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This is a "Post-Print" accepted manuscript, which has been published in "Journal of Experimental Botany"

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Please cite this publication as follows:


You can download the published version at:

https://doi.org/10.1093/jxb/ery288
Understanding and optimizing species mixtures using functional-structural plant modelling

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Word count: 4603
Number of colour figures: 2
Date of submission: 1 June 2018
Abstract

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

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

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

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

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

Process-based simulation models are suited to study the contribution of separate causal mechanisms to the overall behaviour of systems. Traditional crop models, however, suffer from three main drawbacks: 1) They are typically designed to be spatially one-dimensional, just considering differences in canopy or rooting pattern in the vertical direction, making it hard to represent the spatial heterogeneity that characterizes mixtures. Some crop models are two-dimensional, representing heterogeneity of an intercrop or agroforestry system using a block structure (Gou et al., 2017; Van Noordwijk and Lusiana, 1998). 2) They normally do not consider individual plants, while mixture performance is greatly determined by growth of individual plants driven by competition for local resources (such as light, water, nitrogen and phosphorus) and local conditions (such as temperature and humidity). 3) They cannot explicitly account for plant plasticity in growth and
functioning at the organ level in relation to local conditions, because they do not describe the plant structure. In this paper, we set out to show how advanced modelling techniques, based on detailed 3D representations of the structure and functioning of the individual plants and their organs, are suited to unravel the roles and significances of the mechanisms underlying performance of mixtures. This approach will be instrumental to pinpoint those key processes at the organ, plant and population scales and their interactions that lead to high performance of mixtures, and to use that information to sustainably optimize our crop systems.
Spatial plant modelling of simplified mixtures to unravel complex plant-plant interactions

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

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

This spatially heterogeneous canopy development and the interspecific plant-plant interactions during the co-growth period are intercrop features that can be optimally studied and explored using a modelling approach that simulates individual plants growing together, competing for resources and responding in terms of growth and development to each other’s signals. In functional-structural plant (FSP) modelling (Godin and Sinoquet, 2005; Vos et al., 2010; Evers, 2016), plant growth and development is simulated in three dimensions as a function of underlying physiological processes driven by environmental variables such as light (Chen et al., 2014; Evers and Bastiaans, 2016) or nutrients (Gérard et al., 2017; Postma et al., 2017) as resources for growth and/or signals for competition. Temperature is usually included in processes determining development and growth. Key to the FSP modelling methodology is 1) that the mechanisms of growth (e.g. photosynthesis, respiration and resource acquisition and allocation) and development are defined at the levels of the plant organ, and 2) that plant and canopy growth are an emergent model property, resulting from interactions between growing organs within a plant and between growing plants within the stand.
Crucial to the usefulness of FSP modelling is the explicit feedback between plant and their local environment: environmental factors drive plant growth and 3D architecture and functioning, but the plants and their three-dimensional architecture also modify their environment continuously, such as the distribution of radiation intensity and spectral composition within a canopy (Chelle et al., 2007) and the availability of nutrients in the soil (Henke et al., 2014). This feedback between the plants and their local environment is the foundation of simulating plant-plant interactions (Chelle, 2005) and is therefore fundamental to simulating species mixtures and predicting their performance, given the variation in those local environments from plant to plant.

