



Absorbed radiation and radiation use efficiency as affected by foliar diseases in relation to their vertical position into the canopy in wheat

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ABSTRACT

The impact of foliar diseases on crop yield losses is better understood if considering ecophysiological variables together with pathological variables. Although wheat crop losses due to foliar diseases have already been studied with an ecophysiological approach, none of these studies analyzed the vertical diseases distribution into the canopy leaf layers in relation to the canopy size (leaf area index—LAI) and its architecture (light extinction coefficient- k value). Thus, the objectives of the present study were: (i) to understand the importance of the vertical distribution of the foliar diseases in relation to radiation absorption efficiency (RAE) for different LAI levels and canopy architectures and; (ii) to analyze and compare two ways of radiation capture estimations, considering LAI as a total or LAI of each leaf layer separately. The wheat cultivar Klein Pegaso was grown in plots under field conditions during three growing seasons using different nitrogen supply levels and a wide range of severity diseases by using protected and unprotected crops (applying or not fungicides, respectively). Unprotected plots were inoculated with biotrophic and/or necrotrophic pathogens. Biotrophic (*Puccinia triticina*-leaf rust) and necrotrophic pathogens (*Drechslera tritici-repentis*-tan spot; *Alternaria triticina*-leaf blight) constituted the “diseases complex” with different levels and proportions depending on the year and N treatment. Results showed that foliar diseases reduced LAI and GLAI (green leaf area index). GLAI was not only diminished by LAI reductions, but also by increases in NGLAI (non-green leaf area index) due to lesion coverage which reduced light absorption. In spite of the differences observed in LAI between protected and unprotected crops, radiation interception was not affected until LAI dropped down its critical value (i.e. when crop intercept 95% of the maximum radiation possible to be intercepted). The results demonstrated that assuming a uniform distribution of the diseases, lead to underestimations of accumulated absorbed radiation up to 21%, and as a consequence to overestimations of radiation use efficiency (RUE) up to 29% when diseases were concentrated in the lower leaf layers into the canopy. Together with the severity of the pathogen, at the time to decide controlling diseases, farmers should take into account: (i) LAI level, mainly in those crop situations where, during the critical period for yield determination, the LAI is close to or below the critical value; (ii) canopy architecture (k) associated with light distribution into the canopy and (iii) vertical diseases distribution into the crop.

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1. Introduction

Foliar diseases are one of the main reducing factors of yields in wheat (*Triticum aestivum* L.) crops in the Argentinean Pampas region (Annone et al., 2001) and in many other crop regions around the world. In Argentina, yield losses between 6 and 55% depending on environmental conditions and wheat cultivars used, have been found for crops infected with the residue-borne necrotrophic pathogen *Drechslera tritici-repentis* that causes tan spot (Annone et al., 2001 and works cited therein). Tan spot was found to recently increase in South America due to variety composition and expansion of non-tillage practices, becoming one of the main

Abbreviations: APAR, accumulated absorbed PAR; GLAI, green leaf area index; IPAR, accumulated intercepted PAR; LAI, leaf area index; LAR, loss of absorbed radiation; NGLAI, non-green leaf area index; PAR, photosynthetically active radiation; RAE_C, radiation absorption efficiency calculated with canopy model; RAE_L, radiation absorption efficiency calculated with layer model; RIE, radiation interception efficiency; RUE, radiation use efficiency; TSL, totally senescent leaves.

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damaging leaf blights (Duveiller et al., 2007). It is often associated to other blights as *Helminthosporium* leaf blight, a complex of spot blotch caused by *Cochliobolus sativus* and tan spot (Duveiller et al., 2005) or leaf blotch diseases caused by *Septoria tritici* blotch, tan spot and *Stagonospora nodorum* altogether (Wiik, 2009). These wheat leaf blights are often assessed together due to the similarity of symptoms and damages. Losses between 40 and 50% were also found in wheat crops due to early infections of leaf rust caused by the main biotrophic pathogen of wheat *Puccinia triticina* (Annone et al., 2001 and works cited therein).

In wheat as in many other crops, above ground biomass production has been widely related to: (i) the amount of intercepted radiation and (ii) the ability of the crop to convert this intercepted radiation in biomass (i.e. radiation use efficiency: RUE) (Gardner et al., 1985; Johnson, 1987). The proportion of solar incident radiation that is captured by the crop, called radiation interception efficiency (RIE), depends on the leaf area index (LAI) and the canopy architecture, associated with the extinction coefficient (k) as described by Hipps et al. (1983). Thus, k defines the functional relation between the RIE and the LAI of the crop. Foliar diseases could reduce one or both attributes, i.e. RIE (Waggoner and Berger, 1987) and/or RUE (Johnson, 1987). Regarding RIE, the kinetic of Hipps et al. (1983) equation determines a critical leaf area index when the crop intercepts 95% of the maximum radiation possible to be intercepted by the crop (see Eq. (1)). Therefore, LAI reduction below that critical value because of diseases would lead to reductions in RIE; which will be proportionally greater as the values of LAI become lower.

In diseased crops, part of total intercepted radiation is captured by the portions of the leaves affected by diseases, which are not functional, reducing the radiation absorption efficiency (RAE). Thus, total absorbed radiation could be reduced because of GLAI decrease either through lesion coverage, accelerated senescence (Boote et al., 1983) and defoliation or through reduced tillering (decrease leaf area formation). It was previously found in wheat that leaf rust and *S. tritici* blotch in complex did not interact (Robert et al., 2004) and that the overall decrease in GLAI due to both diseases was enough to simulate damages either at the leaf (Robert et al., 2005, 2006) or at the crop level (Bancal et al., 2007). In the same way, Bhathal et al. (2003) shown that tan spot and *Septoria nodorum* blotch caused similar damages in wheat crops.

In addition, foliar diseases effects on the intercepted or absorbed radiation not only depends on their impact on LAI or GLAI per se, but also on the vertical position of the canopy where the diseases appear (Béasse et al., 2000; Robert et al., 2004; Bancal et al., 2007). Gooding et al. (2000) speculated that the upper leaves of the canopy are of particular importance in assimilates contribution to wheat yield because they: (i) are the last senescent leaves; (ii) are in the upper position of the canopy having lesser shadow level than those positioned at the lower layers, being able to intercept more radiation and; (iii) are “vascularly” closer to the spikes than the other leaves. Some evidences showed that a great portion of grain carbohydrates comes from flag leaf (Lupton, 1972). Additionally, leaf nitrogen concentration decreases from the top to the bottom of the canopy in concordance with light attenuation, therefore upper leaves have higher levels of nitrogen content than lower ones (Anten et al., 1995; Dreccer et al., 2000; Bertheloot et al., 2008). Since foliar photosynthesis is dependent on foliar nitrogen content (Sinclair and Horie, 1989; Anten et al., 1995) flag leaves produce higher levels of assimilate per unit area than lower leaves. Likewise, Robert et al. (2004) working with simulated data for wheat suggested that photosynthesis of the upper leaf layer (i.e. flag leaf) contributes with ca. 45% to the total photosynthesis, 20% corresponded to leaves immediately below the flag leaf; and the remaining contribution was ascribed to the

lower ones. Although the role of the upper leaves into the canopy is really important for intercepting solar radiation, the importance of the lower leaves for the capture of radiation may vary according to (i) the canopy coverage (LAI) and (ii) the extinction coefficient (k) which is specie and cultivar dependant. Furthermore, it is crucial to understand damages due to leaf rust and tan spot, as leaf rust, widely wind dispersed often affects upper leaves of the crop late in the season while tan spot is splashed from infected stubble to lower and then to upper leaves during the whole crop cycle (Duveiller et al., 2005).

In a previous paper, Serrago et al. (2009) determined the effects of foliar disease complex on intercepted radiation and radiation use efficiency at canopy level in a wide range of environments, where different cultivars, nitrogen and foliar diseases conditions were considered. They clearly showed that, at canopy level, wheat leaf diseases mainly affected radiation capture efficiency. The present study analyze the effects of foliar diseases on captured radiation and radiation use efficiency at leaf layer level and discuss the advantage and problems of consider the approach at canopy vs leaf level on the main physiological components of aerial biomass accumulated by the crop. Thus, the present paper aims: (i) to understand the importance of the vertical distribution of the foliar diseases in relation to RAE for different LAI levels and canopy architectures and; (ii) to analyze and compare two ways of radiation capture estimations, considering LAI as a total or LAI of each leaf layer separately. Both objectives were carried out under a wide range of crop environment and disease situations which are normally explored by farmers in field paddocks. Thus, to fulfill the objectives, a “foliar diseases complex” constituted by different pathogen with different levels and proportions was generated in different agronomical environments and a wide range of LAI levels was explored due to different nitrogen availabilities and sowing dates used.

