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Does radiation interception or radiation use efficiency limit the growth of wheat inoculated with tan spot or leaf rust?

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ABSTRACT

Tan spot [*Pyrenophora tritici-repentis* (Died.) Drechs., anamorph *Drechslera tritici-repentis*) (Died.) Shoem.] and leaf rust (*Puccinia triticina* Eriks) are major diseases worldwide and some of the main biotic causes of yield and quality reduction in wheat (*Triticum aestivum* L.). Although wheat crop losses due to foliar diseases have already been studied based on an ecophysiological approach, none of these studies analyzed the independent effects of foliar pathogens with different nutritional habits. The aim of the present study was to determine the independent effects of (i) *Py. tritici-repentis* (necrothroph) and (ii) *Puccinia triticina* (biotroph) on the physiological components of biomass production: accumulated intercepted by green tissue photosynthetic active radiation (IGPAR), radiation use efficiency calculated by intercepted radiation (RUEint) as well as by intercepted by green tissue (RUEgt) in a wide range of Argentine commercial bread wheat cultivars growing in two field environments. Field experiments were carried out during two consecutive years combining a large range of wheat bread commercial cultivars and two levels of inoculation to promote infection of Tan spot and Leaf rust diseases, including a control without inoculation. Treatments were arranged in an experimental split-split plot design with three replications, where the main plots were both diseases, subplots corresponded to inoculation treatments 1- without inoculation (WI), 2- low concentration of inoculum of each disease (LC), 3- high concentration of inoculum of each disease (HC) and ten Argentine bread wheat commercial cultivars were the sub-subplots. Area under disease progress (AUDPC), area under percentage of non-green leaf area (AU %NGLA), crop growth rate (CGR) and healthy area duration (HAD) were calculated. Green leaf area index (GLAI), aboveground biomass (AGB), IGPAR and RUE were measured at three different crop stages (GS39, GS61 and GS82). Increases of inoculum concentration decreased AGB between 8 and 20% mainly explained by reductions in HAD and decreases on IGPAR by 14–18% with higher reductions when the crop was inoculated with *Py. tritici-repentis* than with *P. triticina*. Although both diseases reduced the physiological components of accumulated biomass related to radiation interception (IGPAR), RUEint (−23%), RUEgt (−11%) and CGR (−29%) were more reduced, respect to WI, when plants were inoculated with *P. triticina* compared to *Pyrenophora tritici-repentis*. The differential responses in RUE could be associated with the nutritional habit of *P. triticina* that reduces leaf nitrogen concentration, enhance assimilates consume by leaf respiration, reducing radiation use efficiency.

Abbreviations: AGB, aboveground biomass; IGPAR, accumulated intercepted by green tissue photosynthetic active radiation; AUDPC, area under disease progress; CGR, crop growth rate; FL, flag leaf layer; GLAI, green leaf area index; HAD, healthy area duration; HC, high concentration of inoculum; Ieg, interception efficiency by green tissue; IPAR, intercepted photosynthetic active radiation; LC, low concentration of inoculum; %NGLA, proportion of non-green leaf area; RUEint, intercepted radiation use efficiency; RUEgt, intercepted by green tissue radiation use efficiency; WI, control without inoculation.

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1. Introduction

Wheat (*Triticum aestivum* L.) is grown in most regions of the globe due to its importance as a food source, and its enormous genetic phenological plasticity (Slafer and Rawson, 1994). Airborne diseases, and particularly leaf rust (*Puccinia triticina* Eriks) and tan spot [*Pyrenophora tritici-repentis* (Died.) Drechs., anamorph *Drechslera tritici-repentis*) (Died.) Shoem.] are the main foliar diseases in Argentina and in many wheat production areas in the world, causing important yield and quality reduction in this crop. Leaf rust, is the most common rust disease of wheat (Bolton et al., 2008; Huerta-Espino et al., 2011). The fungus is an obligate parasite that cannot carry over from one season to the next on seed, stubble or soil. The most important sources of inoculum are susceptible volunteer wheat plants growing during the summer/autumn known as the 'green bridge'. The urediniospores produced by *P. triticina* can be wind-disseminated and infect host plants hundreds of kilometers from their source plant, which can result in wheat leaf rust epidemics on a continental scale (Bolton et al., 2008). Leaf rust requires moisture (rain or heavy dew) or high humidity for spores to germinate and infect leaves (Beard et al., 2015).

Unlike *P. triticina*, the principal sources of inoculum of tan spot are the seeds, the straw and collateral hosts (Rees and Platz, 1980; Wright and Sutton, 1990). For inoculum dispersal and infection development, temperature among 10–30 °C and moisture among 6–48 h are needed (Sah, 1994). The increasing inoculum of this pathogen has been attributed to the use of conservation tillage systems, shorter crop rotations, continuous wheat cultivation and use of susceptible cultivars (Moreno et al., 2012). Disease severity and time of infection depends on the presence of inoculum, carried over from last season (leaf rust) and/or present in the stubble (tan spot); favorability of seasonal conditions; pathotype virulence and varietal susceptibility (Cotuna et al., 2015). For example, under reduced tillage, where infested residues with *P. tritici-repentis* remains, the onset of tan spot epidemic occurs earlier than under conventional tillage (Mehta and Gaudencio, 1991). Both diseases alter the formation of different yield components, depending on the crop developmental stage at which infection occurs (Madden and Nutter, 1995) as well as the duration and severity of the epidemic (Robert et al., 2004; Serrago et al., 2009). Under severe infections of *P. triticina* yield losses can be up to 50% (Huerta-Espino et al., 2011), whereas under *Py. tritici-repentis* infections losses can range between 3 and 53% (Rees and Platz, 1983), 17–27% (Simón et al., 2011) and 27–42% (Wegulo et al., 2012).

