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plant modelling

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2 **plant modelling**

3

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18 **Abstract**

19 Plant species mixtures improve productivity over monocultures by exploiting species  
20 complementarities for resource capture in time and space. Complementarity results in part from  
21 competition avoidance responses that maximize resource capture and growth of individual plants.  
22 Individual organs accommodate to local resource levels, e.g. with regard to nitrogen content and  
23 photosynthetic capacity or by size (e.g. shade avoidance). As a result, the resource acquisition in time  
24 and space is improved, and performance of the community as a whole is increased.

25 Modelling is needed to unravel the primary drivers and subsequent dynamics of complementary  
26 growth responses in mixtures. Here, we advocate using functional-structural plant (FSP) modelling to  
27 analyse the functioning of plant mixtures. In FSP modelling, crop performance is a result of the  
28 behaviour of the individual plants interacting through competitive and complementary resource  
29 acquisition. FSP models can integrate the interactions between structural and physiological plant  
30 responses to the local resource availability and strength of competition, that drive resource capture  
31 and growth of individuals in species mixtures. FSP models have the potential to accelerate mixed-  
32 species plant research, and thus support the development of knowledge that is needed to promote  
33 the use of mixtures towards sustainably increasing crop yields at acceptable input levels.

34

35 Keywords: diversity, complementarity, resource foraging, phenotypic plasticity, simulation model,  
36 virtual plant

37

## 38 Introduction

39 Global population growth necessitates further increases in global food production and at the same  
40 time a reduction in the ecological footprints of agriculture in terms of land use, exploitation of natural  
41 resources and spill-overs to the environment. The need for a sustainable intensification of agriculture  
42 is fostering interest in ecology-smart approaches for yield increase. In this regard, use of diversity  
43 through mixtures of plant species has large potential: ecological research shows that productivity,  
44 resource-use efficiency and stress resilience all tend to increase with species richness (Loreau *et al.*,  
45 2001; van Ruijven and Berendse, 2005; Isbell *et al.*, 2015). Yet, single-species systems are the norm in  
46 modern agriculture.

47 Compared to monocrops, little work has been done on crop mixtures for yield increase in modern  
48 mechanized agriculture, despite the potential shown for mixed-species systems (Li *et al.*, 2013; Yu *et al.*,  
49 2015, 2016; Fletcher *et al.*, 2016) as well as cultivar mixtures (Tooker and Frank, 2012; Sapoukhina  
50 *et al.*, 2013). Recent research however has started to focus on the mechanisms that explain the  
51 increased performance of mixed-species systems. Lessons are being learned for both agriculture and  
52 ecology, demonstrating the relevance for mixture performance of soil biota (Hendriks *et al.*, 2013;  
53 Qiao *et al.*, 2016), soil resource mobilization (Li *et al.*, 2014), plasticity in root growth (Liu *et al.*, 2015)  
54 and shoot growth (Zhu *et al.*, 2016), and root nodulation (Bargaz *et al.*, 2016). These processes are  
55 tightly linked and operate at integration levels from the plant organ to the population, and it is not  
56 known to what extent they contribute to crop performance. To disentangle the effect of these factors  
57 on crop performance experimentally is very difficult because they occur at the same time and interact  
58 with each other. Moreover, the roles of the different processes underlying mixture performance  
59 depend on the inherently heterogeneous nature of species mixtures, both in time and space. Insight  
60 in key mechanisms contributing to high yield and resource use efficiency in mixed stands is needed to  
61 exploit those mechanisms to improve crop production sustainably.

62 Process-based simulation models are suited to study the contribution of separate causal  
63 mechanisms to the overall behaviour of systems. Traditional crop models, however, suffer from three  
64 main draw-backs: 1) They are typically designed to be spatially one-dimensional, just considering  
65 differences in canopy or rooting pattern in the vertical direction, making it hard to represent the  
66 spatial heterogeneity that characterizes mixtures. Some crop models are two-dimensional,  
67 representing heterogeneity of an intercrop or agroforestry system using a block structure (Gou *et al.*,  
68 2017; Van Noordwijk and Lusiana, 1998). 2) They normally do not consider individual plants, while  
69 mixture performance is greatly determined by growth of individual plants driven by competition for  
70 local resources (such as light, water, nitrogen and phosphorus) and local conditions (such as  
71 temperature and humidity). 3) They cannot explicitly account for plant plasticity in growth and

72 functioning at the organ level in relation to local conditions, because they do not describe the plant  
73 structure. In this paper, we set out to show how advanced modelling techniques, based on detailed  
74 3D representations of the structure and functioning of the individual plants and their organs, are  
75 suited to unravel the roles and significances of the mechanisms underlying performance of mixtures.  
76 This approach will be instrumental to pinpoint those key processes at the organ, plant and population  
77 scales and their interactions that lead to high performance of mixtures, and to use that information  
78 to sustainably optimize our crop systems.