2. Materials and methods

2.1. Treatments and experiments design

Three experiments were carried out in the experimental field of Department of Plant Production of the University of Buenos Aires (Buenos Aires, Argentina, 34°35'S, 58°29'W) during the 2004, 2005 and 2007 growing seasons. To generate a wide range of coverage (LAI) levels and to explore different environmental conditions, different sowing dates and nitrogen availabilities were used. The cultivar Klein Pegaso, which is very susceptible to leaf rust, was sown at 400 plants m^{-2} on 29 June 2004, 3 August 2005 and 24 July 2007 in plots of 10 rows 0.15 m apart and 2.8 m long for 2004 and 2005 and 2.1 m long for 2007 experiments. Variations in flowering time between the extreme sowing dates were of around 20 days (2004 vs 2005).

Treatments consisted in a factorial combination of two contrasting nitrogen availabilities and two diseases (or fungicides) levels. In relation to nitrogen, no fertilized (N_0) and fertilized (N_1) treatments were used. Nitrogen availability in the N_0 treatment (i.e. the nitrogen content in the top 0.6 m of the soil at sowing time) was 28, 13 and 50 $kg N ha^{-1}$ for 2004, 2005 and 2007 experiments, respectively; while in the N_1 treatment the nitrogen availability (i.e. soil nitrogen content at the top 0.6 m plus fertilizer nitrogen) was 180 $kg N ha^{-1}$ for 2004 and enhanced to 300 $kg N ha^{-1}$ for 2005 and 2007 experiments to enlarge differences between N_0 and N_1 treatments. The two levels of diseases treatments were: protected (P), with fungicide application, and unprotected (UP) without fungicides application. The P treatment consisted of maintaining the crop free of diseases during the whole cycle through systematic applications of tebuconazole (Folicur® Bayer SA) at 750 $cm^3 ha^{-1}$ every 15 days.

In the UP treatment diseases development was promoted with different inoculum (pathogen) resources with the aim to generate “foliar diseases complex” constituted by various levels and different proportions of pathogens. Thus, in the 2004 and 2005 experiments, wheat stubble collected from previous diseased crops infected with necrotrophic pathogens (mainly *D. tritici-repentis*-tan spot), was uniformly applied to the ground of all the plots at sowing (inclusive in the P treatment). Infected stubble was not used during the 2007 growing season with the purpose of avoiding necrotrophic pathogen infection and favoring leaf rust appearance on the top leaves. In addition, plots corresponding to UP treatment were inoculated with spores of *P. tritici* (leaf rust) at the onset of stem elongation in 2004 and 2005 experiments and, repeated at middle of stem elongation in 2005 experiment (since, the former inoculation did not succeed neither in 2004 nor in 2005), while in the 2007 experiment inoculation with leaf rust was applied at flag leaf emergence. In all cases, the inoculation was carried out by pulverization of the spores over the plots using water with some drops of surfactant (Tween 20[®]) as a carrier. Specific race of leaf rust for the cultivar Klein Pegaso was used for preparing the suspension. The spores were obtained and provided by Francisco Sacco from the National Institute of Agricultural Technology (INTA), Argentina. For keeping the foliar wet to promote the rust infection, during the 2004 experiment water was sprayed at the evening, just before the spore inoculation, and during the next three evenings. As the wet conditions during that experiment were not as good as expected to promote rust infection, during 2005 and 2007 experiments wet conditions were improved using plastic tents. Thus, after the inoculation at the evening, all the plots (including controls) were covered with plastic tents during the following three nights to increase humidity and foliar wet with the objective of promoting the infection by the pathogen.

In the three experiments herbicides and insecticides were sprayed when necessary to control weeds and insect damages. From the onset of stem elongation onwards nets were installed to prevent lodging.

Treatments were arranged in a split plot design with three blocks. The main plots represented the nitrogen treatments (N_0 and N_1) and the sub-plots corresponded to the fungicide treatments (P and UP).

2.2. Measurements and calculations

From anthesis to maturity, samples of above ground biomass of 0.3 or 0.5 m length were randomly collected from each plot every one or two weeks. At anthesis and physiological maturity 1 m length of the central rows was sampled. Each sample was oven dried at 60 °C until constant weight. Prior to oven drying, a sub-sample of three to four plants was taken from each sample to measure the severity of foliar diseases, the total leaf area index (LAI), the green leaf area index (GLAI) and the non-green leaf area index (NGLAI).

These sub-samples were separated into main stems and tillers and then the leaf blades were grouped according to their canopy leaf layer position. Those leaf blades containing at least a minimal portion of green tissue were pasted on paper sheets, digitalized with a scanner at 300 dpi and then the total, green and non-green leaf area were determined with Assess (Lamari, 2002), an image analysis software for the different leaf layer positions. After digitalization of the images, the sub-samples (leaves and stems) were oven dried until constant weight to be able to extend area measurements to the main sample. Then, LAI, GLAI and NGLAI were calculated as m² of leaf per m² of ground. It is important to note that those leaves that were totally senescent (TSL), i.e. dead leaves, were not digitalized

with the scanner and thereby were not included in the LAI calculations. These TSL were not included in RIE and RAE estimations (see below). For the anthesis sampling date, and after measurements were made, flag leaves were oven dried at 60 °C for 48 h until constant weight and after that they were weighed, and foliar nitrogen content determined using the Kjeldahl method (Lang, 2002).

Visual estimations of foliar diseases severity (percent of diseased area) were made in all the main stem leaves for the same sub-sample used for image analysis. Leaf rust (biotrophic pathogen) severity was assessed as the percentage of leaf area covered by spores (since it was not possible to separated chlorosis and necrosis caused by this pathogen from those caused by natural processes) and disease caused by necrotrophic pathogens (as a whole) was assessed as the percentage coverage of symptomatic area (chlorosis and necrosis due to necrotrophic pathogens). It is important to remark that, whenever a leaf was heavily senescent, symptoms of foliar diseases were not possible to be distinguished. The prevalence of the different necrotrophic pathogens was estimated through incubation of leaf portions with necrotic area randomly collected from the sub-samples. These necrotic portions were incubated under optimal conditions for fungi development and sporulation and then the presence of the different pathogen in each portion was determined using a magnifying glass. The prevalence of pathogens was calculated for each plot as the percentage of portions with each pathogen within the total necrotic portions incubated. These evaluations were made at the middle of the grain filling period only for the 2004 and 2005 experiments as there were no important necrotrophic severity levels in the 2007 growing season.

Radiation interception was measured between heading and anthesis stages during the 2004 and 2005 experiments with a linear ceptometer (LI-191 S, LI-COR Inc., Lincoln, NE, USA). Measurements were made in the central rows of the plots determining the incident radiation (I_0) immediately above the canopy and transmitted radiation (I_t) at the base of the crop (on soil surface) placing the sensor in three positions along the rows (left, centre and right) and taking an average of the three measurements. RIE was calculated as the ratio between the difference of incident and transmitted radiation to incident radiation. Since other works (e.g. Thorne et al., 1988) did not find significant differences between RIE values from instantaneous measurements made at noon and those from measurements integrated over the whole day (24 h), measurements were made on clear days from an hour before to an hour later than solar noon.

The Beer–Bourguier–Lambert Law (Hipps et al., 1983) approximation was used to estimate the RIE and RAE from LAI measurements made on the samples taken during the grain filling period as follows:

$$RIE = a(1 - \exp^{-kLAI}) \quad (1)$$

where a is the maximum value of radiation interception reached by the crop and k is the extinction coefficient. Values of a and k parameters were estimate fitting Eq. (1) to data of RIE and LAI measured between heading and anthesis stages. Since, no significant differences between nitrogen and disease (or fungicide) treatments were found for a and k parameters (see Fig. 3 in Section 3), the whole data set was used to obtain a unique k value. As different works in the literature show that from anthesis onwards the architecture of the plant remains fairly constant no observing differences in the light distribution profile into the canopy (Bertheloot et al., 2008) nor in the k value (Thorne et al., 1988), the calculated value of k was used to estimate RIE from LAI measurements during the grain filling for the different years and treatments.

Two models were used for the estimation of RAE: (i) leaf layer model (RAE_L) and (ii) canopy model (RAE_C). The leaf layer model takes into account the distribution of diseases in the different leaf layers of the canopy and estimates RAE_L for each leaf layer *i*, as follows:

$$RAE_{Li} = [\exp(-kLAI_j)] [a(1 - \exp(-kLAI_i))] \left[\frac{GLAI_i}{LAI_i} \right] \quad (2)$$

where LAI_i and GLAI_i are the total and green leaf area index of a given leaf layer *i* and; LAI_j is the total leaf area index over the leaf layer *i*. The RAE_L for the whole canopy is the summation of RAE_{Li} calculated for each leaf layer *i*.

