Difference in Chemotype Composition of *Fusarium graminearum* Populations Isolated from Durum Wheat in Adjacent Areas Separated by the Apennines in Northern-Central Italy

A. Prodi*1, W. Purahong1,2, S. Tonti1,2, D. Salomoni3, P. Nipoti1, L. Covarelli3 and A. Pisi1

1Dipartimento di Scienze e Tecnologie Agroambientali, Alma Mater Studiorum Università di Bologna, via Fanin 40, 40127 Bologna, Italy
2Faculty of Agriculture and Life Science, Chandrakasem Rajabhat University, 10900 Bangkok, Thailand
3INRAN (ex ENSE-Sezione di Verona), via Ca’ Nova Zampieri 37, 37057 San Giovanni Lupatoto, Verona, Italy
4Dipartimento di Protezione e Valorizzazione Agroalimentare, Viale Fanin 46, 40127 Bologna, Italy
5Dipartimento di Scienze Agrarie e Ambientali, Università degli Studi di Perugia, Borgo XX Giugno, 74, 06121 Perugia, Italy

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Chemotype composition of *Fusarium graminearum* strains, isolated from durum wheat kernels from naturally FHB infected fields in Northern and Central Italy, was investigated by multiplex PCR. The different climatic and environmental conditions of the two examined areas separated by the Apennines affected the composition of chemotypes. 15Ac-DON chemotype was predominant in both the sub areas. Nivalneol chemotype was more frequent in the warmer sub area.

**Keywords:** chemotype, durum wheat, *Fusarium graminearum*, Fusarium head blight

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*Fusarium graminearum* (teleomorph Gibberella zeae (Schwein.) Petch.) is the major pathogen responsible of Fusarium head blight (FHB), an economically crucial and complex etiology disease on cereal crops worldwide (Goswami and Kistler, 2004). FHB has received more attention because of its effect on yield (Parry et al., 1995), grain quality (Liggitt et al., 1997) and grain contamination by mycotoxins (Visconti et al., 2000). FHB resistant cultivars are considered one of the solutions for the problem related to mycotoxin contamination in wheat grains (Lemmens et al., 2004), but unfortunately to date no resistant cultivar is commercially available for durum wheat. Most attention in the analysis of grain affected by FHB was placed on contamination by deoxynivalenol (DON), acetylated forms of DON (3Ac-DON and 15Ac-DON) and nivalenol (NIV).

DON is a mycotoxin that disturbs and/or inhibits DNA, RNA and protein synthesis by binding to the ribosomal peptidyltransferase site leading to a decrease of cell proliferation (Shifrin and Anderson, 1999). It is also known as vomitoxin and it is responsible for hemorrhagic and anorexic syndromes, neurotoxic and immunotoxic effects in mammals (Visconti et al., 2004). DON contamination levels in food and feed were found to be much higher than those observed for NIV (Boutigny et al., 2011), being probably the most negligible toxin due to the small amount usually detected (Yazar and Omurtag, 2008), but with consistent levels in many Asian countries, New Zealand and Brazil (Placinta et al., 1999). However, NIV has shown to have a higher toxicity than DON, for example, in human blood cells (Minervini et al., 2004). This toxin has also shown higher activity than DON in inhibiting DNA, and it may account for various toxic phenomena such as induction of cell death (Poapolathep et al., 2002).

Based on the production of type B trichothecenes, DON and NIV, three *F. graminearum* chemotypes have been described: 3Ac-DON, 15Ac-DON and NIV. Chemotype identification is broadly used to characterize *F. graminearum* for its toxigenic potential (Pasquali et al., 2009). There was a correlation between the presence of *F. graminearum* chemotype and wheat grain mycotoxin content. DON and NIV contents can be successfully predicted by quantifying the fungal biomass of DON and NIV producers with a real-time PCR quantification method (Brandfass and Karlovsky, 2006; Burlakoti et al., 2007; Pasquali et al., 2009).

