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Genetic dissection of resistance to diseases in wheat

Summary – Plant pathogens seriously affect crop productions worldwide from a quantitative and qualitative point of view. The emergence and spread of new virulent races is even facilitated by the ongoing climatic changes. The development of new genetically resistant cultivars, in particular for durum and bread wheat, represents a protective strategy which is effective and sustainable in terms of economic advantage and respect of the environment. The use of resistant cultivars indeed allows a drastic reduction of fungicide applications in agriculture with a great improvement of quality and security of the end products.

Keywords: wheat, disease resistance, QTL mapping.

Introduction

Plant diseases are one of the main biotic constrains which strongly reduce crop productions in many environments, and they are becoming even more threatening especially in the frame of the current climatic changes. Bread wheat (*Triticum aestivum* L.) and durum wheat [*Triticum turgidum* (L.) subsp. *turgidum* (L.) convar. *durum* (Desf.)] are among the most important cultivated crops worldwide. For these species in particular, the damage to grain yield is both quantitative and qualitative with a serious downgrading of the main grain quality parameters.

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Plants can react to a pathogen attack through the activation of two main kinds of immune response. In both cases, large gene families coding for specific enzymes and immune receptors are involved. In the first case, a basal response is activated, in which pattern recognition receptors (PRRs), which are plasma membrane localized, recognize the molecules typical of microorganisms, such as bacterial flagellins or lipopolysaccharides, and fungal chitin or heptaglucosides [1]. As these molecules are expressed by both pathogens and non-pathogenic microorganisms, they are called microbe-associated molecular patterns (MAMPs) [2]. The second mechanism is known as effector-triggered immunity, and it is based on the action of the so-called resistance (R) genes. These code for mainly intracellular proteins which are devoted to the specific recognition of pathogenic effectors, coded by the avirulence (Avr) genes following the «gene for gene» model [3]. R genes form one of the largest gene families in plants, and most of them contain a conserved nucleotide-binding domain (NB-ARC) and leucine-rich repeat domain (LRR) [4]. Plant immune responses mediated by R genes often culminate in a hypersensitive response, which is a programmed cell death event that leads to restricted biotrophic pathogen growth at the site of infection [5]. More than 100 R genes have been cloned in various plant species, and some of them have been mapped through association and linkage mapping. Due to the continue plant-pathogen co-evolution, new pathogen races arise that overcome established R genes in crop cultivars. Therefore it is of extreme importance to identify new resistance sources and transfer them to élite susceptible cultivars through closely linked molecular markers.

In the present review, some examples of identification of genes for resistance to the main diseases of durum wheat are presented.

Linkage mapping as a tool to identify loci for disease resistance in durum wheat

Linkage mapping is one of the marker-based approaches widely used to identify the chromosomal location of loci for the main traits of agronomic interest in crops. It is a highly effective approach for the genetic study of qualitative and above all quantitative disease resistance and has been used frequently in durum and bread wheat to detect resistance genes/quantitative trait loci (QTLs) to several diseases [6-12].

As an example, this approach has been used to study the resistance to a viral disease. Soil-borne cereal mosaic virus (SBCMV) is a furovirus widespread in Europe [13], which can infect durum and common wheat, and numerous other cultivated and spontaneous Gramineae [14]. *Polymyxa graminis* Led., a soil-borne plasmodiophorid protist, is responsible for the transmission of this virus to the roots of its host plants. This virosis is a serious concern for durum wheat productions, as in Italy it is widespread in the main wheat growing areas, especially in the northern and central regions, and it causes grain yield losses often above 50% on susceptible cultivars [15]. Moreover, the *P. graminis* protist can preserve its infectivity in soil for 10 years or more [16]. To date, the only economically viable means of controlling

SBCMV is the adoption of resistant cultivars [17]. In a study carried out in durum wheat, a linkage mapping approach was used to identify a major locus for resistance to SBCMV in the cv. Neodur [7]. A recombinant population of 146 RILs (recombinant inbred lines) derived from the cross Cirillo (highly susceptible) × Neodur (highly resistant) was evaluated in a naturally infected field, and a QTL that explained up to 87% of the observed variability for symptom severity was identified on the short arm of chromosome 2B. The QTL analysis also allowed to identify molecular markers which can be used in marker assisted selection (MAS) programs to transfer this locus to cultivars of interest. Three minor QTLs were also found on chromosomes 3B and 7B. The presence on the genetic map of markers associated to a gene sequence [18] allowed to discover that two markers coding for resistance proteins co-segregate with the major and the minor QTLs on chromosomes 2B and 3B respectively. These can therefore represent potential candidate genes for the two resistance loci. Furthermore, microsatellite markers flanking the major QTL were evaluated on a set of 25 durum wheat genotypes that were previously characterized for SBCMV resistance. The allelic composition of the genotypes at these loci, together with pedigree data, suggest that the old Italian cultivar Cappelli provided the SBCMV resistance determinants to durum cultivars that have been independently bred in different countries over the last century [7].