On the other hand, the canopy model considers a uniform distribution of diseases between the leaf layers and estimates RAE_C for the whole canopy as follows:

$$RAE_C = [a(1 - \exp(-kLAI))] \left[\frac{GLAI}{LAI} \right] \quad (3)$$

The RIE, RAE_L and RAE_C between two sampling dates were obtained by interpolation. With these data and the daily incident photosynthetically active radiation (PAR) obtained from a weather station situated in the site of the experiments, the daily amount of intercepted PAR and the daily amount of absorbed PAR (for RAE_L and RAE_C) were calculated. By summation of the daily data, accumulated intercepted PAR (IPAR) and absorbed PAR (APAR_L and APAR_C) were calculated for the entire grain filling period (from anthesis to physiological maturity).

Radiation use efficiency (RUE) for the grain filling period was estimated as the slope of the relationship between the post anthesis accumulated above ground biomass and the post anthesis APAR for each of the treatments using either RAE_L or RAE_C estimations. For these regressions, data of all the sampling dates were used.

2.3. Statistical analysis

Statistical differences between treatments were tested through standard analyses of variance with first level interactions. When the analysis of variance revealed significant differences, the mean treatment values were compared using Tukey test with significance level of 0.05. The software used for statistical analysis was INFOSTAT Professional v.1.1 (Di Rienzo and Robledo, 2002). Whenever plotting data of a variable (severity, LAI, GLAI, RIE and RAE) in relation to thermal time (°C d⁻¹) from anthesis (XY plots), standard deviations were presented for each point.

2.4. Sensitivity analysis of RIE and RAE_L due to *k* variations and the effects of different vertical distributions of foliar diseases into the canopy

Considering that extinction coefficient (*k*) could vary with genotype, stage of development and/or growing conditions (Thorne et al., 1988), a sensitivity analysis of RIE and RAE_L for changing values of *k* was performed. It is important to note, as was indicated above, that in the data set used in the present study *k* values did not show variation between nitrogen and diseases treatments. Thus, new estimations of RIE and RAE_L (Eqs. (1) and (2), respectively) with different *k* values were made for the 2005 growing season in the UP treatment. The *k* values tested were: (i) the one belonging to the cultivar used in the present study, i.e. *k* = 0.60, and (ii) two other values corresponding to 25% up and down respect to the *k* value obtained in the present study, i.e. 0.75 and 0.45, respectively; corresponding to the range of *k* values for wheat found in the literature (e.g. Abbate et al., 1998 and reference cited therein). The severity value used for these estimations

(12.8%) corresponded to the total severity value (considering non-green leaf area as total diseased tissue) recorded during the 2005 N₁ treatment at the timing of maximum LAI, estimated as the mean (weighted by leaf size) of the three upper leaf layers.

Additionally, with the purpose to understand how losses of absorbed radiation (LAR), due to interception of radiation by diseased leaf area, could vary when considering different vertical diseases distribution into canopies with different *k* values and LAI levels, three hypothetical vertical diseases distribution were considered: (i) all the diseases located in the flag leaf (L1); (ii) all the diseases located in the third leaf from the top (L3) and; (iii) a uniform distribution of diseases within the three upper leaves. It is important to highlight that in each of the three situations the mean severity value was 12.8% (value cited above). Thereby, whenever diseases were uniformly distributed, each one of the leaf layers had a severity value of 12.8%. However when diseases were considered to be all concentrated in one leaf layer (i.e. flag leaf) this leaf layer had a severity value of 38.4% and the others two leaf layers had 0% of severity, being the average between the three leaf layers 12.8%. On the other hand, two contrasting LAI levels were used: (i) maximum LAI of 2005 N₁ treatment (i.e. 6.3) and; (ii) maximum LAI of 2005 N₀ treatment (i.e. 3.1). For all the LAI, *k* values and

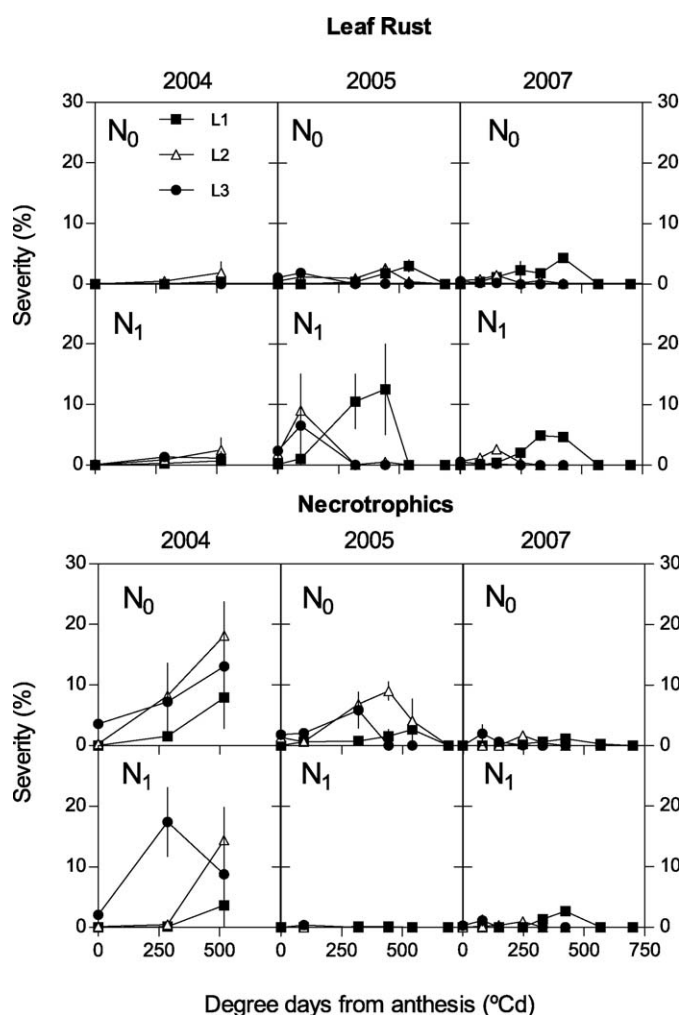


Fig. 1. Severity dynamics of leaf rust (percent of leaf area covered with spores) and necrotrophic pathogens (percent of chlorosis and necrosis due to necrotrophic pathogens) during the grain filling period for the UP treatment. Data from the two nitrogen treatments (N₀ and N₁) and the three years of experiments (2004, 2005 and 2007) are shown. Necrotrophic pathogens are group as a whole. L1 (flag leaf), L2 and L3 are presented as squares, triangles and circles, respectively. Vertical bars indicate standard error.

vertical diseases distribution combinations, the RIE for each leaf layer and for the crop and, the RAE_L for the crop were calculated using Eqs. (1) and (2), respectively. With RIE and RAE_L values for the crop, the LAR due to non-green tissue interception was estimated for each combination as:

$$LAR(\%) = \left[\frac{(RIE - RAE_L)}{RIE} \right] \times 100 \quad (4)$$

3. Results

3.1. Diseases development

In all experiments, diseases in the upper three leaf layers appeared mainly from anthesis onwards (Fig. 1). The levels and proportions of the different type of pathogens (biotrophic and necrotrophic pathogens) within the “diseases complex” varied between years and nitrogen treatments. In 2004 experiments, severity of necrotrophic diseases reached values between 3.7 and 18.2% being higher in the lower leaf layers while symptoms of leaf rust (biotrophic) stayed lower than 2.5%. Conversely, in 2007 experiments, the predominant disease was leaf rust reaching severity values in flag leaf layer of 4.3 and 4.8% in the N_0 and the N_1 treatment, respectively; whereas severity caused by necrotrophic pathogens was never higher than 2.5%. Finally, in 2005 experiments the composition of the “diseases complex” was different depending on the nitrogen treatment. Under high nitrogen availability (N_1) the predominant disease was leaf rust reaching severity values up to 12.5% with no detection of necrotrophic diseases symptoms. On the other hand, under low nitrogen availability (N_0), necrotrophic pathogens predominated in the “diseases complex” reaching values up to 9% while leaf rust did not exceed 3%. Foliar nitrogen content (%) of the flag leaf at anthesis showed significant differences between nitrogen treatments in the 2005 growing season ($p < 0.001$) being higher in N_1 (3.58%) than in N_0 (2.28%) whereas no significant differences ($p > 0.1$) were detected in the 2007 experiments between both nitrogen levels although the trend was similar than that observed in 2005 (i.e. $N_0 = 2.62\%$ and $N_1 = 3.06\%$).

In general terms diseases developed acropetally i.e. infected firstly the lower leaves layers and latter affecting the upper leaves (Fig. 1). This trend was clear for necrotrophic pathogens in the 2004 experiment and for leaf rust and necrotrophic pathogen in N_1 and N_0 treatments in 2005, respectively. In 2007, leaf rust affected mainly flag leaf (L1) but with lower levels than the N_1 treatment of 2005. The necrotrophic pathogens reached higher levels in the lower leaf layers than in the upper ones, whereas the opposite occurred for leaf rust (Fig. 1).

