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Reduction of fungal disease spread in cultivar mixtures: Impact of canopy architecture on rain-splash dispersal and on crop microclimate

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ABSTRACT

Mixtures of cultivars with different disease resistance levels make it possible to manage plant disease in a context of fungicide reduction. The cultivars composing a mixture are often chosen for their contrasted disease resistance levels, whereas their architecture is rarely taken into account. However, canopy architecture has an impact on spore dispersal and microclimate, both of which contribute to disease development. Disease spread by rain-splash occurs over short distances and is expected to be modulated by canopy structure. Our objective was to assess the impact of wheat cultivar mixtures that differ by their canopy architecture on crop microclimate, spore dispersal and the propagation of splash-dispersed disease, septoria tritici blotch, caused by Zymoseptoria tritici. Each cultivar mixture was composed of a susceptible and a resistant cultivar. A single, short susceptible cultivar was used. The resistant companion was either short (homogeneous) or tall (heterogeneous). Two proportions of resistant cultivar were tested in homogenous mixture. Mixtures were compared to pure stands of component cultivars. The level of resistance of each cultivar was assessed through disease measurements in pure stand. A diversity of canopy architecture was obtained at the flowering stage: the leaf area index ranged from 2.2 to 4.4 m^2/m^2 and flag leaf insertion height from 0.65 m (standard height) to 1.20 m (tall plants). Spore fluxes were measured during two rain events and microclimate variables including air temperature, relative humidity and leaf wetness duration were recorded from the booting stage onwards. Disease assessments were carried out weekly in mixtures and pure stands. Disease on susceptible plants was significantly lower in heterogeneous mixtures than in pure stands. In homogeneous mixtures, a high proportion of resistant plants was associated with high canopy density, which led to a microclimate favorable to disease development. Leaf wetness duration was in fact longer in the pure stand constituted of standard height resistant plants, which had the densest canopy. In the two homogeneous mixtures that differed by the proportion of resistant plants, disease reduction was similar. On the other hand, heterogeneous mixtures had a lower canopy density and lower spore fluxes than homogeneous mixtures. Compared to the susceptible pure stand, the area under the disease progress curve of susceptible plants was reduced by 68% in the heterogeneous mixture and by 32% and 34% in the homogeneous mixtures with 75% and 25% of resistant plants, respectively. Our results suggest that the impact of canopy architecture on microclimate and spore dispersal can significantly contribute to the reduction of disease propagation in cultivar mixtures. We therefore suggest that taking cultivar architecture into account, in addition to the level of resistance to disease, could provide a strategy to enhance disease reduction in cultivar mixtures in the case of splash-dispersed diseases.

1. Introduction

Cultivar mixtures allow a reduction in disease progression, which is of real interest in a context of fungicide reduction (Finckh and Wolfe, 2006). The cultivars composing a mixture are often chosen for their contrasted disease resistance levels. Disease reduction in cultivar mixtures is related to physical spore dispersal mechanisms linked to spatial distribution of contrasted plant resistance levels. In a mixture, the mean distance between susceptible plants is greater than in a pure stand, and spore transfer from one susceptible plant to another is therefore lower (density effect). On the other hand, spores are intercepted by resistant plants that are either not at all or little affected by

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disease, and that therefore do not reach susceptible plants (barrier effect). The efficiency of cultivar mixtures has generally been reported for wind-dispersed diseases (de Vallavieille-Pope, 2004), which are characterized by long dispersal distances, thus favoring interactions between cultivars (Garrett and Mundt, 1999). The mixture of plants with contrasted resistance levels is expected to be less efficient in the case of splash-dispersed diseases since shorter dispersal distances lead to more auto-contamination. However, splash dispersal (Saint-Jean et al., 2004; Huber et al., 2006) is also expected to be particularly affected by canopy architecture (Schoeny et al., 2008).

Canopy architecture has significant impacts on both spore dispersal and crop microclimate (Boudreau, 2013), which can affect plant disease (Calonnec et al., 2013; Tivoli et al., 2012; Le May et al., 2009). For example, spore transfer by rain-splash occurs over shorter distances in dense canopies since spores have a high probability of being intercepted close to the site of spore emission (Schoeny et al., 2008; Yang and Madden, 1993). On the other hand, dense canopies also retain humidity, which can lead to favorable conditions for pathogen infection and disease development (Ando et al., 2007; Richard et al., 2013; Deshpande et al., 1995). Plant height and distance between leaves contribute to determining canopy density and have been identified as important plant characteristics (Sim & n et al., 2005; Tavella, 1978) in relation to septoria tritici blotch (STB) caused by *Zymoseptoria tritici* (Orton et al., 2011). In the case of diseases spread by rain-splash over short distances, the range of distances between the leaf source of inoculum and the surrounding leaf targets determines the set of short trajectories that spore-carrying splash-droplets have to travel.

