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Resistance to abiotic stresses in durum wheat: Which ideotype?

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SUMMARY – Resistance to stresses is a complex character. Abiotic stresses affect crop production and despite many decades of research, they continue to be a major challenge to agricultural scientists. Drought, heat and salt are the most important to be considered in the selection of new genotypes. Stay-green trait in durum wheat is also evaluated. When water is limited during the grain filling period, genotypes possessing this trait maintain more photosynthetically active leaves. In this presentation an idea of a new ideotype of plant is discussed.

Key words: Drought, tolerance, stay-green, durum wheat.

RESUME – *"Résistance aux stress abiotiques chez le blé dur : Quel idéotype ?". La résistance aux stress est un caractère complexe. Les stress abiotiques influencent la production des cultures et, bien que plusieurs décades de recherches aient été faites, ils continuent à être la plus grande provocation pour les chercheurs agricoles. La sécheresse, la haute température et la salinité sont le plus important à considérer pour la sélection de nouvelles variétés. Le caractère "semper virens" dans le blé dur est aussi considéré. Lorsque l'eau est limitée pendant la période de remplissage de la semence, les variétés avec ce caractère maintiennent les feuilles actives photosynthétiquement. Dans cet article est discutée une idée de nouvel idéotype.*

Mots-clés : *Sécheresse, résistance, semper virens, blé dur.*

Introduction

Large areas are subjected to more or less severe abiotic stresses. Out of these, water, heat and salt stresses are the most investigated.

Different kinds of drought may occur under different stresses such as heat shocks, water deficit, low air hygrometry, insolation, salinity. Therefore plant response is diversified at various level of organization (molecular, cellular, etc.).

Although drought resistance is considered as a valid breeding target in the stabilization of crop performance, by breeders and molecular biologists, at the moment there is lack of knowledge to measure with precision the plant resistance under drought stress conditions (Blum, 1996).

Plant response to drought can be studied by identification of traits that are in relation to drought tolerance at the physiological, cellular, biochemical and molecular levels. Hence, the study of the diversity of drought tolerance mechanisms can give interesting information on the different possibilities of adaptation.

Developing plants that have an advantage under abiotic stresses conditions is a major challenge for durum wheat improvement programs. Genotypes possessing stay-green trait are potential candidate to assure yield in semi-arid regions.

Here, we reported some considerations for an ideotype of durum wheat plant resistant or tolerant to abiotic stresses in general and to drought stress in particular.

Drought resistance

Drought tolerance is a complex character (independent on the yield potential) which make difficult to find an appreciable genetic correlation between a physiological attribute and yield or plant performance under field conditions. However, drought resistance exists because there are in plants specific mechanisms which are shown under stress conditions (see for a review Blum, 1988). Selection for morphological and physiological components of drought resistance in the early stages of a breeding program may give information when yield is not available (Austin, 1993). As an example, these components may be used to choose parental at the beginning of a breeding program for water deficient field conditions. Alternatively at the end of a yield-based breeding program screening for drought tolerance may introduce characters that improve plant adaptability to a particular environment.

There are different types of plant reactions to a specific water stress that may be resumed, according to Levitt's (1972) terminology, as: (i) stress escape or capability to avoid stress injury; (ii) stress avoidance or capability to decrease damage induced by stress; and (iii) stress tolerance or ability to undergo without injury a stress.

The adaptation mechanisms change with genotype, plant age, environment, type of organ and tissue, for these reasons it is necessary to determine the most suitable conditions in which to observe the type of physiological response that is better related to an improved plant performance. During the last twenty in our Institute we have identified a pool of attributes that may confer adaptation (Table 1). Mechanistic approach (physiological research on fundamental plant processes involved in stress response on a limited number of genotypes) and empirical approach (large scale screening of correlations between plant traits and agronomic index of tolerance) have been adopted.