The analysis of prevalence showed that the predominant necrotrophic pathogens causing foliar diseases were *D. tritici-repentis* (tan spot) and *Alternaria triticina* (leaf blight). During 2004 growing season the prevalence levels were 25.3 and 4.0%, for tan spot and leaf blight, respectively in N_0 treatment; while in N_1 the prevalence values were 20.0% for *D. tritici-repentis* and 9.3% for *A. triticina*. In the N_0 treatment of the 2005 experiment the prevalence was 41.3 and 17.3% for tan spot and leaf blight, respectively. It is important to highlight that diseases caused by necrotrophic pathogens stayed at very low levels in the N_1 treatment during 2005 or in both nitrogen treatments in the 2007 experiment (Fig. 1).

3.2. Leaf area index, RIE and RAE at canopy level

The total and the green leaf area index (LAI and GLAI) at anthesis for the P treatment varied with the growing season. The highest

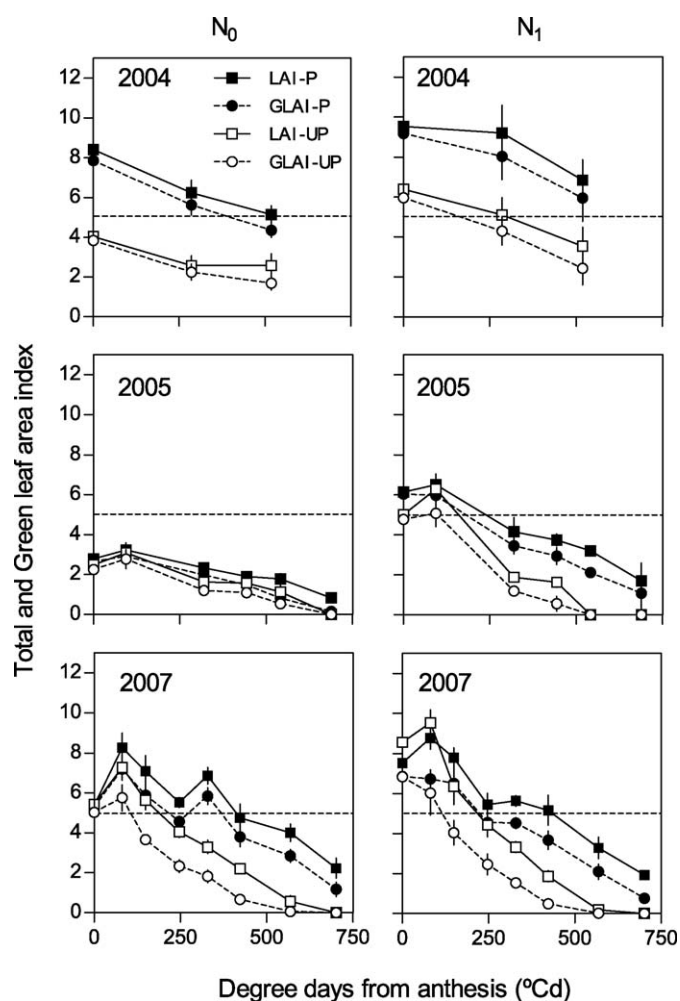


Fig. 2. Dynamics of the total (squares with continue lines) and green (circles with dotted lines) leaf area index during the grain filling period for P (solid symbols) and UP (open symbols) treatments and both nitrogen situations (N_0 and N_1), in three years (2004, 2005 and 2007). Horizontal dotted line indicates critical LAI value (i.e. when crop intercepts 95% of the maximum radiation possible to be intercepted). Vertical bars indicate standard error.

values were found in the 2004 followed by the 2007 experiment, while the lowest ones were observed during the 2005 experiment under the low nitrogen availability. In all experiments, the general trend was that the N_1 had higher LAI and GLAI than the N_0 treatment. Similarly, and as expected, the P treatment showed higher LAI and GLAI values throughout the grain filling period than the UP treatment in all growing seasons (Fig. 2).

Regarding the time course of LAI during grain filling period, it was lower than the critical value at the time of anthesis only in the UP treatment during the 2004 N_0 experiment and during 2005 N_0 for the P and UP treatments. In the rest of the experiments, LAI was at the critical or even over that value at the time of anthesis and after that LAI was reduced by diseases throughout the grain filling period at a rate that changed depending on the year and nitrogen treatment (Fig. 2). Although in the N_0 treatment during 2005 growing season the LAI remained below the critical value, without important differences between both fungicide treatments (P and UP), diseases (UP treatment) brought forward the time when LAI fell below its critical value in the other situations. In relation to N treatment, nitrogen application (N_1) delayed the time when LAI dropped below the critical value in 2004 experiment due to higher maximum LAI reached in N_1 than the N_0 treatment (Fig. 2).

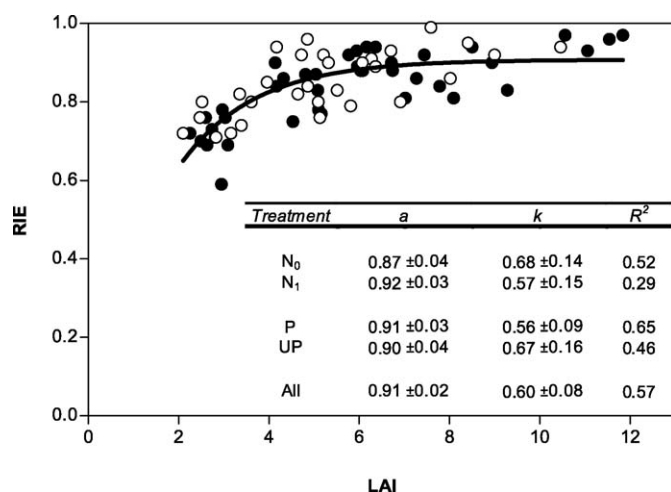


Fig. 3. RIE and LAI measurements used for estimations of a and k parameters by fitting Eq. (1). Solid and open symbols indicate P and UP treatments. The table inset shows parameters estimations ($\pm$ half confidence interval, 95%) for different N availabilities and diseases conditions and for the pool data set (All). R^2 are shown for each situation.

Considering that, diseases did not affect the maximum LAI reached by the crop (except in 2004 N_0 treatment, data not shown), their main impact was an enhanced LAI reduction throughout the grain filling period (Fig. 2). Although reductions of GLAI were consequence of decrease in LAI, when comparing the differences between LAI and GLAI curves (NGLAI), these were greater for the UP than for the P treatment (particularly during 2007) suggesting that lesion coverage increased NGLAI, decreasing GLAI. The higher NGLAI in the UP than the P treatment was clearly denoted when comparing RIE and RAE_L (see Fig. 4) and when observing the accumulated absorbed radiation by non-green leaf area (see Table 2).

Estimations of a and k parameters, by fitting Eq. (1) to RIE and LAI data measured between heading and anthesis stages, were used for RIE, RAE_L and RAE_C calculation from LAI measured during the whole grain filling period. Acceptable fit were found for all the situations as demonstrated by the correlation coefficient values with the exception of N_1 data for which no LAI values lower than 4 were observed and thereby the range of RIE explored was too narrow (Fig. 3). Since k values calculated for different nitrogen and fungicide treatments did not show significant difference, the pool data set was used to obtain a unique a and k values i.e. $a = 0.91$ and $k = 0.60$ (Fig. 3). Thus, both parameters were used for RIE, RAE_L and RAE_C calculations during the grain filling period.

In all cases but in the N_0 treatment of 2004 experiment, the main negative effects of diseases on RIE and RAE_L occurred during the grain filling period (Fig. 4); in fact similar values of both attributes were found at anthesis for P and UP treatments. In spite of the reductions of LAI by diseases from anthesis onwards, RIE in the UP treatment remained either unchanged or slightly affected, until approximately the mid part of the grain filling period (Fig. 4) when LAI dropped below the critical value (Fig. 2). From that moment (i.e. mid part of the grain filling) until the physiological maturity important reductions in RIE due to diseases were observed.

