attempt to clarify one of those solutions, which is based on improved plant genetics.

A survey among laboratories

This study results from a survey conducted among the main players working on plant technology. Of course, identifying plants able to maintain their growth despite lack of water is nothing new and has been part of improvement criteria for as long as Man has been domesticating plants. There are many programmes aiming at extending faming periods or areas, and at better dealing with climatic hazards. Yet recent advances in biotechnology have offered greater analytical power. That is why our approach has been to go and take a closer look, with the researchers themselves, and to see how this research was doing.

The survey was conducted by Laure Gaufichon, who holds a Doctorate (PhD) in Plant Biology, and by Jean-Louis Prioul, Professor Emeritus at the Institute of Plant Biology, University of Paris Orsay. The working method used involved two distinct stages. The first part was a bibliographical analysis, compiling and analysing the works that have been published. This kind of analysis helps establish a roadmap for the research and helps spot those avenues that are favoured, as well as their progress to date. The second part consisted in conducting an onsite survey with laboratories, research teams, public agencies and private-sector companies. The surveys took place in France, Kenya and the United States.

Regarding French public research agencies, FARM teams met with researchers at the National Institute for Agricultural Research (INRA), the French Centre for International Cooperation in Agricultural Research for Development (CIRAD), the Institute of Research for Development (IRD), as well as members of most entities in the Agropolis Cluster in Montpellier. Teacher-researchers at the University of Paris Sud were also interviewed. Regarding seed companies, the survey involved BASF, Monsanto, Limagrain-Vilmorin, Pioneer and Syngenta. In addition to a number of meetings and visits that took place in Europe, a two-week mission to the United States helped gain access to private laboratories. The work of international agricultural research centres (CIRAD), and members of the Consultative Group on International Agricultural Research (CGIAR), was also analysed. A mission to Kenya allowed have discussions with national research institution officials about programmes linking them to private-sector companies with support from the Bill and Melinda Gates Foundation.

The study focuses on cereals for temperate and tropical zones

The study provides a wide panorama of current research and its development prospects. It does not claim to be exhaustive, but it is probably the most up-to-date field-based survey available. Results show the fundamentals about work underway in France, the United States and Africa, and through the seed multinationals, it indicates the basic avenues of research being followed in the private sector. It has little information about research in Asia, particularly China and India, and about Latin America, other than what appears in science publications.

The study has given priority to cereals, which are the foundation of human food. Indeed, those species get the largest share in science investment. Within the list, including maize, wheat, rice, sorghum and millet, maize itself is far ahead of the others. It is in fact one the favoured plants for private-sector companies.

From a geographic standpoint, the survey took into account all climatic zones. Similarly, it looked at both developed and developing countries. Ecological conditions and the way farming is organised are a major component in research strategy. Moreover, the deadlines pertaining to research programmes give some idea of how long we may have to wait before new varieties are disseminated.

Generally speaking, the study strives to describe the facts in the most direct way possible. Yet what is shown here is a structured, organised report which is intended to be read; it is not a verbatim account of the meetings. The writing sticks to scientific, technical facts, which it avoids concealing behind musings that are beyond science and technology. Accordingly, the survey gives equal treatment to the various means of plant breeding, whether conventional breeding or transgenesis.

The report comprises four parts

The first part is a reminder of definitions and of the issues surrounding drought with respect to farming. It re-establishes plant improvement within the wider context of the various options available to farmers to confront the risks and consequences of drought, especially the use of sturdy farming systems or the provision of water through irrigation.

The second part shows the biological mechanics that explain plant sensitivity to water stress. Indeed, all development steps do not have the same vulnerability, and the resulting impact it can have on plant growth, blossoming, or fruit development differ. But those mechanics also give plants greater ability to adapt. The study looks at physiological reactions and at modifications in gene expression, providing the scientific explanations required for a good understanding of the relations between phenomena.

The third part explains the various avenues of research available at this time to geneticists and breeders. This report highlights the progress made through gene sequencing and molecular marking. Biologists now enjoy huge analysing power for genetic resources, which helps save valuable time in matching plant phenotypical traits and genomes.

The fourth part yields a state of the art of the research, species by species, showing acquired results and prospects. Readers who do not wish to go into the technical details of previous chapters may go directly to this chapter.

Major facts

Several observations stem from this analysis. The first relates to the importance of genetic resources (germplasm). Genetic diversity remains the prime capital. Assessing these resources using the modern tools of molecular biology represents a major step.

The second observation is that maize is the plant that is studied the most. Two varieties with drought-tolerant potential will soon be put on the market, one stemming from conventional breeding, the other from transgenesis. Both are intended for the North American market. However, this research will be useful for farmers in Africa where a specific international research programme has united seed companies, national and international public research organisations and American foundations.

The third observation is that progress will be gradual. New varieties are not a silver bullet but represent one small step in the long-term fight against drought. The creation and distribution of drought-tolerant varieties has only just begun . Tests carried out on both the initial varieties soon to be sold in the United States show they can achieve a gain in the order of 6% to 10% under drought conditions. This is encouraging. Yet the fact remains that farming practice is a fundamental factor in tapping into this potential, and that seeds are but one of the factors in farming systems.

The fourth observation concerns the global stakes underlying this research. Its impact in terms of a secure food supply and the adjustment to climate change is considerable. This research is being assigned substantial means by private-sector companies. They are mostly targeting crops with reasonable business potential, although the advances will ultimately benefit farmers in poorer countries. Public research both in the North and South have taken on decisive responsibility for less commercial crops like rice, sorghum or pearl millet. This is an international issue concerning their missions in the public interest. Drought tolerance is one of the major challenges for the future of the planet. It deserves an ambitious, integrated international approach on the level of a worldwide research and development programme supported by the international community.

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① Drought: definitions and farming-related issues

A. Definitions of drought

The term "drought" encompasses a variety of notions. We shall therefore make a distinction between an "occasional" lack of water (drought) and a structural shortage of water (aridity).

Drought describes a non-systematic shortage in rainfall, designated by how much it deviates from average or standard pluviometric values, using the following quantitative aspects:

- Duration (an intermittent or extended drought);
- The period of occurrence;
- The geographic spread;
- The momentum of occurrence (sudden or gradual);
- The time of occurrence as it relates to crop-growing cycles, in terms of its consequences on farming.

Aridity is a systematic shortage in rainfall. It is a structural condition. It concerns part of the areas on the planet that are poorly conducive to farming activities. In regions known as arid, the rainfall is lower than the potential evapotranspiration There are a host of indices and formulae to designate aridity, some of which use climatological criteria, others bio-geographic criteria.

One useful "representation» of aridity is the following aridity index (FAO, 1992): P/PET, where P is for precipitation (rainfall) and PET for potential evapotranspiration, calculated using the Penman method, taking into account atmospheric humidity, solar radiation and wind.

- This index helps define three kinds of arid zones: hyper-arid, arid and semi-arid.Hyper-arid zones (0.03 aridity index): annual rainfall rarely exceeds 100 millimetres;
- Arid zones (0.03 to 0.20 aridity index): rainfall is extremely variable, with annual quantities ranging from 100 to 300 millimetres;
- Semi-arid zones (0.20 to 0.50 aridity index): annual rainfall ranges from 300-600 to 700-800 millimetres with summer rain, and from 200-250 to 450-500 millimetres with winter rain.

Taking the world's total land surface area, hyper-arid zones represent 4.2%, arid zones represent 14.6% and semi-arid zones 12.2%. Thus we see that close to one-third of the world's total land surface area is made up of arid land.

Beyond just the pluviometric shortages, we can distinguish the following:

- "Edaphic" or agricultural drought, caused by insufficient quantities of water in the superficial ground store during the growing season. **This occurs**

when poor ground humidity, combined with water scarcity, halts plant growth, reduces yields and endangers cattle. This is the standard drought in farming, caused by insufficient rainfall during the growing season.

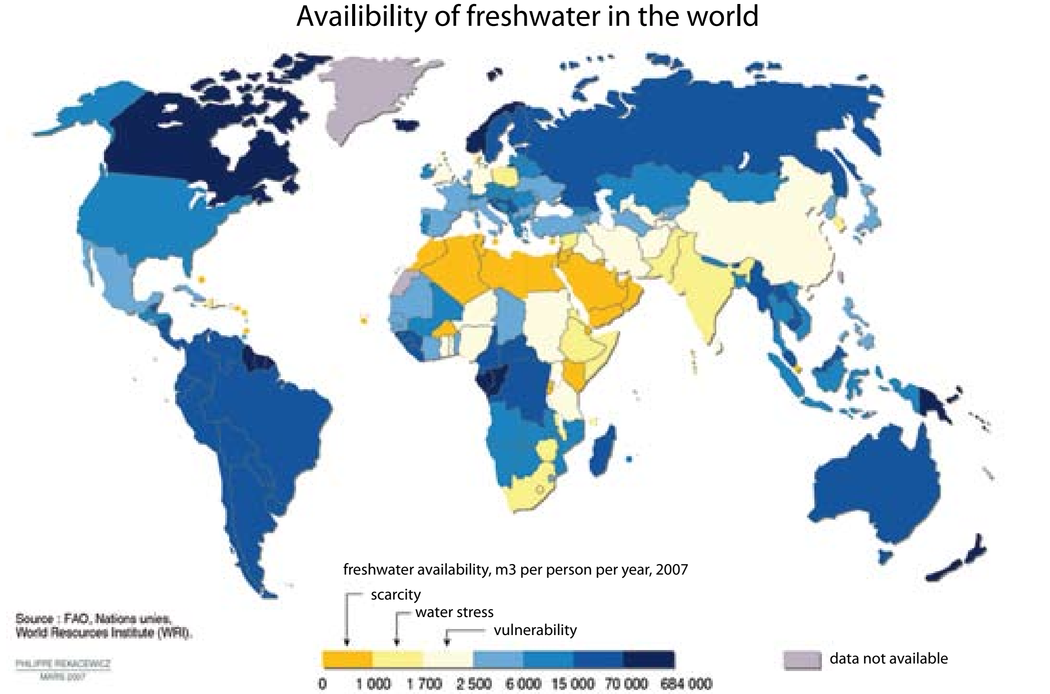
- “Hydrological” drought, caused by a deficient replenishment of hydrological reserves, which is rather the result of insufficient rainfall outside the growing season.
- Drought represents a risk whose frequency, scale, duration and date of occurrence cannot be forecast. Drought is a definite risk whose occurrences are unpredictable. Farmers have therefore developed preventive or hedging strategies to confront that risk.

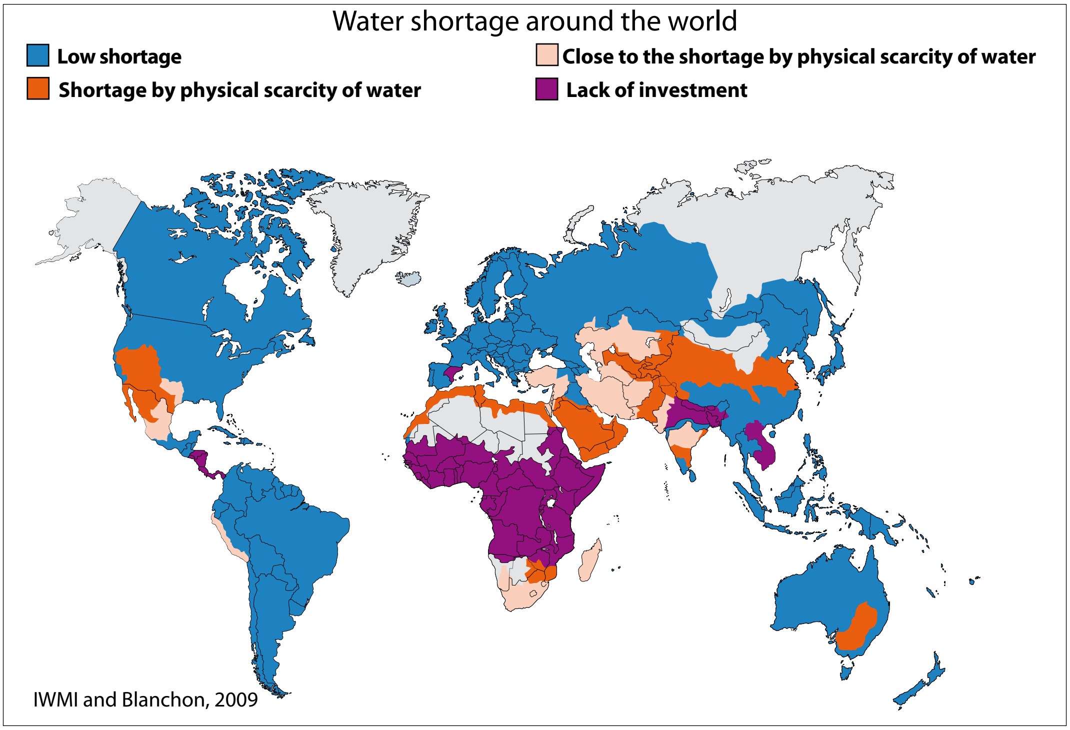
B. Freshwater is a natural resource that is unevenly spread across the planet

Freshwater is a natural resource that is unevenly spread worldwide, in terms of both space and time. On average, freshwater availability is of 6,500 cubic metres per inhabitant per annum on a worldwide scale, which is a sufficient quantity to satisfy human needs and preserve the ecosystem (Blanchon, 2009). There are however substantial discrepancies from one geographic zone or country to another. A zone is considered to be in a situation of water stress if freshwater availability is below 1,700 cubic metres per inhabitant per annum, and in a situation of water scarcity if below 1,000 cubic metres per inhabitant per annum.

We can thus see the outlines (see figure below) of a belt of scarcity stretching from Morocco to Pakistan and India, along the southern Mediterranean coast, extending down Africa’s eastern seaboard from Somalia to South Africa. The rest of Africa is relatively well-endowed, as are North and South America and Oceania. The European situation is mitigated, with some well-supplied

Availibility of freshwater in the world





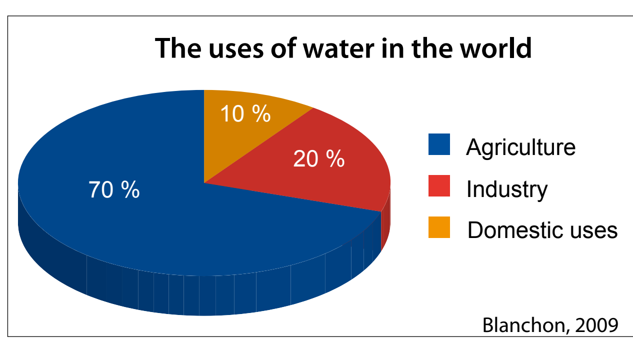
states (Norway) and others where conditions are more difficult (Denmark). China is less well-endowed than its South-East Asian neighbours (Thailand, Vietnam). Although it hosts 60% of the world population, Asia holds only 33% of world freshwater resources.

Water scarcity is a more complex, relative concept depending on conditions of access (see figure above, and Troy et al., 2008). These vary from region to region. The physical scarcity of the resource is a reality in North Africa, where the various uses altogether withdraw over 75% of surface water resources (Comprehensive Assessment, 2007). Some regions in the world, including West Africa, are facing economic scarcity: there is enough water, but its access is limited by the lack of sufficient means to exploit it.

In addition, water has to be shared between domestic needs and, in the first place, drinking water for humans, and agriculture and other uses, especially industrial.