Table 1. Traits expected to lead to improved adaptation of durum wheat in the Mediterranean environment

High pre-anthesis values of leaf area	Wittmer *et al.,* 1982
Great number of grains per inflorescence	Rascio *et al.,* 1984
Weak leaf tensile strength	Rascio *et al.,* 1992a
High potassium, chloride ions, reducing sugars and proline in the leaves	Rascio *et al.,* 1994
Low osmotic potential at full turgor	Rascio *et al.,* 1997
High affinity for strongly bound water (high DWS values)	Rascio *et al.,* 1997a

From path coefficient analysis of yield components it resulted that number of grains per inflorescence exerts the greatest effect on potential yield (Rascio *et al.,* 1984). This effect may be the consequence of the changes in dry matter partitioning toward harvestable yield (Evans, 1988), because it induces greater assimilate demand by the sink. Drought tolerant plants showed escape mechanisms consisting of good winter growth (early vigour), hence high pre-anthesis values of leaf area and leaf area duration, high translocation of pre-anthesis assimilate to the ear (Wittmer *et al.,* 1982) and hence poor dry matter content per unit of leaf area (low specific leaf weight, small leaf thickness) after anthesis (Cedola *et al.,* 1994). The last characteristics may be easily determined measuring Leaf Tensile Strength (LTS), whose expression in field resulted to be not affected by plant growth stage and water regime and for these reasons appears to be a very promising screening test (Rascio *et al.,* 1992). Tensile strength of standard leaf segments resulted much weaker in plants with low drought susceptibility index (Fischer and Maurer, 1978). Correlated with this weakening there was an increase in the proportion of hemicelluloses of the cell walls (Singh *et al.,* 1985; Rascio *et al.,* 1990) and substantial decrease in proportion of crystalline cellulose. These chemical alterations of cell wall composition, reflect the enhanced accumulation of osmotically active compounds at the expense of wall synthesis. Moreover hemicellulose, for its capacity to store and release water may affect positively the water holding capability of the apoplast inducing, indirectly, some decrease in osmotic volume (Rascio *et al.,* 1994).

Direct and indirect solute concentration in the leaves represents in fact a very important drought tolerance mechanism for durum wheat in Mediterranean environment, being K^+, Cl^- ions, proline and reducing sugars the major contributors to osmotic adjustment (Rascio *et al.,* 1994). The trait expression changes with genotype, but is influenced by phenological stage of development, environment and water regime, too. For these reasons the appropriate, simplified and controlled screening environment for solute accumulation capability has been defined (Rascio *et al.,* 1997). Osmotic potential at full turgor, determined at two leaves stage in small pots in controlled environment and under moderate water deficit shows a high level of repeatability of cultivars mean discrimination across stages and may be rapidly determined starting from stem elongation.

Indirect control of osmotic volume by increasing macromolecules capability to retain hydration water represents an other important mechanism of drought tolerance, because it has been observed the existence of high affinity for strongly bound in drought tolerant genotypes (Rascio *et al.,* 1992a; Rascio *et al.,* 1998). Routinely it may be determined through analysis of DWS (Differential Water Sorption) by the leaves between two different temperatures at 33% RH (Rascio *et al.,* 1997a). The technique resulted useful in identifying “mutants for bound water” because may be applied for screening of large sample numbers. The use of mutants gave important contribute to understanding physiological processes, to detect new genes involved in drought tolerance, to evaluate the effect of a single genes (if single gene mutants are available) in the plethora of genes expressed under stress conditions and to increase variability. In fact, large amount of information about a relative low number of plant traits is available. For many others it is not known if selection will improve tolerance, because poor variability or difficulty in large population screening. As an example, mutagenic treatment increased greatly variability for this trait as compared to variability observed, for the same character among commercial wheat cultivars (Fig. 1) (Rascio *et al.,* 1995).