Conversely, RAE_L was reduced by diseases immediately after anthesis and with a higher rate than in P treatment, mainly in the 2007 experiment in both nitrogen treatments (Fig. 4), where the highest values of NGLAI were found as indicated above. The differences between intercepted and absorbed radiation curves in Fig. 4 represent the fraction of incident radiation absorbed by non-green area, including senescent and diseased foliar area. Then,

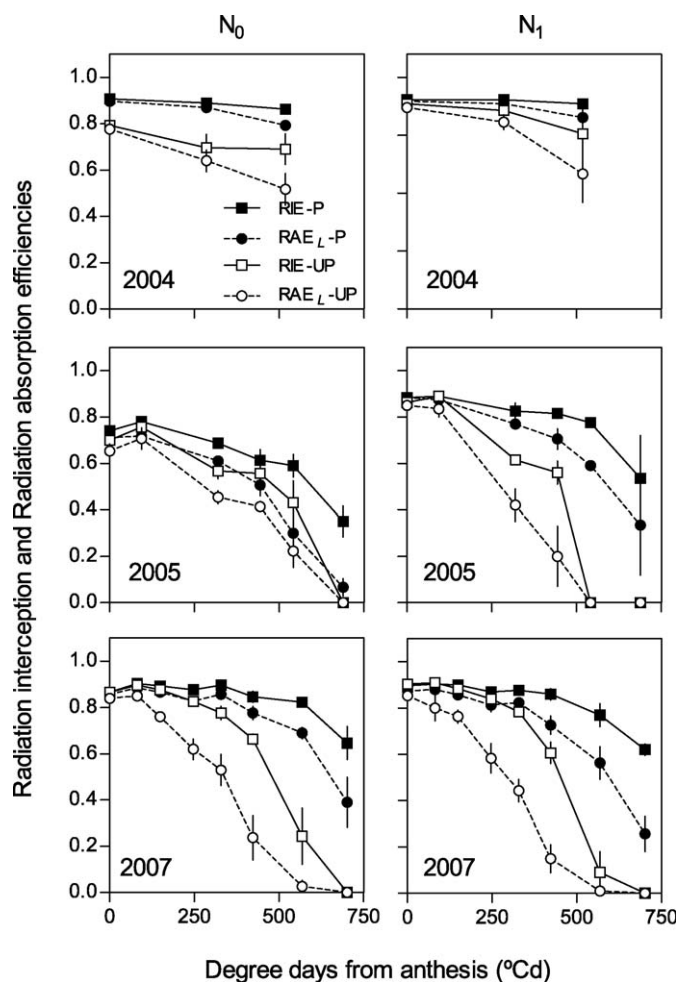


Fig. 4. Dynamics of the radiation interception efficiency (RIE, squares with continued lines) and radiation absorption efficiency calculated by leaf layer model (RAE_L , circles with dotted lines) during the grain filling period for P (solid symbols) and UP (open symbols) treatments and both nitrogen situations (N_0 and N_1), in three years (2004, 2005 and 2007). Vertical bars indicate standard error.

diseases and/or senescent area captured an important amount of incident radiation during the grain filling period reducing, as a consequence, the fraction of absorbed radiation by the crop (Fig. 4). Clearly, these reductions were higher in the UP than in the P treatment in most of the situations (N and years) during an important part of the grain filling period.

3.3. Green leaf area index, RIE and RAE per layer

In general, diseases firstly reduced the GLAI of the lower leaf layers of the canopy reducing after that the GLAI of the upper layers (Fig. 5). In the 2005 and 2007 experiments, the GLAI of the L2 and L3 leaf layers in the UP plots was reduced just after anthesis the reductions reaching ca. 100% at the middle of grain filling period, whereas the GLAI of the L1 (flag leaf) remained unchanged (respect to P treatment) during approximately the first half part of the grain filling period the reduction ranging from 20 to 80%, approximately, at the middle of the grain filling period. In the N_0 treatment during the 2005 experiment the GLAI of the flag leaf in the UP crop was not significantly different from that of the P crop. Finally, in the 2004 experiment, the GLAI of the L2 and L3 leaf layers was reduced by diseases before anthesis (30–45% of reduction at anthesis) but the GLAI of the flag leaf (L1) was not affected during the whole grain filling period remaining with similar GLAI values than those found

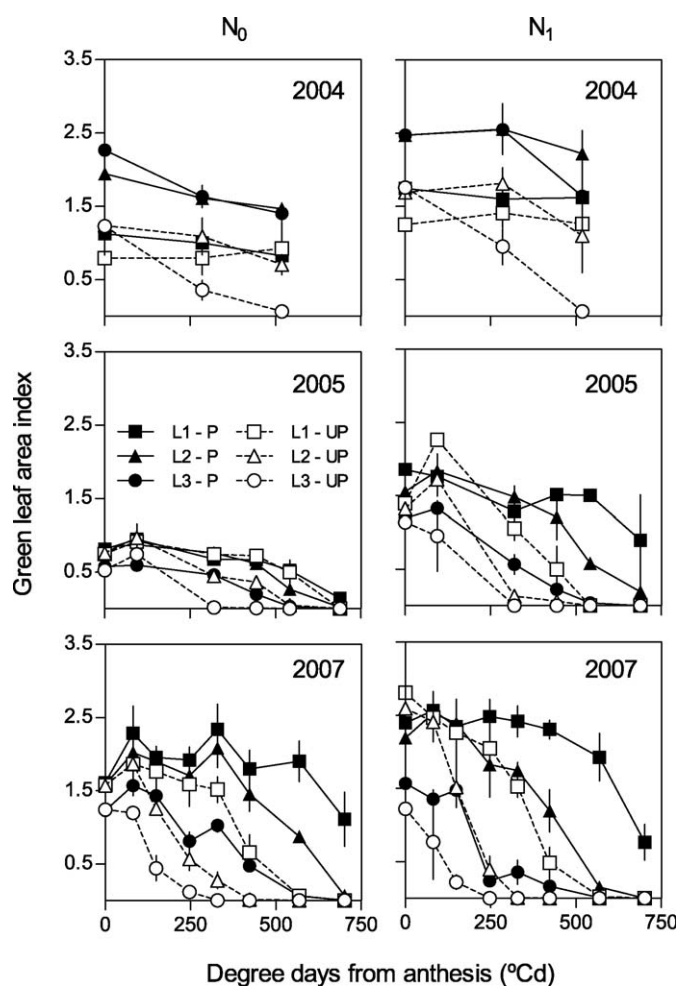


Fig. 5. Dynamics of the green leaf area index for different leaf layers during the grain filling period for P (solid symbols) and UP (open symbols) treatments and both nitrogen situations (N_0 and N_1), in three years (2004, 2005 and 2007). L1 (flag leaf), L2 and L3 are represented as squares, triangles and circles, respectively. Vertical bars indicate standard error.

in P plots (Fig. 5). Thus, it seems to be that GLAI of the flag leaf (L1) was reduced only in those situations where leaf rust was the predominant disease of the “diseases complex” (i.e. both nitrogen treatments in 2007 experiment and N_1 treatment during 2005 growing season).

Given its highest position in the canopy and sometimes its greater size, the flag leaf layer showed greater RAE_L values than those of the lower leaf layers. This difference was more evident in the 2007 experiment in both nitrogen treatments and in the N_1 treatment in the 2004 and 2005 experiments (Fig. 6). Maximum RAE_L of the flag leaf ranged from ca. 40% (2005 N_0) to 75% (2007

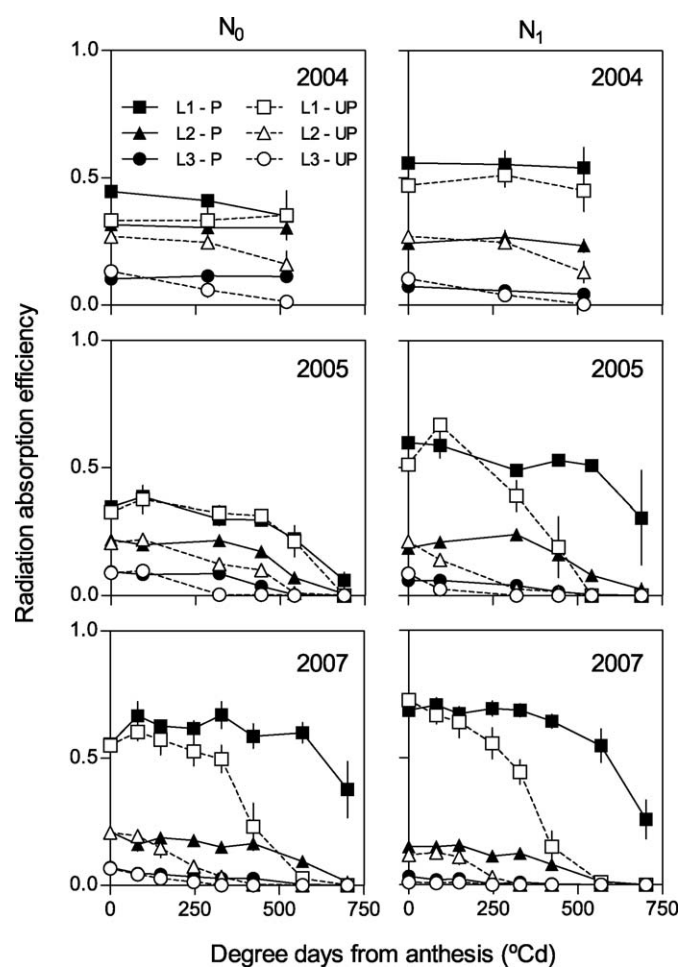


Fig. 6. Dynamics of the radiation absorption efficiency (RAE_L) for different leaf layers during the grain filling period for P (solid symbols) and UP (open symbols) treatments and the two nitrogen situations (N_0 and N_1), in three years (2004, 2005 and 2007). L1 (flag leaf), L2 and L3 are represented as squares, triangles and circles, respectively. Vertical bars indicate standard error.