79 **Spatial plant modelling of simplified mixtures to unravel complex plant-plant interactions**

80 A defining property of species mixtures is their inherent heterogeneity, both in 3D space and in time.  
81 Plants of different species emerge at different times, have different rates of growth and development,  
82 have intrinsically different architectural and physiological traits, and grow at different levels of spatial  
83 clustering. Relay strip intercrops, cropping systems in which two different species are grown in  
84 alternating strips on the same field, can be regarded as mixed vegetation in which this heterogeneity  
85 has been extremely simplified. Since such relay intercrops are known to yield higher than  
86 monocultures at all input levels (Brooker *et al.*, 2015; Yu *et al.*, 2015), they make excellent subjects to  
87 explore the mechanisms responsible for high mixture performance. Such intercrops contain generally  
88 only two species with known emergence and growth characteristics, regularly arranged in strips of a  
89 fixed width.

90 The high performance of relay intercrops can be traced back to their heterogeneity: first plants of  
91 species 1 emerge in their designated strips and start to grow making use of the empty above and  
92 belowground space in the neighbouring strips for resource capture. At some point, plants of species  
93 2 are sown in the empty strips and start interacting with species 1 as they grow in the open areas.  
94 Later, plants of species 1 are harvested and those of species 2 grow on, making use of the extra space  
95 and resources that have become available after the harvest of species 1. Thus, the capture of  
96 resources in the absence of competition outside of the co-growth period, the interaction during the  
97 co-growth period, and the longer total access to resources such as light (Zhang *et al.*, 2008) compared  
98 to monocultures are the main reasons for the high performance of such relay intercrop systems (Yu  
99 *et al.*, 2015).

100 This spatially heterogeneous canopy development and the interspecific plant-plant interactions  
101 during the co-growth period are intercrop features that can be optimally studied and explored using  
102 a modelling approach that simulates individual plants growing together, competing for resources and  
103 responding in terms of growth and development to each other's signals. In functional-structural plant  
104 (FSP) modelling (Godin and Sinoquet, 2005; Vos *et al.*, 2010; Evers, 2016), plant growth and  
105 development is simulated in three dimensions as a function of underlying physiological processes  
106 driven by environmental variables such as light (Chen *et al.*, 2014; Evers and Bastiaans, 2016) or  
107 nutrients (Gérard *et al.*, 2017; Postma *et al.*, 2017) as resources for growth and/or signals for  
108 competition. Temperature is usually included in processes determining development and growth. Key  
109 to the FSP modelling methodology is 1) that the mechanisms of growth (e.g. photosynthesis,  
110 respiration and resource acquisition and allocation) and development are defined at the levels of the  
111 plant organ, and 2) that plant and canopy growth are an emergent model property, resulting from  
112 interactions between growing organs within a plant and between growing plants within the stand.

113 Crucial to the usefulness of FSP modelling is the explicit feedback between plant and their local  
114 environment: environmental factors drive plant growth and 3D architecture and functioning, but the  
115 plants and their three-dimensional architecture also modify their environment continuously, such as  
116 the distribution of radiation intensity and spectral composition within a canopy (Chelle *et al.*, 2007)  
117 and the availability of nutrients in the soil (Henke *et al.*, 2014). This feedback between the plants and  
118 their local environment is the foundation of simulating plant-plant interactions (Chelle, 2005) and is  
119 therefore fundamental to simulating species mixtures and predicting their performance, given the  
120 variation in those local environments from plant to plant.