Besides viruses, the majority of the main diseases for wheat are caused by fungal pathogens, and rusts are among the most widespread diseases for both durum and common wheat.

Among fungal diseases, *Puccinia triticina* Eriks., the causal agent of leaf rust, may cause up to 50% yield losses, mainly associated with a reduction in biomass, harvest index, and kernels per square meter [19]. To date, more than 60 leaf rust resistance genes that originate from *Triticum* species have been characterized and mapped to specific chromosomes, while only few were fine-mapped to more specific genetic locations. *Lr21* [20], *Lr10* [21], and *Lr1* [22] are three leaf rust resistance genes cloned in bread wheat, encoding typical resistance proteins containing coiled coil (CC), nucleotide-binding-site (NBS), and leucine-rich-repeat (LRR) motifs. More recently, two genes for broad resistance to multiple rusts were identified: *Lr34* and *Lr67* which code for an ABC transporter and for a sugar transporter respectively. Both genes promote a basal resistance to the pathogens [23, 24].

Despite the great advances in the characterization of leaf rust resistance loci in bread wheat, a limited progress has been achieved for durum wheat, but in some cases genes corresponding to those present in common wheat were identified. An example is the resistance gene *Lr14a*, mapped on the long arm of 7B chromosome of durum wheat [25]. A similar resistant phenotype was also observed in the Italian durum wheat cultivar Creso, which possesses a high level of durable resistance to leaf rust based on both hypersensitive and non-hypersensitive components. In order to investigate the genetic basis of this resistance, a segregating population composed of 123 RILs derived from the cross Creso × Pedroso, was evaluated for disease sever-

ity in adult plants under field conditions, and in controlled conditions by assessing macroscopically the latency period and microscopically the number and type of pathogen colonies formed following artificial inoculation with a specific isolate. Besides some minor QTLs, one major QTL explaining both reduction of disease severity in the field and increased latency period was found on the long arm of chromosome 7B, and closely associated PCR-based and DArT markers were identified [8]. Based on reaction to the infection, a different allele compared to *Lr14a* was postulated.

Sources of resistance to leaf rust are also wild or domesticated emmer accessions. More recently, the *Triticum turgidum* ssp. *dicoccum* (2n = 4x = 28) accession MG5323 showed a useful level of resistance to leaf rust disease. The analysis of a segregating population of 110 RILs, derived from a cross between the cv. Latino (*T. turgidum* spp. *durum*), susceptible to leaf rust, and MG5323 revealed that this resistance was due to three different regions. More in detail, a major resistance gene was detected on the short arm of chromosome 1B, explaining more than 40% and two additional minor resistance genes located on chromosome 7B explained until 25% of phenotypic variation. Analysis of the leaf rust responses of the RILs demonstrated that only lines bearing resistant alleles at both loci showed effective leaf rust resistance, indicating that the genes identified behave as complementary genes. In all cases, the *T. dicoccum* accession MG5323 contributed the resistant allele [26].

A metaQTL analysis for resistance to powdery mildew in wheat

Genetic maps related to biparental populations and having a certain number of common mapped molecular markers can be merged to obtain much more dense consensus maps [27, 28]. These maps, with a very high marker coverage, can be used for metaQTL analyses, in which collected QTL data from different published studies are used to obtain consensus QTLs across different genetic backgrounds, thus providing a better definition of the regions responsible for the trait, and the possibility to obtain molecular markers that will be suitable for marker-assisted selection. This analysis was used in a study with the aim of identifying metaQTLs for resistance to powdery mildew in wheat. This disease, caused by the fungus *Blumeria graminis* f.sp *tritici*, induces important yield losses in areas with cool or maritime climates. To date, more than 60 powdery mildew resistance genes/ alleles have been reported in common and durum wheat [29]. Some of these were transferred from domesticated as well as wild relatives, such as *Triticum turgidum* var. *dicoccoides* (Körn.) and var. *dicoccum* (Schrank), *T. timopheevii* (Zhuk.), *T. monococcum* (L.), *T. tauschii* (Schmalh), and *Aegilops speltoides* (Tausch), or from more distant species, like *Secale cereale* (L.) [29]. An integrated map was developed for the projection of resistance genes/alleles and the QTLs from the literature, and to investigate their distribution in the wheat genome. Molecular markers that correspond to candidate genes for plant responses to pathogens were also projected onto the map, particularly consid-