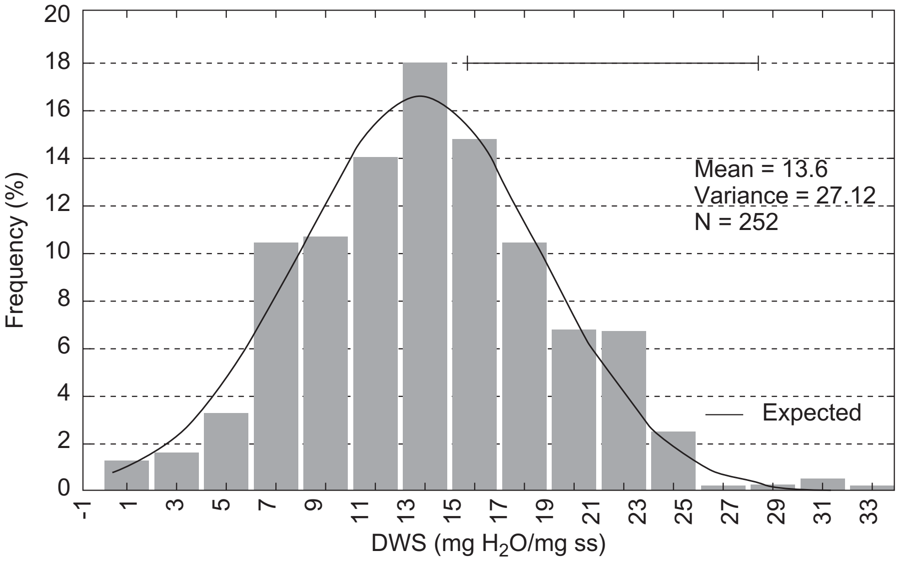

Fig. 1. Frequency distribution of DWS determined at the heading stage of flag leaves of 250 mutagenized plants submitted to the screening procedure in the field. Solid line indicates the variation for DWS character in ten commercial durum wheat varieties grown on the field (Rascio *et al.,* 1995).

Salt stress resistance

Potassium is the only monovalent cation essential for all higher plants (Epstein, 1972), representing the major inorganic constituent of plant cells (Borowitzca, 1981). It is involved in many physiological processes such as turgor potential regulation, cell elongation, growth of shoot and roots, stomatal movement, transpiration.

Under drought conditions, potassium application has shown an effect on growth, water use efficiency and dry matter production or yield (Van deer Paauw 1958; Andersen *et al.,* 1991). Moreover, the ability to accumulate K^+ ions in organs is positive for drought and saline tolerance (Fitter and Hay, 1987 and Hsiao and Lauchli, 1986). K^+ and Cl^- ions accounted for as much as 35% of the recorded osmotic adjustment (Rascio *et al.,* 1994). Hence, the K/Na ratio has been considered as an index of drought tolerance, being higher in tolerant genotypes (Dvorak and Gorham, 1992).

The altered accumulation of K^+ ions in durum wheat mutants may contribute to identify mechanism of K^+ uptake, accumulation and partitioning, as well as to define useful genes to transfer in traditional breeding programs.

Our experiences demonstrated, in general, that in one mutant of durum wheat (422) the growth of dry matter was less limited than wild type under different levels and concentration of salts (KCl, NaCl and KNO_3) (Fig. 2). In addition, the mutant also showed an higher K/Na ratio in leaf tissues.

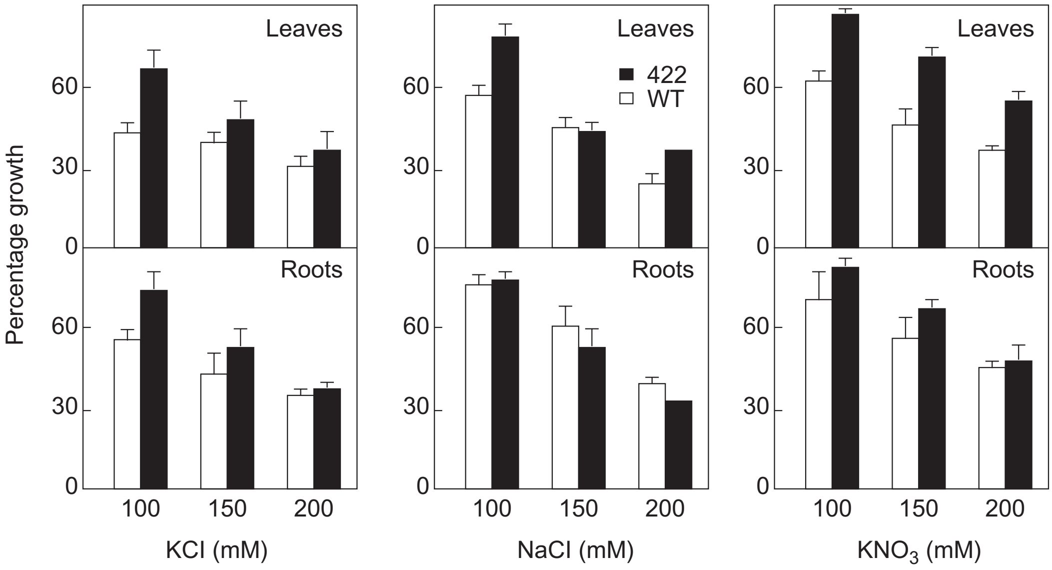

Fig. 2. Effects of salts on dry matter accumulation in leaves and roots of wild type (blank column) and 422 (full column) plants grown for 22 days in saline solutions. Salt effects on growth were calculated as percentage of dry matter accumulated in the absence of added salts. The values are means of four plantlets and error bars denote the SE.

