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Breeding for Drought Resistance Using Whole Plant Architecture – Conventional and Molecular Approach

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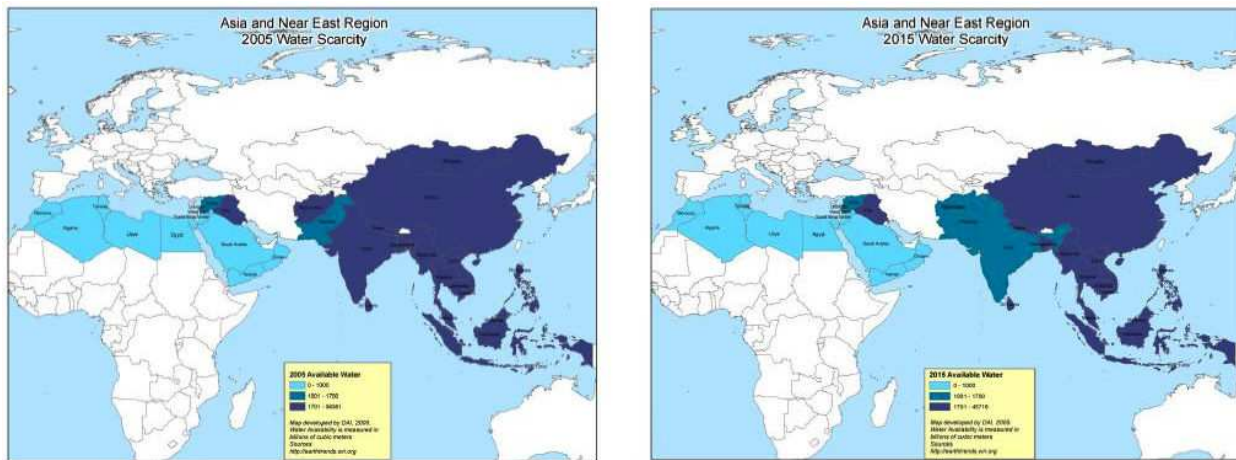
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1. Introduction

Drought, also referred to as low-moisture stress, is a form of abiotic stress. It is a challenge posed by the environment to the survival and productivity of a plant/crop that occupies a large area. This directly translates to economic loss to the farmer(s) who depend on the harvest. The plant has a wide range of genetic and phenological adaptations innate or triggered to cope with the stress. The extent of loss to productivity depends on the periodicity (over years), timing within the season when it occurs, rate of onset of the stress, severity, duration and a few other minor factors. At certain geographical locations, drought occurs at periodical intervals over years in a cycle. Should it occur, all the stages of the crop are likely to be affected. Vulnerability of crops to drought is likely to be intensified due to climate change [1].

When challenged by drought, a plant struggles to survive. If it succeeds to survive, it tries to complete the life cycle, which in annual crops means production of grains. When challenged by stress the phenology of the plant is severely altered. Altered phenology is often reflected as advancing flowering and maturity or by delaying flowering so that the critical stages of the crop do not get severely affected. Either way, it tries to circumvent the stressful period. This is a form of drought escape. The pattern of response will depend on the time of onset, intensity and nature of stress. Alternatively, it triggers a series of biological processes that helps the plant take the challenge 'head on' and complete the lifecycle with high grain yields. It is this pattern of responses that are a subject matter of systematic plant breeding endeavor. Collectively the latter strategy is referred to as drought resistance and scientists seek to study, understand and use it to enable farmers to get as good a harvest as possible.



Dark blue – countries with plentiful water ($>1,700 \text{ m}^3/\text{person}/\text{day}$)
 Medium blue – countries with water stress ($<1,700 \text{ m}^3/\text{person}/\text{day}$)
 Light blue countries with water scarcity ($<1,000 \text{ m}^3/\text{person}/\text{day}$)

Figure 1. Water scarcity map of the most vulnerable parts of the world. Left 2005, Right 2015. Borrowed from “Blue revolution initiative Strategic framework for Asia and the Near East, Bureau for Asia and the Near East, USAID, May 2006. P 37 [2]”

Breeding for drought tolerance in any given crop, has immense value to the farmers as their livelihood depends on the harvest(s). It bears a positive effect on the farmers’ economic health, family well-being and harmony in the society. It affects poor farmers more than the rich ones. Complete or partial loss of harvest in drought years is known to trigger panic reaction, migration and decrease or extinction of flora and fauna of the particular habitat. There have been scores of farmer suicides due to losses caused by drought and associated problems in different States of India [3, 4]. A link between drought and suicides has been established in Australia [5], Africa, and in the South America. Thus as a trait, drought resistance has immense value to the individual farmer and the society. According to [6] the “future imperative is clear – Asia cannot continue to depend on the quantity and quality of freshwater for rice cultivation in the traditional manner”.