The dominant chemotypes of *F. graminearum* vary within geographical areas, i.e. different countries and/or continents (Prodi et al., 2009b), but some host preference may affect the composition of chemotypes of *F. graminearum* population. Within the same country, the different geographical areas (i.e. plain, mountains, valleys, etc.) and distances from the sea, may also affect the composition of chemotypes of a fungal population. Mountains may play an importance role as natural obstacles by inhibiting the
diffusion of *F. graminearum* to other areas and preventing the genetic exchange among populations. The sea may provide humidity and enhance the suitable conditions for *F. graminearum* infection. Different locations have different environmental and climatic conditions, therefore also *F. graminearum* populations should be adapted to the environment under the pressure of natural selection.

The aim of this study was to investigate the chemotype differences of *F. graminearum* populations identified from different regions of Northern-Central Italy, separated by the Apennine mountains.

Durum wheat kernels from different cultivars were collected from naturally FHB infected fields within three Italian regions (Emilia Romagna, The Marche and Umbria) of Northern-Central Italy during the years 2009–2010 (Table 1). Emilia-Romagna and The Marche are separated from Umbria by the Apennines (Fig. 1) and, therefore, we considered two sub areas: Emilia-Romagna and The Marche merged in the sub area 1 and Umbria in sub area 2. Four hundreds kernels from each of 63 samples of wheat collected were washed in sterile water, disinfected in a 2% sodium hypochlorite solution for 2 min, then placed in Petri dishes containing potato dextrose agar (Difco, USA) with 0.3 g L$^{-1}$ streptomycin and neomycin sulphate. The Petri dishes were incubated at 22°C in the dark for seven days (Pancaldi et al., 2010). *F. graminearum* was identified, from

| No. isolates | Field localities | Regions | Cultivars | Chemotypes |
|--------------|------------------|---------|-----------|------------|
| ER 1         | Baricella        | Emilia Romagna | Neolatino | NIV        |
| ER 2         | Baricella        | Emilia Romagna | Normanno  | 15Ac-DON  |
| ER 3         | Budrio           | Emilia Romagna | Iride     | 15Ac-DON  |
| ER 4         | Busseto          | Emilia Romagna | PR22D89   | 15Ac-DON  |
| ER 5         | Cadriano         | Emilia-Romagna | Bologna   | 15Ac-DON  |
| ER 6         | Conselice        | Emilia-Romagna | Tiziana   | 15Ac-DON  |
| ER 7         | Crespellano      | Emilia Romagna | Normanno  | 15Ac-DON  |
| ER 8         | Crevalcore       | Emilia Romagna | Dupri     | 15Ac-DON  |
| ER 9         | Faenza           | Emilia-Romagna | Saragolla | 15Ac-DON  |
| ER 10        | Ferrara          | Emilia-Romagna | PR22D66   | 15Ac-DON  |
| ER 11        | Ferrara          | Emilia Romagna | Levante   | 15Ac-DON  |
| ER 12        | Fiorenzuola d'Arda | Emilia-Romagna | Simeto   | 15Ac-DON  |
| ER 13        | Malalbergo       | Emilia Romagna | Saragolla | NIV       |
| ER 14        | Mezzolara        | Emilia Romagna | Iride     | 15Ac-DON  |
| ER 15        | Molinella        | Emilia Romagna | Normanno  | 15Ac-DON  |
| ER 16        | Molinella        | Emilia-Romagna | Saragolla | 15Ac-DON  |
| ER 17        | Noceto           | Emilia Romagna | 22D78/874928 | 15Ac-DON |
| ER 18        | Noceto           | Emilia-Romagna | 22D89/875015 | 15Ac-DON |
| ER 19        | Noceto           | Emilia-Romagna | 22D40/875011 | 15Ac-DON |
| ER 20        | Ostellato        | Emilia-Romagna | Hathor    | 15Ac-DON  |
| ER 21        | Parma            | Emilia Romagna | Simeto    | 3Ac-DON  |
| ER 22        | Ravenna          | Emilia-Romagna | Saragolla | 15Ac-DON  |
| ER 23        | Ravenna          | Emilia-Romagna | Orobol    | 15Ac-DON  |
| ER 24        | Ravenna          | Emilia Romagna | S. Carlo  | 15Ac-DON  |
| ER 25        | S. Agostino      | Emilia-Romagna | Svevo     | 15Ac-DON  |
| ER 26        | S. Giorgio di Piano | Emilia Romagna  | Neolatino | 3Ac-DON  |
| ER 27        | S. Pietro Capofiume | Emilia Romagna   | S.Carlo   | 3Ac-DON  |
| ER 28        | S. Pietro in Casale | Emilia-Romagna    | Alcione   | 15Ac-DON  |
| ER 29        | Selva Malvezzi   | Emilia Romagna | Anco Marzio | 15Ac-DON |
| ER 30        | Copparo          | Emilia-Romagna | Iride     | 15Ac-DON  |
| ER 31        | Copparo          | Emilia-Romagna | Iride     | 15Ac-DON  |
| ER 32        | Tamara           | Emilia-Romagna | Iride     | 15Ac-DON  |
| ER 33        | Tamara           | Emilia-Romagna | Iride     | 15Ac-DON  |
the single spore cultures obtained, according to morphological criteria described by Leslie and Summerell (2006), DNA from 75 *F. graminearum* strains, morphologically identified, was extracted using a CTAB method (Suarez et al., 2005), modified in this work using seven days fungal mycelium (100–200 mg) and adding 1 μl of proteinase K.