121

122 Few examples of the application of FSP modelling to understand mixture performance exist (Barillot  
123 *et al.*, 2014; Zhu *et al.*, 2015) and these do not go beyond evaluating intercrop effects on light capture:  
124 they ignore growth and the processes that regulate growth. For instance, in relay intercrops such as a  
125 maize-wheat system, plants show different growth patterns depending on their location in the  
126 intercrop stand. Wheat plants growing at the edges of the wheat strips have higher biomass, more  
127 tillers and a larger leaf area than plants in the centre of the strips, which correlated well with the  
128 availability and spectral composition of the light at the strip edges (Gou *et al.*, 2016; Zhu *et al.*, 2016).  
129 The use of FSP modelling made it possible to quantify the contribution of plasticity to complementarity  
130 in light capture (Zhu *et al.*, 2015). Until then, diversity studies implicitly assumed that complementary  
131 resource acquisition between species results entirely from inherent differences between them and  
132 the structure of the plant community. But because plants are plastic they can adjust their phenotype  
133 and associated resource harvesting pattern to the environment created by the other species. Zhu *et al.*  
134 (2015) assessed the extent of this plasticity effect by comparing light capture from simulations of  
135 intercrops with wheat phenotypes representing either the edge row or the inner row phenotype –  
136 something effectively impossible to do in actual field experiments. It was found that plasticity  
137 increased light capture of wheat plants in the mixture substantially. This shows how FSP modelling  
138 can be a useful tool in fundamental ecological and agronomical research on species mixtures.

139 However, light capture is only part of the story. The performance of plant mixtures is only partially  
140 explained by high light capture efficiency through plastic plant responses, and this very much depends  
141 on the plant system itself. Mixtures in which both component species develop largely simultaneously,  
142 i.e. have a large temporal overlap, may still outperform monocultures although they miss out on the  
143 benefit of having a part of the season to themselves (Yu *et al.*, 2015). Mechanisms for overyielding for  
144 species that grow fully at the same time may be competition avoidance belowground (Brooker *et al.*,  
145 2015). Competition avoidance happens when species capture different sections of the resource pool  
146 spatially, temporally or chemically (for nutrients such as P), such that an increase in the acquisition of

147 one species is not at the expense of the uptake of the other species. Such competition avoidance  
148 ensures niche complementarity in resource capture (Mao *et al.*, 2012). Competition avoidance for  
149 light is based on architectural species responses that reduce shading (e.g. increased lengthening of  
150 internodes), but mechanisms for avoiding competition for acquisition of belowground resources  
151 should be expected and need to be further explored in functional-structural modelling studies. Similar  
152 to light capture, the role of such plastic responses to reduce competition depends on the spatial and  
153 temporal configuration of the component species in the system. A suitable combination of spatio-  
154 temporal configuration and plant plasticity may thus lead to an increased resource capture, and hence  
155 increased production and use efficiency. This was shown in an FSP modelling study that was conducted  
156 to explore the value of complementarity in resource uptake in a mixture of maize, bean and pumpkin  
157 (Postma and Lynch, 2012). Simulation of growth of the 3D root systems of all three component species  
158 sharing the same soil volume revealed that the mixed system had higher nitrogen uptake than the  
159 monocultures, due to spatial niche differentiation of the different root systems. The simulations also  
160 suggested that the uptake of less mobile resources, such as phosphorus, may not benefit from  
161 combining these species, depending on soil conditions.

162 FSP modelling in combination with experiments can yield great insight in mixture functioning and  
163 allows for the identification of the most important plant traits and the way in which they may best be  
164 combined, either by configuration, management (e.g. fertilizer) or plastic responses. The  
165 opportunities for FSP modelling in mixed-cropping research will be outlined later in this paper. First,  
166 we will specify the criteria for modelling species mixtures.

167

168 **Criteria for modelling species mixtures**

169 To address mixed crop performance using an FSP modelling approach, the model should contain the  
170 (putative) mechanisms relevant to the mixture performance at the level of the plant organ (leaf, stem,  
171 root) and environmental component (canopy, soil), and produce output at the level of the whole  
172 plants and consequently of the whole mixed-crop system (Fig. 1). Here we discuss the criteria an FSP  
173 model needs to meet to be able to address questions in mixed-species research, starting from the  
174 simulation of single-species systems, and then discussing how single-species models can be amended  
175 to simulate mixed-species systems.

