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Analysing light competition in cereal/legume intercropping systems through Functional Structural Plant Models

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Introduction

Nowadays, agriculture in industrialized countries is characterized by high-inputs, monospecific and morphologically uniform crops. As efforts to achieve sustainable agriculture have to be made, alternative cropping systems have been explored. Mixing two or more crops, referred to as intercropping (Willey, 1979), is regaining interest, at least at the research level, as it enables reductions in the use of fertilizers and pesticides while providing satisfactory yields. In recent decades, research works have mainly focused on improvement of the productivity of intercropping. The efficiency, in terms of inputs and yields, of an intercrop system results from a trade-off between complementarity and competition of the component crops. Cereal-legume intercrops, consisting of a competitive and dominant cereal species (maize, sorghum or wheat) and an associated legume species (bean, cowpea or pea), can be particularly efficient systems (Ofori and Stern, 1987; Tsubo and Walker, 2004). Light capture and sharing between the involved species appear to be key parameters of the intercrop functioning including biomass production and allocation as well as symbiotic nitrogen fixation. Studying light competition between the two component crops requires the use of models which are generally divided in four categories: i) geometrical models; ii) models using the turbid medium analogy; iii) hybrid models which combine the first two ones, and iv) models based on explicit 3D plant description (Sinoquet and Caldwell, 1995). Nowadays, most of light models dealing with intercropping systems are based on the turbid medium analogy that assumes a homogeneous and continuous medium. This allows modelling light extinction through the canopy following Beer-Lambert's law. The assumption of a homogeneous medium, where leaves are small and randomly distributed, could be strongly questioned in the case of cereal-legume intercrops. FSPMs therefore appeared to be a convenient tool for the study of competition for light and its sharing in intercrops as they explicitly take into account the architecture of plants (structure) thus allowing to accurately compute light interception and the subsequent effects on plant functioning.

Our general aim is to analyze light competition in cereal-legume intercrops in order to better characterize the functioning of such systems. In the present study our objective was to build up a simulator able to calculate light sharing between the two component species during the growing cycle and according to different densities and row arrangements. We combined experimental and modelling approaches. 3D reconstructed plants of wheat intercropped with pea were then coupled to a radiation interception model in the Openalea platform.

Material and methods

Experimental design

Experiments were conducted in a greenhouse where intercropped wheat (*Triticum aestivum* L, cv. Apache) and pea (*Pisum sativum* L, cv. Lucy, aphylla type) were grown in 80 cm x 60 cm x 30 cm containers in order to simulate small stands. Plants were sown at three relative densities *i.e.* the percentage of each component crop varied so that each treatment had the same absolute density. The first three treatments consisted of four alternative rows of wheat and pea sown at different proportions of their optimal density: i) 50% wheat and 50% pea (W50-P50 Alternate Row), ii) W30-P70 and iii) W70-P30. The fourth treatment also consisted of 50% wheat and 50% pea but, in contrast with treatment i), plants were mixed within each row (W50-P50 Mixed Row).

Simulation of radiation interception by wheat-pea intercrops

Wheat and pea plants from each treatment were digitized with a 3D digitizer (Polhemus, 2009) in order to track spatial coordinates and orientation of both wheat and pea phytomeres. Three digitizations were carried out during the growing period at 300 Degree Days, 685DD and 1100 DD. Data from digitizing were then imported into the Openalea platform (Pradal *et al.*, 2008) where plants of each species were reconstructed using the “VPlants” library. Leaf length of wheat was computed by recording points along the midrib of untouched lamina, thus keeping their natural bearing. Leaf width and leaf surface were then estimated as in the model ADEL-wheat (Fournier *et al.*, 2003). Stipules surface (St_{surf}) of digitized pea plants was calculated by using an allometric relationship with the maximum length (L_{max}) of stipules, such that: $St_{surf} = \beta * L_{max}^2$, where β is equal to 0.39. This relationship ($r^2 = 0.984$) was established from a destructive sampling of 18 plants. The surface of 434 stipules was measured using a planimeter (LI-3100, LI-COR, Lincoln, NE, USA), while maximum length (L_{max}) was measured with a ruler.

Virtual intercrop stands were then reconstructed by merging both wheat and pea scenes. Intercrop mock-ups were coupled with the nested radiosity model Caribu (Chelle and Andrieu, 1998) thus allowing to compute light interception of each species at the phytomere level.

Preliminary results and discussion

Figure 1 illustrates an output of wheat and pea mock-ups reconstructed from the digitized plants.

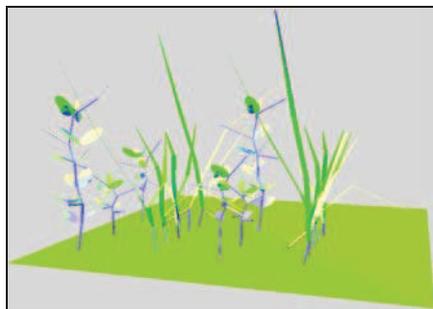


Figure 1. Snapshot of a reconstructed intercropping system of wheat and pea coupled with the radiosity model Caribu in the Openalea platform

Canopy structure parameters of wheat have been widely described in several studies (*e.g.* Fournier *et al.*, 2003). In contrast, the geometrical features of pea plants are poorly documented. The distribution of pea stipules inclination (ranging from 0 to 90°C) is shown in Figure 2. No significant differences of stipule inclination were found in response to the different treatment for any of the three sampling dates. The inclination pattern appeared highly variable between sowing treatments at 300 DD. At this time, regardless of the treatment, 80% of the stipules were within the range 30° to 60°. Afterwards, at 685 and 1100 DD, as the number of stipules per plants increases, the distributions of frequencies became more homogeneous between treatments and between dates, at least in the range 0°-60°. Similar conclusions can be drawn from stipules azimuth distribution (Figure 3) as stipules orientation tends to be more uniform at 685 and 1100 DD.