**Table 1.** Continued

| No. isolates | Field localities | Regions   | Cultivars | Chemotypes |
|--------------|-----------------|-----------|-----------|------------|
| M 1          | Ancona          | The Marche| Saragolla | 15Ac-DON   |
| M 2          | Ancona          | The Marche| Rusticano | 15Ac-DON   |
| M 4          | Castelfidardo   | The Marche| Claudio   | 15Ac-DON   |
| M 5          | Jesi            | The Marche| Liberdur  | 15Ac-DON   |
| M 6          | Jesi            | The Marche| Svevo     | 15Ac-DON   |
| M 7          | Jesi            | The Marche| San Carlo | 15Ac-DON   |
| M 8          | Jesi            | The Marche| Ancomarzio| 15Ac-DON   |
| M 9          | Jesi            | The Marche| Flaminio  | 15Ac-DON   |
| M 10         | Jesi            | The Marche| Levante   | 15Ac-DON   |
| M 11         | Jesi            | The Marche| Saragolla | 15Ac-DON   |
| M 12         | Jesi            | The Marche| Normanno  | 3Ac-DON    |
| M 13         | Jesi            | The Marche| Colosseo  | 15Ac-DON   |
| M 14         | Jesi            | The Marche| Colosseo  | NIV        |
| M 15         | Jesi            | The Marche| Dylan     | 15Ac-DON   |
| M 16         | Jesi            | The Marche| Ciccio    | 15Ac-DON   |
| M 17         | Macerata        | The Marche| S.Carlo   | 15Ac-DON   |
| M 18         | Montefano       | The Marche| Achille   | 15Ac-DON   |
| M 19         | Montefano       | The Marche| San Carlo | NIV        |
| M 20         | San Severino Marche | The Marche | San Carlo | 15Ac-DON   |
| M 21         | Treia           | The Marche| Dorato    | 15Ac-DON   |