176

177 *Single-species FSP models*

178 In FSP models, plant organs such as leaves, internodes and roots are represented in 3D space as  
179 geometric objects, and their creation over time is simulated using simple empirical rules capturing  
180 plant architectural development (Prusinkiewicz and Lindenmayer, 1990; Kurth *et al.*, 2005).  
181 Phenological plant development and organ morphogenesis is not simulated mechanistically in FSP  
182 models that focus on plant growth and performance because it is usually not required for the aim of  
183 the modelling exercise, and would merely decrease computational efficiency without increasing  
184 explanatory power. A comprehensive overview of model approaches that do simulate development  
185 and morphogenesis mechanistically is given in Prusinkiewicz and Runions (2012).

186 Upon their creation, organs start to grow and change size and shape. In actual plants, changes in  
187 organ biomass, size, shape and orientation is driven by a host of different environmental and  
188 physiological processes. Which aspects of plant physiology and environmental regulation are included  
189 in the model depends on the research question that is addressed. For instance, when a study deals  
190 with trying to explain development of a fungal disease in a wheat canopy in relation to plant  
191 architecture, simulation of light capture, photosynthesis and biomass growth is not necessary (Robert  
192 *et al.*, 2008). It is then sufficient to use an FSP model that describes wheat growth and development  
193 over time using empirical relations, extended with provisions to calculate spore dispersal and lesion  
194 development, possibly in relation to canopy microclimate. Similarly, a study that aims at representing  
195 a range of different root system architectures based on genetically determined trait correlations needs  
196 relatively little ecophysiological regulation to be simulated well (Pagès *et al.*, 2014) and can focus more  
197 on trait variation and correlation networks. Conversely, when for instance the research is in the  
198 domain of explaining transport of sugars in a developing plant, processes related to carbon  
199 assimilation and biomass production cannot be ignored (Allen *et al.*, 2005). Thus, as with any  
200 modelling approach, the research question to be addressed determines which ecophysiological  
201 processes need to be taken into consideration and, as a consequence, which can be left out.

202 FSP modelling studies typically use biomass as the performance measure, when the focus is on  
203 understanding competitive relationships between plants. Such a study requires light capture, carbon  
204 assimilation and plant growth to be represented mechanistically (e.g. Evers *et al.*, 2010), but may also  
205 need simulation of belowground resource harvesting and competition (Dunbabin *et al.*, 2013; Postma  
206 *et al.*, 2017) and the interactions between above and belowground resource capture in one dynamic  
207 model (Louarn and Faverjon, 2018). Ultimately, canopy growth is determined by the slowest of a  
208 number of interlocking feedback cycles related to capture of light, nutrients and water (Fig. 1). The  
209 eventual output of such models is a canopy of plants of which the size and biomass is the result of  
210 plant competition for resources during their development.

211

### 212 *Mixed-species FSP models*

213 An FSP model aiming at simulating setups in which plants of different species are competing, is not  
214 fundamentally different from one that simulates a monoculture of plants of a single species. Since  
215 plant growth and development is simulated mechanistically, a simulated plant will cope with any  
216 spatial and temporal heterogeneity in resource availability, regardless of whether this variation is  
217 caused by neighbours of a different or the same species, or even other external reasons such as  
218 imposed shading, fertilization or rain events. It is critical that the model is designed such that  
219 mechanistic simulation of plant growth is based on the inherent plant characteristics, inputs the plant  
220 receives and the influence it has on its immediate environment, and not based on whether or not  
221 plants of a specific species happen to be adjacent. In other words: the effect of neighbours should be  
222 mediated by the local availability of resources and the influence of those neighbours on other (non-  
223 resource) signals. This means that also in mixtures, simulated plant growth behaviour entirely depends  
224 on the functionality implemented at the single plant species level and no special traits are required to  
225 model the effect on or response to neighbours. Additionally, simulated plant growth behaviour can  
226 only depend on the functionality implemented in the model. If plant growth is simulated driven by  
227 light absorption, photosynthesis and assimilate allocation to sink organs, then a mixed-species setup  
228 can only show emergent behaviour based on light competition and associated growth reduction. For  
229 instance, it will never result in a canopy structure shaped by plastic responses to light signals (Ballare  
230 and Pierik, 2017). If such model behaviour is desired, at the level of the species both the cue  
231 (producing a light signal) and the response (plasticity upon receiving a signal), which act independently  
232 of each other, need to be incorporated in the model (done for single species FSP models in Gautier *et al.*  
233 *et al.*, 2000; Evers *et al.*, 2007; Pantazopoulou *et al.*, 2017; Bongers *et al.*, 2018). That way, plant-plant  
234 interaction is emergent from the simulations, rather than imposed. The strength of the interaction  
235 and its consequences for plant performance will automatically follow from e.g. simulated plant