On a world scale, agriculture is the sector that uses the most water. But the breakdown of water uses varies from one continent to the next. It reflects the level of development. Thus in poorer countries agriculture uses 82% of water resources while industry only takes 10%, illustrating their modest industrial development. In high-income countries, agriculture withdraw 30% of water resources and industry 59% (World Water Development Report - Water for People, 2002).

Freshwater as a resource is scarce, poorly distributed and costly. Urbanisation and economic growth will increase the need for domestic water, and the degrading climate will exacerbate fears of scarcity. Reducing water use in agriculture is therefore becoming a worldwide challenge.



C. Climate change will heighten the risks of drought for the most vulnerable agricultural environments

The foremost consequence of climate change looming over tropical and Mediterranean farming is an increase in the chances of drought. There is quasi-unanimous consensus regarding the truth of global warming (a rise in the average temperature of the Earth's surface). Its effects on agriculture can already be seen: the earlier flowering season in orchards, vineyards, harvesting, etc. is an illustration. These rising temperatures have a direct impact on the demand for water (an increase in evaporation through a growing deficit in air saturation), and an indirect impact on the crop development cycle (a longer vegetation period for perennials and a shorter cycle for annuals, etc. (Amigues et al., 2006)).

Regarding changes in rainfall levels and distribution in space and time, prediction models are less consistent than they are for changes in temperature. Available scenarios rather tend to forecast sharper regional and seasonal differences, as well as heightened risks of the occurrence of extreme events.

Accordingly, the IPCC (2007) expects a rise in temperature of between 1.1 and 6.4°C by 2090–2099 as compared to 1980–1999. The impact on water and agriculture worldwide is shown in the table below.

In France, with respect to the water supply of crops, the main reason for concern is the expected drop in summer rainfall, especially in the South, which would exacerbate the risks of edaphic drought. Yet there is no way of knowing whether the drop in rainfall will be evenly distributed over the years, or whether it will amount to more years of substantial drought than in the past (Amigues et al, 2006).

In Africa, global circulation models indicate that the African climate will be more changeable in the 21st century. Experts fear a rise in the occurrence of extreme events, particularly during periods of drought. For agriculture, climatic deterioration would also involve more variances in the duration and starting date of the rainy season (Troy et al, 2008). Climate changeability is already a major concern in many regions: for instance, the Niger River's average annual flow has been cut by half between the 1960s and 1980s (Blanchon, 2009).

The fact that farming in poorer countries should adapt to climate change should be seen as the international community's responsibility. This actually is one of the issues in climate negotiations. Yet such an adaptation depends first and foremost on controlling the consequences of drought. This is why the needed investments should be committed as quickly as possible, whether they involve research or land settlement and hydro-agricultural works.

D. Good farming practice contributes in fighting drought

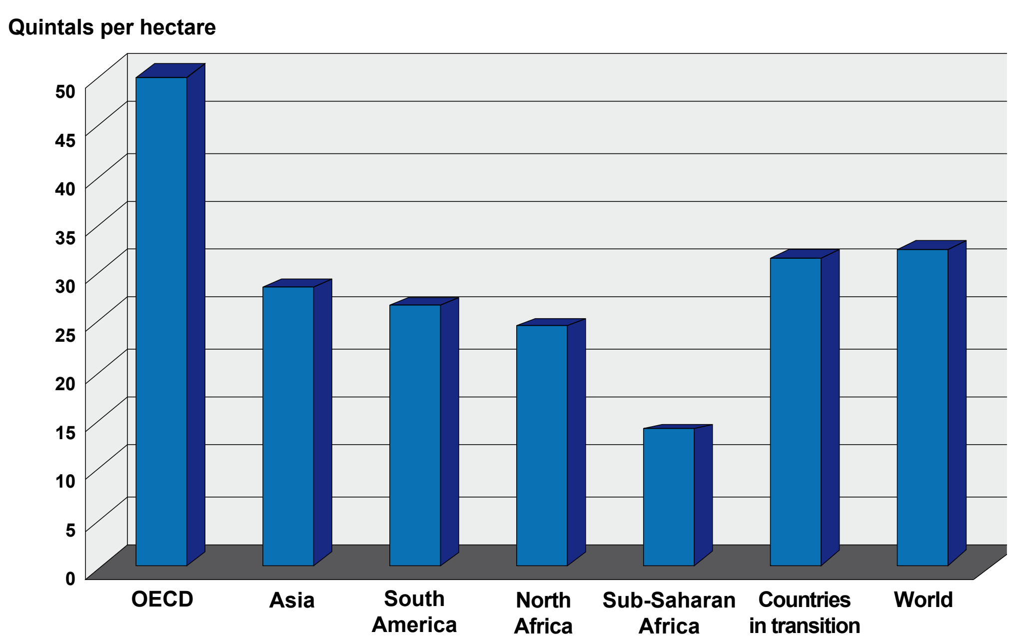
The consequences of drought vary considerably depending on how intensive the farming is, as well as on farming practice. Cereal yields, expressed as an average per continent, range from 1.3 tonnes per hectare in Sub-Saharan Africa to 5 tonnes per hectare in industrialised nations. But those averages conceal much wider regional discrepancies of a factor of 1 to 10, ranging from under 1 tonne per hectare in pluvial farmland in the Sahel to over 10 tonnes in some parts of Europe.

Losses due to lack of rain during the growing season could amount to the loss of the entire harvest in Africa. On the other hand, using inputs, together with the possibility for irrigation during rainy periods, help achieve reasonable yields. For instance, proper control of maize cultivation in Burkina Faso or in Mali can lead to yields in the order of 3 to 5 tonnes. Such low intensive farming achieves the highest gains with multiplying factors ranging from 3 to 5.

Farming practice represents the frontline protection against drought. The techniques used mostly aim at strengthening the ability of soil to maintain its fertility in the event of a drought, which leads to:

- Managing soil balance through chemical and organic fertilisers ;
- Fighting erosion by any means and techniques that can help protect soils and reduce evaporation, especially through direct seeding and cover crops ;
- Crop combinations, often practiced in subsistence farming in the tropics, represent a hedging method against the risk of drought through a principle of mutual compensation between species ;
- Choosing sowing dates so as to use the least risky growing period ;
- Techniques such as Zai, a traditional method used in the Sahel. Zai is based on the making of holes or pits filled with manuring to retain water and fertilising elements.

Cereal yields in the world



Ref : FARM, based on FAO, 2006

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Sowing under cover crops

The practice of sowing under cover crop reduces loss through evaporation and helps preserve a stock of water in the ground. The method consists in doing away with ploughing and keeping harvest residue, or even using cover plants that will fix atmospheric nitrogen, such as legumes. The soil cover represents a protection that can reduce or even put an end to erosion. Water infiltration is facilitated rather than runoff. In addition, the plant cover improves the soil's organic balance and increases its ability to retain humidity. These techniques started out as early as the 1930s in the United States and Latin America. They have experienced a considerable boom from the year 2000 since their use went from involving 62 million hectares in 2000 to 100 million hectares in 2005 (Bollinger et al, 2006). Those techniques are key elements in so-called conservation agriculture. However, the fight against weeds makes it necessary to use herbicides, with their resulting costs and dependency. In fact, direct sowing under cover is a complex farming practice. Its use requires a comprehensive modification in cultivation systems and work organisation. It implies having proper access to inputs. The technique may cause a drop in yield during the initial years if all conditions are not met. For all of those reasons, its dissemination in Africa is impeded.

Generally speaking, farming practice contributes in fighting drought since it aims at achieving two major objectives: improving soil water storage and attaining the right edaphic conditions for adequate plant growth. "Healthy" plants will have better resistance against water stress. Yet their biological potential is not affected, and that is precisely the objective of genetic improvement.

E. Irrigation is essential but not sufficient to feed the planet

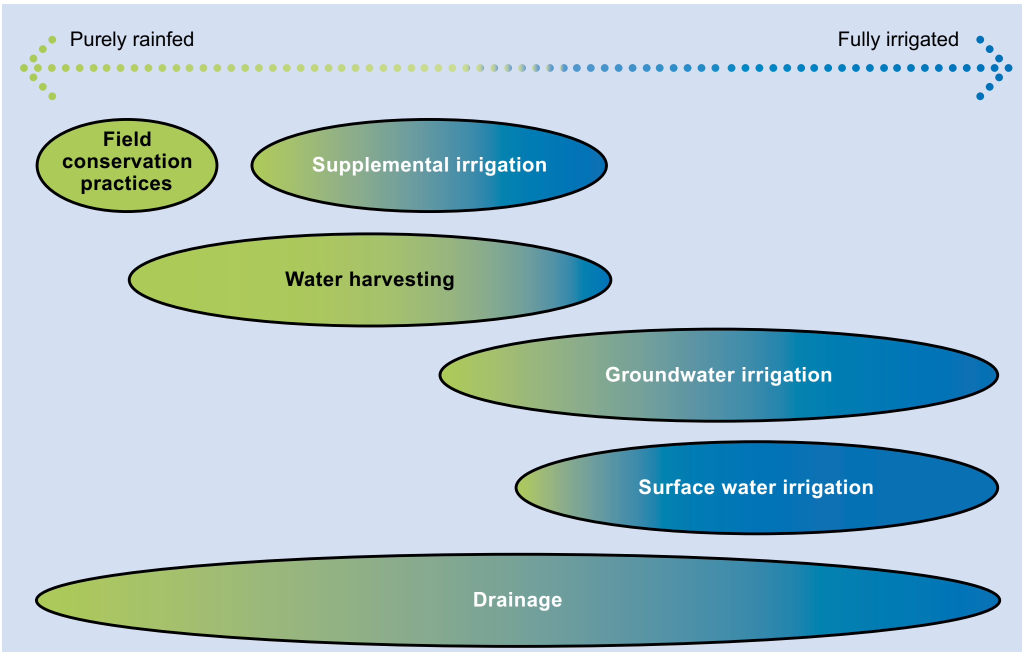
Rain fed agriculture (without irrigation) supplies 45% of agricultural production over 1,100 million hectares that have no irrigation or drainage system. 15% comes from the 130 million hectares cultivated under rain fed farming and using a drainage system.

Irrigated farming uses up 270 million hectares, representing 18% of cultivated land, but produces 40% of the world's food supply. Irrigation uses on average 70% of the world's freshwater, compared to 20% for industry and 10% for drinking water. To meet increasing demographic pressure (9 billion people by 2050), it is estimated that irrigated land in developing countries will have to expand by 40 million hectares by 2030 (Troy et al, 2008). This expansion will mainly have to occur in Sub-Saharan Africa where surface areas should double, and in Latin America.

Agricultural water management is a continuum that goes from rain fed farming to large scale irrigation schemes, including systems irrigated by surface or ground water, supplemental irrigation, water harvesting techniques and drainage (Comprehensive Assessment, 2007).

Catchment management and local works such as contour bunds open up possibilities for irrigation on a village scale. Similarly, using supplemental irrigation in the event of drought episodes during the growing period can help salvage a harvest.

The management of agricultural water



Ref : Comprehensive assessment 2007

Moreover, there is great potential in managing water more efficiently between the various users. Such management can take the shape of agreements on water allocation negotiated between all stakeholders and concerning the catchment area. Setting up agricultural water users associations is an important step in structuring the management of agricultural water requirements at the catchment scale.

F. Indexed insurance initiatives to cover the risks linked to drought

The consequences of drought are not the same depending on whether a farmer is rich or poor. The way in which climatic hazards are handled varies according to the economic and institutional background. The disparities between farming in developed countries and farming in poor countries can be expressed in terms of access to information, access to inputs, access to capital and the existence or not of safety nets. Beyond the availability itself of water resources, their use is conditioned by what means there are to exploit them. Besides, European and American farmers have access to a wide range of information about the climate and to technical advice.

But another thing separating the poor from the rich is the existence or not of schemes for insuring against climatic hazards. Developed nations are in a position to launch exceptional public compensation measures in the event of natural disasters. In addition, there are increasing numbers of harvest insurance schemes depending on private management and on individual, conscious decisions on the part of farmers.

The lack of such systems in Southern nations has led various players to launch individual insurance initiatives in those countries. Indexed insur-

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ance is insurance that is linked to an index such as rain, temperature, humidity or the harvest yield. The most widespread application in developing countries is to use an index of pluviometric sums to insure against harvest losses related to drought. According to Olav Kjorven, Assistant Administrator and Director of Bureau for Development Policy for UNDP, "Only a fraction of three percent of the world population is insured today. The poor in this world have been completely neglected, although they are precisely those who are the most vulnerable, and who need protection the most. Drought, floods and hurricanes often strip entire communities of their goods and resources. Indexed insurance could, at long last, allow millions of poor people to be better prepared for climatic disasters and recover from them faster."

Within this context, a few insurance projects based on climatic indices are being developed in the South.

Indexed insurance offers several benefits. It is accessible to small producers in developing countries. It can be managed by private insurers while enjoying public subsidies. It is based on objective facts that are available to all, and it improves the spread of information. It opens access to credit.

Those schemes are risk coverage tools. They thereby contribute to the spread of innovations that always carry an additional risk. Their spread would represent a considerable advance which could foster investment into the other kinds of technology, whether irrigation, fertility or improved varieties.

Indexed insurance

BASIX is an Indian microfinance institution which started a drought micro-insurance scheme in 2003. It covers expenses released for a year's harvest. In 2008, close to 10,000 insurance policies were sold. Compensatory damages, capped at about thirty Euros, are paid out by ICICI (an Indian bank) and Lombard (a Canadian insurance company). The products being insured are mainly peanut and castor bean. In 2004, premiums ranged from €6.9 to €8.6 per hectare.

The SYNGENTA Foundation launched the Kilimo Salama initiative. Kilimo Salama is an insurance product for farm inputs, which has been developed in Kenya since 2008 to protect producers against drought and floods. 200 producers signed up in 2009, rising to 11,500 producers in 2010. They purchase their inputs in a store belonging to the programme, paying a additional 5% which represents the insurance premium. Reimbursements are triggered automatically on the basis of data collected from weather stations and transferred via an electronic payment system on to an appropriate mobile phone provided at the time of taking out the insurance (the M-Pesa mobile payment system).

An indexed micro-insurance scheme was established in Malawi through the work performed by the Commodity Risk Management Group (CRM) and is used to prefund seeds. If the rainfall is insufficient, the producers are not obliged to reimburse the credit they were granted for inputs. The premium is around €4.9 per hectare to insure a €25 credit for inputs. In 2006, this scheme involved 1,700 producers. It was originally meant to insure coffee and peanut crops, then maize. The scheme insures both the producer and the seed supplier.

Harita is a pilot project established in Northern Ethiopia and funded by Oxfam America. Confronted both with the lack of climatic data and with the fact that the poorest are unable to pay the insurance premium, the Harita project allows producers to work for a few extra days to earn the extra to pay for the premium. The insurance concerns teff, a local cereal, and covers against drought. Producers also get increased access to products from local microfinance.

So there are four main ways for farmers to guard against drought. Farming practices, the provision of water through irrigation and indexed insurance are the first three. Using improved varieties for this purpose is a fourth way, and will be the topic for the remainder of this report.

② To die of hunger or to die of thirst, why do plants need a lot of water?

This chapter will show the biological mechanisms that explain how and why plants are so sensitive to water stress, as well as their adaptability. Water requirements differ according to the species and the stages of development involved.