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

However, light capture is only part of the story. The performance of plant mixtures is only partially explained by high light capture efficiency through plastic plant responses, and this very much depends on the plant system itself. Mixtures in which both component species develop largely simultaneously, i.e. have a large temporal overlap, may still outperform monocultures although they miss out on the benefit of having a part of the season to themselves (Yu et al., 2015). Mechanisms for overyielding for species that grow fully at the same time may be competition avoidance belowground (Brooker et al., 2015). Competition avoidance happens when species capture different sections of the resource pool spatially, temporally or chemically (for nutrients such as P), such that an increase in the acquisition of
one species is not at the expense of the uptake of the other species. Such competition avoidance ensures niche complementarity in resource capture (Mao et al., 2012). Competition avoidance for light is based on architectural species responses that reduce shading (e.g. increased lengthening of internodes), but mechanisms for avoiding competition for acquisition of belowground resources should be expected and need to be further explored in functional-structural modelling studies. Similar to light capture, the role of such plastic responses to reduce competition depends on the spatial and temporal configuration of the component species in the system. A suitable combination of spatio-temporal configuration and plant plasticity may thus lead to an increased resource capture, and hence increased production and use efficiency. This was shown in an FSP modelling study that was conducted to explore the value of complementarity in resource uptake in a mixture of maize, bean and pumpkin (Postma and Lynch, 2012). Simulation of growth of the 3D root systems of all three component species sharing the same soil volume revealed that the mixed system had higher nitrogen uptake than the monocultures, due to spatial niche differentiation of the different root systems. The simulations also suggested that the uptake of less mobile resources, such as phosphorus, may not benefit from combining these species, depending on soil conditions.

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

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

Single-species FSP models

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

Upon their creation, organs start to grow and change size and shape. In actual plants, changes in organ biomass, size, shape and orientation is driven by a host of different environmental and physiological processes. Which aspects of plant physiology and environmental regulation are included in the model depends on the research question that is addressed. For instance, when a study deals with trying to explain development of a fungal disease in a wheat canopy in relation to plant architecture, simulation of light capture, photosynthesis and biomass growth is not necessary (Robert et al., 2008). It is then sufficient to use an FSP model that describes wheat growth and development over time using empirical relations, extended with provisions to calculate spore dispersal and lesion development, possibly in relation to canopy microclimate. Similarly, a study that aims at representing a range of different root system architectures based on genetically determined trait correlations needs relatively little ecophysiological regulation to be simulated well (Pagès et al., 2014) and can focus more on trait variation and correlation networks. Conversely, when for instance the research is in the domain of explaining transport of sugars in a developing plant, processes related to carbon assimilation and biomass production cannot be ignored (Allen et al., 2005). Thus, as with any modelling approach, the research question to be addressed determines which ecophysiological processes need to be taken into consideration and, as a consequence, which can be left out.
FSP modelling studies typically use biomass as the performance measure, when the focus is on understanding competitive relationships between plants. Such a study requires light capture, carbon assimilation and plant growth to be represented mechanistically (e.g. Evers et al., 2010), but may also need simulation of belowground resource harvesting and competition (Dunbabin et al., 2013; Postma et al., 2017) and the interactions between above and belowground resource capture in one dynamic model (Louarn and Faverjon, 2018). Ultimately, canopy growth is determined by the slowest of a number of interlocking feedback cycles related to capture of light, nutrients and water (Fig. 1). The eventual output of such models is a canopy of plants of which the size and biomass is the result of plant competition for resources during their development.