| Sub area 2   | No. isolates | Field localities | Regions | Cultivars | Chemotypes |
|--------------|--------------|-----------------|---------|-----------|------------|
| U 1          | Perugia      | Umbria          | Avispa  | 15Ac-DON  |
| U 2          | Perugia      | Umbria          | Saragolla | 15Ac-DON  |
| U 3          | Perugia      | Umbria          | Grecale | 15Ac-DON  |
| U 4          | Perugia      | Umbria          | Avispa  | NIV       |
| U 5          | Aquasparta   | Umbria          | Iride   | NIV       |
| U 6          | Capanne      | Umbria          | Unknown | NIV       |
| U 7          | Casalina     | Umbria          | Latinur | 15Ac-DON  |
| U 8          | Casalina     | Umbria          | Latinur | 3Ac-DON   |
| U 9          | Casalina     | Umbria          | Latinur | 3Ac-DON   |
| U 10         | Clitunno     | Umbria          | Grecale | 15Ac-DON  |
| U 11         | Colombella   | Umbria          | Avispa  | 15Ac-DON  |
| U 12         | Corciano     | Umbria          | Clairedo| 15Ac-DON  |
| U 13         | Foligno      | Umbria          | Sorrento| 15Ac-DON  |
| U 14         | Spello       | Umbria          | Unknown | NIV       |
| U 15         | Magione      | Umbria          | Unknown | NIV       |
| U 16         | Marsciano    | Umbria          | Unknown | 15Ac-DON  |
| U 17         | Panicarola   | Umbria          | Ermocolle| NIV      |
| U 18         | Castiglioni del lago | Umbria | Unknown | 15Ac-DON  |
| U 19         | Pozzuolo     | Umbria          | Duilio  | 15Ac-DON  |
| U 20         | S. Fatucchio | Umbria          | Latinur | NIV       |
| U 21         | Marsciano    | Umbria          | Saragolla| 15Ac-DON  |
| U 22         | Pozzuolo     | Umbria          | Quadrato| 3Ac-DON   |
Chemotype Composition of Fusarium graminearum Populations

(20 mg/ml) to CTAB-grinding buffer shortly before the use. F. graminearum DNA was analyzed with specific primers Fg16F/Fg16R under the conditions described by Nicholson et al. (1998), to determine the identity of all the strains.

F. graminearum was isolated from all the samples, no more than two isolates of F. graminearum per sample were chosen, and 75 isolates were used for further studies (Table 1). The molecular results confirmed the microscopic identifications, based on macroconidia characteristics, with the presence of the expected band of 410 bp.

The potential capacity of F. graminearum isolates to produce trichothecenes was evaluated using a multiplex PCR version (Starkey et al., 2007) as described by Prodi et al. (2009b). Primers, designed in the region of the Tri12 gene located in the terminal gene cluster for trichothecene biosynthesis, can distinguish three subgroups depending on the type of β-trichothecene produced. One primer is common to all chemotypes (12CON) and the others are chemotype-specific for 15Ac-DON (12-15F), 3Ac-DON (12-3F) and NIV (12NF) (Starkey et al., 2007).

All three chemotypes were found in both sub areas at each side of the Apennines (Table 1) and verified with the presence of the expected band of 670 bp for 15Ac-DON chemotype, of 410 bp for 3Ac-DON and of 840 bp for NIV. Sixty-four strains were found to be DON producers (57 strains 15Ac-DON and 7 3Ac-DON). Eleven strains showed to be NIV chemotype. Although in both areas the 15Ac-DON chemotype was dominant, the percentage of 15Ac-DON was variable. In Emilia Romagna and The Marche (sub area 1), the 15Ac-DON chemotype was accounting to 84% followed by 3Ac-DON and NIV at 8% (Fig. 2). In Umbria (sub area 2) 15Ac-DON chemotype was accounting to 54%. NIV was accounting to 32% and 3Ac-DON to 14% (Fig. 2).

This study is consistent with previous studies and reveals that F. graminearum 15Ac-DON chemotype is prevalent in Italy, while 3Ac-DON and NIV chemotypes are much less frequently detected (Gale et al., 2007; Prodi et al., 2009a). Prodi et al. (2009b) found only two isolates of NIV from a total of 74 isolates of F. graminearum in 43 fields of a restricted area of Emilia Romagna.