A. Plant sensitivity to water stress is closely related to the stage of development and the species involved

Generally speaking and during their vegetative development, the quantity of water being used by crops is similar from one species to another when they are subjected to the same climate. Accordingly, crop water use mostly depends on how long their cycle of development is and on what climatic events happen during that cycle. However, plant species' sensitivity to drought is uneven. This depends on the general way in which the plants function, at what stage of development water stress happens, and on the cultivating methods the farmers have used. Within the framework of this study, we chose to focus on cereals. It is possible to rank them according to their sensitivity, or their tolerance, with respect to drought:

- Some species, like wheat, whether the winter or spring variety, are not particularly tolerant to water deficit, but since their growing cycle mostly happens in autumn and winter, their exposure to water deficit and therefore to water stress, is low. So they are considered as using water efficiently since climatic requirements are low during their development cycle;
- Other species, whose growing cycle runs in spring and summer (in a temperate climate), have intrinsic tolerance to water stress, whether it is during the development of their vegetative system or during the appearance of their reproductive organs. This is the case with barley and sorghum, which can be grown without irrigation;
- Lastly, the case of maize should be considered apart from other cereals. Although it is highly efficient in the way it uses water, thanks to its growth potential and to response mechanisms that are especially effective whenever it is subjected to water stress during vegetative development, maize is extremely sensitive to drought during flowering and grain formation. This is the paradox that justifies both irrigating this crop in cases of frequent risk and the research efforts focussing on its tolerance to drought.

The impact of drought on yield therefore depends both on the species concerned, and so on its genetic potential, and on cultivation techniques that are often related to local growing conditions and to the existing climatic scenario. In the course of evolution, plants have worked out strategies to protect themselves against moderate water stress by setting up a series of responses to simply help them survive and ensure their line of descent. Those responses follow three kinds of strategy:

- **Evasion** is an adaptation to the environment allowing plants to avoid periods that are critical in their development. Farmers use this plant strategy to position the growing season within periods where conditions are favourable. For instance, the idea is to avoid summertime cultivation, or to develop varieties with a shorter development cycle in order to avoid those periods in the year that are the most stressful to plants. Evasion only makes sense on the scale of farms and cultivation systems;
- **Avoidance** helps plants to limit the impact of stress through adaptations such as leaf wilting or curling. This strategy promotes survival at the expense of productivity;
- **Tolerance** helps maintain cellular functions that are critical to survival through specific, targeted responses.

Generally speaking, one only rarely sees plants dying from drought within a farming context. Farmers know the average risk for a given plot under a given climate, and so adapt the crops they grow and adapt the cultivation methods accordingly. Yet the determination to extend plant cultivation beyond those geographic zones that meet optimal environmental conditions, together with the intensification of instances of drought in some parts of the world, demand a change in cultivation techniques and the development of varieties that are better adapted to local cultivation conditions.

B. Water efficiency

Plant water use efficiency is defined as the ratio between the biomass produced and the water transpired. Efficiency can vary, particularly according to the species and to the climate. Crops with the highest water efficiency are maize and sorghum.

Total water requirements of some plants (rainfall and irrigation)

Plant	Water uptake (L/kg DM)
Maize*	238
Banana	346
Maize (grain)*	454
Barley*	524
Potato*	590
Wheat*	590
Soybean	900
Upland Rice	1600
Flooded Rice	5000

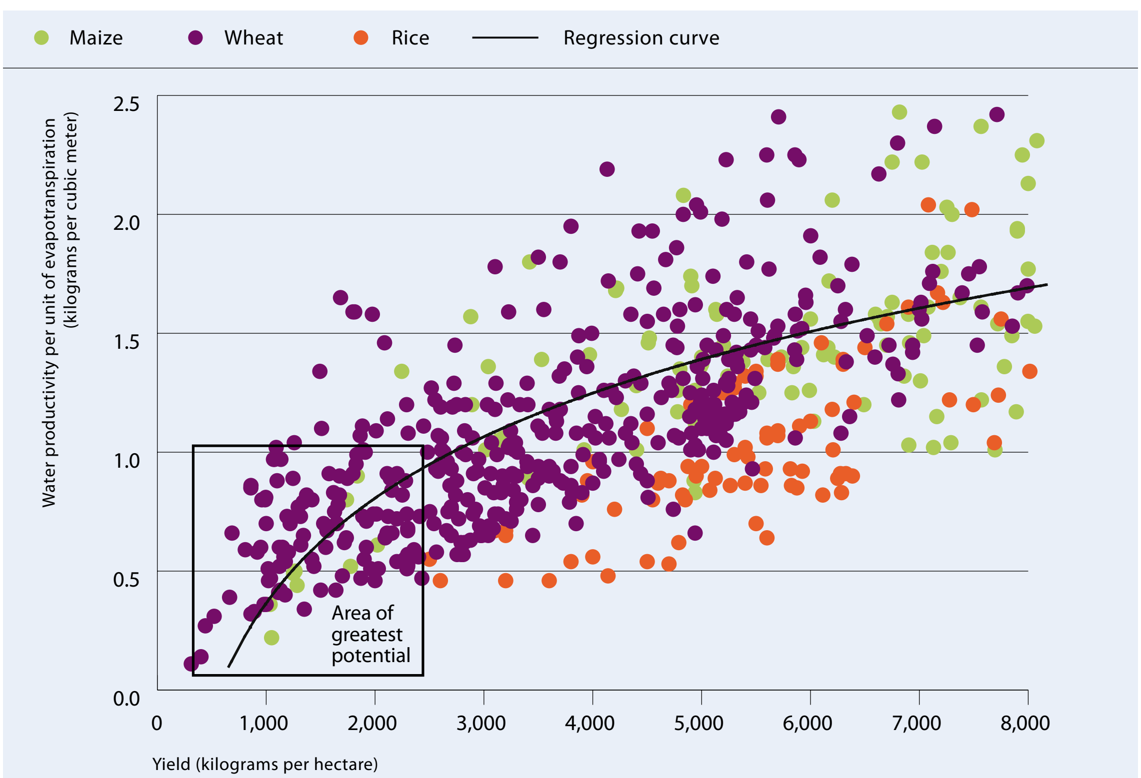
** in temperate areas*
Ref : AGPM-Info Technique-N°353, December 2006.

This concept is similar to that of water productivity: by definition, water productivity is the ratio between the product and the water used during the production process. Strictly speaking, the product is the consumable biomass produced, expressed in terms of mass, in terms of energy content or market value.

The following table shows the water consumed by various plants to produce one kilogramme of dry matter, meaning the opposite of water efficiency.

One of the most powerful levers for boosting water productivity is to increase low yields (i.e. below 2 tonnes per hectare, Schultz et al, 2008), for instance through better fertilisation. If all yields were above 2 to 3 tonnes per hectare, on the basis of constant worldwide production, water use worldwide would be reduced by about 1,500 cubic kilometres per annum (against 4,000 cubic kilometres withdrawn by all sectors in 2000). The reduction is related to a better ground cover by leaves, and so a better water interception by plants and lower evaporation. Low yields are a priority target, because the gain in water productivity in cereals is higher when yield is around 1-tonne per hectare than for yield around 2 tonnes per hectare or more, as shown in figure below.

The potential increase of water productivity is higher for low yields agriculture



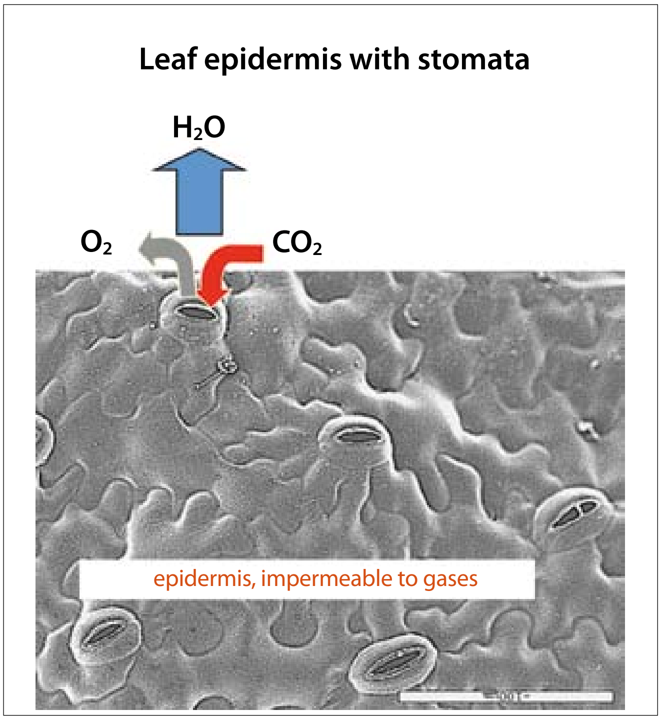
Source: Adapted from Zwart, S.J., and W.G.M. Bastiaanssen, 2004, "Review of Measured Crop Water Productivity Values for Irrigated Wheat, Rice, Cotton and Maize," *Agricultural Water Management* 69 (2): 115–33; chapter 7.

Comprehensive assessment 2007

C. Plants have, like all non-aquatic organisms, worked out water loss reduction mechanisms so as to maintain a water-rich inner medium, while at the same time allowing the atmospheric CO2 input vital to photosynthesis and so to growth

1. A plant is a "water pump": 300 to 500 litres of water are needed to fix one kilogram of carbon!

Plant tissue is mostly made up of water. The water content may vary from one species to the next: from 78% of total mass for potatoes to 95% for lettuce. Plants draw water from the ground, together with the nutrients required for their growth, thanks to their roots. Contrary to animals, plants do not have a central pumping system to circulate water through the tissue, but membrane ionic pumps and carriers that participate in moving water around. The water and nutrients constitute the sap, known as raw sap, which is taken from the roots to the shoots through xylem vessels using the leaf transpiration process. Transpiration is a plant-specific water "evaporation" that occurs through the stomata, small pores spread across the leaves' surface, and it helps the water rise from the roots to the stems and leaves. This phenomenon originates from a powerful aspiration which depends on the difference in water potential between the soil and the air. Water potential defines the water's bond energy. Put more simply, it is the energy needed to bring a water volume unit to a free state, meaning a liquid and pure state. It is expressed in pressure units (MPa). Thus, on the scale of the plant, water circulates from the ground, where water potential is poorly bonded, meaning the water is almost in a free state, to the shoots where it is discharged in the air. The intensity of transpiration is such that the amounts of water stored by the plant or used in its metabolism are insignificant when compared with the amounts it absorbs: the mass of water found inside a plant at a given moment in time is low compared to the flow of water that transits through it in a day.



Leaf transpiration occurs through microscopic pores called the stomata. Stomata consist of two cells, called guard cells and which delineate a pore, the ostiole. They are unevenly spread on the upper and lower side of leaves, and their density varies from one plant species to another (from 50 to 500 per mm^2 of leaf). Ostioles help gas exchange between the plant and the air. Therefore, **stomata are the seat of both water output, that is to say transpiration, and carbon dioxide (CO_2) input**. In leaves, CO_2, the mineral form of carbon, is used in photosynthesis, a process that leads to the synthesis of carbohydrate components, like sugars, used by cells in their functioning. This series of reactions is called carbon assimilation. It is easy to understand that since water output and CO_2 input in leaves occurs through stomata, transpiration and carbon fixation are two closely related processes. One should add that the incoming flow of CO_2 is very small compared to the outgoing water flow, since it takes about 500 grams of water to fix 1 kg of CO_2.

2. A plant adjusts the amount of grains it produces to its capacity for growth: the early reproductive phase is therefore particularly sensitive to all forms of stress, for this is a natural adaptation

Plants are static organisms. Yet this basic statement conceals complex workings and a need to adapt, since plants cannot escape the environmental constraints they are confronted with. Plants therefore have to adapt their metabolism and physiology to the availability of nutrients in the soil, to soil salinity or even, among other abiotic constraints, to thermal stress and drought. A plant's growth capacity depends on its cultivation conditions.

Plants have evolved by favouring the formation of seeds that are viable for the continuation of the species. It is important at this point to define the concepts of sink organs and source organs. In plants, the development of a new organ, say a root or a bud, requires the importation of photosynthates such as sugars or nitrogenous components, such as amino acids, which come from organs known as source organs, like adult leaves. Grains are importers, so as such they are sink organs. This means that in the event of stress, causing a reduction in photosynthesis (a source function), the plant's priority is to preserve its capacity to produce at least one viable seed. So it implements an abortion process for those seeds that will not be filled owing to insufficient resources. Accordingly, since the amount of grains a plant produces is related to its capacity for growth, the yield depends to a large extent on what kind of environmental conditions the plant is subjected to, whether it is during its vegetative development (the growth of stems and leaves) or during the appearance of its reproductive organs.

D. Plants have a host of physiological mechanisms for adapting to drought

Plants are able to set up a whole series of physiological responses to help them act upon their own water status so as to adapt to environmental conditions, to limit the effects of stress upon their metabolism and at the most, ensure their survival and their reproduction. Once drought conditions are established, one observes the following, in this order: a slowdown in growth, a modification in water movements related to metabolic readjustments, and lastly a stomata closure.

1. The growth of leaves and stems ceases, that of roots is less affected

In most species, water stress materialises through a slowdown in the setting up of new shoots, meaning the leaves and stems, and by slower growth among pre-existing organs. Those modifications occur as a result of an increased rate of cell division in the plant tissues (Granier et al, 2000) and of a modification in the physical-chemical properties of the cell walls, which become more rigid, thereby inhibiting their expansion (Cosgrove et al, 2005). Over the long term, these processes will limit the surface of exchange between the plant and the air, and so limit water loss via transpiration. Recent data show that slower growth is not a passive consequence of the lack of water in the cells, but a controlled, programmed response of the plant, the result of which is to anticipate severe events in water stress. The response is therefore preventive, and not endured.

While the shoot growth is altered in the event of water stress, the growth of roots is less affected. Indeed, a plant will favour setting up deep roots so it may access deeper groundwater resources (Wu and Cosgrove, 2000).

2. In leaves, conductivity and water availability are modified

If on the scale of the plant, water is transported from the roots to the leaves via xylem vessels, on the scale of tissues, water circulates from cell to cell using two mechanisms:

- passing freely on the surface of the walls surrounding the plant cells, known as the apoplastic path.
- using a transport mechanism allowing it to pass through the membranes, referred to in this case as the symplastic path.

It was recently demonstrated that in plants, as in animals, transmembrane water exchanges occur through pores formed by proteins found in cell membranes and called aquaporins (Luu and Maurel, 2005). In the event of water stress, the opening and distribution of aquaporins among the membranes is modified, which helps to modulate the route taken by the water among the tissues or organs (Zhu et al, 2006) and to adapt water conductivity within the plant to the water which is available in the soil.

For the proper functioning of plant cells, water has to be under pressure therein. This phenomenon is called turgor pressure. In the event of water deficit in the soil, the plant tissues may lose water. Yet the plant is able to maintain cell turgor pressure thanks to the controlled accumulation of molecules called osmoprotectants. These are, among other things, amino acids, sugars or even ions (Zhang et al, 1999, Abebe et al, 2003). This phenomenon is osmotic adjustment, helping maintain a correct cellular volume despite the water loss caused by water stress.