An experiment carried out to evaluate the percentage of seeds germination under different types and increasing levels of salts demonstrated again the superiority of mutant respect to wild type. As an example, 80% of seeds germinated in presence of 200 mM KCl against 20% of wild type.

As a consequence of high K/Na ratio, the mutant selected limits Na^+ accumulation in leaves tissues and therefore shows a higher capability to resist under salt condition. Thus, it may represent an ideal material to study the genetic basis of potassium accumulation and identify the gene(s) responsible of salt stress tolerance in tetraploid wheats.

Heat stress resistance

Wheat plants grown in many areas of the world may be subjected to temperatures exceeding 35ºC for several hours during a normal growing season, resulting in the synthesis of heat shock proteins (HSPs) in many tissues of plant (Necchi *et al.,* 1987; Krishnan *et al.,* 1989; Helm and Abernethy, 1990; Weng and Nguyen, 1992). The appearance of these proteins is associated with the concomitant reduction in normal protein synthesis and has been positively correlated with acquisition of thermo-tolerance (Krishnan *et al.,* 1989).

Durum wheat synthesized HSPs in multiphasic fashion with changes in the profile of HSPs depending on the duration (4, 7 or 12 h) of the heat shock (Necchi *et al.,* 1987). However, comparison of wheat genotypes differing in thermal tolerance provides evidence that heat-tolerant cultivars synthesised low molecular weight HSPs earlier during exposure to heat shock and at higher level than did heat susceptible cultivars (Vierling and Nguyen, 1992; Weng and Nguyen, 1992). Finally, periods of high temperature (above 30ºC) increased the synthesis of different hsp mRNAs and of the corresponding protein in the wheat seed, demonstrating that in the seed the mechanism of response to the heat shock was strongly activated (Treglia *et al.,* 1999). This may also indicate the importance for the plant of protecting the embryo from damage caused by external factors.

The effect of thermal regimes during grain filling on quality, measured by the variations in W, P and L alveograph parameters, were significantly confirmed by the imposed treatments (Borghi *et al.,* 1995). In fact, in presence of a long period of temperature in the range of 30-35ºC a dough strengthening effect was observed, while frequent episodes of daily maximum temperature above 35ºC led to dough weakening effect. These results were observed both in durum and bread wheat.

Stress tolerance based on the regulation of carbon partitioning

Most critical phase for yield is grain filling period. It is well-known that the final weight of each grain depends on the rate of supply and storage of assimilate and that the grains of apical, middle and basal part of one spike vary in size, such as weight and dimension (Daynard *et al.,* 1971; Evans and Wardlaw, 1976; Gallagher *et al.,* 1976; Sofield *et al.,* 1977). Bingham (1969) emphasized the relationships between sink and source organs of plant and several studies have been carried out to verify if the final grain weight was either sink- or source-limitant (Walpole and Morgan, 1974; Fisher and Laing, 1976; Martinez-Carrasco and Thorne, 1979; Winzeler *et al.*, 1989).

Studies to investigate sink-source relationship in abiotic stress condition are very rare. Based on our preliminary studies under field condition in a typical Mediterranean environment, the alteration of source (removal of flag leaf or awns or together) or sink (removal from spike of 2 or 4 spiklets) on *Triticum durum* Desf. (cvs. Simeto and Messapia, different in kernel size) and *Triticum dicoccum* plants are here discussed to underline changing of grain weight from apical, middle, and basal spike parts (Troccoli *et al.,* 1997).