This is the first study that provides data suggesting a different chemotype composition of F. graminearum within two adjacent geographical areas separated by natural obstacles. Emilia Romagna and The Marche are separated from Umbria by the Apennine mountains and their climate is classified as humid subtropical while Umbria has a Mediterranean climate (Peel et al., 2007). Humid subtropical climate is characterized by cold winters with average temperatures around 0/1 °C (winters usually colder than those of some countries at higher latitudes), hot summers (average temperature 22/24 °C), high precipitations and absence of a dry season. Mediterranean climate has hot and dry summer, mild winter and rainy autumn. In Umbria, the Apennines act as a barrier to the influence of the Adriatic sea and to the North-east cold air but, several changes in altitude and geographical position can generate a huge variety of climates. The geographical differences in the two sub areas create a specific different climate and environment that may affect the fitness of some chemotypes (Ward et al., 2002). Jennings et al. (2004) proposed that environmental favorable conditions explain the distribution of F. culmorum chemotypes in different geographical areas. We suppose that this hypothesis may also be valid in the case of F. graminearum. In China, Zhang et al. (2007) reported how temperature affects the different distribution of F. graminearum chemotypes and they showed that DON producers were present in cooler regions with the annual average temperatures of 15 °C or lower. On the other hand, NIV chemotype and the new subpopulation of 15Ac-DON producers are mostly present in warmer regions where the annual average temperatures are above 15 °C. This finding somehow supports our results on the different chemotype composition between the two sub areas located on different

Fig. 1. Map of Northern-Central Italy, indicating the two sub areas studied (Sub area 1: Emila-Romagna and The Marche; sub area 2: Umbria).

Fig. 2. Frequency of the three F. graminearum chemotypes in sub area 1 (A) and sub area 2 (B).
sides of the Apennines. In the warmer region with Mediterranean climate (Umbria) F. graminearum NIV producers are present three fold more than in cooler regions (Emilia Romagna and The Marche) where we observed a high percentage of DON producers (total 92%; 15Ac-DON=84% and 3Ac-DON=8%).

However, our results do not show a clear cut like reported by Zhang et al. (2007). In Umbria, the warmest region, the percentage of DON producers was still high (total 68%; 54% for 15Ac-DON and 14% 3Ac-DON). In our experiment this could be explained with two hypothesis: first, F. graminearum NIV chemotype, mentioned by Zhang et al. (2007), is in lineage 6, so in some way they may behave differently from F. graminearum population of Northern-Central Italy (lineage 7), exclusively isolated from durum wheat. On rice Lee et al. (2009), observed that the different ecological ability between lineage 6 isolates and lineage 7 isolates were not directly related to the mechanism of pathogenicity; second, it is possible that some chemotypes of F. graminearum could be transported to other locations by seed shipping and long-distance spore transportation influencing chemotype composition (Guo et al., 2008). In fact in Western Canada, between 1998 and 2004, it was detected an increase of more than 14-fold of F. graminearum 3Ac-DON producers: that was linked to an introduction of a 3Ac-DON pathogenic population that was more toxigenic and vigorous, with a selective advantage above 15Ac-DON chemotype (Ward et al., 2008).

We can conclude that the different climatic and environmental conditions of the two examined areas separated by the Apennines affected the chemotypes composition of F. graminearum. 15Ac-DON was predominant in both the sub areas while NIV chemotype was more frequently detected in Umbria, the warmest sub area.

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References

Boutigny, A. L., Ward, T. J., Van Coller, G. J., Flett, B., Lamprecht, S. C., O’Donnell, K. and Viljoen, A. 2011. Analysis of the Fusarium graminearum species complex from wheat, barley and maize in South Africa provides evidence of species-specific differences in host preferences. Fungal Genet. Biol. 48: 914–920.

Brandfass, C. and Karlovsky, P. 2006. Simultaneous detection of Fusarium culmorum and F. graminearum in plant material by duplex PCR with melting curve analysis. BMC Microbiol. 6: 4.