N_1). Since the flag leaf layer absorbed proportionally most of the incident radiation with respect to the other leaf layers, the highest differences in RAE_L between P and UP treatments were observed in those treatments where diseases reduced GLAI of that flag leaf layer (i.e. 2007 in both nitrogen levels and 2005 N_1 treatment, the ones where leaf rust disease dominated the “foliar diseases complex”). In the N_0 treatment during the 2005 experiment, diseases reduced RAE_L in the L2 and L3 leaf layers, without any effect on the RAE_L of the flag leaf, while in the 2004 experiment, small differences were found between P and UP treatments for RAE_L values, without any clear trend among leaf layers (Fig. 6).

Table 1

Recalculations of radiation interception efficiency (RIE) for the crop (Total) and for L1 (flag leaf), L2 and L3 leaf layers and; calculation of total loss of absorbed radiation (LAR) assuming new hypothetical k values (25% up and down the real k value). Different diseases distribution were considered: (i) all the diseases located on the flag leaf (L1), (ii) all the diseases located on the third leaf layer from the top (L3) and; (iii) diseases uniformly distributed among the three upper leaf layers (Uniform). Percent of RIE of each leaf layer regards to total RIE are in brackets. A severity value of 12.8% (mean of the three upper leaf layers) was considered for the simulations.

LAI	k value	RIE				LAR (%)		
		L1	L2	L3	Total	L1	L3	Uniform
3.1	0.45	0.31 (46)	0.21 (32)	0.12 (18)	0.67	18.2	7.1	12.2
	0.60	0.39 (51)	0.23 (30)	0.11 (15)	0.76	20.3	5.8	12.3
	0.75	0.45 (56)	0.23 (29)	0.10 (12)	0.81	22.3	4.7	12.4
6.3	0.45	0.59 (69)	0.19 (22)	0.07 (8)	0.86	21.6	3.8	12.6
	0.60	0.68 (77)	0.16 (17)	0.04 (5)	0.89	24.1	2.4	12.7
	0.75	0.75 (83)	0.12 (14)	0.03 (3)	0.90	26.1	1.4	12.7

Table 2

Accumulated intercepted photosynthetically active radiation during the post anthesis period by: (i) green leaf area (absorbed radiation, $APAR_L$), (ii) non-green leaf area and; (iii) total leaf area (intercepted radiation, IPAR) for P and UP treatments under high (N_1) and low (N_0) nitrogen availabilities during 2004, 2005 and 2007 growing seasons. Statistical analysis of the main effects of nitrogen (N), fungicide (F) and their interaction ($N \times F$) are included.

Year	Treatment	Accumulated intercepted radiation ($MJ\ m^{-2}$)					
		Green leaf area		Non-green leaf area		Total leaf area	
		P	UP	P	UP	P	UP
2004	N_0	231.4	167.5	12.7	30.5	244.1	198.0
	N_1	237.5	195.0	11.2	30.1	248.7	225.2
	N		ns		ns		*
	F		***		***		**
	$N \times F$		ns		ns		ns
2005	N_0	177.5	147.5	54.6	38.0	232.2	185.5
	N_1	254.5	129.9	36.7	42.2	291.1	172.1
	N		*		ns		*
	F		***		ns		***
	$N \times F$		***		*		***
2007	N_0	273.5	142.9	28.1	77.2	301.6	220.1
	N_1	254.0	128.2	43.5	78.9	297.5	207.1
	N		*		ns		ns
	F		***		***		***
	$N \times F$		ns		ns		ns

Asterisks indicate the level of significance as: (*) $p < 0.1$, (**) $p < 0.05$ and (***) $p < 0.01$; ns: non-significant differences.

Although for the data set used in the present study, no significant differences were found in the k value due to nitrogen and/or diseases, this crop trait could be modified (for a different genotype for example) affecting RIE, RAE_L and loss of absorbed radiation (LAR). Thus, different k values combined with both low and high LAI levels and with three vertical patterns of diseases distribution into the canopy led to important changes in RIE (Table 1). The impact on RIE due to changes in k values from 0.45 to 0.75 was greater in a crop with low than with high LAI. Thus, for a crop with a LAI of 3.1 RIE increased from 0.67 to 0.81, respectively, while when the LAI was almost doubled (i.e. 6.1) RIE increased from 0.86 to 0.90, respectively (Table 1).

In relation to the contribution of each leaf layer for a k value of 0.6, in a canopy with LAI of 3.1 the RIE of L2 + L3 leaf layers represented 45% of total RIE, whereas when the LAI was 6.3 the RIE of L2 + L3 leaf layers represented only 22% of the total RIE (Table 1). On the other hand, when changing k values from 0.45 to 0.75 considering a LAI of 6.3 the relative contribution of L2 + L3 leaf layers to the total RIE was 30 and 17%, respectively. These results highlight the relevance of lower leaf layers in the radiation interception in crops with low LAI and/or low k values with respect to those with high LAI and/or high k values. For example, in crops with a LAI of 3.1 and k of 0.45 the light interception by L3 reached 18% of total RIE, whereas in crops with combinations of LAI of 6.3 and k of 0.75 the L3 leaf layer intercepted only 3% of total RIE (Table 1).

Considering a plant severity level of 12.8% (mean of the three upper leaves, see Materials and Methods) with all the symptoms concentrated in the L3 leaf layer, the difference in the interception levels described above (i.e. 18 and 3%) determined loss in absorbed radiation by the canopy of ca. 7% and only 1.4% for the former and the last situation, respectively. On the other hand, if a uniform vertical diseases distribution into the canopy was considered the reduction of radiation absorption was higher than when diseases were located in the lower leaf layers (L3) and lower than when diseases appeared in the upper leaf layers (L1) for all LAI and k combinations (Table 1).

3.4. Accumulated intercepted PAR (IPAR), accumulated absorbed PAR (APAR), biomass and RUE

Similarly to that observed in RIE and RAE_L , foliar diseases reduced both IPAR and $APAR_L$ during the post anthesis period

($p < 0.05$ in all experiments) (Table 2). In the 2005 experiment there was an interaction between nitrogen and fungicide treatments ($p < 0.01$), i.e. the reductions caused by diseases in IPAR and $APAR_L$ were greater in high than in low nitrogen treatment. As was explained above, in this experiment the composition of the “foliar diseases complex” was different depending on the nitrogen treatment. While in the N_1 treatment the predominant disease was the leaf rust, in the N_0 predominated necrotrophic pathogens, mainly tan spot (*D. tritici-repentis*) (Fig. 1).

There were important reductions in IPAR by diseases ranging from ca. 10 to 40% when the UP plots were compared to the P ones (Table 2), the reductions being higher in those situations where leaf rust was the predominant pathogen of the “foliar diseases complex”. However, non-green leaf area (diseased and senescent) intercepted part of the incident radiation, decreasing the amount of $APAR_L$ by the crop (Table 2 and Fig. 4), especially in the 2004 and

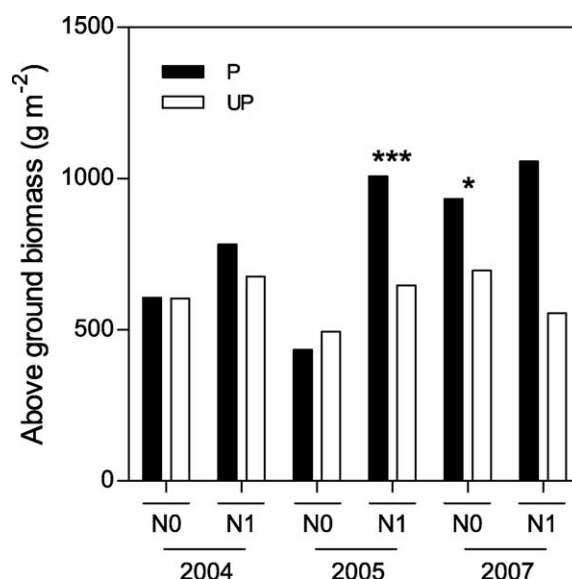


Fig. 7. Accumulated above ground biomass during post anthesis for P (solid bars) and UP (open bars) treatments under high (N_1) and low (N_0) nitrogen availabilities in the three years of experiments (2004, 2005 and 2007). Asterisks indicate the level of significance for the differences as: (*) $p < 0.1$, and (***) $p < 0.01$ between P and UP treatments.

Table 3

Post anthesis absorbed radiation use efficiency estimated by the leaf layer model (RUE_L) for P and UP treatments under low (N_0) and high (N_1) nitrogen availabilities in the three years of experiments. Statistical analysis of the main effects of nitrogen (N), fungicide (F) and their interactions ($N \times F$) are included.

