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Adaptation of durum wheat to a changing environment

Cattivelli Luigi¹, Franco Miglietta², Alessandro. Zaldei³, Fulvia Rizza¹, Anna Maria Mastrangelo³, Pasquale De Vita³, Elisabetta Mazzucotelli²

¹ CRA, Genomics Research Centre, Fiorenzuola D'Arda, Italy

² CNR-IBIMET, Firenze, Italy

³ CRA, Cereal Research Centre, Foggia, Italy

Abstract. The expected climatic changes will lead to an environment characterized by elevated atmospheric CO₂, increased temperatures and increased risks for drought due to an elevated atmospheric evaporative demand. Therefore the traits involved in the adaptation to abiotic stresses, particularly drought and heat, as well the capability of the plants to adjust their metabolism to the increased CO₂ concentration will play a key role to sustain yield (and yield quality) in the durum wheat crop in the next years. This report summarizes a number of studies dedicated to the understanding the physiological and molecular basis of durum wheat adaptation to environmental stress. The overall findings highlight the existence of a significant degree of genetic variation that will allow the selection of new cultivars with a specific adaptation mechanism for the new or changed climatic conditions.

Keywords. Durum wheat – Stress tolerance – Molecular response – Stress related genes.

Adaptation du blé dur à un environnement changeant

Résumé. Les changements climatiques attendus devraient conduire à un environnement caractérisé par une augmentation du CO₂ atmosphérique, la hausse des températures et des risques accrus de sécheresse en raison d'une demande évaporative atmosphérique élevée. Par conséquent, les caractères intervenant dans l'adaptation aux stress abiotiques, en particulier la sécheresse et la chaleur, ainsi que la capacité des plantes à ajuster leur métabolisme par rapport à la concentration accrue de CO₂, joueront un rôle déterminant pour maintenir le rendement (et la qualité du rendement) de la culture de blé dur dans les prochaines années. Dans ce travail, nous présentons les grandes lignes d'un certain nombre d'études centrées sur les bases physiologiques et moléculaires de l'adaptation du blé dur au stress environnemental. Les conclusions générales indiquent l'existence d'un degré significatif de variation génétique qui permettra la sélection de nouveaux cultivars, dotés d'un mécanisme d'adaptation spécifique aux conditions climatiques nouvelles ou modifiées.

Mots-clés. Blé dur – Tolérance au stress – Réponse moléculaire – Gènes liés au stress

I Stress tolerance is a main component of yield stability

During the past century breeding activity has been characterized by the constant release of leading cultivars that in turn became progenitors of new cultivars, selected to perform well under intensive crop management and characterized by an increased yield potential (De Vita *et al.*, 2007). Nevertheless, in recent years average grain yield has not increased at the pace registered from the 1950s to the 1990s. In many crops and certainly in durum wheat, an insufficient yield stability has been recognized as one of the main factors responsible for the gap between yield potential and actual yield, particularly in drought-prone environments. It is worthy to noticing that enhanced yield potential places a greater demand on field resources, thereby resulting in greater stress frequency unless the higher yield potential is associated to an increased stress tolerance. As a consequence, yield stability and stress tolerance are highly associated, and in many cases stress tolerance represents the main factor limiting yield stability (De Vita *et al.*, 2010).

A work describing the changes in adaptation and yield stability achieved over the last century in a historical collection of Italian durum wheat genotypes (landraces, old and new cultivars with different years of release and advanced breeding lines) has been carried out by De Vita *et al.* (2010). The breeding strategies adopted during the last decades have contributed to reduce the interaction of genotypes with environments selecting genotypes with better stability across a wide range of locations and years, as a consequence the modern genotypes outperformed the old ones in all tested environments with a strong yield capacity in highly fertile environments. This trend suggest that the traditional breeding has been able to select, indirectly, for abiotic stress tolerance; nevertheless a number of evidences highlights that many specific stress tolerance mechanisms that can be found in old cultivars/landraces have been lost during the selection.

II – Ofanto and Cappelli, a couple of varieties with contrasting drought response strategies

Senatore Cappelli (generally named Cappelli) is an old, low yielding, tall cultivar selected from a Tunisian landrace and released in 1915. When Cappelli was compared to a typical modern high yielding short cultivar (Ofanto, released in 1990), constitutive differences in Water Use Efficiency (WUE) and adaptive strategies were noticed. Integrated WUE, as recorded by grain isotopic discrimination, consistently showed a higher WUE of the variety Cappelli, associated with lower stomatal conductance over a wide range of relative soil water contents. The differences in WUE thus turned out to be constitutive (Rizza *et al.*, 2012). These finding suggest that the durum wheat cultivars Ofanto and Cappelli can represent an ideal experimental system to investigate the water and heat stress responses in durum wheat.