Burlakoti, R. R., Estrada, Jr. R., Rivera, V. V., Buddeda, A., Secor, G. A. and Adhikari, T. B. 2007. Real-time PCR quantification and mycotoxin production of Fusarium graminearum in wheat inoculated with isolates collected from potato, sugar beet and wheat. Phytopathology 97:835–841.

Gale, L. R., Ward, T. J., Balmas, V. and Kistler, H. C. 2007. Population subdivision of Fusarium graminearum sensu stricto in the upper Midwestern United States. Phytopathology 97: 1434–1439.

Goswami, R. S. and Kistler, H. C. 2004. Heading for disaster: Fusarium graminearum on cereal crops. Mol. Plant Pathol. 5: 515–525.

Guo, X. W., Fernando, W. G. D. and Seow-Brock, H. Y. 2008. Population structure, chemotype diversity, and potential chemotype shifting of Fusarium graminearum in wheat fields of Manitoba. Plant Dis. 92:756–762.

Jennings, P., Coates, M. E., Turner, J. A., Chandler, E. A. and Nicholson, P. 2004. Determination of deoxynivalenol and nivalenol chemotypes of Fusarium culmorum isolates from England and Wales by PCR assay. Plant Pathol. 53:182–190.

Lee, J., Chang, I. Y., Kim, H., Yun, S. H., Leslie, J. F. and Lee, Y. W. 2009. Genetic diversity and fitness of Fusarium graminearum populations from rice in Korea. Appl. Environ. Microbiol. 75:2389–3295.

Lemmens, M., Buerstmayr, H., Kraska, R., Schuhmacher, R., Grausgruber, H. and Ruckenbauer, P. 2004. The effect of inoculation treatment and long-term application of moisture on Fusarium head blight symptoms and deoxynivalenol contamination in wheat grains. Eur. J. Plant Pathol. 110:299–308.

Leslie, J. F. and Summerell, B. A. 2006. The Fusarium Laboratory Manual. Blackwell Publishing Professional, Ames, IA, USA.

Liggitt, J., Jenkinson, P. and Parry, D. W. 1997. The role of saprophytic microflora in the development of Fusarium ear blight of winter wheat by Fusarium culmorum. Crop Protect. 16: 679–685.

Minervini, F., Fornelli, F. and Flynn, K. M. 2004. Toxicity and apoptosis induced by the mycotoxins nivalenol, deoxynivalenol and fumonisin B1 in a human erythroblastic leukemia cell line. Toxicol. In vitro 18:21–28.

Nicholson, P., Simpson, D. R., Weston, G., Rezanaoor, H. N., Lees, A. K., Parry, D. W. and Joyce, D. 1998. Detection and quantification of Fusarium culmorum and Fusarium graminearum in cereals using PCR assays. Physiol. Mol. Plant Pathol. 53:17–37.

Pancaldi, D., Tonti, S., Prodi, A., Salomoni, D., Dal Prà, M., Nipoti, P., Alberti, I. and Pisi, A. 2010. Survey of the main causal agents of fusarium head blight of durum wheat around Bologna, northern Italy. Phytopathol. Medit. 49:258–266.
Parry, D. W., Jekinson, P. and Mcleod, L. 1995. *Fusarium* ear blight (scab) in small grain cereals a review. *Plant Pathol.* 44: 207–238.

Pasquali, M., Giraud, F., Brochot, C., Cocco, E., Hoffmann, L. and Bohn, T. 2009. Genetic *Fusarium* chemotyping as a useful tool for predicting nivalenol contamination in winter wheat. *Int. J. Food Microbiol.* 137:246–253.

Peel, M. C., Finlayson, B. L. and McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* 11:1633–1644.

Pasquali, M., Giraud, F., Brochot, C., Cocco, E., Hoffmann, L. and Bohn, T. 2009. Genetic *Fusarium* chemotyping as a useful tool for predicting nivalenol contamination in winter wheat. *Int. J. Food Microbiol.* 137:246–253.

Peel, M. C., Finlayson, B. L. and McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* 11:1633–1644.