3. Stomata close and photosynthesis diminishes

In the event of water stress, a signalling mechanism allows the plant to close its stomata. The immediate result is a reduction in water loss through transpiration and an improvement in the cells' water status since the roots can, provided the stress is moderate, continue absorbing water from the soil. However, since the stomata also allow the input of carbon dioxide used through photosynthesis in synthesising organic carbon compounds, this adaptive plant response to water stress will inevitably have a significant impact upon the plant's general metabolism and, should the stress persist, upon biomass production and so upon plant productivity.

E. Molecular mechanisms responsible for physiological responses to drought in plants

Research conducted for years on plant response to drought can help us gradually identify the active molecular mechanisms behind those adaptations.

1. Water stress causes a change in the expression of numerous genes

The physiological modifications mentioned earlier are based upon the setting up of coordinated cellular responses as a reaction to a specific stress, namely water stress. Those responses imply some signalling process that from stress detectors called receptors, will trigger a signal making the synthesis of proteins required possible synthesis in the adaptation process.

The proteins are coded by the genes, meaning that a given DNA (deoxyribonucleic acid) sequence will contain the information needed to synthesise a given protein. Protein synthesis is the result of two successive readings of genetic information: the transcription of DNA into messenger RNA (ribonucleic acid), and then the translation of messenger RNA into protein consisting of amino acids. All of the genes in a given organism make up its genome and the amount of genes varies from one organism to another, but in so-called higher animals and plants, the amount ranges from 20 to 30,000. Gene expression can be modified according to environmental conditions (availability of water and nutrients in the soil, air temperature, etc.), as a result of being attacked by pathogens (virus, bacteria, fungi, etc.), but first and foremost it varies during the plant development cycle. For the past ten years or so, the progress achieved in molecular biology allows the quantification of messenger RNA or coded protein by each of the genes in the genome. Those high-efficiency techniques are called respectively “Transcriptomics” and “Proteomics”. It is then possible to determine the genes whose expression is augmented or diminished and so identify the proteins which are potentially involved in the plant cellular responses during water stress (Seki et al, 2002, Shinozaki et al, 2003). Several hundred or thousand genes have their expression modified by water stress (Harb et al, 2010).

2. Abscisic acid is the plant hormone most often involved in cellular response to water stress

Gene expression is controlled by transcription factors, proteins able to fix on gene promoters (DNA sequences that are upstream of the coding part) in order to regulate their transcription. These transcription factors are themselves synthesised by cells in response to various stimuli perceived by the plant, and in a “stress-specific” way, they will help block or unblock the expression of genes that code the proteins involved in the responses appropriate to the given conditions.

Transcription factors involved in the response to drought have been identified, and have helped uncover two main signalling paths. One of them involves a hormone called abscisic acid (ABA) and is produced whenever a plant suffers water stress. Abscisic acid will initiate a cascade of signalling at the cellular level involving transcription factors called AREB

(ABA Responsive Element Binding, Abe et al, 1997, Uno et al, 2000). The other path is independent from that hormone and involves other transcription factors (DREB for Drought Responsive Element Binding, Yamagushi-Shinozaki and Shinozaki, 2005). Genes whose expression is regulated by both those signalling paths will code proteins possessing a variety of biological functions, but all involved in setting up or maintaining response to water stress (Shinozaki et al, 2010). For instance, abscisic acid is an effector for stomata closure or for the synthesis of osmoprotectants (Tardieu and Davies, 1993).

A signaling pathway is initiated by the perception of a stress and results in the adaptation of plant behavior

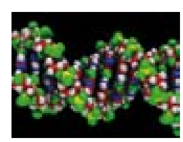
Perception of drought by the plant cells

↓

Synthesis of transcription factors (proteins)

↓

Changes in gene expression



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Changes in protein contents

↓

Morphological, physiological and metabolic responses

3. Sugars are involved in the grain abortion process in the event of water stress

Certain cereals including rice and, more significantly, maize are highly sensitive to water stress at flowering time. Indeed, a drought at that point in the development cycle will cause grain abortion. Even though the mechanism(s) behind this process has(have) not yet been fully identified, it appears that the fact that a reduction in sugars, especially sucrose, being supplied to the cobs contributes to the failure of grain development and an abortion (Boyle et al, 1991, Zinzelmeier et al, 1995). Nevertheless, the cellular signal that triggers deficiency in sugar and the abortion are yet to be identified.

In the event of water stress, the plant is therefore confronted with a delicate, contradictory situation. Indeed, perception by the plant of a water deficit in the soil leads it to set up a host of cellular responses that have a substantial impact on its functioning. The plant has to protect itself from the effects of stress by considerably modifying its metabolism while attempting to maintain its growth and production potential. There are numerous adaptive plant responses to water stress and they are based on complex cellular mechanisms involving numerous proteins and genes. It is important to understand that every one of those mechanisms can be considered as avenue possible area of research, and that the genes identified as intervening within those mechanisms are all, right down to the last one, potential candidate genes in the genetic improvement of drought tolerance.

③ Genetic plant improvement now calls upon a variety of biotechnological strategies

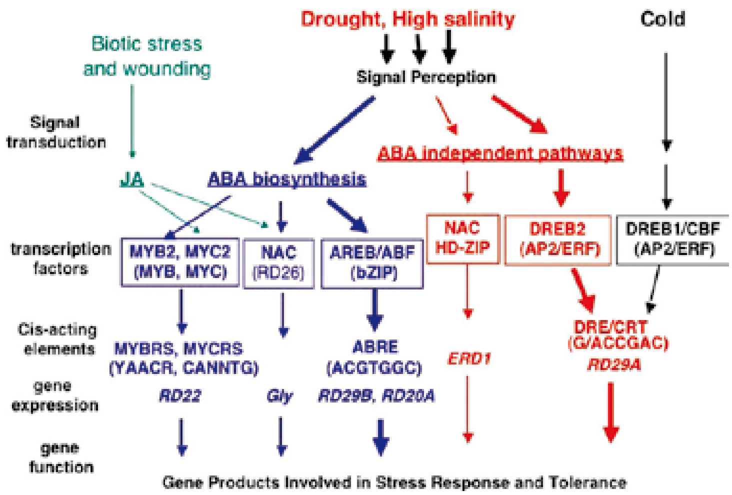
A. The past thirty years have seen considerable advances in molecular biology, leading to better understanding of the mechanisms involved in drought tolerance and to the modernisation of the tools available to plant breeders

1. Determining gene functions: transgenesis as a tool of knowledge

The possiblity of sequencing genomes in plants represents a fundamental advance in our understanding of how they work, whether it is under standard cultivation conditions or under stress conditions. Sequencing a genome consists in reading the full DNA sequences of which it is comprised and in identifying all of the genes found along those sequences. The first plant species, whose genome was entirely sequenced, in 2000, was mouse-ear cress (*Arabidopsis thaliana*). Then it was rice in 2005, followed by the poplar tomato, maize (2009), potato and lastly vine. *Arabidopsis thaliana*, a small crucifer related to rape, is what is known as a model organism. It has become a focus of interest for a host of research laboratories that use it to understand the mechanisms underlying the functioning of plants, their metabolism and their responses to biotic or abiotic constraints.

Once they have sequenced and identified the sequences of genes inside a genome, scientists aim at assigning each one a biological function, meaning they want to determine what the protein, which it encodes, actually does within the organism. This work is partly based on the knowledge already acquired through other organisms, as generally speaking certain parts of the gene sequences are highly conserved throughout the kingdoms, but also thanks to the study of the impact of the lack or the

Signaling pathways involved in plant biotic and abiotic stress responses



Source ; Shinozaki and al. 2007

overexpression of those genes on the plant functioning and morphology. Let us explain this point. Thanks to transgenesis, scientists are now in a position to knock out or to overexpress any gene from plant or other genomes within specific cells, and to assess the impact of those modifications on its behaviour under a given cultivation condition, on its metabolism or on the expression of other genes involved in the same cellular process. This approach, known as functional genomics, used on a wide scale nowadays with *Arabidopsis thaliana*, but also with rice, has helped determine the function of numerous genes among the roughly 30,000 that the genomes of both plants contain. This approach is logically applied to the understanding of drought tolerance mechanisms. It is in this way that the role of AREB and DREB transcription factors mentioned in the previous chapter have been identified, since the lack and overexpression of those genes respectively lead to poorer and better plant behaviour under water stress conditions either in A*rabidopsis thaliana* or in rice. It is also the case with genes coding aquaporins, or with genes coding the enzymes involved in the synthesis of osmoprotectants able to maintain sufficient cellular pressure for proper cell function.

The benefit of working on model plants is to have access to the most efficient genetic and molecular tools for understanding cellular and physiological mechanisms underlying the plants functioning. In the longer term, acquired knowledge can be transferred to other closely related plant species. For instance, *Arabidopsis thaliana* is an excellent model for rape, while rice represents a model for most other cereals.

B.Identifying the favourable genomic regions for a given trait

Thanks to sequencing, it is possible to “label” the genomic regions in plants which will give them the desired agronomic traits. The technique is based upon the identification of DNA sequences, known as molecular markers, whose positions within the genome are known thanks to the prior establishment of chromosome maps. Molecular markers can help determine the form of the gene, co called the allele, found in the individuals being studied. By pairing a genetic analysis of molecular markers among a set of individuals, as well as an analysis of their phenotype (observable and/or measurable traits), one will seek to detect statistically-reliable relationships between the presence of a marker and the value of the measured trait (the amount of grains, for instance). It will then be possible to conclude that certain molecular markers are within close proximity to small regions of the genome coding for some of the traits under study. These regions are called QTLs (Quantitative Trait Locus). Since this analysis is based upon the differences between individuals for the traits under study (the size of the grain, for instance), it will also help determine whether the QTL allele for those individuals is more or less favourable to the trait being studied.

QTLs may be identified through the genetic analysis of individuals resulting from crossing where traits are segregating, but also through an approach known as association genetics. Association genetics consists in searching for correlations between molecular markers and the traits of interest through a wide collection of plants that best represent the diversity of the species (Thornsberry et al, 2001).

It should be mentioned that identifying and locating the QTLs will provide no information about the function of the gene or genes present in each QTL region. Yet it can be a first step in identifying candidate genes and in conducting studies in functional genomics. As we shall see later, it will be possible to use this information for varietal improvement thanks to marker-assisted breeding.

QTL detection to improve a given trait is nowadays an area of research favoured by many laboratories. This is particularly the case in drought tolerance improvement. Initial work began on maize about twenty years ago, but whether we think of the model plant *Arabidopsis thaliana*, rice or wheat, a host of studies are underway to identify genomic regions and alleles that are favourable to that trait. For instance, let us mention the early identification in maize of a QTL for ABA content which co-locates with a QTL for root development (Tuberosa et al, 1998), in *Arabidopsis thaliana* of a QTL linked to a substantial accumulation of ABA in the leaves and to increased yields under water stress conditions (Landi et al, 2001), or in maize once again, the identification of QTLs promoting the maintenance of leaf growth even under water deficit conditions (Reymond et al, 2003).

While just a few years ago, the genome sequencing of a single individual in a given species was a technological feat, the boom in sequencing technology has made it possible nowadays to have access to the genomic sequence of numerous individuals for each species, quickly and at a relatively low cost. Together with the development of bioinformatics data processing, this will revive our ability to explore live genetic diversity and to understand its functionalities.

Genes that have been selected during the domestication of crop plants and during their adaptation to new environments display a diversity that is structured in a different way than that of other genes. The genome in living organisms thus retains an imprint of their evolutionary history. By studying the diversity of crops at the very fine DNA sequence level, it is possible to detect this imprint. The detection of genomic zones selected during the adaptation to special environmental conditions, and which are thus involved in the genetic determinism of special characteristics, is a different, complementary approach to QTL search approaches, used to get closer to identifying the genes that are truly involved in those adaptations.

C. Conventional genetic selection through carefully selected cross breeding, enables scientists to obtain the highest performing lines for a particular trait that is sought for improvement in a given environment

Varietal improvement consists in combining the desired traits from a set of more or less genetically homogenous individuals called “variety”. This is not the prerogative of public or private research, for farmers worldwide have for time immemorial brought changes to their varieties, or have created new ones. This trend continues in farming systems in which seeding systems are basically founded upon using local varieties (as opposed to varieties known as “improved”).

The breeding which we shall refer to here as “conventional” (although it can be the subject of innovative methodologies) is the most widespread strategy used with most crop species. Creating a variety that is tolerant to a specific environmental constraint requires crossing two varieties that have been chosen on a sound basis. One variety supplies the “genetic background”, meaning the entire range of genes favourable to good productivity, while the other brings in traits of tolerance towards the targeted constraint. After an initial crossing, descendants featuring all of the desired traits are selected thanks to an assessment of phenotypic criteria favouring plants that are tolerant to the stress concerned. These descendants in turn will then be backcrossed, about six to eight times on average, with the high-yielding parent variety, selecting at each generation the conservation of the drought tolerance trait.

This breeding is based upon an exploitation of the natural variability existing within a species, and requires access to as wide a range of genetic resources as possible, meaning access to biodiversity. It is easier nowadays on account of new knowledge being acquired about targeted traits and the molecular bases underlying them, as well as the development of techniques developed from the considerable advances in molecular biology over the past thirty years.

D. Marker-assisted breeding helps target and speed up the breeding process

The identification of QTLs favourable to a given trait and that of genes involved in the plant adaptive responses to a given environmental constraint are all biotechnological tools that will help breeders target and speed up the breeding process for the plants’ genetic improvement.

Marker-assisted breeding adds a genetic assessment to the phenotypic assessment underlying the plants’ standard breeding process. It is based upon the species’ genetic variability and the QTL detection in order to speed up the breeding process by directing in a reasoned manner the choice of genotypes combining the maximum amount of favourable traits. Once a QTL has been detected, the favourable allele for the trait being studied can be transferred into the genome of an elite plant through successive backcrossing. At each step, individuals that have inherited the favourable allele are identified and bred thanks to the related molecular markers. This approach allows a reduction in the amount of backcrossing from 6 - 8 to 4.

E. Transgenesis helps transfer genes that can improve the desired trait

Transgenesis (obtaining GMOs) consists in transferring towards a plant a gene whose function or expression data imply that is favourable to the trait under study. The biological origin of the genes being used may be diverse. Accordingly it is possible to have expression from a gene coming from another plant species or a different organism altogether (fungi, bacteria) via the host plant's cell transcription and translation machinery, and thus to considerably extend the genetic resources. The biotechnological advances achieved over the past few years now allow the simultaneous introduction of several genes. This is important to consider within the context of improvements in drought tolerance, since this complex process is based upon responses that involve a large number of genes.

④ Where current research stands on the improvement of drought tolerance in crops; Results obtained and desired progress.

This overview will present the progress of research on maize, rice, sorghum, pearl millet and wheat.

A. Maize

Together with rice and wheat, maize is one of the three most cultivated cereals in the world. The worldwide average yield for maize in the temperate industrialised nations is 8.2 tonnes per hectare as compared to 3.5 tonnes per hectare in less developed tropical countries (ISAAA report, Drought Tolerance in Maize: A New Reality). However, these yields are capped at 1 tonne per hectare in many low-intensity farming tropical regions, particularly in a large part of Sub-Saharan Africa. In both kinds of countries, drought is one of the most significant environmental constraints maize producers are faced with (as a reminder, irrigated maize produces over 20 tonnes per hectare). The capacity farmers have in controlling this risk explains in large part the disparity in yields between temperate and tropical farming.