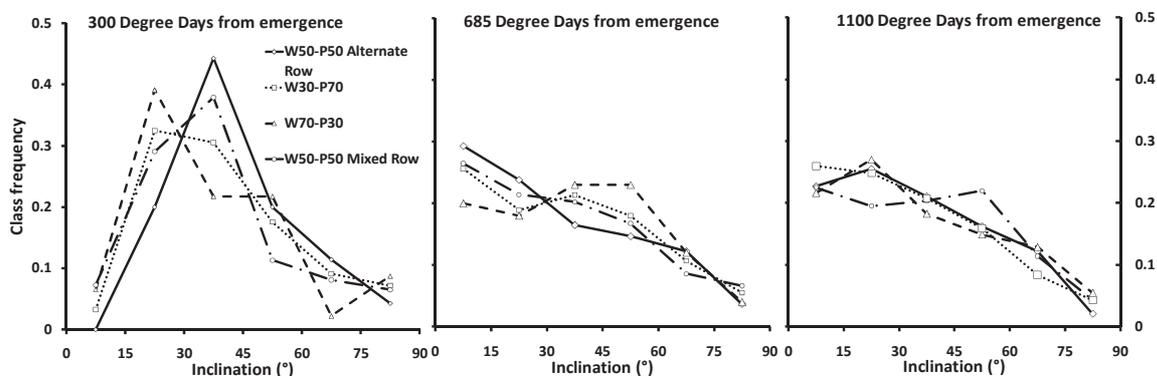


Figure 2: Class frequency of the inclination of pea stipules at three different stages (300 Degree-Days; 685 DD and 1100 DD) according to the different sowing densities and arrangements.

Modifications of geometrical properties such as those described above are ignored when the turbid medium approach is embedded in crop models. This can lead to differences in the computation of light sharing between component species compared to the outputs of our simulator. Indeed, measurement of light transmission reveals different kinetics according to the growing period (Figure 4). Moreover, at 500 DD, the fraction of light transmitted to the soil could be linked to the density of pea as the transmitted light in the W30-P70 treatment was only half of that in the W70-P30 treatment.

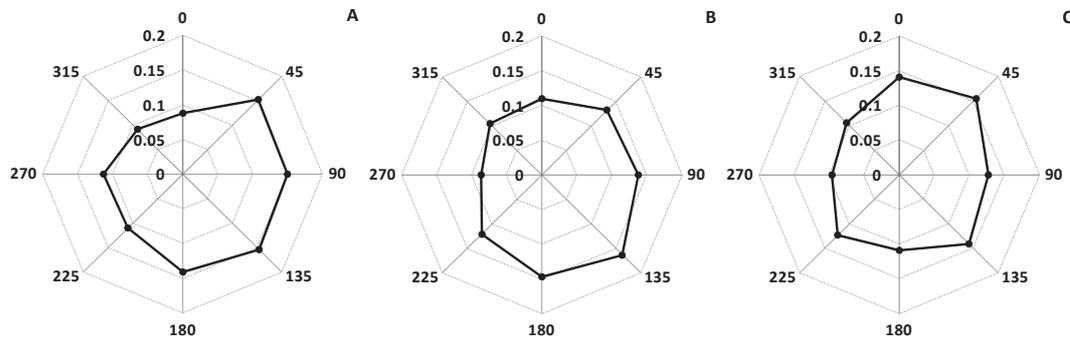


Figure 3: Class frequency of the azimuth (°) of pea stipules at three different stages (A: 300 Degree-Days; B: 685 DD and C: 1100 DD). Data represent the mean azimuth of pea stipules for the four treatments.

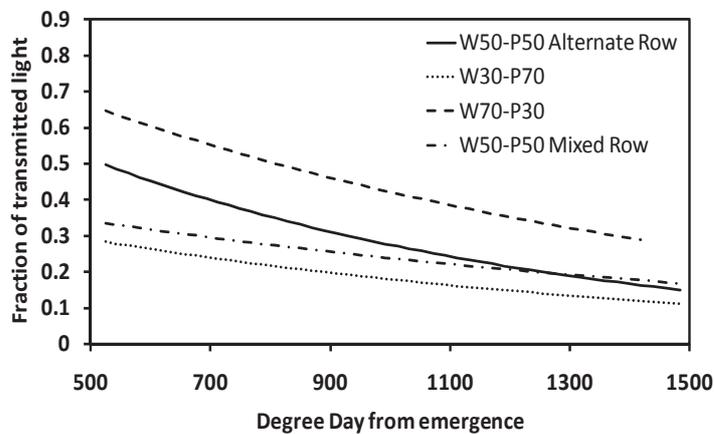


Figure 4. Fraction of transmitted light, at soil level, during the growing period and according to different sowing densities and arrangements. Each curves were obtained by fitting the exponential decay function: $y = y_0 * \exp^{-k * DD}$

To our knowledge, this study is the first attempt to use FSPMs framework to provide new insights into competition for light in cereal/legume intercrops. FSPM concepts enable us to analyze how light interception affects the functioning of the intercrops (*e.g.* biomass accumulation or nitrogen acquisition) and the subsequent effects on plant structures (photosynthetic area, leaf inclination...). The simulator could also be used to analyze the spectral photon distribution within the mixed canopy that differentially impact wheat and pea morphogenesis. Beyond that, it could be also used to test new ideotypes, exhibiting contrasted architectures, in order to minimize interspecies competitions for light while maximizing the benefits of intercropping systems.