In general, source limitation treatments, carried out at the heading stage, determined in the plant of both species of Triticum a significant reduction of final kernel weight with respect to control spike, even though it was very low in *T. dicoccum*. A significant reduction of final kernel weight was displayed when the awn (-15.5%) more than flag leaf (-9.6%) were removed from spike. Awn removal treatment caused a higher loss of kernel weight in cv. Simeto (-20.8%) against cv. Messapia (-14,8%) and *T. dicoccum* (-11.3%).The removal of both organs (flag leaf+awn) decreased in average the kernel weight for 16.2%, resulting cv. Messapia more susceptible (-25.4%) respect to cv. Simeto (-17.8%) and *T. dicoccum* (-6.3%).

The average increase of final kernel weight was of 6.2% or 9.8% when 2 or 4 spiklets, from central part of spike, were removed. For each treatment, *T. dicoccum* showed a significant increase of final kernel weight (+9.7% or +12.0%) similar to cv. Simeto (+6.9% or +11.4%) but superior to cv. Messapia (+2.0% or +5.8%).

With regard to sink-alteration on the spike, only removing 4 spiklets the excess of photosynthates equally distributed in apical (31%), middle (37%), and basal (32%) part, determining an average final kernel weight superior to 40 mg (42, 46, and 45 mg respectively).

The ideotype of plant for high source/sink efficiency should have a higher development and longevity of the awn organ, a lower presence of grains, maximum 2 for each spiklets, in the middle part of the spike, preferring a distribution of grain into a spike slightly longer. This should provide a weight of grains into spike non inferior to 40 mg and therefore a lower presence of shrivelled grains. In the future, studies under stress condition are recommended.

New perspectives in environmental stress genetic improvement

Stay-green phenotype

Leaf senescence comprises a series of biochemical and physiological events which include the final stage of development, from the fully expanded state until death. During leaf senescence, the photosynthetic apparatus is dismantled and nutrients are exported to young growing tissues or storage organs.

Genetic variation exists for foliar senescence and genotypes and plants with leaves which remain green for longer than normal are defined stay-green. Over fifty years ago it was realised that most of the diversity in yield for most crops is a consequence of variation in the duration, rather than the rate of photosynthetic activity (Watson, 1952), and so, delayed leaf senescence (i.e., stay-green), has long been considered to be a desirable trait in cereals breeding.

In cereals as *Avena sativa, Oryza sativa* and *Triticum* spp., relationship between grain yield and duration of the areas of the total canopy and of specific leaf have been observed (Thomas and Smart, 1993). So far, the relationship between stay green phenotype and drought tolerance in these species has not been studied yet. Since maintaining green leaf area during post-anthesis drought increase grain yield, compared with senescent genotype, our aim in the next few years should be to delay the onset of leaf senescence or to reduce its rate.

Examples of stay-green phenotype have been identified in a number of crop species (Thomas and Smart, 1993) and two different types of functional stay green can be distinguished, involving either a delayed onset of leaf senescence or the regulation of its rate of progress. Genes involved in the generation of these types (probably regulatory genes) have not been cloned yet. Identification of mutants that are defective in a senescence function allows an alternative approach to the analysis of senescence process and to clone genes of interest.

In crops adapted to semiarid areas such as maize, sorghum and wheat, genotypes with delayed senescence that retain their leaves in an active photosynthetic state during the grain filling period enhances the stress tolerance by increasing the assimilate supply for grain filling and maintaining the root function and water uptake, or both (van Oosterom *et al.,* 1996). In maize and sorghum, stay-green trait, is a component of tolerance to post flowering drought. As a result of delayed senescence, stay-green sorghum phenotype, accumulates more soluble sugars in the stem than does senescent sorghum, both during and after grain filling, while in maize the major effects connected with delayed senescence are higher water in the leaves at physiological maturity and higher water and sucrose content in the stem and the leaves at grain filling (van Oosterom *et al.,* 1996).

Stem reserve mobilisation is a solid (and probably the only) source of carbon for grain filling under drought stress simply because photosynthesis is inhibited (Blum, 1996a). However, in some cases delay of senescence and utilization of stem reserves are mutually exclusive (Blum *et al.,* 1994). The availability of durum wheat mutants characterized by a stay-green like phenotype offers the opportunity to understand the real contribution of stem reserves in stay-green wheat under drought stress conditions.