Plant architectural traits (Godin, 2000) such as plant height, leaf dimensions or leaf curvature can vary strongly between cultivars of the same species. Canopy architecture results from plant architectural characteristics and agronomical practices. Canopy architecture can be more or less heterogeneous depending on the contrast between the plants that make up the canopy. Standard recommendations for the design of cultivar mixtures in mechanized agricultural systems (Wolfe, 1985) include avoiding differences between cultivars in terms of straw height and precocity in cultivar mixtures in order obtain homogeneous canopy structure and to limit competition and simplify harvest. However, mixing cultivars of cereal species with a marked difference in plant height has led to positive effects on yield (Fang et al., 2014; Essah and Stoskopf, 2002), grain quality (Jackson and Wennig, 1997), lodging (Revilla-Molina et al., 2009), water use efficiency (Fang et al., 2014) and weed suppression (Kiær et al., 2012). This type of mixture has also led to a reduction of airborne diseases (Li et al., 2012; Zhu et al., 2005; Jackson and Wennig, 1997). For example, mixtures of a tall traditional susceptible glutinous rice cultivar with a shorter modern resistant cultivar have led to a good control of panicle blast disease caused by *Pyricularia grisea* (wind-dispersed) through reduction the of canopy moisture (Zhu et al., 2005). Furthermore, a reduction of septoria tritici blotch has been observed in mixtures of wheat cultivars with plant height differences (Jackson and Wennig, 1997).

Choosing cultivars not only according to their resistance level to disease but also to their architecture could be a way to amplify disease reduction in cultivar mixtures. Our objective was to quantify the impact of wheat cultivar mixtures characterized by diverse canopy architecture on spore dispersal, canopy microclimate and splash-dispersed disease, septoria tritici blotch.

2. Material and methods

We designed a field experiment to investigate the effects of canopy architecture of wheat cultivar mixtures on microclimate, spore dispersal and STB disease propagation. Treatments included three cultivar mixtures with similar or contrasted straw height, sown in different proportions, and the three pure stands of the corresponding cultivar mixture components. Plant and canopy architecture were characterized at the flowering stage. At this stage, the architecture of wheat is relatively stabilized. All organs have appeared and reached their final size. This is also a critical stage of the epidemic when it gains in importance and when the differences between cultivar mixtures and pure stands are most visible. Spore fluxes were measured during two rain events and several microclimatic variables were recorded in well-developed canopies. Disease assessments were carried out weekly in order to quantify and compare disease progression in mixtures and pure stands.

2.1. Experimental design

The experiment was carried out at INRA-Grignon Research Station (48°′ N, 1° 56′ E), 40 km west of Paris, France. Winter bread wheat cultivars were grown in pure stands and in binary mixtures within 3.5 m wide × 10 m length plots with 0.175 m inter-rows. Plots were divided into two equal parts: one was used for destructive plant sampling, the other for non-destructive measurements (spore dispersal, microclimate and disease assessment). Plots were separated by 1.75 m wide triticale strips of the cultivar Tribeca (a tall plant, resistant to STB), in order to avoid disease spread between neighboring plots. A randomized block design was used with three replicates per treatment. Crops were sown on October 24, 2014, at a density of 220 seeds m^{-2}, which was comparable to common practices in the region. Nitrogen fertilization was adjusted according to the balance-sheet method (Rémy and Hébert, 1977) with a target yield of 7 t/ha. A single nitrogen application took place at the beginning of stem elongation, around the growth stage (GS) 30 (Zadoks et al., 1974). A single herbicide treatment was applied in the early spring. No fungicide treatment was applied.

Three cultivars were used in the experiment, including two cultivars with standard height (called hereafter “short”), with an average ear height of 0.81 m (Maxwell and Sogood) and a tall cultivar with an average ear height of 1.44 m (Barbu de Champagne). Maxwell (ShoR – Short Resistant) is among the most commercially-available STB-resistant wheat cultivars, with a resistance score of 7 (on a scale from 1 – most susceptible – to 9 – most resistant). Sogood (ShoS – Short Susceptible) is fairly susceptible (score 4). Barbu de Champagne (TallR – Tall Resistant) is a French landrace, characterized as being resistant to STB in local field trials. Resistance genes have not been investigated in this study, and should be quite different since one cultivar is a modern and the other is a landrace. Here, resistance level of cultivars to STB was assessed through disease measurements in pure stands performed the previous year. Both resistant cultivars had similar resistance levels to STB in field. In the present experiment, the area under the disease severity progress curve (AUDPC in % · °Cd) of the three top leaves of the cultivars in pure stands was 685, 877 and 5616 for Maxwell, Barbu de Champagne and Sogood, respectively.

All mixtures consisted of a susceptible (S) and a partially resistant (hereafter called “resistant”, R) cultivar. Straw heights of cultivars composing a mixture were either similar (hereafter referred to as homogeneous mixtures, HOM) or contrasted (heterogeneous mixtures, HET). Mixtures were sown in equi-proportion (1S:1R), except for the homogeneous short mixture that had either 25% (HOM-1S:3R) or 50% (HOM-1S:1R) of susceptible cultivar seeds. All the cultivars composing the mixture were sown in pure stands (PUR), allowing comparisons with the mixture.

2.2. Plant and canopy architecture

Plant and canopy architecture was characterized in mixtures and pure stands. The height of the highest ligulated leaf was recorded at six dates, from the beginning of stem elongation (GS 30) to flowering (GS 65). Plant architectural traits were characterized at flowering. Eight main stems with ears were randomly sampled in each plot, including four axes of each cultivar in the case of cultivar mixtures. The insertion height of leaves was measured. Leaf curvature was measured using a 3D digitizer (3SF002, 3space® fasttrack™Polhemus, USA). Leaf blades were