2. What is drought resistance?

The ability of a plant to maintain favorable water balance in its tissues (turgidity/turgor) when exposed to drought stress is a manifestation of drought resistance. Turgidity refers to the condition of the leaf when it is wide open and fully facing the sky. When a leaf loses turgor it rolls (in crops like rice) wilts (in crops like legumes) and ultimately dries up. Loss of turgor is an indication that the transpiration demand is more than the water being supplied from the soil through the plant. Sometimes, the loss of turgor can be a temporary phase during high temperatures prevalent during midday.

Maintenance of turgor under low-moisture conditions is crucial. It implies continued transpiration. This requires the stomata to be open thus facilitating gas exchange, a prerequisite for

photosynthesis. The transpiration pull thus generated provides the suction force (one of the requirements) for water uptake by roots. This also keeps the leaf cool and prevents drying and subsequent dying. Thus, a favorable water balance under drought condition is a key to a plant's survival and productivity.

While continued transpiration has many advantages to the plant/crop survival, the final and economically useful manifestation of drought resistance is the magnitude of grain yield that is obtained at the end of the season, when the crop has been challenged by drought. Maintenance of turgor, transpiration, biomass or greenness is of little use to the farmer who wishes grain yield. While maintenance of turgor and survival under stress are of academic interest, grain yield is of practical value. Thus, ultimately, in grain crops the grain yield is the manifestation of drought resistance. Even under non-stress conditions, it is the grain yield (or the economic product in non-grain crops) that is a measure of a plants' performance [7]. Any trait that contributes to this would be a useful selection criteria in a breeding program.

The pattern of responses that a plant chooses to trigger has been collectively referred to as drought resistance. Further classifications of responses fall into three categories namely, drought escape, dehydration avoidance and dehydration tolerance [8]. Dehydration avoidance is a reaction when the plant maintains a high level of water status or turgor under conditions of increasing soil-moisture deficit. Finally, drought resistance is referred to as a plants' ability to sustain the least injury to life functions at decreasing levels of tissue water status or turgor. Drought escape refers to the ability of the plant to complete its lifecycle before the onset of drought or adjust its phenology so that the crucial developmental stages escape the adverse impacts of drought [9]. Delayed flowering, is one such phenological adjustment.

Broadly, plants adopt two strategies, which involve reducing their water expenditure called "water savers" or "pessimistic plants" or accelerating water uptake sufficiently so as to replenish the lost water called as "water spenders" or "optimistic plants". A plant can maintain turgor by adopting one or both of the following strategies depending on genotype and environmental factors.

1. The mechanism of conserving water: includes stomatal mechanism, increased photosynthetic efficiency, low rate of cuticular transpiration, reduced leaf area, effect of awns, stomatal frequency and location.
2. Improving the water uptake: the mechanisms are efficient root system, high root to shoot ratio (R/S), difference in the osmotic potential of the plants and conservation of water.

The drought resistant variety or hybrid that is developed is also expected to possess the ability to contend with excess moisture. Many times low-moisture and excess moisture can also cause stress to the crop within the particular season. The variety or hybrid must also possess certain degree of resistance to common diseases or pests that are prevalent in the area that is targeted.

3. What characters are associated with drought resistance?

All parts of the plant are affected by drought stress. Conversely, all parts of the plant can potentially contribute to augment/enhance stress resistance. Among the plant species that inhabit the earth a wide range of traits enable plants to either tolerate excess water (submergence) or very low-water (drought). Each species has a wide range of characters accumulated during the course of evolution to adapt to the habitat. Crops have evolved over centuries in a particular habitat and have, over time, adapted to the adverse conditions. All the crops occupying a habitat share the same/similar set of adaptive traits as per the law of homologous series of variation [10]. For example, in rice there are accessions, which tolerate short span to long periods of submergence. They outgrow the water level and produce panicles above (like lotus flowers) or kneel down when water recedes, all the time keeping panicles facing upwards. On the other hand, there are accessions of rice, which tolerate prolonged periods of drought. Referred to as upland rice, these accessions grow like other arable crops with no need for standing water, ever. In the middle of this wide range are genotypes, which grow under submerged soils (irrigated rice).