236 arrangement or architectural differences between species (Fig. 2). Thus, in FSP models of species  
237 mixtures that are used to understand performance, plant competition for resources is an emergent  
238 property. The effects of competition for resources on vegetation performance is the consequence of  
239 all individual plants requiring and acquiring resources. Competition is not incorporated as a distinct  
240 process with separate equations and parameters, but an outcome of resource acquisition by individual  
241 plants growing together in a local environment where resources are shared. Any additional  
242 mechanism that influences competition, such as light signalling aboveground (Ballare and Pierik, 2017)  
243 or facilitation belowground (Li *et al.*, 2007, 2014), merely contributes to the ability of plants to gather  
244 resources, and should be included as such if the research question demands it.

245

246

247 **Opportunities for FSP modelling in mixed-species research**

248 FSP modelling is a promising tool to analyse the competitive relationships between component  
249 species in mixtures at plant level. As the plant is modelled at organ level with representation of both  
250 structure and physiology, FSP models may be used to study the consequences of structural as well as  
251 physiological plant traits for crop performance in relation to management. Specifically, these domains  
252 provide opportunities: 1) improved understanding of how plant-plant interactions in mixtures  
253 determine plant and canopy growth and thus performance; 2) species ideotyping by the identification  
254 of combinations of architectural and physiological traits that lead to optimal performance of plants in  
255 mixtures; and 3) optimization of crop planting patterns and temporal overlap that maximize the  
256 interaction effects on performance within the boundaries set by mechanization.

257

258 1) In the most simplified view, canopy performance is determined by interlocking feedback cycles with  
259 plant growth as an integrator, and capture of light, nutrients and water by the plant structure as the  
260 basic resources for growth (Fig. 1). The rate at which these cycles operate is determined by resource  
261 availability and capture traits, and modulated by mechanisms such as facilitation of nutrient uptake  
262 and avoidance of competition for resources by plastic plant responses. The plant can grow as fast as  
263 the slowest feedback cycle allows, but the rate of each cycle is affected by that of the others. This view  
264 of integrated multi-resource capture by the individual plant applies to monocultures as well as to  
265 mixtures. However, due to variation in local conditions and neighbour interactions in mixtures, these  
266 feedback cycles differ more strongly between plants in mixtures than in monocultures. For example,  
267 we know that root exudates of one species can make nutrients available to the second species (Li *et*  
268 *al.*, 2007, 2016), but it is unclear how plant traits and soil conditions jointly shape the way this  
269 facilitation process interacts with above-ground growth and light harvesting and thus contributes to  
270 overall system performance across environments. Also, it has been established that wheat plants in  
271 the border rows of wheat strips in mixtures with maize are more efficient in capturing light, due to a  
272 greater number of tiller and a larger leaf area per plant, than plants in the middle of those strips (Zhu  
273 *et al.*, 2015), but it is not at all clear how this local advantage translates to biomass production e.g.  
274 when soil resources are limiting, or when plant responses to the border position are weak, or when  
275 efficiency of light conversion is low. FSP modelling allows us to explore such scenarios, by varying  
276 availability of soil resources and introducing differences in plant responses. Even though predictions  
277 of biomass accumulation might not be very precise, the qualitative change in biomass over time can  
278 help us understand which processes are important or limiting at which moment in the development  
279 of the canopy. This can then aid in the design and optimisation of experiments, treatment  
280 combinations and measurements. Thus a combination of FSP modelling and dedicated experiments

281 will be instrumental in advancing our understanding of the interactions between processes and the  
282 consequences for performance in species mixtures.