1. Maize is a species that uses water efficiently, but is highly sensitive to water scarcity at certain times in its development cycle

Maize has a complex behaviour with respect to water and water stress. It is a species known as C4, which has a special carbon fixing mechanism during photosynthesis that is different from that of most other crops like wheat, rice or sunflower. This mechanism is seen as an adaptation, among other things, to water stress and it provides maize with optimal water use and high growth capacity since it has highly efficient regulation mechanisms and it controls efficiently closure or opening of its stomata according to existing environmental conditions. The quantity of water used per gram of fixed carbon is therefore much lower than it is in grasses of temperate origin (wheat, barley, etc.). Yet maize is highly sensitive to water stress, especially during its flowering period, since a water deficiency at that point in the cycle will cause grain abortion and lead to substantial yield reductions. Irrigation is essential for maize crops in most of the regions of the world because it is highly sensitive to drought, especially at flowering time, when it requires even greater quantities of water for its vegetative development.

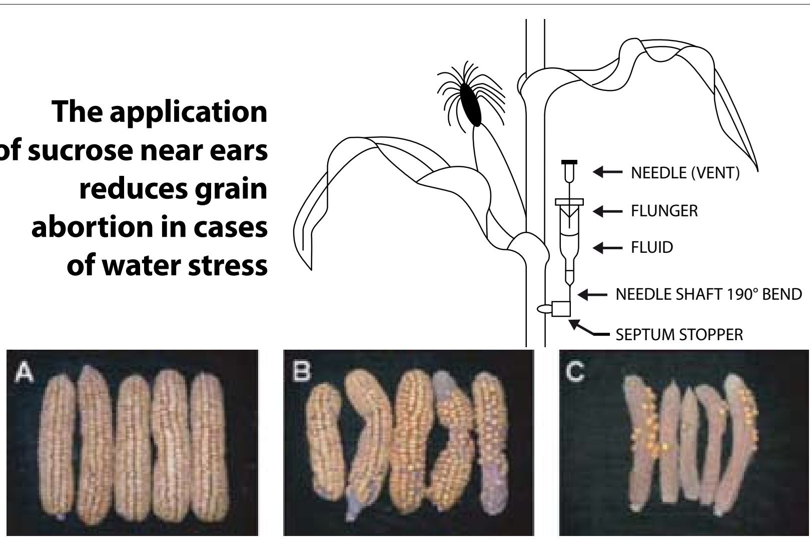
2. Maize sensitivity to water deficit during the reproductive stage is related to late female flowering

Contrary to other cereal species like wheat or barley, in maize the detrimental effect of drought on grain production is not due to sterile grains of pollen (Westgate and Boyer, 1986b). In maize, as in sorghum, a consequence of water stress is an extended period between male and female flowering times. This reduces the number of fertilisation occurrences and as a result the production of grains. Thus the lag in maturity between male flowers and female flowers, known as the anthesis-silking interval or ASI, is a vital genetic criterion in improving drought tolerance in maize, especially for tropical species subjected to a water deficit that is frequently severe at flowering times.

3. Grain abortion is also an unfortunate consequence of water stress at flowering time

In the event of a water deficit, it frequently happens that within the few days following fertilisation, the development of the fertilised ovule ceases. This phenomenon, resulting from severe water stress, appears to occur at random on the same cob. Although the visual difference between grains that are due to abort and healthy grains can only be detected a dozen days after fertilisation, experiments appear to show that abortion is initiated very early, even before the embryo has had time to develop. The mechanisms that lead to this abortion are still poorly described. In particular, the signal that sparks the onset in the process remains to be determined, even though many studies seem to demonstrate that sugars are involved (Boyle et al, 1991, Zinzelmeier et al, 1995).

The application of sucrose near ears reduces grain abortion in cases of water stress



Normal culture conditions — Water stress + sucrose — Water stress – sucrose

Source ; Boyle and al. 1991

4. Water stress also has a significant impact on vegetative development in maize

While maize sensitivity to a water deficit is at its maximum during the reproductive phase, a drought occurring during the plant's vegetative growth is far from harmless and can have severe consequences on yield. One of the adaptation mechanisms set up by plants, especially that of maize, to combat water stress is a limitation of leaf transpiration. This requires less of leaf growth resulting in a minimum, of surface areas of exchange with the atmosphere, and a partial, controlled closure of stomata to limit water loss. On the other hand, root growth is less affected, and the development of the root system helps maintain access to water resources. These processes, which aim at preserving the water taken from the soil for as long as possible, are part of the survival strategy set up by the plant. Yet while this strategy helps protect the plant and reduce its stress levels, it greatly penalises photosynthesis which is strongly linked to water loss by transpiration since it depends on the leaf surface and to what degree the stomata are open.. As a result, those adaptive responses in plants to water stress occurring during their vegetative development may have severe consequences on productivity since they irreversibly affect (i) the traits of the root system, (ii) the plant's entire biomass and the leaf's surface, and (iii) the setting up and development of reproductive organs.

5. Genetic criteria chosen by breeders to improve drought tolerance in maize

Yield loss caused by water stress is a direct consequence of physiological responses set up by plants for their protection and to minimise the impact of this stress on their development and their ability to reproduce. The study of those responses will help breeders determine which endogenous mechanisms they should target, and thus select the best criteria to improve drought tolerance. In maize, this mostly means reproductive growth maintenance (ASI), stomata conductance maintenance, leaf growth and the improvement of the root system. In order to identify the lines that are most resistant to water stress, the plants are cultivated under stress conditions , and so-called phenotypical criteria are measured, which to agronomists are the visible manifestation of metabolic and physiological change. It mainly involves the time period between male and female maturity (ASI), curling and senescence in leaves (yellowing), leaf size and yield components (the amount of cobs/ears per plant and grains per cob/ear).

6. Generally speaking, maize improvement through conventional breeding has produced hybrids that are more drought-tolerant

Traditional breeding methods implemented since 1930, when the first hybrids were introduced, have helped improve the yield in maize not only under normal irrigation conditions, but also under water deficit conditions. Multi-local tests performed on hybrids developed by the Pioneer seed company from 1953 to 2001 have shown a constant increase in yield of 189 kg per hectare per annum for irrigated maize, and of 146 kg per hectare per annum when plants are cultivated under moderate drought conditions (Campos et al, 2004). Generally speaking, sensitivity to water stress at flowering time in the most recent genotypes does not seem as high as that observed in the oldest genotypes. This trait was not necessarily part of breeding objectives, and this improvement probably comes partly from an indirect impact brought about by better plant vitality due to the effects of hybridisation (heterosis effect or hybrid vigor).

7. Breeding programmes aimed at improving drought tolerance are dependent on having access to the largest possible range of genetic resources

Pioneer was the first seed company to commercialise maize hybrids in the 1930s. Their very first work, concerning the improvement of water stress tolerance, was the result of a severe drought in 1930 in Iowa where the company is based. The anecdote is amusing because practically all of the hybrids that were being tested in the field at the time had been unable to withstand the lack of water, the few that did survive were used as base genetic material in the first project aiming at improving the trait. In the 1950s, programmes intensified, and over the years they helped develop ever more efficient plant collections with respect to water stress, which under drought conditions showed a constant improvement in yields of about 1% per annum.

The CIMMYT (International Maize and Wheat Improvement Centre www.cimmyt.org) has been involved for about thirty years in breeding programmes in Africa, South America and India, aiming at identifying and commercialising the lines of maize best suited to local cultivation conditions. The breeding focused on yield, but also on traits considered as providing reasonable tolerance to a water deficit, especially ASI (Edmeades et al, 1999, Bruce et al, 2002). In Africa, the CIMMYT, the IITA (International Institute of Tropical Agriculture) and private seed companies have all collaborated to assess and distribute the grains from varieties developed in these institutes. The most promising among those new drought-tolerant varieties, ZM521, is now cultivated in more than a million hectares in Southern and Eastern Africa. The success of this combined breeding, of the evaluation scheme and the grain distribution was the driving force behind development and funding by the Bill and Melinda Gates Foundation and the DTMA project (Drought Tolerant Maize for Africa). The project objective is to create a collection of lines of drought-tolerant maize within 5 to 10 years. Project managers are announcing their objective as a yield increase of one tonne per hectare, or a productivity increase of 20% to 30% as compared to current low-intensity farming averages (1 to 1.5 tonnes peThese conventional breeding programmes, implemented by numerous seed companies and national or international research institutes, explore maize's natural genetic variability to select the most favourable genotypes with respect to drought tolerance. They have helped take inventory of the local genetic variability, but also to enhance it for putting in place collections of lines that are preserved and utilised in most of those programmes. These collections are called germplasms. It is important to stress that this so-called traditional breeding is exclusively based upon phenotypic traits (visible under in-field conditions), the principle being to use the natural variation existing throughout and within the species. So it assumes access to genetic resource banks (germplasms) that are as exhaustive as possible. CIMMYT has thus opened a seed bank in Mexico City which houses maize's worldwide genetic diversity. The same goes for private breeders.

The CGIAR

The Consultative Group on International Agricultural Research (CGIAR) is a partnership between 15 International Agricultural Research Centres (IARCs) spread all over the world, and the backers, both bilateral and multilateral, who fund them. The centre's mission focuses on plant production, animal production, forests and fishing. In 2009 the budget was €629 M, including 9 million dollars from public credits and the rest fromfoundations.

Among the centres, two are specialised in research on rice, the IRRI (International Rice Research Institute) based in Los Baños in the Philippines and holding a worldwide mandate, and the Africa Rice Centre, formerly the WARDA (West Africa Rice Development Association) based in Cotonou, Benin, holding a regional mandate. Another centre, the CIMMYT (Centro International de Mejoramiento de Maiz y Trigo or International Maize and Wheat Improvement Centre) works on wheat and maize and is based in Mexico.

There are four centres whose mission focuses on ecological areas: (i) the ICARDA (International Centre for Agricultural Research in Dry Areas) for arid areas, based in Aleppo, Syria, (ii) the ICRISAT (International Crop Research Institute for the Semi-Arid Tropics) for semi-arid areas, based in Patancheru, near Hyderabad, India, (iii) the IITA (International Institute of Tropical Agriculture) for tropical areas, based in Ibadan, Nigeria and (iv) the CIAT (International Centre for Tropical Agriculture) for high-altitude areas, based in Cali, Colombia. There are three other centres that perform cross-functional missions, focused on genetic resources (Bioversity International) from Rome, on water management (International Water Management Institute –IWMI) from Sri Lanka, and on farming policies from Washington. The IARCs conduct shared, innovative programmes about major issues. Those programmes are known as "Challenge Programmes".

Ever since its creation in 1971, the CGIAR has given the greatest attention to genetic improvement and varietal creation. The distribution of high-potential varieties of rice, wheat and maize was behind the inception of the green revolution. More recently, the "New Rice for Africa" programme, known as NERICA and conducted by the Africa Rice Centre, is combining the high yield of Asian rice with the resistance of African varieties to disease and to pests. There are also 11 CGIAR centres administering international germplasms, thus ensuring the preservation and distribution of a wide range of phytogenetic resources.

8. Progress achieved in molecular biology can now help speed up selection through marker-assisted breeding

One example of this strategy is CIMMYT using female flowering delay (ASI) QTLs to obtain tropical varieties that are more drought resistant (Ribaut et al, 1996, 1997, 2002). The introduction of those chromosome regions (introgression) into genetic material is one successful example in obtaining genotypes that are more drought-resistant. Marker assisted breeding aiming at the introgression of other traits like stomata opening and their sensitivity to hormones, root architecture modification or the maintenance of leaf growth during water stress have all been attempted, but the mechanisms are so complex that no usable results have so far been obtained through breeding (Collins et al, 2008).

Marker-assisted breeding is used on a wide scale by seed companies in developing conventional varieties of maize that are more drought-resistant. Through its DroughtTolerance I programme (DTI), which calls upon traditional breeding and marker-assisted breeding, Pioneer will be commercialising in the United States next year (2011) a variety of maize purported to provide a 6% yield increase under water stress conditions. The Swiss company Syngenta is also communicating about the commercialisation in the United States in 2011 of a conventional maize promising, under drought conditions, a 15% higher yield than that of the best hybrids currently on the market. Such programmes require extremely efficient laboratories for the molecular analysis of large amounts of genotypes, and the selection of the best lines for crossbreeding in a large amount of test plots (about 200 in some cases). Seed companies have developed genotyping and phenotyping platforms which facilitate very high-throughput analyses.

9.The commercialisation of a GMO maize in the United States in 2012 is the first result of research using transgenesis

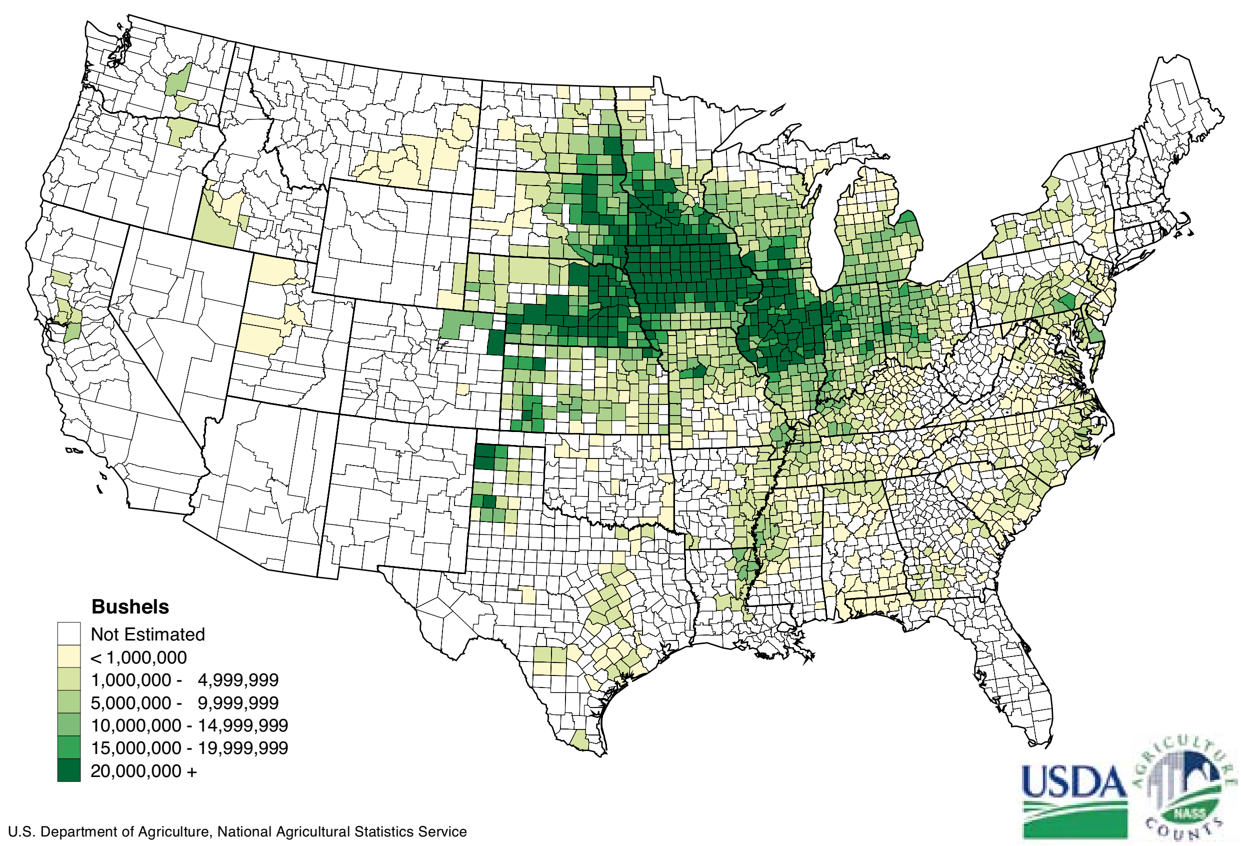
Transgenesis consists in transferring, towards a target genotype, one or more genes whose function or expression data imply that they are favourable to the targeted trait. Seed companies are currently involved in a wide range of work projects to improve drought tolerance in maize thanks to transgenesis by seeking new genes, using systematic screening of all genes known to be involved in responses to stress in the living world, as well as using more targeted approaches based on knowledge of adaptive mechanisms.

