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Genetic of adaptation to drought of cultivated species and consequences on plant breeding

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Summary.- Among various methods used in wrestling with drought. genetic improvement holds badly exploited cards which should enable it to play one of the leading parts. Among others, improvement based directly on physiological characters of adaptation to drought is involved. For the most important cultivated species, informations are gathered in form of the available data concerning genetic variability of these adaptive characters, the nature of correlations between each other and between them and the production characters, and lastly their heredity. This stage enables us to point out the blanks in our knowledge of these different components of selection, to identify the limits of the classical selection method based on production in dry conditions and finally to work out a more effective approach of genetic improvement of adapted complex ideotype.

This method needs an enlargment of the genetic variability which is studied, the application of selection based on the various characters of adaptation and production, the parting of long-term improvement led by recurrent selection with the short-term one led by classical varietal selection, and the parting of selection for productivity with selection on adaptive characters.

Résumé.- Parmi les différentes méthodes utilisées pour lutter contre la sécheresse, l'amélioration génétique possède des atouts mal exploités qui devraient lui permettre de jouer un rôle de première importance. Parmi ceux-ci, l'application d'une amélioration directe des caractères physiologiques d'adaptation à la sécheresse est particulièrement importante. Chez les principales espèces cultivées, les principales données disponibles sont présentées sur la variabilité génétique de ces caractères adaptatifs, sur la nature des corrélations existant entre ceux-ci et avec les caractères de production et enfin sur leur hérédité. Cet examen permet de mettre en évidence les lacunes dans nos connaissances de ces différentes composantes intervenant dans la sélection, de mettre *en* évidence les limites des méthodes de sélection classiques basées sur la production en conditions sèches, et finalement de proposer une approche plus efficace de l'amélioration génétique des idéotypes d'adaptation complexes.

Cette approche repose sur un Qlargissement de la variabilité génétique qui est travaillée, sur l'application d'une sélection basée sur différents caractères d'adaptation et de production, sur la dissociation de l'amélioration à long-terme menée par sélection récurrente, de l'amélioration à court-terme menée à l'aide des méthodes de sélection classiques, et enfin sur ladissociation de la sélection pour la productivité de la sélection des caractères adaptatifs.

Key words : drought -adaptation - selection - genetic - variability - heredity.

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INTRODUCTION

In order to achieve an improvement of adaptation of cultivated species to different types of drought they go through, it is clear that the involved methods - plant breeding, improvement of farming tecnics, among others recourse to irrigation, development and management of soils - are to be parts of a whole.

Among these methods, breeding is abble to play a part of major importance by creating better adapted varieties related to various drought conditions. Its advantages, which are not sufficiently exploited, lies in the use of a wide inter- and intra-species variability, in the application of strides of physiology on the understanding of adaptive mechanisms and in the choice of breeding methods adapted to each case.

Among these advantages, the application of physiology is particularly neglected. Very few breeding programs from all over the world associate physiology to their approach as a part of a whole, although such an association would, without any doubt, present a great potential. This remark would apply to gcnetic improvement of characters depending on the whole physiology of the plant. This is the case of productivity.

The first signs of a reasoned use of "the physiological tool" for breeding are becoming discernible. This use is one of the ways which should allow genetic progress ; which has been for more than 60 years by breeding, to remain firm. Other potential approaches, as far as we can now identify them, deal with a bettcr long term management of genetic variability and with the use of biotechnologies.

From a genetic point of view, three fondamental components, concerning physiological characters of adaptation to drought will shape the leading of breeding. They are :

- genetic variability of adaptive characters ;
- nature of correlations between these characters ;
- their heredity.

1.- GENETIC VARIABILITIES OF ADAPTIVE CHARACTER

As Ahmadi (1983) mentions it : "Adaptation to drought appears as the result of numerous anatomical, morpbological, physiological and biochemical characteristics, constituent or inductible, which interact in order to make possible the keeping of growing and development processes under conditions of climates and soils called drought". In order to simplify, we will call "physiological characters of adaptation" all these mechanisms.