Extensive studies of gross morphology and hard pan penetration ability of roots among traditional and improved accessions of rice had brought out the fact that the most deep-rooted accessions were traditional accessions and improved varieties had relatively shallow roots. The traditional accessions had greater hard pan penetration ability compared to improved accessions [11]. Most likely, this was due to the natural selection over decades/centuries or crop improvement efforts in well-endowed habitats. Most traditional accessions manifested low grain yield, but had high degree of tolerance to drought [12] but improved varieties were susceptible to drought, shallow rooted and were high yielders. Based on the germplasm study, it almost appeared that the drought resistance and grain yield were under such a genetic control that bringing them together was impossible. This would have been the case if the two sets of traits were pleiotropic. Extensive QTL mapping studies for root traits and grain yield in the same mapping population in similar habitats contradicted this [13].

Considerable amount of investment has been made by the scientific community in studies associated with drought resistance. Several crops have been studied. A wide range of traits is found to be associated with drought resistance (Table 1). Ironically, the only trait that the farmer is interested in is that which fetches him/her an income from what constitutes a marketable produce [6]. Thus, finally, for practical breeding purposes, manifestation of drought resistance can be summarized as increase in the economic product(s). In food crops, it would be the grain, in fruit crops it would be fruit and in vegetable crops it would be the edible part, whatever it is root, leaves or stem. Thus, yield is one single trait that could be considered as a manifestation of drought resistance. As yield is a result of a well-grown plant, biomass could be the cause or a prerequisite to high yield. Further, good biomass is a result of adequate quantity of water and nutrients made available at appropriate growth of the plant. This implies a well-endowed root system. As a breeding objective, the plant traits that could be selected among segregants are robust and efficient root systems, well-endowed shoot system and finally grain yield. This means selection for the entire plant characters and not only

for shoots that are easy to see, measure and select. Every part of the plant, above-ground or below-ground should be subjected to selection pressure.

Traits associated with drought tolerance	
Morphological & Anatomical:	Grain Yield; Maximum Root length, Root Volume, Root Dry Weight, Root Thickness; Root surface area, above-ground Biomass; Harvest index; Leaf drying; Leaf tip firing; Delay in flowering. Aerenchyma, Leaf Pubescence.
Phenological:	Earliness; Delay in Flowering; Anthesis-Silking Interval; Seedling vigor; Weed competitiveness; Photosensitivity; perennially.
Physiological & Biochemical	Osmotic Adjustment; Carbon Isotope Discrimination; Stomatal conductance; Remobilization of stem reserves; Specific leaf weight; ABA; Electrolyte leakage; leaf rolling, tip firing, Stay-green; Epicuticular wax; Feed forward response to stress
Oxygen scavenging;	Heat shock proteins; Cell Wall proteins; Leaf water potential; Water use efficiency; Aquaporins; Nitrogen use efficiency; Dehydrins;

Table 1. Development of drought tolerant quality rice varieties

All the traits fit well in the well-known formulae given below

Grain Yield – Transpiration x Water Use Efficiency

Finally, for a trait(s) to be of use, it should be correlated with or causally related to yield, easy to select for and should not be a drain on the energy reserves of the plant. For a breeder to use such a trait there should be ample genetic variability for the trait in the germplasm accessions. The heritability of the trait must be greater than heritability of the grain yield per se.

4. Genetic elements associated with drought resistance

Drought resistance is a complex trait/phenomenon [14]. Some people think that it is not an individual trait and refers to the response of a plant/crop to an environmental condition. Purported complexity of the trait deterred many scientists to work on the trait in several crops. Most of the investment in the green revolution era was focused on favorable habitats. The research investment in terms of time, effort and funds on unfavorable habitats was significantly less compared to the favorable ones and this was due to the high rate of returns on the investment (in the private sector). One of the favorite arguments extolling the difficulty in breeding for drought resistance was that the genetic basis of the trait was not discerned and that it was controlled by many traits. In fact literature is replete with many reasons to almost dissuading a not so determined breeder/researcher.

As an avocation, breeding for any trait can be done irrespective of the complexity of the trait. Neither is it necessary to fully understand the trait's inheritance. Crop improvement can be

accomplished in spite of this. The argument is amply exemplified by the rapid strides and break-through accomplished in the 1. Semi-dwarfism, 2. Heterosis 3. Development of synthetic varieties of *Triticum aestivum*, L. and 4. Continuous improvements in grain yield and quality parameters across crops over years Table 2. In all cases listed above, one common issue is that the genetic basis is still not 'clear'. While concerted efforts are underway in several crops to discern the mode of action, number of genes governing the trait, the promoters, QTLs, etc., plant breeders have gone ahead and improved each one of the traits.