Monsanto, in collaboration with BASF, has for some years now been announcing the commercialisation of the first transgenic maize to react better to water stress. This variety results from about ten years work and hopes to be launched in the American market in 2012. The selected gene stems from the *Bacillus subtilis* bacterium and is known as *cspB* for Cold Shock Protein B. It was introduced with a sequence that only authorises its expression in the shape of protein coding in the event of water stress. The protein coded by the *cspB* gene is known as a chaperone protein and bears the same name, cspB, as the corresponding gene. It facilitates the assembly of complex protein structures. In the event of water stress, the plant sets up numerous cellular responses to minimise the effects of stress. One such response is an overall slowdown in metabolism. The plant goes on “standby” thanks to, among other things, a diminution of the translation of messenger RNAs into proteins. This diminution results from a change in conformation for RNAs, which “huddle up” and are no longer available to the translation machinery. The chaperone cspB binds with messenger RNAs so as to keep them unfurled, and so allow the synthesis of the proteins they code, as would be the case if there were no stress. Thus the expression of this gene in maize helps maintain photosynthesis and thus growth, both at the vegetative stage and the reproductive stage, whenever plants are experiencing a water deficit. Monsanto is announcing yield increases in the order of 6% to 10% when compared to the most efficient hybrids currently on the market. In order to facilitate commercialisation, an insurance system that guarantees a minimum increase in yield of 5% will be set up.

Pioneer is also developing a programme aiming at improving drought tolerance in maize: Drought Tolerance II (DTII). Many candidate genes have been identified and are currently being tested among the most efficient lines. So the objective is to find as quickly as possible the best gene combination for commercialising the variety containing several transgenes within 5 to 7 years in the United States. It would appear that in this case, the plant’s energy and strength are to be improved rather than its drought-tolerance *per se*, the effect on the latter being indirect.

Despite having worked for a long time on grain abortion via the influence of sugar deprivation, Pioneer seems to have abandoned this trait in favour of a stable metabolism even under water stress conditions through signalling depending on plant hormones like abscisic acid and ethylene. Syngenta and the French company Limagrain are carrying out the same sort of programme with similar deadlines.

Maize production in 2009 in the United-States



10. Genetics are the corner stone of maize research programmes

While transgenesis is a powerful biotechnological tool that can speed up the genetic improvement of drought tolerance in maize, the foundation of this work is still based on the diverse genetic resources that have been collected over decades. Indeed, the programmes that seed companies have been developing over the past decade aim at introducing genes or alleles that have been identified as providing better drought tolerance in the most efficient conventional lines under given cultivation conditions.

For example, the transgenic maize developed by Monsanto/BASF and which is expected to be launched in 2012 is targeting a precise region in the United States: the Western Maize Belt, i.e. Nebraska, Colorado and Kansas, which suffers droughts of fluctuating severity every year.

Accordingly, the *cspB* gene was introduced to the hybrids best suited to the cultivation conditions in the region. The same goes for the transgenic variety developed by the DTII programme by Pioneer, due to be launched for farmers based in the plains of the American Far West.

In order to successfully complete those heavy-investment programmes, Monsanto, Pioneer and Syngenta use their germplasm, their expertise in marker-assisted breeding, their gene banks and their substantial phenotyping potential. Field tests in the various target areas help assess the real yield increases generated by the various events in genetic transformation. These companies have numerous test sites in the regions in the world that are of interest to them for the development of so-called 'drought tolerance' programmes (roughly 200 sites). Therefore in those various test sites, many genes have been and are still being tested among the lines best adapted to local cultivation conditions. Genes selected to develop commercial varieties are those that provide the best resistance to water stress in the largest number of lines, so as to optimise investments committed to these programmes and the number of potential markets worldwide.

11. New markets are also emerging in Africa, Asia and South America

Sub-Saharan Africa is an area where Monsanto and Pioneer, to name but two, believe there is no market at this time. They are however taking part, in association with NGOs, in non-profit programmes to provide farmers with improved varieties for such crucial traits as drought tolerance or a more efficient use of nitrogen. Tests are currently taking place in East Africa , an interesting area because the annual rainfall is fairly similar to that in the Midwest, but maize yields are 10 times lower on average, especially for smallholder farmers who seldom harvest more than one tonne per hectare. Those differences are mainly due to (i) an uneven rainfall distribution during the course of the year, (ii) a modest use of hybrids (13% as compared to 100% in the United States) and (iii) a limited access to inputs. The WEMA project (Water Efficient Maize for Africa) was initiated in South Africa and East Africa in 2008 with the support of the Bill and Melinda Gates Foundation. It aims at delivering as quickly as possible to the African market varieties of tropical maize adapted to local cultivation conditions and showing improved drought tolerance. It unites various players in plant biology research and agronomy, including the CIMMYT and Monsanto who have made their genetic resources available. The project's objective is to provide farmers with varieties of improved maize that will help them increase their yield under drought conditions from 20% to 35% by 2017. Those varieties will be obtained though traditional and marker-assisted breeding. The transgenetic path will also be explored, since Monsanto is providing freely the project with the *cspB* gene, and other genes identified in the United States as providing improved drought tolerance. The introduction of those genes will be performed in locally-adapted lines that have been developed over the years by CIMMYT and by Monsanto in South Africa.

Seed companies are also turning towards Eastern Europe, Latin America (especially Mexico, Brazil and Argentina), India, China and South-East Asia for the development of 'Improving Drought Tolerance' programmes.

WEMA (Water Efficient Maize for Africa)

Within the framework of this study, we travelled to Kenya, one of the five countries taking part in the WEMA project, to meet researchers and breeders working in the various laboratories involved in the project around Nairobi (CIMMYT, Monsanto and KARI, the Kenya Agricultural Research Institute). Funded partly by the Bill and Melinda Gates Foundation, the project is ambitious and requires continuous dialogue between the various partners involved. WEMA raises great hopes among governments, but also and especially among farmers. Beyond the launch of varieties of improved conventional maize (2012 objective) and/or transgenic maize (2017 objective), the project helps developing national research in the countries involved. This is in fact a significant aspect for WEMA since CIMMYT and Monsanto actively contribute to the education of scientists at the research institutes with which they work: AATF (African Agriculture Technology Foundation, www.aatf-africa.org) oversees the project, its mission being to help governments put in place a legislative framework allowing the cultivation of transgenic plants. Among the five countries involved in WEMA, only South Africa enjoys such a comprehensive legislation. The process is complete in Uganda, and it is underway and nearing completion in Kenya, Tanzania and Mozambique. Those countries should hopefully be able to run the initial trials on the transgenic lines developed in the project as early as 2011. The homogeneity of the seed batches supplied to farmers is a sine qua non condition for their acceptance by farmers, especially the poorer ones, who cannot take any risks. The countries involved are working at setting up reliable production channels for the seeds, calling upon local seed companies and national institutes that already have the capacity to duplicate the grains, as in the case of Kenya.

12. Conclusion: Drought-tolerance improvement in maize is only in its early stages

Drought tolerance calls upon a host of molecular elements. This complexity is all the more significant in maize whose sensitivity at certain periods in its development cycle further complicates the breeders' work. This goes a long way to explaining the difficulties that were experienced during research programmes and the substantial delays before being put on the market. There is no such thing as a 'silver bullet' solution developed by introducing a single gene or the introgression of a single QTL, and there never will be. Solutions will keep on coming from the introduction of several traits via transgenesis and/or standard breeding. Breeders are increasingly talking about gene stacking. Moreover, breeding objectives are determined by the cultivation systems they are confronted with. Research results will be assessed according to their local success. Which raises the issue, besides, of the transfer period for improvements achieved in developed countries towards developing countries.

The transgenic maize to be commercialised soon by Monsanto and BASF in the United States contains only one transgene. However, both companies are actively continuing to identify and test other genes involved in drought tolerance improvement, and they have announced the publication of another serious molecular contender in the not too distant future. The next generation of water-stress-tolerant transgenic plants will be the result of research programmes like these or like DTII, conducted by Pioneer, aiming at finding the best gene combination (probably 2 to 5) for optimising yields under water deficit conditions. It is important to mention that those varieties of transgenic maize will also integrate herbicide- and insect-resistant genes, which are technologies that have already been commercialised by most major seed companies in the past few years and which correspond to a demand by farmers, especially in the USA.

B. Rice

1. The most cultivated cereal in the world, rice nowadays is subjected to substantial environmental constraints

Rice is one of the most cultivated cereals worldwide. It is the primary source of energy for over half of the world's population, especially in Asia where it is the staple food. In South America and Africa, rice consumption is growing yearly, to the detriment of maize, sorghum and pearl millet. Domesticated about 10,000 years ago in Asia and probably around the same time in Africa, this cereal belongs to the botanical genus *Oryza,* which includes 23 species. Among them, 2 species are cultivated today: *Oryza glaberrima*, which originated in West Africa, and *Oryza sativa*, which originated in Asia. The latter, the most widespread, is sub-divided into two sub-species, *indica* and *japonica*. The varieties in both sub-species are adapted to different modes of cultivation since rice *indica* is grown in irrigated or in deep water in tropical zones, while *japonica* varieties on the other hand are grown in irrigated temperate or high-altitude zones and pluvial (rain-fed) in tropical zones. In Africa, the 'historical' *Oryza glaberrima* variety has been superseded by *Oryza japonica*.

Rice is an illustration of the amazing genetic diversity bred by Man in crop plants since their domestication. Tens of thousands of rice seed varieties are preserved in national and international gene banks. The International Rice Research Institute (IRRI) alone, based in the Philippines, stores over 100,000 samples of two species of cultivated rice.

While rice owes its success to its great capacity to adapt to a wide range of cultivation conditions, rice-growing nowadays is subjected to significant environmental constraints. The irrigated method, the most popular since its comprises over 55% of the harvested surface, requires substantial quantities of freshwater, which is becoming a rarity, while the pluvial method is subjected to increasingly frequent episodes of drought, particularly in the tropical zones. The United Nations forecast for demographic growth indicates that there is a need to increase rice production by at least 40% by 2030. Reaching this objective is impossible without developing new varieties able to provide higher yields than current varieties, regardless of environmental conditions.

2. Rice has become a model plant and numerous research projects worldwide are focusing on identifying the genes and QTLs that could be used to improve the plant's drought tolerance

As a result of its economic standing and of the relatively small size of its genome, the international scientific community chose to make rice one of the model plants in plant genetics. Its genome sequencing was completed in 2005 thanks to an international research effort and the founding in 1999 of the IRGSP Consortium (International Rice Genome Sequencing Project)

This model plant status has made rice the centre of scientists' attention seeking to dissect the cellular and molecular mechanisms used in the response to water stress. As mentioned earlier, part of the cellular responses set up during water stress is initiated via two signalling paths, the one dependent on abscisic acid, the other independently of the hormone. Many genes intervening in those signalling paths have been identified in rice. One of them is the code for transcription factor DREB1A which, independently from abscisic acid, favours expression in genes involved in plant drought tolerance. This gene's overexpression, whether in rice or in a model plant *Arabidopsis thaliana,* appears to significantly increase resistance to water stress (Dubouzet et al, 2003, Ito et al, 2006). While this work represents a fine example of the identification of a candidate protein for drought tolerance in rice or other cereals like maize, the lack of any conclusive results in-field or under agricultural conditions is impeding the advancement of that discovery towards the development of improved var

3. Although numerous genes and QTLs able to intervene in the response to drought have been identified in rice , the specific genetic criteria to target in improving water stress tolerance has not yet been clearly identified

Rice reacts to water stress in the same way as most cereals do, setting up an evasion, avoidance or tolerance strategy according to the kind of drought involved. As with maize, the development phase most sensitive to water stress during the development cycle of rice concerns the few days prior to and after flowering. However, for the time being, research projects are targeting a variety of criteria such as: (i) root growth modification in the event of water stress, especially in aquatic rice (deep-water cultivation), (ii) osmotic adjustment, (iii) leaf curling (to regulate the leaf surface and limit stomata transpiration), (iv) water use efficiency and (v) the synchronisation of cultivation cycles, for which there is significant variance, even if it is still poorly defined in rice. QTLs have been identified for each one of those traits. For example, a correlation was found between leaf growth sustainability and an osmotic adjustment QTL (the accumulation of solutes in the cells) (Zhang et al, 1999). A comprehensive summary of the research studies carried outon rice is summarised in this publication, "Candidate genes for drought tolerance improvement in rice (*Oryza sativa*)", Vinod, 2006.

To date, while the genetic bases of all those traits for the adaptation of rice to drought have been explored to improve water stress tolerance in the long term, no one particular route is favoured. The research done over the past thirty years has generated a massive amount of crucial information which must be cross-referenceed in order to understand the comprehensive mechanisms of drought tolerance in rice and to present breeders with validated molecular candidates.

4. Researchers have decided to get to the root of the problem

In rice, pluvial varieties have a dense root system that can, under certain conditions, reach over one metre in length. This characteristic, which is not found in irrigated rice that grows in waterlogged soil, helps the plant to access water resources deeper in the soil. CIRAD (French Centre for International Cooperation in Agricultural Research for Development) chose to focus on this morphological trait through various closely-related research projects.

One of the projects aims at describing and simulating plant behaviour thanks to the development of an eco-physiological model known as Eco-Meristem. The objective is to model root growth when plants are grown under standard water conditions or under drought conditions during their vegetative development, using software that can help forecast plants' architectural development under a variety of agronomic, ecological and climatic conditions (http://amap.cirad.fr/fr/equipe2). Another project uses the identification of genes involved in the function of the root meristem, a cellular zone from which root tissues are differentiated, and where new roots are formed. The *CROWN ROOTLESS1* gene is one of them. In order to understand its precise operating mode, links are sought between the genes' various alleles and the root system's architectural traits within different varieties of rice (Courtois et al, 2009). The objective is to determine which alleles favour plant growth in the event of water stress, so as to transfer them in the long term into receiving varieties, either via marker-assisted breeding or via transgenesis.