In the data-boards presented in appendixes 1, 2, 3 (Khalfaoui, 1988), we list the various physiological characters of adaptation according to Levitt's classification (1981) and point out : their influence on productivity, their reversibility, their aptitude for easy selection, and their effectivencss in relation to different types of drought. These data-boards extensions from Turner's one (1981), with a differcnt opinion concerning the influence of some characters on productivity and their aptitude for easy selection.

Concerning the main species, a bibliographical study of the works led in order to point out the existence of genetic variabilities in the manifestation of adaptive characters, allows us to build the data-boards of appendixes 4, 5, 6. Their analyse makes clear a great disparity between the levels of various species and various adaptive characters, reached through research. For example, the gcnetic

Appendix 1.- Mechanisms of drought escape

MECHANISMS	Effect on Productivity	Reversibility on relief of stress	Easiness in screening	Drought at		Drought during the culture		
				arly tages f the ulture	late stages of the culture	Steady small rains	Drought periods	
							during the sensi- tive stage	contin- gent
- Earliness		I		+	+	O	O	O
- Shifting of the sensitive stage during the cycle	(-)	NR	difficult	O	O	O	+	O
- Developmental plasticity	0	R	easy to difficult according to species	+	O	O	+	+

- = negative effect ; + = positive effect ; 0 = without effect ; ? = unknown effect ; ( ) = uncertainly established effect ; R = reversible ; I = irreversible ; PR = partially reversible.

variability of adaptive characters of the wheat is pretty well known ; on the contrary, informations concerning ***Phaseolus vulgaris*** L. are very fragmentary. In the same way, the genetic variabilities of the parameters of root development are pretty well known for the main species although those concerning the keeping of photosynthesis have been studied for very few species. Beyond making clear the adaptive characters of species, this points out the important effort of research that is still to be done in the field of characterization of their genetic variability.

Consequences for breeding

According to the type of drought which the varieties to be created will have to be adapted to, the choice of characters, in addition to agronomic characters, defines an ideotype of selection. The existence of a genetic variability at disposal for each adaptive character is the necessary condition to their genetic improvement. It is the reason why stomatal control of wheat (Fisher et *al.*, 1979 ; Sojka et *al.*, 1979 ; Clarke et *al.*, 1982) and rice (Ahmadi, 1983), glucidic reservcs in the roots of peanut (Khalfaoui, 1988) and osmotic adjustment of rice (Culter *et* al., 1980) cannot be improved *for* lack of sufficient genetic variability although tbere are physiologically effective for each of these species.

2.- PIIYSIOLOGICAL AND GENETIC CORRELATIONS BETWEEN CI-IARACTERS

We make a distinction between two kinds of correlations between adaptive characters and between them and agronomic characters. The first one regroups physiological direct correlations and the second one indirect genetic correlations.