An other important aspect in a stay-green phenotype is also related to the sugar contents in the leaf. The demand by the sink and the longer photosynthetic activity are primary factors in determining sugar concentrations in the leaf. The sink limitations that we could have with extension of green leaf, may also increase the sugar concentrations (sucrose, fructose and glucose) in the leaf itself. In these cases the sugars levels can be determinant for the osmotic adjustment that the leaf will use in drought conditions. In one stay-green variety which has been studied in some detail (FS854 which is credited with the world record yield for non-irrigated maize), carbohydrate accumulation in the leaf does not appear to accelerate leaf senescence (Thomas and Smart, 1993) and so, the increase of sugars concentrations in the leaf does not seem to affect genes that are implicated in the photosynthetic process.

Drought tolerance seems to be the most important trait in stay-green phenotype and can also represent the trait of interest in many applied breeding programmes. However, a better understanding of the basis for the onset of senescence in plants and isolation of genes involved in the senescence process should be fundamental for future agronomic improvement.

Ideal crops for the breeders should come out by a balance between extension of photosynthetic activity in a single flag leaf or in the whole canopy, and drought tolerance during grain filling period.

Sub-cellular drought tolerance and mechanisms preventing photooxidative stress

Under low water potential consequent to environmental stress conditions, chloroplastic and mitochondrial metabolisms may be severely damaged, so decreasing the energetic supply to the plant by ATP synthesis.

In the last decade in our Institute we have identified different metabolic indicators of drought tolerance in durum wheat, relative to chloroplastic and mitochondrial functionality; they are reported in Table 2 in comparison with some physiological parameters highly correlated to yield stability under stress and suitable to be used in a breeding programme for a Mediterranean environment.

Table 2. Metabolic and physiological indicators of drought tolerance in durum wheat

Metabolic parameters	
Photochemical quenching of chlorophyll fluorescence	Flagella *et al.,* 1994
Inhibition of mitochondrial proline oxidation	Flagella *et al.,* 1994a
Quantum yield of photosynthetic electron transport (ϕ_{PSII})	Flagella *et al.,* 1995
Mitochondrial oxidative phosphorylation	Flagella *et al.,* 1996a
Non assimilatory Φ_{PSII}	Flagella *et al.,* 1998a
Physiological parameters	
Cell membrane stability	Flagella *et al.,* 1986
Different *in vitro* tests	Flagella *et al.,* 1987
Water retention capability evaluated by near infrared reflectance	Flagella *et al.,* 1992

Under environmental stress conditions limiting photosynthetic assimilation of CO_2, leaves are exposed to photon fluxes well in excess of those that can be used with high efficiency. So a photooxidative stress due to light-dependent generation of reactive oxygen species (ROS) may occur in chloroplasts. Moreover, also mitochondria are reported to be a major site of ROS generation under stress (Alscher *et al.,* 1997).

Different defence mechanisms may be used by plants in order to prevent photooxidative stress i.e. to develop a highly efficient antioxidative defence system and to avoid overreduction of the photosynthetic and mitochondrial electron transport chain.

In particular, the antioxidative defence system existing in all plant cells to counteract the toxicity of ROS is composed of both enzymic and non enzymic constituents. The non enzymic antioxidants are generally small molecules such as ascorbate (vitamin C), glutathione and a α-tocopherol, together with the carotenoid pigments. The enzymic antioxidative components are a prerequisite for life in oxygen. They include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (AsPOD) and the enzymes involved in the synthesis and regeneration of the low molecular mass antioxidants (Foyer *et al.,* 1994). Preliminary results obtained in our Institute show that the increase in SOD and glutatione reductase (GR) activities and in ascorbate and dehydroascorbate acids seems to have a key role in durum wheat drought tolerance (Flagella *et al.,* 1998).

At chloroplastic level the maintainance of the electron transport when CO_2 assimilation is limited, may be due to photorespiration (Wu *et al.,* 1991), cyclic electron transport and Mehler peroxidase reaction termed also pseudocyclic electron flow. Both photorespiration and the Mehler peroxidase reaction sequence have repercussions for the regulation of the quantum efficiency of PSII (Φ_{PSII}) and are important components of the overall regulation of electron transport termed photosynthetic control (Foyer *et al.,* 1994). The photochemical quenching and the quantum yield of Φ_{PSII}, evaluated by chlorophyll fluorescence analysis, during the transient of the induction, has a predictive value for drought tolerance in durum wheat (Flagella *et al.,* 1994, 1995, 1996). That highlights the key role of regulatory processes such as the Mehler peroxidase reaction and possibly also cyclic electron transport in limiting overreduction under stress (Flagella *et al.,* 1998a).