283

284 2) Genotypes currently used in crop mixtures have been bred to give high performance in  
285 monocultures, but it is not clear whether their phenotypes are also optimal for growing in mixtures,  
286 as mixtures may require a different set of traits than monocultures do (Brooker *et al.*, 2015). For  
287 example, depending on the conditions and plant arrangement, plants may need to show high  
288 tolerance to shade at the seedling stage when the companion species has been sown earlier. Plants  
289 may need to have a steeper leaf angle, when the second species has an erect stature. Plants of one  
290 species may need to root deeper early on than would be required in monoculture to provide an  
291 optimal root distribution, when the companion species extends its roots horizontally through the top  
292 soil layers. Exploring all potential combinations of traits by experiments alone is not feasible or at least  
293 very costly. FSP modelling is an ideal tool to explore opportunities for trait optimization, by performing  
294 virtual ideotyping: determining which combinations of traits (which phenotypes) perform optimally in  
295 mixtures for a given (range of) conditions. Traits here can be architectural such as stem length or root  
296 angle, physiological such as photosynthetic efficiency or nutrient uptake, but also the strength of  
297 responses to environmental cues such as shade avoidance. Trait optimization can be performed for  
298 combinations of traits simultaneously across different environmental conditions and/or planting  
299 patterns, providing ideotypes for very specific conditions or generic ideotypes for a broad range of  
300 conditions. Furthermore, co-selection of species needs to be considered: the optimal traits of species  
301 A in a species A and B mixtures will depend on the traits of species B, and *vice versa*. This co-selection  
302 is further complicated by the fact that spacing and timing of A and B relative to each can be varied and  
303 itself optimized (see point 3 below). Limited application of FSP modelling in the domain of ideotyping  
304 has been initiated for monocultures and mixtures (Sarlikioti *et al.*, 2011; Barillot *et al.*, 2014) but an  
305 integrated model that includes the major contributors to plant performance (Fig. 1) still needs to be  
306 developed.

307

308 3) Performance of a species in a mixture may very much depend on the planting pattern used.  
309 Numerous experiments have been performed in which intercrop strip width, the number of rows in a  
310 strip, species temporal overlap, and population density in the strip have been evaluated for  
311 performance, showing substantial variation between treatments (e.g. Zhang *et al.*, 2008; Gou *et al.*,  
312 2016). In general, these experiments show that the less heterogeneous the plant arrangement is (for  
313 instance wide strips with many rows), the more the intercrop resembles a collection of small  
314 monocultures, and thus the less involved interspecific interactions are in determining crop

315 performance. These observations would point towards maximizing species mixing, without reducing  
316 the effect of canopy structural heterogeneity, thus optimally exploiting the potential of the  
317 interspecific plant interactions. However, a meta-analysis of empirical evidence indicates that  
318 alternate row intercrops do not perform as well as narrow strip intercrop (Yu *et al.*, 2015). Further  
319 work is needed to explore further if and why the spatial resolution of a species mixture has an  
320 optimum for maximum stand performance. Increasing the resolution of a mixtures comes at the  
321 expense of manageability of the system: mechanical sowing, spraying and harvesting requires certain  
322 strip widths and distances, as well as some extent of species temporal overlap, to be efficient and  
323 economically feasible under current technologies. FSP modelling can be applied to help find the  
324 balance here: for given species characteristics, which planting pattern and amount of overlap gives  
325 what performance. With such information trade-offs between performance optimisation and farm  
326 management can be made. But the information may also hint at options for revision of technologies  
327 given potential performance gains. In combination with the phenotype optimization mentioned  
328 above, FSP modelling provides the possibility to optimize the entire system, giving breeders,  
329 agronomists and bio-systems engineers suggestions for the actual development of efficient, high  
330 yielding and manageable intercropping systems.  
331

332 **Concluding remarks**

333 Species mixtures are fundamentally more complex than monocultures. The level of complexity is  
334 determined by the species and their traits, which includes their reactions to neighbours, as well as the  
335 patterns and timings at which they grow. This introduces numerous interactions that make  
336 experimental analysis of mixtures very difficult. Modelling is an effective tool to complement and  
337 direct this experimental work: existing knowledge can be integrated, lack of knowledge can be  
338 identified, and hypotheses can be generated, that can subsequently be tested in experiments.  
339 Specifically, FSP modelling provides us with the framework to explicitly simulate interactions between  
340 plants of different species based on feedback relations with environmental factors, and the 3D spatial  
341 and temporal heterogeneity characteristic of mixed-species plant systems. FSP modelling can boost  
342 experimental work in the domain of mixture performance, allowing us to sustainably increase crop  
343 performance at optimized input levels.