Direct physiological correlations cannot be modified by selection. An

Appendix 2.- Mechanisms of drought avoidance

	Effect on Producti-vity	eversi-ility on elief of tress	Easiness in Screening	Drought at: early stages of the culture (limited WR)	Drought at: late stages of the culture, deep WR	Drought at: late stages of the culture, limited WR	Drought during the culture: Steady small limited WR	Drought periods during the sensitive stages: deep WR)	Drought periods during the sensitive stages: limited WR	Drought periods contingent: deep WR)	Drought periods contingent: (limited WR)
) Reduction of water loss											
Reduction of leaf area :				O	ø	+	+	+	+	+	+
* Constituent characters		I	easy								
* Inductible characters :		PR									
. leaf size			easy								
. leaf senescence			difficult								
High stomatal resistance :											
* rapid stomatal closure		R	easy	+	+	O	+	+	+	+	+
with glucidic reserves			quite easy	O	+	O	+	+	+	+	+
* low transpiration rate at											
complete aperture		I	easy	+	+	+	+	+	+	+	+
* stomatal density and size :		I	easy	+	+	+	+	+	+	+	+
according to species { high low											
{ low high											
High cuticular resistance :	O	I	easy	+	+	+	+	+	+	+	+
* epicuticular wax.											
* cohesiveness of cells											
leaf pubescence	O	I	easy	+	+	+	+	+	+	+	+
Reduction of interception of radiations :											
* reduction of leaf area (above)											
* high leaf reflectance :	(-)	I	easy	+	+	+	+	+	+		+
. epicuticular wax											
. foliage color											
* leaf angle	(+)	I	easy	+	+	+	+	+	+		+
* leaf movements :	O	R	easy	+	+	+	+	+	+		+
. wilting											
. rolling											
. paraheliotropy											
* spikelets	+	I	easy	+	+	+	+	+	+		+
I Water absorption											
Root growth :		I	difficult								
* rate of initial growth											
* depth											
* root density											
→ low	to			-			+	-	+		+
high	to *			+	+			+			-
Hydraulic resistance of roots											
* diameters of xylem vessels			quite easy								
* number of xylem vessels			easy to diffi. (Species)								
→ high				-			+	-			+
low				+	+			+			

Fegend : Appendix 1. WR = water reserve of the soil.

example is given by the opposition for tbe restriction of transpiration by closure of stomats to the keeping of photosynthetic activity (Cowan et *al.*, 1977). From a genetic point of view, the phenomenon of pleiotropism is involved. It is the kind of correlation with production under conditions of drought that the characters studied must show, in order for them to be effectively adaptive.

But, in numerous cases, a genetic indirect correlation betwecn characters determined by distinct genes is involved. Given expressions may have been associated in the same genotypes under the effect of natural and human selcction pressures. If these genes are linked, it will be very difficult, even impossible, to dissociate their allels by genetic recombination in segregating material. On thc other hand, if there is no linkage effect between genes, associations of allels will be modified by genetic recombination.

Appendix 3.- Mechanisms of drought tolerance

MECHANISMS	Effect on Productivity	Reversibility o n lief of stress	Easiness in re- screening	Drought et early stages of the culture	Drought et late stages of the culture	Drought during the culture: Steady small reins	Drought during the culture: Drought periods during the sensitive stage	Drought during the culture: Drought periods continge
▪ Germination under high osmotic pressure	0	I	difficult	+	0	+	0	0
▪ Tolerance to dehydratation (and heat) :	?			+	+	+	+	+
stability of protoplasmic membranes	(-)	?	easy					
. stability of proteins (among others those involved in photosynthesis)		I	difficult					
Maintenance of turgor :			difficult	+	+	+	+	+
. osmotic adjustment		R						
. tissue efasticity	?	I						
Maintenance of photosynthesis :								
amount of proteins/unit of leaf are.3	+	I	easy	+	+	+	+	+
spikelets	+	I	easy	O	+	+	+	+
Maintenance of harvested organs production :	0							
change in allocation of assimilates		(R)	difficult	0	+	+	+	+
compensatory effect of production components		NR	easy	0	0	+	+	+
Modification of metabolism (plant hormones)	?	R	difficult	+	+	+	+	+

Legend : Appendix 1

This phenomenon has a direct consequence on physiological interpretations. Actually, physiological studies deal with varietics which have been created by natural and human selection. Some correlations between characters and between them and productivity may lead to think wong, about physiological direct correlations, therefore links between causes and effccts, exist although they actually depend on genetic indirect correlations. The risk of genetic indirect correlations increases when, willing to present a complete approach of the species bchaviour, research workers associate in their studies varieties representative of ideotypes of adaptation very different drom each other. Without any linkage cffcct, expressions will be dissociated in the individuals issued from a cross between these varietics. An example is given by the case of precocity of peanut (Khalfaoui, 1988). A study of correlation for a group of varieties representative of the collection has pointed out a very important positive correlation (- 0,98^{+++}) between flowcring precocity and fruit maturation precocity. After prime analysis,