5. From participatory breeding to marker-assisted breeding, many projects seek to improve the tolerance of rice to environmental stress

In Africa, rice consumption is on the rise. However, although rice-growing is intensifying, the continent is still far from being self-sufficient. It is in this context that the Africa Rice research centre in West Africa and South Africa has for some years already been developing new varieties of rice adapted to African cultivation conditions. Historically, the species most cultivated in Africa is *Oryza glaberrima*. To Africa rice researchers, this pluvial species represents a store of genes providing sturdy resistance to the kind of environmental stress rice-growing is subjected to in Africa, i.e. drought, soil salinity and high temperatures. Thanks to some sound crossbreeding between *Oryza glaberrima* and *Oryza sativa,* a species with a higher yield, Africa Rice succeeded in developing rice varieties with a faster development cycle (30 - 50 days less compared to non-improved varieties), that could avoid the critical drought periods. Those new varieties are known as NERICA (New Rice for Africa) and are experiencing increasing success with African farmers as they provide them with yield increases of close to 50% when plants are grown without fertiliser, and over 200% when grown with added inputs (http://www.warda.org/nerica flyer/technology.fr).

For the past few years, we have been seeing projects that include the latest biotechnological advances in terms of breeding as well as the identification of numerous genes or alleles that could potentially provide better tolerance to water stress. Among them, the STRASA project (Stress Tolerant Rice for poor farmers in Africa and South Asia) intends to develop throughout Africa and South Asia, using marker-assisted breeding and/or transgenesis, varieties of rice that are resistant to a range of major environmental stress factors including drought and soil salinity, an issue which is every bit as important to rice as water stress tolerance. Funded by the Bill and Melinda Gates Foundation, the project involves Africa Rice as well as the IRRI. While it greatly relies on biotechnology, it also calls upon the local varietal diversity inventoried in every participating country thanks to help from farmers to adapt the proposed solutions as best as they can to the agrosystem considered (http://beta.irri.org).

C. Sorghum

1. Sorghum is a close relative to maize, but it is less sensitive to water stress

Sorghum, like other summertime species such as sunflower or barley, stands out for its strong intrinsic drought tolerance producing an acceptable yield even without irrigation. Sorghum is a species with a C4 metabolism, like maize, which helps it efficiently regulate the opening of its stomata according to environmental conditions. However, although maize is highly sensitive to drought during its reproductive stage, sorghum has a high tolerance to water stress at the time in its cycle.

2. More resistant to drought than maize but less so than pearl millet, sorghum often has to compete with the other species

Sorghum is a species which is well-adapted to areas with low rainfall or with a short-lived rainy season, and more generally speaking to arid regions. In Africa for instance, it is cultivated in areas where there is from 600 to 900 mm of rainfall in the rainy season. Sorghum is often seen as a replacement crop for maize whenever the rainfall has been insufficient. This is particularly true in the tropical zones, especially in Africa and Central America, but can also be seen in the United States or in Europe.

Frequently the subject of crop rotation because it can use the residue of the fertiliser from the previous crop (often cotton), sorghum has a poor reputation as a staple food in some African countries, so whenever possible, pearl millet is chosen instead.

3. "Photoperiodism" and "Stay-Green" are the traits targeted by research programmes seeking to improve drought tolerance in sorghum

CIRAD is interested in photoperiodism in sorghum. Photoperiodism is an adaptation in certain plants that can only flower when there is sufficient continuous daylight. This trait, which could be seen as an adaptation to drought, occurs at the end of the cultivation cycle. It is a synchronisation of the plant'sdevelopment cycle with the rainy season, and this regardless of the sowing date, highly variable in some parts of the tropical zones since it is linked to the start of the rainy season. Photoperiodism helps synchronise the plant's flowering with the end of the rainy season, ensuring an easier end to it's cycle and avoiding water stress conditions. The aim of many breeding programmes, especially in West Africa, is to maintain photoperiodism in local varieties by involving farmers when choosing those varieties. The programmes are mainly conducted in Mali and in Burkina Faso within the framework of a project funded by the AFD (French Agency for Development), who involves NGOs and farmers' associations on site who are in charge of setting up the production and distribution of seeds. It should be noted however, that Photoperiodism is not applicable in the drier areas.

Stay-Green consists in maintaining a certain amount of green leaves after flowering to ensure the grains will get adequate nitrogen compounds and sugars. This trait has been targeted by Australian breeding programmes which have brought about the development of a smaller but more vigorous sorghum, yielding a high-quality harvest. Even though it is uncertain whether or not Stay-Green would be transferrable to African varieties, the CIRAD still wants to look into it through a breeding programme that has just been initiated (Interview: Gilles Trouche of CIRAD). Stay-Green QTLs have been identified thanks to a comparative approach with rice (Srinivas et al, 2009).

Getting farmers to participate in the breeding of new sorghum varieties in Burkina Faso and in Mali

In Burkina Faso and in Mali, sorghum represents between half and one third of crops produced in pluvial cultivation. Sorghum has many advantages; particularly its flexibility, its hardiness and its multiple uses. Since the late 1990s, the Rural Economy Institute in Mali (IER), the Agricultural Research Institute in Burkina Faso (INERA) and CIRAD have been conducting phased research aiming to enhance the local genetic diversity, with the support of the French Fund for the World Environment.

Sorghum cultivation in Burkina-Faso is vital for the population to become self sufficient, especially in areas where the rainfall is equal to below average but erratic. Sorghum is cultivated in all agro-ecological areas, from the North and its Sahelian climate to the extreme South-West and its North-Guinean climate, bearing in mind that its area of predilection is the zone between the isohyets for 600mm and 900 mm (the North Sudanese area). Within a same climatic zone, the inter annual and spatial rainfall variability is significant, especially in the early rainy season, and parasite pressure is highly variable for they greatly depend on climatic conditions. Given this context, Burkinabé farmers have adopted a risk-reduction strategy by each cultivating several varieties of sorghum at one time.

However, 'improved' varieties of station-produced sorghum have not been a great success with African farmers. This failure can be explained by the fact that improved varieties are poorly adapted to the ecosystems concerned and to the needs of the locals. The cause could also be that contrary to local varieties, the varieties that were produced through research have lost their sensitivity to daylight duration (photoperiodism) and require a precise sowing date to be able to ripen under favourable conditions. On the other hand, traditional varieties will adapt the duration of their cycle to the duration of daylight, so as to mature on a fixed date matching the end of the rainy season: if they are sown late in the season, their cycle is short, and if they are sown earlier in the season, their cycle is longer.

The region though has great biological diversity, including local varieties, but that biodiversity was threatened by the spread of other species, especially maize. The research project carried out in the year 2000 had as a prime objective to create, using local ecotypes, improved varieties which met the diversity of agro-ecosystems as well as the needs of producers and users. Among breeding objectives, adaptation to climate via photoperiodism ranked highest, as well as productivity and grain and hay quality.

The working method was based on recurring breeding cycles to dynamically preserve genetic diversity according to a varietal creation approach along participatory, decentralised lines. The aim was to help farmers test the new varieties available over several years, under their own cultivation conditions and according to their own production objectives and they themselves select the varieties which met their particular constraints. The project helped identify several varieties which showed improved performance. Accordingly, in Burkina Faso there are now five varieties being propagated and commercialised by farmer associations. However, the breeding applied specifically to drought resistance is not conclusive, because given the rather random nature of this stress, it would have required farmers to carry out trials over several years to get results that can only be assessed over time.

4. Genetic improvement in sorghum could use marker-assisted breeding, but not transgenesis for the time being

Photoperiodism and Stay-Green are two genetic criteria chosen by breeders to directly or indirectly improve yields in sorghum under water stress conditions. Other possiblities are being explored, especially as part of the Generation Challenge Programme.

The ICRISAT (International Crop Research Institute for the Semi-Arid Tropics, www.icrisat.org), located in India and Africa (Nairobi, Kenya and Niamey, Niger) is carrying out breeding research programmes for sorghum. The improvement of drought tolerance in the species is not a priority for the institute, which is focusing on developing varieties that possess better nutritional qualities, especially higher zinc and iron content (Interview: Said N Silim of ICRISAT).

Although some research has helped identify genes or QTLs that can be used in the genetic improvement of sorghum, the genetic variability available in the world where sorghum is grown remains to be studied.

The Generation Challenge Programme (GCP)

The CGIAR (Consultative Group on International Agricultural Research) is a consortium of 15 international institutes that together cover the main cultivated plants, livestock farming, fishing and forestry. It sets up time-limited programmes aiming at fostering public and private research partnerships . The GCP (Generation Challenge Programme) is one such project. It is a consortium comprising 18 members, representing in total about 200 partners worldwide. Drought tolerance improvement is GCP's main theme and research is underway on 18 different species simultaneously (maize, sorghum, cowpea, pearl millet, rice, etc.). Phase I of the programme (2004-2008) has set up a network and partnerships between various laboratories in Northern and Southern countries. Phase II, currently underway, aims at providing everyone with reliable tools for marker-assisted breeding. Accordingly, the GCP is in transition. The priority has become the management and smart processing of data, as well as ensuring that the data is shared between the partners. The programme is currently setting up an "integrated breeding" platform. A website will provide a range of services to facilitate marker-assisted breeding and data analysis. The objective is to facilitate access to markers, especially for national research institutes and small private companies in developing countries, or any national or international public research laboratory. The platform should be widely accessible from 2012. It is funded to a large extent by the Bill and Melinda Gates Foundation, but the GCP hopes it will be financially self-sufficient by 2014 through user fees. Interview: Jean-Marcel Ribaut.

D. Pearl millet

1. Pearl millet is a species with 'naturally' good defences against drought and very popular in Africa

In Africa pearl millet is cultivated in the most arid regions and in the poorest of soils. The northernmost limit of pearl millet cultivation, north of the Sahelian zone, is in fact the limit of all possible cultivation. While it can cope with 250mm rainfall per rainy season, pearl millet is generally cultivated in areas where it rains from 400mm- 600 mm per annum. Sometimes competing with sorghum, pearl millet is often favoured to the detriment of sorghum. This is especially true in West Africa, where pearl millet has an excellent reputation, particularly with women, due to its high nutritional qualities.

2. Pearl millet though is sensitive to water stress during the reproductive stage

Although it is considered as a drought-tolerant species since it requires little water for its development, pearl millet is sensitive to water stress during the few days before and after flowering. A lack of water at that time in the cycle will cause grain abortion and could have a disastrous affect on yield.

3. The shortening rainy seasons witnessed in Africa results in a shortening of the pearl millet's development cycle

Rainfall is in constant decline in Africa, a consequence of climate change,. For example, the annual rainfall has dropped to close to 30% in Niger over the past 50 years (between 1960-2010), whilethe amount of is affected, so is the duration since it starts later and ends earlier. There is early pearl millet and late pearl millet. The lower the amount of rainfall, the earlier the variety of pearl millet cultivated. Some varieties, cultivated in the vicinity of Lake Chad, are able to complete their development cycle in less than three months, while the late variety, cultivated further south, require over four months from sowing to harvest. This fine correlation between cycle duration and amount of precipitation available is a perfect example of evasion. As a direct consequence of the above phenomena, pearl millet cultivated in Africa is of an increasingly earlier variety, and research efforts in terms of drought tolerance improvement in millet is therefore focussing its attention on developing early varieties with synchronised flowering (Interview: Yves Vigouroux of IRD and Thierry Robert, University of Paris-Sud. Visit: JL Prioul to the ICRISAT in Niamey).

4. Pearl millet improvement programmes are being developed but they are lacking financial and human means

The IRD (Institute of Research for Development) is currently in the process of identifying the genes causing early flowering in pearl millet, using a genetic association approach(Saïdou et al, 2009) and detection studies with respect to traces of breeding (Mariac et al, 2010). Those genes are molecular candidates available to breeders in developing new varieties. Pearl millet breeding and improvement programmes are mainly conducted by the ICRISAT in India and Africa and by national agricultural research institutes. However, the number of breeders is decreasing in those institutes as is the financial support, especially in Africa, to make best use of the knowledge obtained about the mechanism linked to early flowering with the intention to develop improved varieties, which would lead to an increase or at least stability in yields from one year to the next.

The ICRISAT is conducting a significant pearl millet improvement programme for farmers. Its head office is in India but it has several test and research stations located in Africa. The largest is located near Niamey, Niger. The benefit of the breeding working closely with farmers can be illustrated by the initial failure of short-stemmed varieties, developed a few years ago by the ICRISAT. In Africa the stems of the pearl millet plant are used to build fences or shelters, so farmers did not adopt the short stem varieties. In 2003, the institute chose to practice participatory breeding to extend the genetic base of local diversity. The idea was to make farmers take part in the breeding process so as to determine precisely the farmers' and consumers' needs and provide varieties that were adapted to the climate and cultivation conditions.. Several varieties resulting from that breeding process are now available in Niger (Interview: Thierry Robert, University of Paris-Sud XI. Visit: JL Prioul at the ICRISAT in Niamey).

The benefit of improved varieties to farmers depends for the most part on the geographic area and the economic background. In some African regions, despite the disparity in rainfall, there is nonetheless some stability from one year to the next, so investing in improved varieties can be worthwhile as long as farmers are provided with loans to purchase the seeds and fertiliser. The experiment run for the past three years in DogonDoutchi, Niger with support from the Orsay-DogonDoutchi Association and more recently from the French Ministry of Foreign Affair*s* shows a threefold increase in the yield per hectare, which helps farmers reimburse their loan, and even make a healthy profit. The success of this system also implies the existence of local seed production companies to reproduce the varieties from the ICRISAT. Indeed, since pearl millet is an allogamous (cross fertilisation) species, there is a very high probability of crossbreeding between cultivated millet and wild millet, making it difficult to reuse the grains from one year to the next (Interview: Thierry Robert, University of Paris-sud 11)

E. Wheat

1. Wheat is a species with a complex genome

With an annual worldwide production of about 600 million tonnes, wheat is the most cultivated and most consumed cereal by Man. While there are several kinds of wheat, two kinds enjoy major economic status:

- Durum wheat (*Triticum turgidum* ssp *durum*) is mostly cultivated in dry, warm areas either in Southern Europe or North Africa. With a high gluten content, it is used in semolina and pasta.
- Spring wheat or bread wheat (*Triticum æstivum*), the most cultivated, is produced in the most temperate zones in the American continent and in Northern Europe to produce bread-making wheat.

The wheat we use today comes from a long and complex breeding process, the starting point of which was Aegilops, and other kinds of diploid wheat, a hardy but poorly productive cereal still cultivated in the Middle East. While Aegilops is diploid, with a genome consisting of **two** batches of 7 chromosomes each, current durum and spring wheat are respectively tetraploid (four batches of 7 chromosomes) and hexaploid (**six** batches of 7 chromosomes). This polyploidy could explain why the wheat genome is so complex, with a size equivalent to five times that of the human or maize genome and forty times that of the rice genome.

2. Sequencing the wheat genome amounts to a formidable challenge to scientists, and will be crucial for all improvement programmes concerned

Given its very large size compared to most other plant species mentioned in this report, the wheat genome has not yet been fully sequenced, and the retrieval of molecular markers was difficult. The sequencing of the wheat genome was initiated a few years ago. It requires substantial international cooperation, which was achieved in 2005 with the founding of a consortium called the IWGSC (International Wheat Genome Sequencing Consortium), whose objective was to facilitate and coordinate international efforts in order to complete the full sequence of the wheat genome as fast as possible. The consortium groups laboratories belonging to national research institutes, numerous universities throughout the world, international research agencies like the CIMMYT, as well as seed companies including Limagrain and Syngenta. It is co-chaired by coordinating laboratories from North America, Australia, Switzerland, Japan and France.

The sequencing of the wheat genome which will soon be available thanks to big progress in high throughput sequencing, will facilitate the identification of interesting genes and the development of a genetic map sufficiently complete and precise to intensify marker-assisted breeding programmes.