No.	Trait	Crop
1	Grain yield	Rice, Wheat, Finger millet, Bajra
2	Heterosis	Maize, Sorghum, Cotton, Tomato,
3	Semi-dwarfism	Wheat and Rice
4	Synthetics (reconstituted allo-hexaploid genome)	Synthetic wheat
5	Genome diploidization	Triticale, Synthetic wheat

Table 2. Traits for which genetics has not been discerned but have been subject of continued improvement over decades.

5. Breeding for drought resistance – Selection environment

Breeding for drought must be conducted with adequate concern for the selection environment. Adequate care and appropriate consideration must be given to the genotype X environmental interaction during selection of parents and segregants at each filial generation. Ideally, the selection environment(s) must adequately represent the target environment(s) for which the variety/hybrid is being developed. Usually the target environment is highly variable in edaphic, climatic and hydrological status. Every cubic centimeter of soil is different from the other. Aboveground also, the plant faces differences in climatic condition during the day/night, across the season and over year(s). Thus, every cubic centimeter aboveground and belowground is likely to be different and the plant has to adapt to this. If the habitat covers a large geographic area, so as to explain the variability that exists, it is usually referred to as a 'population of habitats'.

Any significant deviation between the selection environment (where the parents and the segregants chosen are evaluated/advanced) and the target population of habitats would make the final selected variety/hybrid inadequately adapted contributing to failure of the crop improvement program. An alternative to having the selection environment geographically isolated or distant from the target environment is to perform selection in the target environment itself. The farmers of the target habitat(s) could be involved in the selection process. Such

a breeding program, conducted on the farmers' fields (target environments) involving target farmers is referred to as 'participatory plant breeding'.

Unjustifiably it is perceived that breeding for drought resistance is difficult because

- a. It is a complex trait,
- b. There are too many secondary traits associated with it and heritabilities are low,
- c. There is inadequate knowledge about the inheritance mechanism involved,
- d. Predicting the magnitude of drought that might occur, if at all it occurs, is difficult and
- e. No single trait manifests direct correlation with grain yield under stress.

This argument is invalid because breeders, over years, have been improving traits and crop plants without adequate knowledge about the genetics of the trait they are breeding for. Four classic examples are given in Table 2. Thus, complexity of a trait or lack of information on the inheritance mechanism of a trait has not bothered breeders much. The innovative selection strategies applied in a well understood environment has yielded results year after year in crop after crop. Thus, while breeding for drought resistance too, not having 'complete' knowledge of inheritance of traits, will not be a deterrent.

With reference to the inability to predict the occurrence of drought and the stage at which it would occur within the cropping duration, it is prudent to build drought resistance to a genotype irrespective of the crops' developmental stage. A plant should be able to face the challenge, posed by low-moisture regime, whenever, should it occur [13].

Genetic variability for traits is harnessed by the breeders in a breeding program. There is ample variation for all traits in the germplasm accessions within a given species and across species that are amenable for use. Selection strategies need to be designed to be able to select for traits especially if it involves destructive sampling (example, root traits). Studying roots in segregating populations is not as easy as studying shoot traits and grain yield. A plant has to be uprooted to expose roots for analysis. This would kill the plant if it is not already mature. The root traits are ideally studied at peak vegetative stage. At maturity there would be decline in the root traits. Thus innovative selection strategies need to be adapted depending on the mode of propagation, reproduction etc. Traits associated with drought resistance valuated under the stress-full environment manifest lower heritability values making selection an unattractive proposition. This is because of the high G x E interactions. This is manifested by 'crossover interactions' typical of improved and traditional accessions when evaluated in the same study [15, 16]. Any effort to improve the Environment (E) in the experimental site might contribute to improve heritability (H) values. But increase the risk of misrepresenting the target population of environment. Crossover effects are not universal and it is possible to break the trend and select for high productivity under stress and relatively high yields under non-stress habitats too [14, 17].

Two examples where selection for root traits was seamlessly incorporated into the breeding program are discussed below in detail.