ering NBS-LRR and receptor-like protein kinases. Twenty-four MQTLs were found on wheat 15 chromosomes. The co-location of the resistance QTLs and genes was investigated. Moreover, from analysis of the sequences of DArT markers, 28 DArT clones mapped on wheat chromosomes were associated with the NBS-LRR genes and positioned in the same regions as the MQTL for powdery mildew resistance. Furthermore, the analysis of the co-localization of resistance loci and functional markers provided a large list of candidate genes, useful for the fine mapping and isolation of resistance genes, and for the marker-assisted improvement of resistance in wheat [9].

Dissecting the genetic bases of resistance to fungal diseases through association mapping

Beside linkage mapping, a second approach for mapping resistance loci is association mapping, where genotype-phenotype relationships are explored in germplasm collections or natural populations. This approach is based on linkage disequilibrium (non-random association of alleles at adjacent loci) that tends to be maintained between linked loci over many generations [30]. Association mapping can be conducted directly on relevant breeding material, thus allowing direct inference from data analysis to the breeding program, or on wild or domesticated accessions. In this case a much higher mapping resolution is observed compared to cultivars, due to a lower extension of linkage disequilibrium blocks. Furthermore, phenotypic variation is observed for most traits of interest and polymorphism is higher than in biparental populations [31]. In both tetraploid and hexaploid wheat, linkage and association mapping have already proven to be effective strategies for identifying marker-trait associations for agronomically important traits [32, 33] including resistance to stem rust [10, 34-39]. Stem rust, caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn. (*Pgt*), is one of the most destructive diseases of wheat, in many regions of the world [40]. During severe epidemics, the disease can cause yield losses exceeding 50-70% in both hexaploid (*T. aestivum* L.) and tetraploid (*T. turgidum* ssp.) wheats (http://www.ars.usda.gov/). Additionally, wheat infected by stem rust can also suffer reduced end use quality and food security [34]. Combinations of different stem rust resistance (*Sr*) genes were successfully introgressed into wheat cultivars worldwide since the 1950s, effectively controlling the disease for many years [35]. However, the discovery of a new aggressive race (TTKSK, isolate Ug99) of *Pgt* in Uganda in 1999 [41] threatens wheat production due to its wide virulence on over 80% of wheat cultivars worldwide [42]. Moreover, at least eight variants with different virulence patterns have been described from the «Ug99 lineage» of African stem rust races, further complicating the resistance breeding process (rusttracker.cimmyt.org).

To identify QTLs conferring resistance to African stem rust race TTKSK at the seedling stage, an association mapping panel consisting of 230 tetraploid wheat accessions was evaluated under greenhouse conditions by [43]. Thirty-five resistance

QTLs were identified on all chromosomes, and seventeen are of particular interest as identified each by several markers located in the same chromosomal region. Many of the identified resistance loci were coincident with previously identified rust resistance genes, while nine, located on chromosomes 1AL, 2AL, 4AL, 5BL and 7BS were declared novel. A search for candidate resistance genes was carried out in the regions where QTLs were identified, and many of them corresponded to NBS-LRR genes and protein kinases with LRR domains.

Conclusions

The continuous plant-pathogen co-evolution needs that new resistant alleles are continuously introduced in the wheat breeding programs worldwide to face the emergence of new virulent races. This need is even more urgent in light of the ongoing climatic changes, which help the new races to spread in areas previously characterized by non-optimal growing conditions. Mapping approaches and QTL/gene cloning are the best way to produce genetically resistant wheat cultivars to limit the damage of pathogens to productions in a sustainable and economically-friendly manner. The recent availability of hexaploidy and tetraploid wheat genomes will further speed up this process [44,45].

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