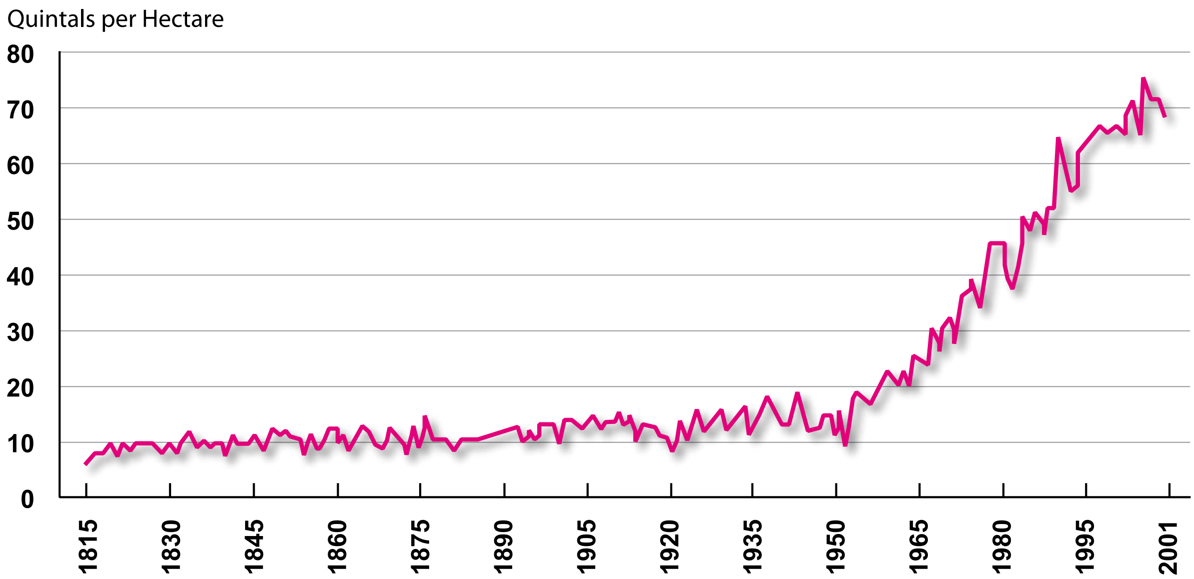
3. Wheat varietal breeding is in the midst of great changes

There is great diversity in the wheat grown throughout the world today, since at last count there were over 30,000 different varieties. While almost all genetic improvement programmes in maize or rice now call upon marker-assisted breeding and/or transgenesis, those that concern wheat at this time practically all use the genetic variability found in local populations and related species. However, the large number of markers now available speeds up their use. CIMMYT has a substantial germplasm for wheat which it utilises intensively to create, via basic crossing between cultivated and wild wheat, wheat genotypes known as synthetic, meaning they do not exist in nature, which help enhance the store of diversity in wild wheat, especially for traits of tolerance to biotic or abiotic stress. At this time, about 15% of the crossing performed in CIMMYT programmes involves synthetic wheat (Reynolds, Rajaram and Sayre, 1999).

This "biotechnological" delay in the genetic improvement of wheat mostly stems from the difficulty there is in getting genetic markers and in sequencing its genome, and to the difficulty experienced by scientists in setting up a stable, reliable transgenesis protocol for the species. While those scientific reasons are significant, other more economic and political reasons are inhibiting the development of genetic improvement programmes for wheat in general and the marketing of transgenic wheat. The first reason is economic, owing to the fact that the profit margin on the price of wheat seeds is low and that farmers can keep part of their harvest for sowing the following year. As a result, in most wheat-producing countries, the development and ownership of wheat varieties is public or it involves small companies. Up to now, major seed companies have considered that it was hard to break even with costly breeding programmes using marker-assisted breeding or to an even larger extent transgenesis (personal communication, Monsanto and Limagrain). Another hurdle regarding transgenesis is a fear on the part of farmers of producing GMOs for major markets, particularly the European market, resistant to the cultivation and consumption of products made from transgenic plants.

However, while the development of new varieties helped achieve a constant average increase of 1.2 quintal per hectare per annum in France from 1956 to 1995, annual yield increases have been almost nonexistent for the past ten years. This stagnation can also be seen in North America and Australia, and has been behind the forsaking of wheat cultivation to the benefit of maize in some areas, especially in the Western United States, as well as discontent among farmers who are increasingly demanding the development of more efficient varieties, regardless of how they are obtained. French company Limagrain has in fact just announced the commercialisation by 2016 of the first-ever transgenic wheat in North America. As far as this variety was concerned, work did not focus on improving drought tolerance, but on an efficient use of nitrogen, a trait considered by seed companies to be the most appropriate with respect to bringing the first GMO wheat to the marketplace (personal communication, Monsanto and Limagrain).

YIELDS OF BREAD WHEAT IN FRANCE



Source : Ministry of agriculture, Sigma

4. Increased water efficiency in wheat, a fine example from Australia of improved drought tolerance

Wheat is a winter or spring species. In either case, even though sowing occurs at different times, the harvest takes place prior to summer. So wheat cultivation cycle takes place for the most part during a period of the year when any risk of water deficiency is low. This is therefore an evasion strategy. Wheat has good overall tolerance, and good water efficiency related to low transpiration demands during its vegetative cycle. However, for areas that suffer severe drought, like Australia, water efficiency is a genetic criterion that is chosen to improve drought tolerance in wheat.

In Australia, breeding aiming at increasing water efficiency has most often led breeders to select plants showing low stomata conductance so as to limit water loss through transpiration, and this throughout their entire vegetative development. Thus, as is the case with the avoidance strategy, the cumulative photosynthesis is reduced and ground water is "saved" so as to be used at the end of the cycle. Yet this kind of approach has most often led to a reduction of the biomass produced and to a reduction in yield when cultivation conditions are favourable and water stress limited (Condon et al, 2002). Another breeding programme, also carried out in

Australia, has succeeded, by using isotopic discrimination of the photosynthetic process as a phenotypic criterion, in breeding wheat showing both a high stomata conductance and high water efficiency (Rebetzke et al, 2002), providing a significant increase in yield under particularly dry conditions.

According to a study led by Arvalis and INRA, the stagnation in yields that have been observed for over a decade in Europe could be due to the onslaught of short periods of heat between March and June and to late springs that are getting increasingly dry, which have an irreversible impact on the filling of wheat grains. This conclusion could be decisive in fostering the intensification of drought tolerance improvement programmes in wheat, especially in Europe and the United States. Monsanto, Syngenta and Limagrain have in fact already expressed their determination to deliver transgenic wheat with higher resistance to water and thermal stress on to the marketplace in about ten years time.

⑤ Conclusion

A. Optimising the way in which plants use water: two inseparable pillars, farming practices and genetic improvement

1. Preserving groundwater for the benefit of cultivated plants

Water scarcity is one of the main environmental factors that can limit plant growth and productivity, for photosynthesis can only happen through considerable water loss (300 to 500 litres of water for 1 kg of carbon). While genetically improving the water stress tolerance trait is Man's response to achieve increased yields under drought conditions, for optimal results it should be associated to an improvement in farming practices. Indeed, certain cultivation techniques, such as no till prior to sowing, associated with herbicide, adapting density to the kind of soil and to the variety sown, or maintaining the organic matter content in the soil, are all founded on efforts to preserve groundwater reserves. The history of progress in farming shows that improvements in cultivation techniques is invariably related to genetic improvements, meaning a reasoned utilisation of the genetic resources of every species so as to make the best use of the cultivation background. So that one approach benefits the other and vice-versa.

2. Genetic improvement uses natural adaptation mechanisms of plants to drought and the genetic variability found in every species

Throughout evolution, plants have set up adaptation mechanisms to water stress to help them survive in the event of moderate drought and to maintain their ecological niche by adapting their water requirements to the local climatic offering. Those mechanisms, being genetically controlled, are based upon a wide range of morphological and physiological responses, given that drought is a phenomenon that can happen unpredictably at any time during the plant's development cycle, and which can last for a variable, random length of time. While there is a wide range of responses, they can be classified into three categories, each reflecting a different strategy: evasion, avoidance and tolerance.

For centuries, not to say millennia, Man has been using those adaptation mechanisms, unconsciously at first, and then consciously by selecting those natural varieties able to produce larger grains and more grains, and this on a regular basis and in every environment. This approach has helped extend the cultivation zones of major species cultivated outside their original area. For instance, in tropical regions it has been founded on choosing short-cycle species performing their development cycle during the rainy season (pearl millet), or in the case of more productive varieties, on the crossing of varieties featuring efficient avoidance or tolerance strategies. Thanks to genetic understanding, reasoned breeding has helped make better use of the genetic biodiversity of species being studied and of related wild species, leading to the development of increasingly efficient varieties for a given environmental background. This biodiversity, represented for each gene by the amount of variable forms known as alleles which provide the same properties but with greater or lesser efficiency, makes up the genetic resources. The crucial nature of the preservation of our genetic heritage has led to the creation of public grain banks, for crop species, which store tens of thousands of local varieties, thanks to international efforts (CGIAR, the Consultative Group on International Agricultural Research). For instance, those banks are located in Mexico for wheat and maize (CIMMYT) and in the Philippines for rice (IRRI).

B. Genetic improvement in plants is now taking advantage of the boom in biotechnology

1. What biotechnology is bringing to the understanding of the genetic foundations of drought tolerance

In a species, the variability in the efficiency of responses to water stress is based upon the presence or not of alleles, the kinds of genes that are most favourable to that trait. The past thirty years have seen advances in molecular biology in the fields of gene identification, expression and sequencing, which have helped us gradually discover the molecular mechanisms involved in adapting to drought. Advances in sequencing have also helped us make better descriptions of genetic resources. Within this fundamental research approach, transgenesis is an essential tool for knowledge for it provides the means to demonstrate the intervention of one or more candidate genes in a beneficial response to drought. This demonstration implies using in-field tests to fully validate results.

2. Marker-assisted breeding speeds up the improvement process and makes it more accurate

Advances in molecular biology have considerably boosted our understanding of allelic variations in genes. Using neutral genetic markers, it is now possible to locate the chromosomal regions that control the quantitative value of any measurable trait (the mass and amount of grains, the amount of leaves, etc.). This has paved the way to a very powerful kind of biotechnology, namely marker-assisted breeding, which helps select in a predictive way within a line of descent those individuals combining the maximum amount of favourable alleles for every gene. In the case of drought resistance, one of the initial successful uses of this technique was performed by the CIMMYT, an international research centre and CGIAR member, who succeeded in obtaining tropical maize which was more drought-resistant. High-throughput sequencing techniques that now give access to an understanding of all of the genes in a species and their variations have further boosted the power of this technology, which is now used on a wide scale by all major seed companies.

3. Transgenesis makes an additional contribution

Transgenesis made a dramatic entry into the field of plant improvement, for it makes it possible to introduce genes that do not exist into the species one wants to improve. This is the case with herbicide-tolerant genes, or synthetic insecticidal genes. Regarding drought resistance, a variety of maize bearing a drought-resistant gene of bacterial origin will be commercialised in 2012 on the American market. However, the effects of transgenesis are not a substitute for those of marker-assisted breeding, for transgenes only take on their full meaning with varieties that are already adapted, and the expected improvement is not on an “all or nothing” basis, but rather incremental in nature. This is especially true with such polygenic traits as drought resistance.

4. Progress depends on the species involved

How far along we are in utilising these biotechnological techniques differs from one species to the next. For both biological and economic reasons, maize is by far the species generating the most efforts. Biologically, in maize as in most cross-fertilised species (allogamous), crossing two inbred lines will produce a much larger and more productive hybrid than both parents (this is the “hybrid vigour” phenomenon). This property, used in the USA since the 1930s and then worldwide, has also helped raise the genetic understanding of this species. Private research has played a major role in intensifying maize research thanks to the benefits generated by annual sales of hybrid seeds. On the other hand, wheat and rice, being self-fertilised species (autogamous), have little hybrid vigour and have generated much lower profit margins. This explains why, in the case of rice, progress to date has mostly been due to public research. Regarding wheat, the situation is changing as a result of requests from farmers.

5. A strategy that includes technical and socio-economic progress is a guarantee of success; there is more room for growth in Southern countries than in Northern countries

At this time, all of the major seed companies have called upon biotechnology in developing most of their new varieties. Those genetic advances are founded on two primary pillars: access to the largest possible store of genetic resources, and marker-assisted breeding. A third pillar is transgenesis, which helps further increase genetic variety by using genes from other species and that cannot be introduced through conventional breeding. Obtaining plants that are more drought-tolerant requires calling upon the entire range of those biotechnological resources, which implies human and material investments whose cost is further increased by the fact that the local, multifaceted and random nature of drought requires finding solutions that are adapted to each climatic region. There is no such thing as an overall solution (no silver bullet). The idea is not to come up with a single improved variety, but a series of locally-adapted varieties. The profitability imperative attendant to investments requires having access to solvent markets, which implies a difference in approach and in funding schemes between Northern and Southern countries.

In the South, international organisations like the CGIAR maintain public genetic resource banks and provide low-cost access to biotechnological resources such as marker-assisted breeding via the Generation Challenge Programme. Those countries have, or will soon have, access to the same tools as those in the North. One of the conditions for the proper operation of breeding programmes is the presence within national research institutes of a sufficient number of breeders who are trained in those modern techniques. In addition, for farmers to successfully take ownership of those techniques and use improved seeds, there needs to be an overall approach taking into account the entire farming business chain including agricultural practices, access to credit and commercialisation. All this must be done with the objective of improving the farmers' income, with due consideration towards the requirements of the populations. When all those conditions are met, the enhancement of technical advances is much higher than it is in Northern countries, quite simply because the starting point is far from the species highest potential.

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This study's objective is to present the state of the art on research conducted on crops, and their availability to farmers, with respect to a better reaction to drought than the current varieties. Indeed, drought, one of today's environmental constraints, is also poised to become one of the major consequences of climate change.

The working method used was two-fold. It began with a bibliographical analysis followed by a survey involving laboratories in public research agencies and private sector companies. Those surveys took place in France, and further afield in Europe, the United States and Africa, namely Kenya. This is the reason why the results show the most important aspects of the projects underway in France, the United States and Africa. The study focused on cereal crops cultivated in both developed and developing countries (maize, wheat, rice, sorghum and pearl millet) and looked at the different research options in plant breeding, including both conventional breeding and transgenesis.

Two varieties of maize showing higher tolerance to drought will soon be commercialised in the United States, where demand is strong among farmers. One is a standard variety, stemming from a conventional breeding process, while the other stems from transgenesis. Even though these varieties are aimed at the North American market, African farming may benefit from this research since an international programme bringing together seed companies, national and international public research organisations and American foundations was launched a few years ago to apply the progress achieved with maize to tropical species.

The analysis has shown that while the progress achieved in plant biology over the past thirty years has helped speed up, target and facilitate the breeding process, genetic resources remain the keystone of improvement programmes. Furthermore, this progress is dependent upon economic and biological criteria relating to the species concerned. Accordingly, maize currently claims the lion's share of investments made by private research to improve crops' drought tolerance. Besides, it is crucial to remember that since drought tolerance is based on complex biological processes, research is on-going and the path will be a long one. Lastly, it will not be possible to exploit the potential of enhanced seeds without a simultaneous improvement in farming practices, and increase investment in agriculture, especially in developing countries.

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