6. Breeding for drought resistance — Marker-assisted selection

Marker-assisted selection is expected to boost the pace of crop improvement especially for complex traits. This was the feeling of molecular biologists who want about discovering DNA markers in large numbers. Overtime, the markers have evolved. There is always a search for ideal markers which can be used by breeders. Characteristics of ideal markers are as follows

1. Tightly linked to gene that controls the trait either individually (monogenic trait) or in groups (polygenic trait)
2. Co-dominant in inheritance. It will help identify heterozygotes and homozygotes with ease. Dominant markers are also useful but they identify only one of the homozygous allelic combination
3. PCR based so that it can be analyzed faster. It would be better if the amplified bands could be resolved on agarose gels or data acquired as quickly as possible.
4. The marker should account for a large proportion of the genetic variability for the trait of interest.
5. The marker must be able to identify all other allelic forms associated with the trait.

The first QTL tagging work, for root traits was done by IRRI, Philippines in 1995 [18]. Ever since a very large number of QTLs have been discovered for every component trait expected to contribute to drought in several crops. Each one of them, proposed that the QTLs discovered would help MAS for drought. A large number of QTLs associated with traits related to drought have been tagged to different kinds of molecular markers [13, 19]

So far, the only documented success stress with MAS for root traits has been the work of [20] in rice. In this paper too, out of the five loci selected for MAS, only one locus of chromosome 9 had a significant and positive effect on root traits. Phenotyping done among the transgressants aided in the selection process.

A novel upland rice variety, BirsaVikasDhan 111 (PY 84), has recently been released in the Indian state of Jharkhand. It was bred using marker-assisted backcrossing with selection for multiple quantitative trait loci (QTL) for improved root growth to improve its performance under drought conditions. It is an early maturing, drought tolerant and high yielding variety with good grain quality suitable for the direct seeded uplands and transplanted medium lands of Eastern India. PY84 is the first example of a rice variety bred through the combined use of marker-assisted selection and client-oriented breeding, and a rare success story for the use of marker-assisted selection to improve a quantitative trait. It out-yields the recurrent parent by 10% under rain fed conditions. The variety was developed in a collaborative partnership between CAZS-NR; GraminVikas Trust, Ranchi, Jharkhand, India and Birsa Agricultural University (BAU), Ranchi, Jharkhand, India. The target QTL was first identified by Adam Price (Aberdeen University, UK) and Brigitte Courtois (CIRAD, France/IRRI, Philippines) [20].

In this marker assisted backcrossing program (MABC) was used. The strategy was to pyramid different QTLs situated on different chromosomes. All these QTLs were related to root traits.

An Indian *indica* rice variety was used as the recurrent parent. The donor for deep-rooting and grain aroma was Azucena, a *japonica* from Philippines. Five segments on different chromosomes were targeted for introgression; four segments carried QTLs for improved root morphological traits (root length and thickness) and the fifth carried a recessive QTL for aroma. Twenty-two near-isogenic lines (NILs) were evaluated for root traits in five field experiments in Bangalore, India by Dr. H.E. Shashidhar. The target segment on chromosome 9 (RM242-RM201) significantly increased root length under both irrigated and drought stress treatments, confirming that this root length QTL from Azucena functions in a novel genetic background. No significant effects on root length were found at the other four targets. Azucena alleles at the locus RM248 (below the target root QTL on chromosome 7) delayed flowering. Selection for the recurrent parent allele at this locus produced early-flowering NILs that were suited for upland environments in eastern India (Figure 2).