Appendix 4.- Genetic variability of mechanisms of drought escape for the main studied species

MECHANISMS	GRAMINACEOUS						LEGUMINOUS				OTHERS			
	BARLEY	MAIZE	PEARL MILLET	RICE	SORGHUM	WHEAT	BEAN (PHASEOLUS VULGARIS)	COWPEA	PEANUT	SOYBEAN	COTTON	OIL PALM	POTATO	SUNFLOWER
- Earliness	+	+	+	+	+	+	+	+	+		++		+	+
- Shifting of the sensitive stage during the cycle		+												
Developmental plasticity	+	+			+	+	+	+	+		++		+	+

+ = existence of genetic variability ; + • = lack of genetic variability ; 0 = absence of genetic variability ; ( ) = uncertainly established effect

this correlation seemed to be due to a direct physiological link between the two characters. But, a study of the F3 generation conducted on segregating material showed a total absence of phenotypical (0, 01) and genetic cor-relation (- 0, 02). Thus, it seems important that, when studies are held in order to explain physiological mechanisms involved in the plant behaviour, correlations discovered between characters of the varieties have to be confirmed using segregating genetic material before any physiological interpretation.

Consequences for breeding

The kind of correlation between characters will either facilitate or impede breeding of the adaptation ideotype.

Direct physiological cor-relations or genetic ones with a strong linkage effect can be directly exploited if they benefit the plant. They allow, among othcr things, to adopt early tests as done in the case of the link between roots development at juvenile and grown up stages observed for many species (Hurd, 1974 ; Townley-Smith *et al.*, 1977 ; Ahmadi, 1983 ; de Souza *et al.*, 1984 ; Coleman, 1986 ; Khalfaoui, 1988). On the contrary, if they don't benefit the plant, they will lead to try to find out a compromise. This is the case of physiological adaptive characters presenting a cost towards productivity. This compromise will be obtained by applying a certain selection pressure on each character during the whole breeding program.

When there is no strong linkage effect, a genetic correlation between adaptive characters will lead either to co-select the allels in order to keep their association when one is of some benefit, or to counter-select them in order to separate them when the initial association is of negative effect towards the available varieties.

Appendix 5.- Genetic variabilities of mechanisms of drought escape for the main studied species

MECHANISMS	GRAMINACEOUS						LEGUMINOUS				OTHERS			
	BARLEY	MAIZE	PEARL MILLET	RICE	SORGHUM	WHEAT	BEAN (PHASEOLUS VULGARIS)	COWPEA	PEANUT	SOYBEAN	COTTON	OIL PALM	POTATO	SUNFLOWER
1) Reduction of water loss														
- Reduction of leaf area :														
* constituent characters			+		+	+					+			
* inductible characters :		+												+-
. leaf size					+									
. leaf senescence		+												
- High stomatal resistance :														
* rapid stomatal closure		+	+	+	+-	O	+	+	+	+	+	+		
with glucidic reserves					+	+			O		+	+		
* low transpiration rate at complete aperture	+		+		+	O			(O)		+	+	+	
* stomatal, density and size :	+	+		+	+	+	+	+	+	+	+		+	+
- High cuticular resistance :	+			+	+	+		+	(O)	+	+	+	+	
* epicuticular wax.	+-			+	+	+						+		
* cohesiveness of cells														
- Leaf pubescence						+			+					+
- Reduction of interception of radiations :														
* reduction of leaf area (above)														
* high leaf reflectance :														
. epicuticular wax (above)														
. foliage color	+								+					
* leaf angle	+			+										
* leaf movements :														+
. wilting														
. rolling		+	+	+	+	+								
. paraheliotropy														
* spikelets	+					+								
Water absorption														
Root growth :														
* rate of initial growth		+		+	+	+			+	+	+		+	
depth	+	+	+	+	+	+			+	+	+		+	
* root density	+	+	+	+	+	+			+				+	
Hydraulic resistance of roots														
* diameters of xylem vessels				+		+								
* number of xylem vessels						+-								

Legend : Appendix 4

3.- IIEREDITY OF ADAPTIVE CIIARACTERS

In appendixes 7 and 8, the principal bibliographical data conccrning the heredity of avoidance and tolerance characters are presented for some specics mainly studied. The figures of these different studies are not easily comparable with one another because of the disparity of genetic materials, of technics, of gcnerations, of environmental conditions and of models of estimate ; this is the reason why these figures have been replaced by qualitatives appreciations.

