Modelling intercropping highlights importance of resource competition and possibly direct plasticity effects

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Abstract
Modelling of intercropping systems involves competition for resources and plasticity effects. We reviewed models that fall in these two categories and highlighted their limitations. Light capture mechanism is the predominant process modelled across all models however, competition for water and/or nutrient and interactions are only captured in some. Limitations of these models are related to the canopy architecture, the method used for resource sharing and priority assignment of the shared resources, lack of interactions and feedbacks between plants, plant organs and local environment, and also the monoculture framework used to build intercropping models. Plasticity effects in intercrops have been quantified in very few studies focusing mainly on crop response to light. Frameworks such as the 3D functional–structural plant (FSP) models have been proposed as useful tools that can unravel and simulate interactions and feedbacks between intercrops and local environmental factors. These tools can model both resource use and plasticity and should help untangle interactions and feedbacks between resources and the intercrop components from the plant organ to crop level. The tools need testing in field experiments to establish the utility of intercrops in modern agriculture beyond the experimental sites.

Keywords
Functional-structural plant models

Introduction
Crop models are useful tools in advancing the understanding of intercropping systems in new and varied environments, and for better decision making. Most models are built on monocrop systems and lack the framework to adopt intercrop systems (Chimonyo et al. 2016). The main mechanisms in intercropping are i) use of resources which involves direct competition, facilitation, complementarity and resource use efficiency (Pinto et al. 2019, Fletcher et al. 2016) and ii) plasticity which is plant adaption and response in the presence of another plant and also due to interactions between plant organs and resources (Evers et al. 2019). A key challenge for researchers is understanding and incorporating these complex mechanisms in crop models. In this paper we reviewed the literature to examine how contemporary crop models simulate intercropping and their limitations to advance intercropping science.

Methods
We used existing review papers and other modelling study papers to identify crop models that can simulate intercropping systems and then categorized them according to their component configurations, mechanisms of resource share/utilization and reported their performance in predicting the yield and resource use efficiency. The models reviewed are APSIM (Asseng et al. 1997), DSSAT (Jones et al. 2003), FASSET (Jacobsen et al. 1998), FSP (Yu, 2016), STICS (Brisson et al. 2004), SWAP (Kroes et al. 2017) and WaNuLCAS (Van Noordwijk and Lusiana 1998).

Results
The mechanisms of intercrop growth and development in these models can be categorized with respect to a) resource use and b) interactions between above and belowground resources and intercrops. Key variables used to define canopy structure in models and to determine resource sharing and interactions are summarized in Table1.

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Table 1. Key variables (bulleted) used to define canopy structure, resource (light, water and nutrients) use and above- and belowground interactions in crop models

	Canopy structure	Light capture	Water and Nutrients	Interactions (above- and belowground)
APSIM	• Crop height (Canopy layers are defined by intercrop heights)	• Crop height • LAI (green and dead) • Extinction coefficient	• Resource amount (Uptake of resource by intercrop occurs on alternating days)	
DSSAT	• Crop height • Shading capacity	• Crop height • Shading capacity • Micro-climate variables (A shading algorithm is used with modified micro-climate variables, crop height and shading capacity)		
FASSET	• Canopy height • Canopy area (Canopy is divided into several equal layers)	• Green leaf area • Canopy height • Extinction coefficient	• Resource amount • Potential uptake (Algorithm on resource competition is based on when all/none/some intercrops can fulfil their demands)	
STICS	• Dominant canopy • Understorey (shaded and sunlit) canopy	• LAI (dominant canopy) • Understorey canopy (using Beer's law) (The shaded and sunlit parts influence crop growth processes and resource budgets. Shoot growth is impacted by the understorey shaded crop growing under limiting radiation)	<u>Water</u> • LAI • Light partitioning (Water requirements for intercrops rely on light partitioning and surface resistance of the canopy based on LAI. <u>Nutrients</u> • Resource demand • Root depth and distribution (Nitrogen uptake depends on demand, root distribution and depth penetration)	• LAI • Canopy surface resistance (Water requirements are linked to light partitioning • Soil permeability • Soil water content (These two variables influence interactions between root systems of intercrops)
(SWAP 2x1D)	• Canopy height (Two canopy layers limited by intercrop heights	• LAI • Homogeneous (H) and compressed (C) canopies (A weighted average of radiation between H and C is used)	<u>Water</u> • Soil hydraulic conductivity • Crop belowground coverage	• Crop belowground coverage (Crop belowground coverage (relative root dominance) influences soil water exchange)
WaNuLCAS	• Crop height (Canopy layers are equal to number of intercrops	• LAI • Relative crop height (Intercrops in a canopy layer are assumed to have uniform leaf spread)	<u>Water and Nutrients</u> • Potential uptake rate • Relative resource demand • Relative root length density (RLD) (Nutrient supply is at a given soil water content)	• Relative root density (RLD) (Resource uptake is a function of intercrop RLD, and the RLD and resource demand of neighbour crop)
FSP	• Leaf surface • Canopy	• Reflectance and transmittance coefficients (A shade avoidance algorithm is used)		