Year	Treatment	RUE_L (g MJ ⁻¹)	
		P	UP
2004	N_0	2.96	4.19
	N_1	4.04	3.92
	N		**
	F		ns
	$N \times F$		ns
2005	N_0	2.95	3.17
	N_1	3.95	4.67
	N		**
	F		ns
	$N \times F$		ns
2007	N_0	2.66	3.50
	N_1	3.13	2.90
	N		ns
	F		ns
	$N \times F$		ns

Asterisks indicate the level of significance as: (*) $p < 0.1$, (**) $p < 0.05$ and (***) $p < 0.01$; ns: non-significant differences.

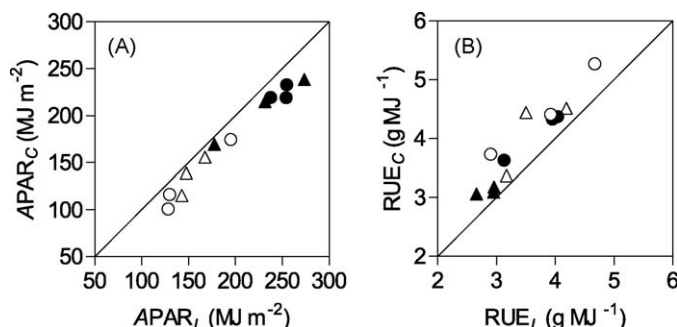


Fig. 8. (A) Accumulated absorbed photosynthetically active radiation calculated with the canopy model ($APAR_C$) against accumulated absorbed photosynthetically active radiation calculated with the leaf layer model ($APAR_L$) during post anthesis and; (B) radiation use efficiency calculated with the canopy model (RUE_C) against radiation use efficiency calculated with the leaf layer model (RUE_L) during post anthesis. Solid and open symbols indicate P and UP treatments, respectively. N_0 and N_1 are represented as triangles and circles, respectively. Data corresponding to the 2004, 2005 and 2007 experiments were included. Diagonal line indicates the 1:1 relationship.

2007 experiments ($p < 0.01$). The overall mean proportion of the IPAR that was intercepted by NGLAI (lesion coverage plus senescent tissue of non-dead leaves) was close to 24% in the UP treatment and was only 12% in the P treatment.

With the exception of the 2004 N_1 and 2005 N_0 the general trend was a reduction of the post anthesis above ground biomass production in the UP when compared to the P treatment. However, the differences were significant in statistical terms only in the N_1 ($p < 0.01$) and the N_0 treatment ($p < 0.1$) of 2005 and 2007, respectively (Fig. 7). The general trend was the higher the reduction of $APAR_L$ by diseases the higher the decrease of biomass (Table 2, Fig. 7). In fact, variations in above ground biomass accumulation during grain filling period were significantly correlated ($R^2 = 0.74$, $p < 0.05$) to variations in post anthesis $APAR_L$. Thus, the highest reductions in biomass due to diseases were observed in those cases where leaf rust was the main pathogen in the “foliar diseases complex”.

Averaging data from nitrogen treatments and years, RUE_L was found higher for the UP (3.72 ± 0.66 g MJ⁻¹) than for the P (3.28 ± 0.57 g MJ⁻¹) treatment. In four of the six situations RUE_L

was higher in the UP treatment, although the differences between the UP and the P treatment were not significant in statistical terms ($p > 0.1$) (Table 3). RUE_L ranged from 2.96 to 4.04 g MJ⁻¹ in the P treatment and from 2.90 to 4.67 g MJ⁻¹ in the UP treatment. As expected, significant difference in RUE was observed between nitrogen treatments in the 2004 and 2005 experiments ($p < 0.05$), the lower the nitrogen availability the lower the RUE_L .

The comparison between the leaf layer and the canopy approximations for APAR and RUE calculations showed evident differences (Fig. 8). APAR was underestimated when the canopy instead of the leaf layer model was used (Fig. 8a). The underestimation of $APAR_C$ compared to the $APAR_L$ ranged from ca. 5 to 14% and from ca. 6 to 21% in the P and UP treatments, respectively. Conversely and probably as a consequence of the underestimation of the APAR, RUE was overestimated when calculated from the $APAR_C$ (Fig. 8b). The overestimation of RUE_C when compared to RUE_L was higher in the UP (from 6 to 29%) than in the P (from 5 to 16%) treatment. In addition, and in the same way as shown in Tables 2 and 3, Fig. 8 shows that the main impact of diseases was through APAR reductions whereas there was not a clear trend for RUE variations between P and UP treatments.

4. Discussion

The environmental variations generated in the present study by different growing seasons (years), inoculum resources and nitrogen treatments produced canopies with important variations in LAI as well as a wide range of foliar diseases levels with different compositions of the “foliar diseases complex” (necrotrophic and leaf rust). Thus, the experimental frame used allowed us to evaluate how foliar diseases reduced biomass production through their effects in different ecophysiological variables in a wide range of crop and diseases situations.

As was previously shown by Serrago et al. (2009), in the present study foliar diseases mainly reduced radiation intercepted and absorbed by the crop through LAI and GLAI reductions, without significant effects on RUE. The highest reductions of IPAR and APAR were found in those experiments and treatments where leaf rust was the main disease affecting the crop (both N treatment in 2007 and N_1 treatment in 2005), the reductions in the capture of radiation being lower when necrotrophic pathogens (mainly tan spot) dominated the “foliar diseases complex” (both N treatments in 2004 and N_0 treatment in 2005). The higher reduction of APAR in plots mostly affected by leaf rust than in those mostly affected by necrotrophic pathogens (*D. tritici-repentis* mainly) was due to leaf rust caused higher GLAI reductions of the upper leaves (i.e. with the highest levels of interception) than the reductions caused by tan spot. Different evidences in the literature (Tiedemann, 1996; Robert et al., 2002) showed that leaf rust (biotrophic pathogen) was promoted under high leaf nitrogen content as was the case of N_1 treatment in 2005 in the present study and both nitrogen treatment during 2007 growing season. Conversely, when crop was grown under low nitrogen availability and thereby evidencing a low nitrogen concentration in foliar tissues, as was observed in N_0 treatment of 2005 experiment, necrotrophic pathogen (mainly tan spot) dominated the “foliar diseases complex”.

Considering that in most of the situations the maximum LAI reached by the crop was not different between P and UP treatments, reduction of LAI was probably due to increases in the totally senescent leaves (TSL). The results of the present study showed that, the impact of foliar diseases on RIE depends on the value of LAI reached at the moment of the diseases appearance (Cornish et al., 1990; Paveley et al., 2001), being the impact smaller or null in those situations where the diseases did not reduce LAI below the critical value (i.e. when crop intercept 95% of the maximum radiation possible to be intercepted). A similar

conclusion can be raised from a re-interpretation of different data from the literature (Madeira et al., 1994; Béasse et al., 2000; Jesus Junior et al., 2001). In addition, the curvilinear relationship between LAI and RIE (Hipps et al., 1983) implies that, for a same level of LAI reduction (below the critical value) due to diseases, the decrease in RIE will be proportionally greater in crops with low LAI values than in crops with high LAI values. In the same way, Bingham et al. (2009) stated that crops with large LAI levels might be expected to tolerate a greater green leaf area loss without important changes in light interception when compared with crops with small canopies. In fact, the reasoning behind Bingham et al. (2009) speculation is the buffer capacity of the LAI depending on the time that LAI can be maintained above the critical value (i.e. 95% of incident radiation intercepted).

However, diseases not only decreased LAI, but also reduced GLAI by lesion coverage thus increasing NGLAI in non-TSL. In fact, the difference between IPAR and APAR_L observed in the present work highlighted that diseased or senescent part of the still-leaving leaves (NGLAI) intercepted an important amount of solar radiation. The non-green leaf tissue of a given leaf layer intercepts part of the radiation that could otherwise be used by the lower leaf layers (Bastiaans and Kropff, 1993), thereby, leading to a net loss of radiation for the crop growth. Some works calculated RAE (and thus APAR), by replacing the LAI by GLAI in Eq. (1) (Madeira et al., 1994; Bryson et al., 1997; Kumudini et al., 2008). This kind of estimation does not take into account the radiation intercepted by non-green leaf area of the upper leaf layers (lost radiation): it considers that this radiation could be used by the green parts of the lower leaf layers, thus leading to an overestimation of the absorbed radiation. However, as argued in the literature (Madeira et al., 1994), when diseases cause directly defoliation more than leaf lesions coverage as it was shown in some leguminous species, this approach is quite acceptable.