Overreduction may be also prevented by exporting to the cytosol reducing equivalents such as by malate-oxalacetate and triosephosphate shuttles. The reducing equivalents might be then oxidated by mitochondria.

On the other hand also mitochondria are potentially exposed to the most severe environmental conditions with respect to the production of ROS and ensuing oxidative damage. Electron flow via the respiratory chain can produce ROS, which are assumed to severely damage cells. In particular, ROS generation is enhanced when plants are subjected to unfavourable environmental stimuli (Scandalios, 1993; Alscher *et al.,* 1997; Foyer *et al.,* 1994). Since mitochondrial functions are severely damaged under conditions of oxidative stress (Kowaltowski and Vercesi, 1999), plant mitochondria are expected to possess efficient defence systems.

Of particular interest are the mitochondrial defence systems against oxidative stress. Besides antioxidants and enzymatic ROS scavenging systems, three different energy-dissipating pathways, that can prevent ROS generation by plant mitochondria itself, have been described, namely the alternative oxidase (AO) (Vanlerberghe and McIntosh, 1997) the PUMP (Vercesi *et al.,* 1995) and the PmitoKATP (Pastore *et al.,* 1999).

In conclusion a tolerant genotype should be characterized by an efficient antioxidant defence system constituted by both enzymic and non enzymic components and by efficient mechanisms for preventing overreduction of the chloroplastic and mitochondrial electron transport chain (Fig. 3) in order to limit ROS production under stress.

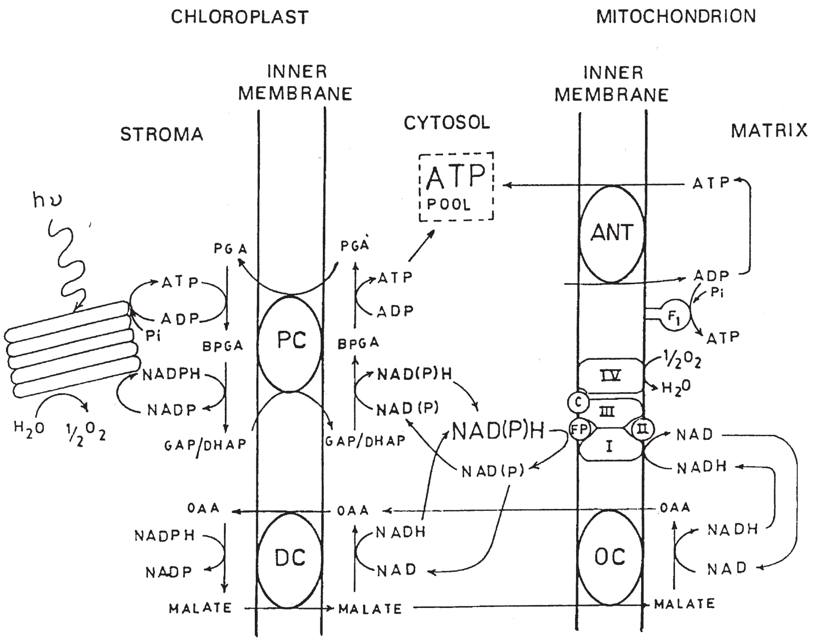

Fig. 3. Metabolite shuttles between chloroplasts and mitochondria via the cytosol are proposed to be the biochemical basis for the interaction between photosynthesis and respiration. The net result is that mitochondria help to prevent the over-reduction of chloroplasts and cytosol. Similarly, choloroplasts could prevent the over-oxidation of mitochondria and cytosol. c, cytochrome c; F_1, coupling factor; GAP, glyceraldehyde-3-phosphate; BPGA, glycerate 1,3-bisphosphate; PC, phosphate carrier; DC, dicarboxylate carrier; ANT, adenine nucleotide translocator; OC, oxalacetate (OAA) carrier; FP, external NAD(P)H dehydrogenase. Adapted from Raghavendra *et al.* (1994).

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