Yield can be described by the cumulated biomass throughout the growing period and the proportion of biomass that is partitioned to the grain (Harvest index). Biomass production depends on the ability of the canopy to (i) intercept the incident radiation, which is a function of leaf area index (LAI) and canopy architecture (extinction coefficient -*k*-) and (ii) the efficiency at which the solar energy is converted into biomass (radiation use efficiency-RUE-) (Miralles and Slafer, 1997; Reynolds et al., 2005). Damage to leaf tissue through infection by foliar pathogens modifies plantís carbon metabolism due to reductions in the capacity of the crop to intercept and absorb the photosynthetic active radiation (IPAR-IGPAR) and/or as a consequence of reductions in RUE, response that is associated with the nutritional habit of the pathogen (Boote et al., 1983; Johnson, 1987; Bingham et al., 2009). According to their nutritional relationship with the host, fungal pathogens can be classified as necrotrophs, biotrophs or hemi-biotrophs (Oliver and Ipcho, 2004). Necrotrophs (like *Py. tritici-repentis*) destroy tissue during the colonisation by fungal hyphae through the secretion of toxins and cell wall degrading enzymes (PtrToxA, PtrToxB and PtrToxC), leading to a loss of green area and shrinkage of the leaf surface (Gooding et al., 2000; Wegulo, 2011). When necrotic regions are retained on leaves, they continue to intercept some light but without contributing to photosynthesis determining reductions in IGPAR (Dimmock and Gooding, 2002). On the other hand, biotrophs (like *P. triticina*) derive their resources for growth and sporulation from living host cells (Voegele and Mendgen, 2011), altering source-sink relations within the leaf and directing host nutrients to the fungal mycelium (Scholes and Rolfe 2009; Bancal et al., 2012; Ney et al., 2013). The host response to biotrophs tends to be more complex than that of necrotrophs. Infected leaves by biotrophs generally determine increases in respiration rate, reductions in the rate of photosynthesis and losses of chlorophyll (McNew, 1960; Scholes and Rolfe, 1995; Robert et al., 2005; Carretero et al., 2011) that could be associated with decreases on RUE. Most of the studies conducted to analyze the effect of foliar diseases in wheat have documented detrimental effects on IPAR/IGPAR but not in RUE, however, these studies have been focused on the effect of a complex of diseases (Serrago et al., 2009; Carretero et al., 2010) or natural infections (Bryson et al., 1997; Bancal et al., 2007), so it is difficult to ascertain the individual effects of a necrothroph pathogen (*Py. tritici-repentis*) or a biotroph pathogen (*P. triticina*) on the IGPAR and RUE. In the present study, both pathogens were inoculated independently to assess the individual effects of each disease on the physiological attributes related to biomass accumulation in wheat.

Traditionally, diseases management decisions on wheat are based on the use of thresholds constructed from empirical relationships relating the percentage of reduction of yield and the level of disease in a given time, often calculated based on incidence, severity and AUDPC parameters (Gaunt, 1995; McRoberts et al., 2003; Serrago et al., 2009). The problem that arises from this view is that they do not consider ecophysiological aspects related to biomass and yield formation (LAI, GLAI, % non green leaf area -%NGLA-), limiting the extrapolation to a wide range of genotypes, environments, years and locations (Gaunt, 1995; Bryson et al., 1997; Paveley et al., 1997; Savary et al., 2006). An eco-physiological approach focused on the impact of pathogens with different nutritional habits (biothrops-necrothrops) on attributes associated with the biomass production could be useful to improve the quantification and modelling of crop losses and thus contribute to the management of these diseases. Several authors reported that the use of this approach to predict the diseases effects is more accurate and robust than those models that only consider a phytopathological perspective (Waggoner and Berger, 1987; Serrago et al., 2009; Carretero et al., 2010). However, well-known models as WHEAT-PEST (Willocquet et al., 2008) does not include the effects of tan spot and consider only partially the effects of leaf rust. We hypothesize that *Pyrenophora tritici-repentis* is mostly a light stealer reducing radiation interception while *Puccinia triticina* is a light stealer and also removes soluble assimilates from host, therefore it reduces the green LAI (lesion area + virtual lesion area) and outflows assimilates from the pool of assimilates, processes that could be associated not only with reductions in intercepted radiation but also in RUE.

The present study was designed to determine the effects of independent artificial inoculations of foliar diseases with different nutritional habit 1) *Pyrenophora tritici-repentis* (necrotroph) and 2) *Puccinia triticina* (biotroph) on the physiological components of biomass production: Accumulated intercepted by green tissue photosynthetic active radiation (IGPAR) and radiation use efficiency (RUE) in bread wheat crops.

2. Materials and methods

2.1. General conditions

Field experiments were carried out in 2012 and 2013 at the Experimental Station J. Hirschhorn, Faculty of Agriculture and Forestry Sciences, National University of La Plata, Province of