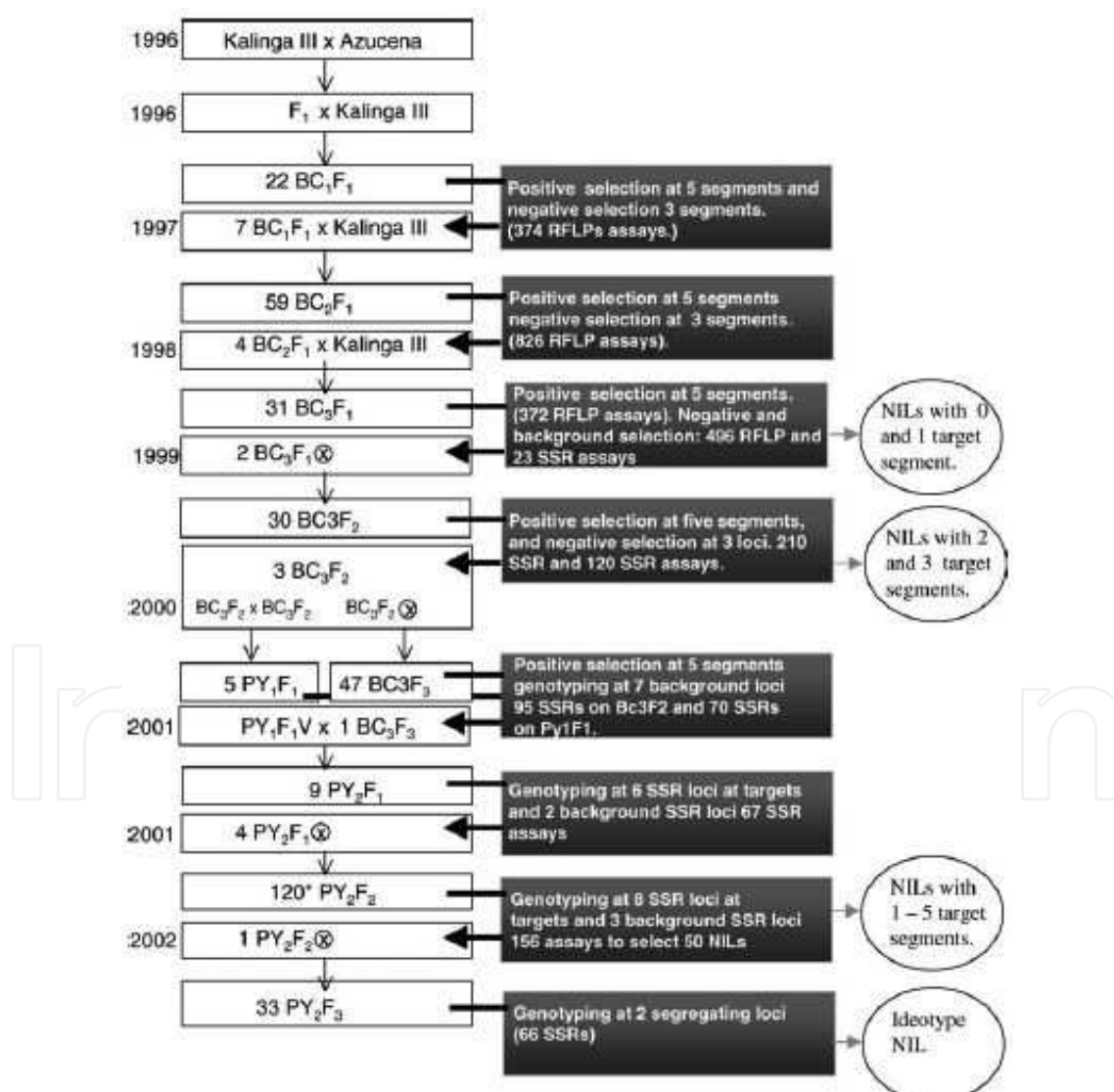


Figure 2. A flow chart for MAS for drought resistance.

7. Breeding for drought resistance — Conventional approach

Selection in the target habitat has been the standard way of breeding for drought resistance across crops. Over the past decade several OPVs and Hybrids have been developed with the active participation of the national programs across the target countries (Table. 3). Grain yield and other shoot traits has been the focus in most of their projects. This is a typical case of plant breeding. Selection for a plant's performance would have been better understood and most effective selection would have resulted probably by using root characters in the parental selection and breeding program.

In rice, an innovative strategy was adapted to breed for drought resistance. The donor for characteristic deep root was a local variety Budda. The donor for grain yield was IR-64. The generations were advanced by raising the families derived from F3 onwards in farmers' fields and involving farmers in the selection process. Each of the F3 families was divided into two parts with one being directly sown and maintained under well-watered conditions, while the other one was maintained under drought stress. Water was provided to each one (WW and LMS) by precise measurements. While WW set received 80 % of the water lost due to evaporation, the other one (Stress) received 60 % of water evaporated (Evaporation was measured by installing and maintaining a pan-evaporimeter in the field). Data was recorded on grain yield and biomass at harvest. Selection at each generation was based only on biomass. High biomass types under both conditions were forwarded to next generation. In the next generation, one tiller from each plant was grown in PVC pipes to study root traits (Figure 3). All subsequent generations were forwarded in three places. Two in field (WW and drought) and one in PVC tubes. The selection was based on all three traits: Good Roots + Shoots + Grain yield [21].



Figure 3. Manifestation of transgressive segregation for root traits in rice.