First of all, these data-boards draw the extremcly limited extend of our knowledge in the field of the heredity of adaptive characters. Few species have been studied and in a very fragmentary way. However, these data are necessary for optimizing breeding methods adapted to each case. They belong to a field of research that has to be better explored.

Several adaptive characters seem to depend on a reduce number of genctic factors (major genes or major groups of genes). For example, the presence of spiklets on ears (Evans et *al.*, 1972) and the accumulation of wax at the cuticle

Appendix **6.-** Genetic variabilities of mechanisms of drought **tolerance** for the main studied species

MECHANISMS	GRAMINACEOUS						LEGUMINOUS				OTHERS			
	BARLEY	MAIZE	PEARL MILLET	RICE	SORGHUM	WHEAT	BEAN (PHASEOLUS VULGARIS)	COWPEA	PEANUT	SOYBEAN	COTTON	OIL PALM	POTATO	SUNFLOWER
▪ Germination under high osmotic pressure'	+	+			+	+			+	+				
▪ Tolerance to dehydratation (and heat) :														
. stability of protoplasmic membranes		+	+		+	+			+	+	+	+	+	+
. stability of proteins						+								
(among others those involved in photosynthesis)		+	+			+							+	
▪ Maintenance of turgor :														
. osmotic adjustment			+	O	+	+		O		O				O
. tissue elasticity				-		+	+							
Maintenance of photosynthesis :						+			+	+	+			
. amount of proteins/ unit of leaf area					+									
. spikelets	+					+								
Maintenance of harvested organs production :														
. change in allocation of assimilates					+									
. compensatory effect of production components						+								
Modification of metabolism (plant hormones)	+	+ +	+		+	+	+		+					

Legend : Appendix 4

level (Blum, 1975 ; Richard, 1982 ; Avato et *al.*, 1985). The rest of the characters are polygenic heredity type with, in most cases, a marked preponderance of additive genetic effects over non additive ones (dominance and epistasis). In spite of a limited genetic complexity, due to additive effects, the estimates of broad and narrow sense heritabilities are often low or very low because of marked intervention of environment in phenotypical expression and because of an important interaction between genotypes and environments.

Consequences of breeding

When adaptive characters are determined by a very limited number of genetic factors, it will be easy to transfer a positive expression to agronomically interesting varieties. The best adapted breeding method is, in this case, the Back-cross one. Essentially, it allows transfer of the favourable allels with very little modification of the genotype of the interesting cultivar and thus, if pleiotropism is

Appendix 7.- Heredity of mechanisms of drought avoidance for the main studied species

MECHANISMS	Graminaceous						Leguminous	Other
	Barley	Maize	Pearl Millet	Rice	Sorghum	Wheat	Peanut	Cotton
) **Reduction of water loss**								
- Leaf area	A h_n= 1 to H					A >> NA h_n = 1 to H		
- Stomatal resistance :								
. stomatal closure				A ♀			A ≃ NA	A > NA h_n = 1
with glucidic reserves								h_b = 1
. stomatal density and size	A h_n= 1 to H	A, NA fewgen		A, NA	A >> NA			
- Cuticular resistance :					A	A > NA h_n= 1 to M		
. epicuticular wax		polygen			A >> NA ♀ fewgen	monogen		
- Reduction of interception of radiations :								
. leaf area (above)								
. leaf reflectance :								
* epicuticular wax (above)								
* leaf angle	h_n= 1 to M			h_b= 1 to H monogen				
* spikelets						monogen		
) **Water absorption**								
- Root growth :		A > NA						
. rate of initial growth				A > NA ♀	A, NA	A	A > NA	h_b = M
. depht			NA ≥ A	A ≥ NA h_n = M		A > NA	A >> NA	
. number of roots			NA ≥ A	A ≥ NA		A > NA ♀	A	
- Hydraulic resistance of roots :								
. diameters of xylem vessels				A > NA h_n = M		h_n = M		
. number of xylem vessels						h_n = M		