III Ofanto and Cappelli show a largely different molecular response to high temperature and drought

When a transcriptomic analysis of the molecular response to drought, heat, and to a combination of both stresses was carried out in plants of Ofanto and Cappelli, two largely different responses were found. For instance, Ofanto activated a large set of well-known drought-related genes after drought treatment, while Cappelli showed the constitutive expression of several genes that in Ofanto are induced by drought and a minimal modulation of gene expression in response to stress. Assuming that the extent of gene modulation (number of genes modulated in response to stress) is a consequence of the stress signal perception, the same experimental conditions had a different impact both on stress signalling in Cappelli and Ofanto. Despite the lower Relative Water Content of Cappelli compared to Ofanto, the former cultivar showed minimal gene activation in response to drought. The lower stomata conductance and the constitutive expression of some drought-related genes might contribute to limit the effect of drought and the stress perception in Cappelli which, in turn, is reflected in a minimal drought-induced gene expression (Aprile *et al.*, 2013).

Durum wheat often faces water scarcity and high temperatures, two events that usually occur simultaneously in the fields. The combination of drought and heat stress in plants is a unique stress sharing a marginal portion of the molecular responses activated by drought and heat stress alone. With respect to the response to the combination of heat and drought conditions, Ofanto and Cappelli are characterized by two opposite stress-responsive strategies. In Ofanto the combination of drought and heat stress led to an increased number of modulated genes, exceeding the simple cumulative effects of the two single stresses, whereas in Cappelli the same treatment triggered a number of differentially expressed genes, lower than those altered in response to heat stress alone (Aprile *et al.*, 2013).

IV The RIL population of Ofanto x Cappelli offers a tool for the dissection of the genetic basis of trait associated to stress tolerance

Given the significant differences observed in terms of physiological and molecular mechanisms involved in the adaptation to abiotic stress condition, a RIL population was derived from the cross Ofanto x Cappelli and used to build a molecular marker map. A total of 618 molecular markers were assembled into 30 linkage groups that covered all of the durum wheat chromosomes except 1A (Marone *et al.*, 2012a, 2012b).

This genetic map was used to dissect the genetic bases of leaf porosity (a stomatal-conductance-related trait) measured under field conditions as well as the loci controlling the expression of a gene differentially expressed in response to stress between the two parental lines. Six QTLs were detected for leaf porosity, among them, the one located on chromosome 3B appeared to be more stable across different environments (Paino *et al.*, 2012). A gene of unknown function having the greatest expression difference in response to drought stress between the two cultivars was selected and used for expression QTL analysis, a single e-QTL with a strong effect (more than 90% of explained phenotypic variability) was mapped on chromosome 6B (Aprile *et al.*, 2013). The fact that the e-QTL was coincident with the locus of the position of the gene strongly suggests that the main factor controlling its expression relies in the gene sequence itself.

The mapping of the QTLs controlling leaf porosity and of the e-QTL controlling the expression of a stress related gene, provides clear evidences that the genetic system based on Cappelli and Ofanto represents an useful tool for the genetic dissection of the molecular response to drought and heat stress in durum wheat.

V – Functional analysis of selected stress responsive genes

The analysis of gene expression often leads to a list of candidate genes that need to be further validated to understand their role in the stress response. Early works on gene expression have identified a number of genes with potential regulatory role in the response of durum wheat to cold and drought stress (Mastangelo *et al.*, 2005, De Leonardis *et al.*, 2007, Aprile *et al.*, 2009). One of them, *TdRF1* a gene encoding an E3 ubiquitin ligase, was then subjected to a functional characterization. Its E3 ligase activity was demonstrated and a network of proteins interacting with TdRF1 was described. The E3 enzymes are responsible of recruiting the proteins targeted by the ubiquitination process, which in turn drive the proteins to degradation through the 26S-proteasome. Furthermore, the functional characterization of TdRF1 has highlighted a small interactome represented by 4 interacting proteins, besides TdRF1, the following proteins were involved: the mitogen-activated protein kinase TdWnk5 was able to phosphorylate TdRF1 *in vitro*, the transcription factor WBLH1 was degraded in a TdRF1-dependent manner through the 26S proteasome *in vivo*, and the RING-finger protein WVIP2 was shown to have a strong E3 ligase activity. Furthermore, *TdRf1* and the genes coding for the TdRF1 interactors were all responsive to cold and/or drought stress, and a negative regulative function in dehydration tolerance was observed for the barley homolog of *WVIP2* (Guerra *et al.*, 2012).

The involvement of E3 ubiquitin ligases in the response to drought and cold stress points out the role of post-translational modifications of proteins in the adaptation to environmental changes in durum wheat.

Besides the genes whose role in stress tolerance is postulated based on their expression profile, other sequences can be identified because involved in metabolic pathways modulated during stress response. An example is represented by the Phospholipases A2 gene family known to

mediate signalling cascades during plant growth and development, as well as biotic and abiotic stress responses. A specific study was undertaken to assess the involvement of specific PLA2s in durum wheat response to drought stress. Three sequences encoding putative PLA2s were found modulated by drought stress suggesting that PLA2 in durum wheat that have roles in orchestrating the plant response to drought (Verlotta *et al.*, 2013).

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