Several varieties have been developed in different countries adopting conventional plant breeding principles (Table 3). Some of these have been accomplished using markers and some without.

No.	Variety	Trait + Selection Strategy	Crop	Developing Institute, Country
1	Ashoka 228 (BVD 109)	MAS+ PPB, Root+Shoot+Yield	Rice	GrameneVikas Trust, BAU, Jharkhand, India
2	Ashoka 220 (BVD 110)	MAS + PPB, Root+Shoot+Yield	Rice	GrameneVikas Trust, BAU, Jharkhand, India
3	PY 84	MAS + PPB, Root+Shoot+Yield	Rice	GrameneVikas Trust, BAU, Jharkhand, India and UAS, Bangalore
4	ARB6	Conventional Pedigree PPB + Root + Shoot + grain yield	Rice	UAS, Bangalore, India
5	MAS946-1	Conventional breeding Pedigree	Rice	UAS, Bangalore, India
	MAS26	Conventional breeding Pedigree	Rice	UAS, Bangalore, India
6	Poornima	Conventional breeding Pedigree	Rice	IGKV, Raipur, India
7	Danteshwari	Conventional breeding Pedigree	Rice	IGKV, Raipur, India
8	Indira BharaniDhan 1	Conventional breeding & selection for roots	Rice	IGKV, Raipur, India
9	Kamaleshwari	Conventional breeding Pedigree	Rice	IGKV, Raipur, India
10	Han Dao 502	Conventional Pedigree	Rice	China Agril. University, India
11	Han Dao 297	Conventional Pedigree	Rice	China Agril. University, India
12	Jin Dao 305	Conventional Pedigree	Rice	China Agril. University, India
13	ZM 309, 401, 423, 523, 623, 625, and 721	Conventional	Maize	South Saharan Africa
14	KDV1, 4, and 6	Conventional	Maize	South Saharan Africa
15	WS103	Conventional	Maize	South Saharan Africa
16	Melkassa 4	Conventional	Maize	South Saharan Africa
17	WH 403, 502 and 504, ZMS402 and 737	Conventional	Maize	South Saharan Africa
18	Rd 12, and 33	Conventional	Rice	Thailand
19	Hanyou 2 and 3 (Hybrids)	Conventional and MAS	Rice	Zhejiang Yuhul Agro-technology Company Zhejiang

MAS= Marker-assisted selection, PPB= Participatory plant breeding, ARB = Aerobic rice Bangalore

Table 3. Drought resistant lines/ list of varieties developed

In conclusion, breeding for drought resistance can do only as much as develop a genotype that can tolerate to moisture stress and respond to incremental water inputs should that be possible in the given habitat. The final answer to maximizing productivity comes from an integrated approach where genotype, agronomy, management, economics and policy come together to maximize the water productivity, the key limiting natural resource. Water is not equitably distributed in the world and the scarcity of water is assuming ominous dimensions (Figure 3).

8. Time tested tips for breeding for drought across crops

A deluge of information and knowledge has been generated over time. Considerable investment has been made by the international community and funding agencies. The collective intelligence can be summarized as under.

1. Screen parents and segregants in a habit that most closely represent/ resemble the target population of habitats.
2. Repeat phenotyping over years and seasons so that maximum possible variations in the environmental conditions are represented.
3. Impose selection starting from early generation (not F₂) in well-watered and stress conditions. This will ensure selection for potential productivity (should stress not occur in the farmers' fields) and still maximize productivity under stress (should it occur). This will ensure that the farmer is likely to harness the full potential of every incremental drop of water above the threshold called drought.
4. Quantify the water that is received by the field during the experimental period. Input of water could come in the form of rainfall or surface irrigation. It would be ideal to also document the evapotranspiration from the field. This will help budget water at the level of each genotype/segregant/plot. With such data, water productivity could be computed for each segregant, genotype.
5. While stability of the drought variety is highly desirable, local adaptability is also very important. A genotype may manifest low stability and may be use-full for the particular habitat.
6. High yield under favorable conditions (moisture regimes) can be combined with the high degree of drought resistance. Thus, traits associated with drought need not be a penalty to the plant under well-watered condition.
7. Selection for root and shoot morphology can be judiciously combined in ongoing breeding program while selecting for resistance to diseases and pests.
8. Instead of incorporating growth stage specific drought resistance (vegetative stage drought resistance, reproductive stage drought resistance etc.) it is more appropriate to make any and every growth stage of the crop drought resistant as the timing of occurrence of drought, if at all in the farmers' field is unpredictable. It would be counterproductive

if stage specific drought resistance is built into a variety and should drought occur at some other stage. Breeding effort would be futile.