absent, of its general behaviour. The difficulty which is often met is due to environmental conditions which affect genes expression. It is the case, for example, for the quantity of epicuticular wax in sorghum (Blum et *al.*, 1978 ; Blum, 1985) and the maturity at harvesting in peanut (Khalfaoui, 1988). This phenomenon dictates to homogenize as much as possible the environmental conditions, which is made possible by the limited number of plants worked upon by Backcross. When the ***in-vitro*** technic of genes transfer will be mastered, genetic engineering will be an effective and rapid method of transfer to efficient varieties of favourable behaviour determined by monogenic characters.

In the case of adaptive characters with polygenic heredity, the task will

Appendix 8.- Heredity of mechanisms of drought toterance for the main studied species

	GRAMINACEOUS		LEGUMINOUS		OTHER
	BARLEY	MAIZE	PEANUT	SOYBEAN	COTTON
Germination under high osmotic pressure		A >> NA ♀ fewgen			
- Tolerance to dehydratation (and heat) : . stability of protoplasmic membranes		A ≃ NA	A >> NA	h_n = M to H	hb = 1 to M

be more difficult. Two possibilities may arise. First, the ideotype of adaptation to be created depends on the expression of a small number of physiological charactcrs which are found in distinct varieties, agronomically interesting. Breeding can be conducted successfully with classical breeding methods of pedigree type, performed with crosses between few genotypes. It is necessary to breed the favourable characters from important effectives and to give preference to choices taking family performances into account, in order to take into account wcak heritabilities.

Secondly, the more complex ideotype concerns several adaptive mechanisms in order to face the given type of drought in a compatible way with a good agronomical value. The classical breeding method for adaptation to drought used until today, consists in an indirect selection according to productivity under dry conditions (Sullivan, 1972 ; O'Toole et *al.*, 1977), of pedigree type with simple crosses at its basis. But, in the case of a complex ideotype of adaptation, this method is greatly limited ; for this reason, a new approach is rccommendcd (Khalfaoui, 1985). This one is based on four principles :

1 - Extension of the genetic variability which is worked

On the classical breeding method is conducted with simple crosses bctween unusually not more than three cultivars at its basis. But the number of characters selected demands a multiplication of genotypes in order to regroup favourable expression inside the genetic material which is workcd on. Moreover, an important genetic variability determines, according to the fundamental theorem of natural selection (Fisher, 1930), a high rate of genetic progress as generations follow one another.

2 -Application of direct selection on adaptive characters

The classical breeding mcthod deserves the term of indirect since it does not estimate the level of adaptation of individuals by a determination of their behaviours in relation to physiological adaptive characters but by paying attention to the effects on productivity under drought conditions of the resultant of the expressions on adaptive characters. The more productive genotypes are the best adapted ones. This approach has two drawbacks :

First, drought in a given place being qualitatively and quantitatively variable according to the year, the selection pressure applied on each generation is variable. Genetic progress is contingent and tends to hit the ceiling. Application of direct selection on adaptive characters allows the homogenize the selection pressure and makes steadier and more continuous the genetical progress.