Additionally to this lost radiation due to interception by NGLAI, diseases could directly reduce the photosynthesis rate of the remaining green tissue of diseased leaves. Bastiaans (1991) observed the development of virtual lesion (lesion in green parts of the leaves which can be considered visually healthy tissue) by *Pyricularia oryzae* in leaves of rice (*Oryza sativa*) but he did not observed virtual lesions in wheat leaves infected by *P. tritici*. Other evidences showed that photosynthesis of green (apparently healthy) area from wheat leaves infected by *P. tritici* (biotrophic pathogen) was not reduced (Robert et al., 2005) or slight reduced (Robert et al., 2004) while a slight reduction was observed for leaves infected with *S. tritici* (hemi-necrotrophic pathogen) (Robert et al., 2004, 2006). Reduction in photosynthetic capacity of green leaf area of diseased leaves might cause RUE reduction at crop level, however, in the present study no significant differences were observed for this crop attribute when P and UP treatments were compared within each nitrogen treatment and year, suggesting that photosynthesis capacity of the visually healthy area was not affected by diseases. Similar results were observed by Bancal et al. (2007) for leaf rust and *S. tritici* blotch in complex at the crop level.

The vertical position of the diseases into the canopy should also be considered for the calculation of APAR since the contribution of the different leaf layers to radiation interception strongly decreases from the top to the bottom positions into the canopy. In agreement with that observed by Robert et al. (2004) and Bancal et al. (2007), in the present study foliar diseases initially reduced the GLAI of the lower leaf layers then progressing to the upper leaves. Thus, as the highest portion of intercepted radiation is concentrated in the upper leaf layers, the absorbed radiation was not significantly reduced until diseases reached these layers. In this way, Rabbinge et al. (1985) working with simulated data for a wheat crop infected by mildew (*Erysiphe graminis*) showed that reductions in daily gross assimilation were greater in canopies

where a same severity of mildew was either uniformly distributed or concentrated in the upper leaf layers, than when it was located in the lower leaf layers. Similar results were found by Bastiaans and Kropff (1993) working in rice (*O. sativa*) infected with leaf blast (*P. oryzae*).

Regarding the vertical position of diseases, the consequences on radiation absorption when they are present in the lower leaf layers depends on the LAI level and canopy architecture (k value). In this sense, Bingham et al. (2009) also speculated that, when diseases are located in the lower layers of the canopy, negligible impact on light interception would be expected in crops either with large LAI or with planophile leaves (high k value). The simulation results of this study showed that the reductions in RAE when diseases appear in the lowest leaf layers would be greater in crops with low k values (allowing higher levels of light to reach lower leaf layers) than in crops with high k values where most of the radiation is absorbed by the upper leaf layers. Similarly to the simulation of Rabbinge et al. (1985) in wheat affected by mildew, the results of the present study showed that when diseases appear in the lowest leaf layers larger reductions of absorbed radiation would occur in crops with low LAI than in crops with high LAI. Therefore, it can be summarized that the lower the k or LAI values the higher the reduction of light absorption is expected when diseases appear in the lower leaf layers. Conversely, the higher the k or the LAI values, the higher the reduction of light absorption when diseases are located in the upper leaves. In this sense, when necrotrophic splash dispersed pathogens (*D. tritici-repentis* mainly) appeared, they reduced mainly GLAI of the lowest leaf layers of the canopy with slighter effect on the flag leaf layer, whereas, as was stated above, leaf rust (a wind spread pathogen) caused important GLAI reductions of the upper leaf layers. The potential advantages of high k values in wheat tolerance cultivars to leaf diseases appearing in the lower leaf layers, as previously hypothesized by Bingham et al. (2009), was supported by the simulation approach made in the present study. However, the hypothesis should be validated using selected wheat cultivars differing for their k value combined with leaf diseases localized at the top or at the bottom part of the canopy.

The consequence of ignoring the vertical diseases distribution into the canopy may conduce to an underestimation of APAR (up to 21%) and consequently to an overestimation of RUE (up to 29%), especially in crops where foliar diseases appeared predominantly in the lower leaf layers. The values of RUE_L found in the present work were similar or slightly higher than those reported for many unstressed crops in the literature (Johnson, 1987; Sinclair and Horie, 1989; Bastiaans and Kropff, 1993; Bancal et al., 2007), confirming that not accounting for the vertical diseases distribution into the canopy may lead to an overestimation of RUE (or underestimation of APAR).

Although significant differences in RUE_L were not found between P and UP treatments, the RUE_L values of the UP treatment were consistently higher than the values of RUE_L of the P treatments. Wang et al. (2001) observed in wheat plants that when shadowing the peduncle plus leaf sheath or the spike during the grain filling period the grain mass of each ear was reduced around 35%. Robert et al. (2004) working with simulated data in wheat crops infected by foliar diseases suggested that, when stem photosynthesis was not considered, plant growth was underestimated by around 14%. Considering that in the present study radiation interception by the stem was not taken into account in the APAR calculations and that it may become an important component of total absorption when GLAI highly decreases, an underestimation of APAR could have occurred leading to an overestimation of RUE. The earlier GLAI decline in the UP than in the P treatment during the grain filling period could determine a more important role of the stem and/or spike in relative terms of

radiation absorption in the UP treatment, resulting in a greater overestimation of RUE in this treatment as it is observed in this study.

In addition, it has been demonstrated that net assimilation rate per unit leaf area decrease with the age of the leaf associated with a diminishing foliar nitrogen concentration (Evans, 1983; Connor et al., 1993). Sinclair and Horie (1989) showed that changes in foliar nitrogen content were linked to changes in canopy RUE through foliar nitrogen effect on leaf photosynthesis. In the present study, leaves of the UP plots died earlier, and thereby younger, than those of P plots. Therefore, plants of P treatment grew during a longer time than plants of UP treatment but with aging leaves showing up a decrease in their photosynthesis rate determining lower RUE_L values in P than in the UP crops. When only the period of time during which leaves in the UP plots were alive (i.e. some portion of leaves remaining green in the UP treatment) was considered for the calculation of RUE_L (using data from 2005 and 2007 experiments), the values obtained in P and UP treatments were very similar (i.e. $3.36 \pm 0.81 \text{ g MJ}^{-1}$ and $3.27 \pm 1.00 \text{ g MJ}^{-1}$, respectively), supporting the speculation that the age of the leaves plays an important role in the calculation of RUE_L when P and UP treatments are compared.

5. Conclusion

This study clearly shows that foliar diseases in wheat mainly reduced radiation capture with no clear effect on RUE. Diseases reduced IPAR due to reductions in LAI (increase of TSL-dead leaves), with slight reductions in APAR due to increases in the NGLAI of leaves still alive. The higher reductions of radiation capture were observed in the experiments and treatments where leaf rust (wind spread) appeared as the main disease, as it caused higher GLAI reductions of the upper leaf layer than the necrotrophic pathogens (splash dispersed) which mainly affected the lower leaves into the canopy. The impact of diseases on the RIE was dependant in the LAI level, being important only when LAI dropped below its critical value. As the upper leaf layer intercepts the highest proportion of incident radiation, the assumption of a uniform distribution of diseases into the canopy may conduce to an overestimation of light absorption reduction due to diseases whenever they remain in the lower leaf layers of the canopy. Additionally, the proportional contribution of the lower leaf layer to the total interception may vary according to the LAI levels and/or canopy architecture (*k* value).

One of the ecophysiological traits proposed to improve RUE at canopy level was to modify leaf architecture promoting more erect leaves (low *k* values) trying to get a better light distribution profile into the canopy, reducing the light-saturated wasteful leaves on the upper positions and increasing light availability for non-saturated lower leaves (Reynolds et al., 2009). Although selecting plants with that ideotype is feasible by breeding, as was early proposed by Donald (1968), genetic diseases resistance in those plants is critical since usually diseases affected leaf layer at the bottom of the canopy and an important part of incident radiation is capture by these leaves in open canopies (i.e. low *k*) as it was shown in the present study.

In terms of crop management, farmers usually consider the severity and/or incidence indices as the main decision tool at the time of applying agrochemicals for controlling foliar diseases. However, the data of the present study demonstrated that other aspects, together with these pathological indices, should be taken into account at the time to decide controlling diseases: (i) LAI level, mainly in those crop situations where during the critical period (in which yield definition is occurring) the LAI reached is close to or below the critical value to intercept 95% of the maximum incident radiation possible to be intercepted (in the field a visual

determination of canopy covered could be used to estimate the distance from the critical LAI) and; (ii) canopy architecture associated with light distribution into the canopy together with (iii) vertical diseases distribution into the crop. Regarding the second and third point, special attention should be paid to open canopies or to cultivars with low *k* values when diseases appeared in the lower leaf layers, as an important proportion of total intercepted radiation is captured by these layers under such situations. Some airborne diseases, as leaf rust, may infect the crop once all the leaves are expanded affecting mainly the upper leaf layers. In these cases, close canopies (high LAI and/or *k* value) that reduce light penetration into the canopy could be prone to losses more than open canopies where lower leaf layers contribute more to RAE.

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