**Mixed-species FSP models**

An FSP model aiming at simulating setups in which plants of different species are competing, is not fundamentally different from one that simulates a monoculture of plants of a single species. Since plant growth and development is simulated mechanistically, a simulated plant will cope with any spatial and temporal heterogeneity in resource availability, regardless of whether this variation is caused by neighbours of a different or the same species, or even other external reasons such as imposed shading, fertilization or rain events. It is critical that the model is designed such that mechanistic simulation of plant growth is based on the inherent plant characteristics, inputs the plant receives and the influence it has on its immediate environment, and not based on whether or not plants of a specific species happen to be adjacent. In other words: the effect of neighbours should be mediated by the local availability of resources and the influence of those neighbours on other (non-resource) signals. This means that also in mixtures, simulated plant growth behaviour entirely depends on the functionality implemented at the single plant species level and no special traits are required to model the effect on or response to neighbours. Additionally, simulated plant growth behaviour can only depend on the functionality implemented in the model. If plant growth is simulated driven by light absorption, photosynthesis and assimilate allocation to sink organs, then a mixed-species setup can only show emergent behaviour based on light competition and associated growth reduction. For instance, it will never result in a canopy structure shaped by plastic responses to light signals (Ballare and Pierik, 2017). If such model behaviour is desired, at the level of the species both the cue (producing a light signal) and the response (plasticity upon receiving a signal), which act independently of each other, need to be incorporated in the model (done for single species FSP models in Gautier et al., 2000; Evers et al., 2007; Pantazopoulou et al., 2017; Bongers et al., 2018). That way, plant-plant interaction is emergent from the simulations, rather than imposed. The strength of the interaction and its consequences for plant performance will automatically follow from e.g. simulated plant growth.
arrangement or architectural differences between species (Fig. 2). Thus, in FSP models of species mixtures that are used to understand performance, plant competition for resources is an emergent property. The effects of competition for resources on vegetation performance is the consequence of all individual plants requiring and acquiring resources. Competition is not incorporated as a distinct process with separate equations and parameters, but an outcome of resource acquisition by individual plants growing together in a local environment where resources are shared. Any additional mechanism that influences competition, such as light signalling aboveground (Ballare and Pierik, 2017) or facilitation belowground (Li et al., 2007, 2014), merely contributes to the ability of plants to gather resources, and should be included as such if the research question demands it.
**Opportunities for FSP modelling in mixed-species research**

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

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

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

3) Performance of a species in a mixture may very much depend on the planting pattern used. Numerous experiments have been performed in which intercrop strip width, the number of rows in a strip, species temporal overlap, and population density in the strip have been evaluated for performance, showing substantial variation between treatments (e.g. Zhang et al., 2008; Gou et al., 2016). In general, these experiments show that the less heterogeneous the plant arrangement is (for instance wide strips with many rows), the more the intercrop resembles a collection of small monocultures, and thus the less involved interspecific interactions are in determining crop
performance. These observations would point towards maximizing species mixing, without reducing
the effect of canopy structural heterogeneity, thus optimally exploiting the potential of the
interspecific plant interactions. However, a meta-analysis of empirical evidence indicates that
alternate row intercrops do not perform as well as narrow strip intercrop (Yu et al., 2015). Further
work is needed to explore further if and why the spatial resolution of a species mixture has an
optimum for maximum stand performance. Increasing the resolution of a mixtures comes at the
expense of manageability of the system: mechanical sowing, spraying and harvesting requires certain
strip widths and distances, as well as some extent of species temporal overlap, to be efficient and
economically feasible under current technologies. FSP modelling can be applied to help find the
balance here: for given species characteristics, which planting pattern and amount of overlap gives
what performance. With such information trade-offs between performance optimisation and farm
management can be made. But the information may also hint at options for revision of technologies
given potential performance gains. In combination with the phenotype optimization mentioned
above, FSP modelling provides the possibility to optimize the entire system, giving breeders,
agronomists and bio-systems engineers suggestions for the actual development of efficient, high
yielding and manageable intercropping systems.
Species mixtures are fundamentally more complex than monocultures. The level of complexity is determined by the species and their traits, which includes their reactions to neighbours, as well as the patterns and timings at which they grow. This introduces numerous interactions that make experimental analysis of mixtures very difficult. Modelling is an effective tool to complement and direct this experimental work: existing knowledge can be integrated, lack of knowledge can be identified, and hypotheses can be generated, that can subsequently be tested in experiments. Specifically, FSP modelling provides us with the framework to explicitly simulate interactions between plants of different species based on feedback relations with environmental factors, and the 3D spatial and temporal heterogeneity characteristic of mixed-species plant systems. FSP modelling can boost experimental work in the domain of mixture performance, allowing us to sustainably increase crop performance at optimized input levels.

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

We thank J. de Vries for providing an illustration of root architecture for fig. 1.

References


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).