The second drawback of indirect selection based on productivity under drought conditions lies in heredity of adaptive characters. Indeed, we have seen that most of these characters are polygenic. Heritability is variable according to characters because of a genetic complexity degree and of an environmental intervention degree in their expression which are variable. Applying indirect selection on productivity, which is the resultant of the whole of the adaptive and productive characters, the selection pressure acts in preference on the more heritable characters, genetically the less complex. It has little influence on gcnctically complex characters which tend to escape selection. This phenomenon, taken into little account, is one of the main reasons of our slack times in genetic progress that we face nowadays after natural and human selections both related to productivity. One may suppose that this pause is probably not due to a physiological definitive limitation but to a temporarly genetic one, because there is still some potential genetic important spare progress linked to complex polygenic cbaracters. This potential can be exploited by applying direct selection on these characters using methods allowing to work on additive genetic effects and also on dominance and epistasis effects which are important and even sometimes preponderant. Improvement of this type of genetic effects demands the carrying out of the largest number of combinations of allels of the different genes in order to keep the best genic associations. But the classical breeding methods of pedigree type lead to a very rapid fixing of the combinations by homozygoty which impedes their multiplication. In addition, the high selection pressure applied puts aside the favorable combinations which are rare and whose expression is highly under environmental influences. On the contrary, recurrent selection methods, by a multiplication genic combinations thanks to repeated intercrosses, allows to a multiplication of allelic "drawings" and, thus the best combinations can be selected.

3 - Dissociation of long genetic improvemtxt from a short term one

From the initial genetical variability, the classical breeding methods of pedigree type imposes a high selection pressure on individuals. It leads to a very rapid restriction of genetical variability and thus to a pause in medium and long term genetical progress. On the contrary, a low selection pressure would allow to preserve and optimize genetic variability but would prevent us from obtaining a high rate of genetical progress and, therefore interesting varieties quickly popularizable. Tndeed, selection pressure is the second component, with genetical variability, which determines the rate of genetic progress between generation (Fisher, 1930). Tis' ufndamental opposition of long against short term improvement of complex genetic characters leads to dissociate long from short term inprovement processes. Long term improvement is managed by methods of selection of recurrent type applied on populations of wide genetic variability. Thanks to a moderate selection pressure they enable us to make optimum the genetic variability. Short term improvement is managed by classical breeding methods of new varieties taking for basis populations improved by recurrent selection. Thanks to a high selection pressure they enable us to quickly create improved popularizable varieties.

4 - *Dissociation of breeding for productivity from selection based on adaptive characters*

We have seen that lots of adaptive physiological cbaracters create costs for the plant productivity (Fisher, 1979 ; Richard, 1982) and are certainly a genetic charge for productivity.

Secandly, conditions of water supply favorable to the breeding of some pbysiological characters of adaptation to drought are different from conditions of water supply favorable to the breeding of productivity (Quisenberry, 1983 ; Richard, 1982). Indeed, physiological characters, completely or partially inductive, need intervention of marked water stresses, as in the case of protoplasmic resistance and osmotic regulation, while differences between genotypes for productivity characters will appear at their maximum under optimum conditions of watcr supply according to the concerned region which correspond to an absence of hard drought.

Negative physiological correlations between some adaptive characters and productivity and moreover the opposition of water supply conditions favorable to brecd for adaptive characters to those favorable to breed for productivity, lead to dissociate breeding for productivity from breeding for adaptive characters.

Recurrent selection is able to lead both of them according to two processes which are developpcd at the same time. From a population, one part of the individuals are screened under controled conditions for their physiological adaptive characters to drought, after inducing drought. The advantage of its application lies in its relative reproductibility which makes possible to keep a constant selection pressure, important factor of selection optimization. A second part of the individuals is selected for productivity and agronomical characters according to the result of a comparative essay on the field. A topping-up irrigation may be added in order to avoid serious stresses. Individuals which have passed the physiological tests are then intercrossed with those chosen in the agronomic essay in ordcr to associate thcir respective qualities in the same genotypcs. The result of these crosses is an improvement population which will be selectcd by the same processes. This plan of selection may be called “divergent-convergent”.

Following the principle of dissociation of long from short term genetic improvement, the improved populations by recurrent selection are used as the starting point for classical breeding method of new varicties.

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