9. Need to select for combination of stresses that challenge the crop in the farmers' field rather than only drought resistance. This will ensure longer survival of the variety in the farmers' field [22].

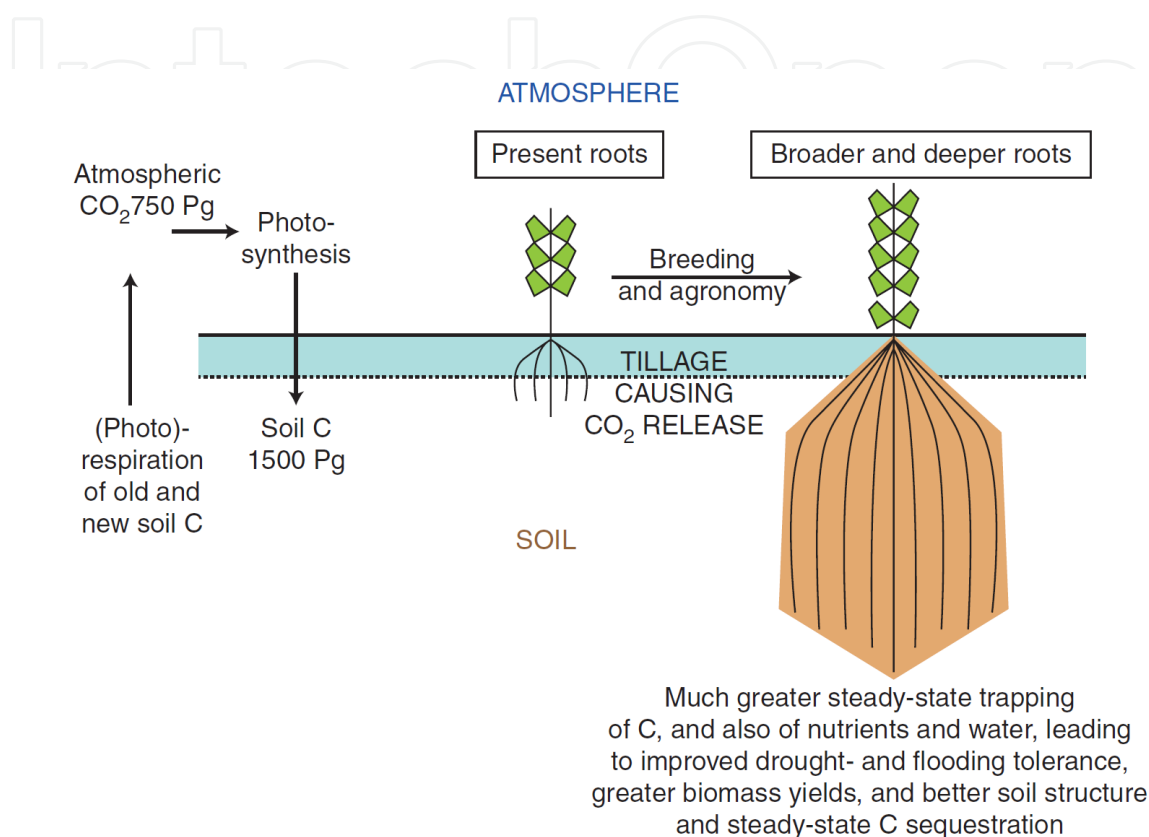


Figure 4. Borrowed from Kell DB, *Annals of Botany*, pp 1-12.[23]

This calls for ushering a blue revolution [2, 23], the water equivalent of green revolution, where it is envisaged that the water productivity in agriculture is addressed along with equity of water distribution between urban aspirations and rural needs. Finally [24] proposes that roots do much more than supply water to plants, they capture carbon and a well-endowed root system is not only important to the plant but also as a means to mitigate climate change, by trapping carbon in the form of increased microbial activity and dry matter accumulations. Thus, roots not only provide anchor, water, nutrients but also contribute to carbon sequestration and one of the means to mitigate global warming.

Finally, using all shoot and root characters of the plant, be it morphological, physiological, biochemical, phenological, anatomical or responses to environment would provide more opportunities for enhancing drought resistance of the crop. The characters of the plant have to be matched with the appropriate agronomic practices to maximize the expression of the traits. This is a holistic approach to plant breeding for drought resistance and also referred to as 'whole-plant breeding'.

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