Placinta, C. M., D'Mello, J. P. F., MacDonald, A. M. C. 1999. A review of worldwide contamination of cereal grains and animal feed with *Fusarium* mycotoxins. *Anim. Feed Sci. Technol.* 78:21–37.

Poapolathep, A., Ohtsuka, R., Kiatipattanasakul, W., Ishigami, N., Nakayama, H. and Doi, K. 2002. Nivalenol-induced apoptosis in thymus, spleen and Peyer's patches of mice. *Exp. Toxicol. Pathol.* 53:441–446.

Prodi, A., Tonti, S., Nipoti, P., Pancaldi, D. and Pisi, A. 2009b. Identification of deoxynivalenol and nivalenol producing chemotypes of *Fusarium graminearum* isolates from durum wheat in a restricted area of Northern Italy. *J. Plant Pathol.* 91:611–615.

Prodi, A., Tonti, S., Nipoti, P., Pancaldi, D. and Pisi, A. 2009a. Presence of deoxynivalenol and nivalenol chemotypes of *Fusarium graminearum* isolated from durum wheat in Italy. *J. Plant Pathol.* 91 (4, Supplement): S4.81.

Shifrin, V. I. and Anderson, P. 1999. Trichothecene mycotoxins trigger a ribotoxic stress response that activates c-Jun Nterminal kinase and p38 mitogen-activated protein kinase and induces apoptosis. *J. Biol. Chem.* 274:13985–13992.

Starkey, D. E., Ward, T. J., Aoki, T., Gale, L. R., Kistler, H. C., Geiser, D. M., Suga, H., Toth, B., Varga, J. and O’Donnell, K. 2007. Global molecular surveillance reveals novel *Fusarium* head blight species and trichothecene toxin diversity. *Fungal Genet. Biol.* 44:1191–1204.

Suarez, M. B., Walsh, K., Boonham, N., O'Neill, T., Pearson, S. and Barker, I. 2005. Development of real-time PCR (Taq-Man®) assays for the detection and quantification of *Botrytis cinerea* in planta. *Plant Physiol. Biochem.* 43:890–899.

Visconti, A., Solfirizzo, M., Avantaggiato, G. and De Girolamo, A. 2000. Strategies for detoxification of *Fusarium* mycotoxins and assessing in vitro the relevant effectiveness. In: Proceedings of Brighton Crop Protection Conference – Pests and Diseases, pp 721–728.

Visconti, A., Haidukowski, E. M., Pascale, M. and Silvestri, M. 2004. Reduction of deoxynivalenol during durum wheat processing and spaghetti cooking. *Toxicol. Lett.* 153:181–189.

Ward, T. J., Bielawski, J. P., Kistler, H. C., Sullivan, E. and O’Donnell, K. 2002. Ancestral polymorphism and adaptative evolution in the trichothecene mycotoxin gene cluster of phytopathogenic *Fusarium*. *Proc. Natl. Acad. Sci. USA* 99:9278–9283.

Ward, T. J., Clear, R. M., Rooney, A. P., O’Donnell, K., Gaba, D., Patrick, S., Starkey, D. E., Gilbert, J., Geiser, D. M. and Nowicki, T. W. 2008. An adaptive evolutionary shift in *Fusarium* head blight pathogen populations is driving the rapid spread of more toxigenic *Fusarium graminearum* in North America. *Fungal Genet. Biol.* 45:473–484.

Yazar, S. and Omurtag, G. 2008. Fumonisins, trichothecenes and zearalenone in cereals. *Int. J. Mol. Sci.* 9:2062–2090.

Zhang, J. B., Li, H. P., Dang, F. J., Qu, B., Xu, Y. B., Zhao, C. S. and Liao, Y. C. 2007. Determination of the trichothecene mycotoxin chemotypes and associated geographical distribution and phylogenetic species of the *Fusarium graminearum* clade from China. *Mycol. Res.* 111:967–975.