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Resource use

(1) Aboveground resources

Intercrop competition for light is dependent on canopy architecture, optical properties of leaves, and soil and incident radiation. The approaches used to describe light competition differ between models. As shown in Table 1, some models assume a canopy divided into layers based on crop height (APSIM, SWAP 2x1D) while others further subdivide the canopy layers based on shaded and sunlit parts in the canopy layer (STICS) and canopy area at a given height (FASSET). More robust models focus on the architecture of heterogeneous canopy (STICS, WaNuLCAS). Main factors considered for light capture in these models are i) use of any/combination of crop height, LAI and extinction coefficients (APSIM, FASSET, WaNuLCAS), and ii) shading capacity in addition to (i) (DSSAT, FSP). Other methods include use of weighted average between two reference radiation values (SWAP 2x1D), and reflectance and transmittance coefficients (FSP). Discrepancies between observations from field experiments and model simulations have been reported due to the representation of light capture and canopy in models. For instance, Corre-Hellou et al. (2009) using field data in a pea/barley mixture showed that maximum height was reached after maximum LAI, different from STICS simulations where canopy height is a function of LAI.

(2) Belowground resources

Most models represent the belowground interactions as 1D and use biomass partitioning coefficients to simulate shoot and root growth. Some models consider competition for both water and nutrients (APSIM, FASSET, WaNuLCAS) while others consider only one of these (SWAP 2x1D). Models such as DSSAT and STICS do not include competition for these resources. STICS simulates root growth and N demand in the sole crop model. It can simulate the advantage in N sharing for a crop with fast root growth and early rapid shoot growth and it assumes that the influence of the intercrops' root systems on each other is due to the influence of the soil status in the root system. Simplistic approaches for competition for water and nitrogen uptake are used in models like APSIM where each of the intercrops is given the opportunity for resource uptake on alternating days. Other models use algorithms that are based on potential resource uptake, relative root length density and resource demand (WaNuLCAS), soil hydraulic characteristics (STICS, SWAP 2x1D) and belowground coverage of the crop (SWAP 2x1D). Pinto et al. (2019) using SWAP 2x1D to simulate radiation and water interactions in strip intercropping found the effect of lateral water exchange on the soil water storage to be significant.

Plant plasticity

Plant plasticity can occur in intercrops due to interactions between the plants, plant organs and resources (Evers et al. 2019). Plasticity can be captured in models such as the FSP as described in Evers et al. (2019) due to their 3D functional–structural plant approach. In this approach, mechanisms of growth and development are at the plant organ level which considers interactions and feedbacks between plants and their local environment. Models such as STICS, SWAP 2x1D and WaNuLCAS partly address the interspecific interactions (Table 1). The light sharing and nitrogen competition processes in STICS have recently been improved to simulate interspecific (cereal/legume) interactions.

Discussion

The intercropping models reviewed here have incorporated only some of the key features in intercropping systems namely resource competition and interactions. All the models have some form of light capture based on their representation of the canopy structure. However, only a few incorporate sharing of water and nutrients resources while fewer consider interaction between resources and intercrops. Other limitations are due to i) the monoculture framework used to build intercropping models; ii) the canopy architecture e.g. a canopy structure that is 1D disregards the spatial dimension which is important for simulating shade effects and light capture; iii) the method used for resource sharing and priority assignment of the shared resources e.g. when priority is given to one plant component, an overestimation of resource capture may occur. It is imperative that resource capture is done simultaneously and thus avoid priority assignment; iv) neglecting below ground interactions which may lead to more efficient resource uptake by some crops than others. Root architecture is more important than its absorption capacity in the competition for water and solutes (Knörzer et al. 2011); and v) not implementing plasticity in most models though it influences resource acquisition and as an emergent property, it integrates all aspects of an intercropping system. Other models such as CROPSYST, WATERCOM, GEMNINI and INTERCOM can provide useful insights and should be evaluated too.

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Conclusion

Crop models reported here can simulate some of the aspects that characterize intercropping systems. There is need for intercropping models to consider canopy design, resource capture and use, and interaction between intercrops and the local environment. The spatial architecture of the canopy has been shown to be important as it facilitates better sharing of light and can address effects of shade. In addition, competing root systems and root architecture are crucial to avoid more resource uptake by one crop over another. Plant plasticity is believed to be crucial since it integrates more aspects observed in intercropping systems. Modelling studies that have quantified plasticity effects have focused mainly on crop response to light - excluding water and nutrients - however, plasticity was found to alter light capture, root growth and N uptake rate. Frameworks such as the three-dimensional Functional-Structural approach that model both resource use and plasticity are useful tools to help untangle interactions and feedbacks between resources and the intercrops from the plant organ to crop level. There is need to establish strong design and testing systems with data interoperability from diverse sources to develop robust intercropping models.

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