344 Additionally, the relationships that emerge from FSP modelling can potentially be used to improve  
345 crop models (e.g. Brisson *et al.*, 2003; Keating *et al.*, 2003; Van Ittersum *et al.*, 2003; Jones *et al.*, 2003).  
346 Crop models are strong at predicting yields for many crop species grown as monocrops across different  
347 environments and soils, using a limited number of input parameters. Species mixtures are however  
348 not easily captured by such models, since they normally cannot represent spatiotemporal  
349 heterogeneity nor interspecific plant-plant interactions very well. FSP models can be used to derive  
350 descriptive relationships for specific species combinations, for example between light extinction and  
351 crop developmental stage. Such relationships can then be incorporated into more conventional crop  
352 models allowing yield predictions to be done efficiently. This will extend the applicability of crop  
353 models beyond the traditional limitations of monocultures.

354

355

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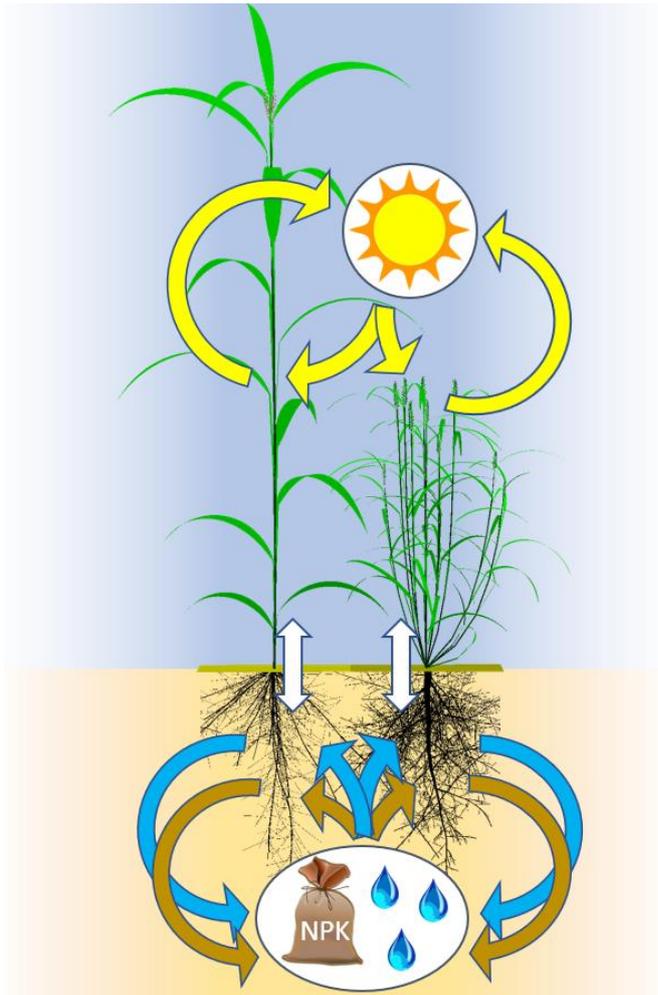


Figure 1. A number of main feedback cycles in the growth and resource acquisition of plants determine the overall growth process of individual plants. Leaf area growth drives light acquisition, which determines photosynthesis and availability of C for above-ground growth (feeding back on the 3D distribution of light in the canopy) as well as below-ground growth. The feedback cycle through light harvesting is illustrated by the yellow arrows. Root growth is driven by C supply, but root elongation is also driven by the 3D pattern of water and nutrient availability in the soil. Both the uptake of water and nutrients affects the potential for above and belowground growth, through providing the water for transpiration and the nutrients for building biochemical compounds. The feedback cycle through water acquisition by roots is shown by blue arrows, while the feedback cycle through nutrient acquisition is shown by brown arrows. The plant as a whole maintains a balance between the shoot and the root growth to tune the rate of the three cycles. In mixtures, plants are competing with neighbours that are not like themselves, and that may be either more or less competitive for light, water, and nutrients. Evidently, the competitive balance is dynamic and relates to the phenological program of growth of the competing species in combination with plastic responses to resource availability. This results in complex system dynamics that may be well explored using FSP models.



Figure 2. Visual output of a maize-wheat intercrop canopy simulated using FSP modelling, showing the spatial resolution at which plants and their organs are represented. In this particular model, plant and organ sizes are the result of competition for light only, based on the cycle light capture – photosynthesis – assimilate allocation – organ growth – light capture. Details on model functionality can be found in Evers and Bastiaans (2016).