HAL open science

Evaluating a new intercrop model for capturing mixture effects with an extensive intercrop dataset

Dereje T Demie, Daniel Wallach, Thomas F Döring, Frank Ewert, Thomas Gaiser, Sofia Hadir, Gunther Krauss, Madhuri Paul, Ixchel M Hernández-Ochoa, Rémi Vezy, et al.

To cite this version:

Dereje T Demie, Daniel Wallach, Thomas F Döring, Frank Ewert, Thomas Gaiser, et al.. Evaluating a new intercrop model for capturing mixture effects with an extensive intercrop dataset. Agriculture, Ecosystems & Environment, 2025, 378, pp.109302. ⟨10.1016/j.agee.2024.109302⟩. ⟨hal-04747808⟩

HAL Id: hal-04747808

https://hal.inrae.fr/hal-04747808v1

Submitted on 22 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

Agriculture, Ecosystems and Environment 378 (2025) 109302

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Evaluating a new intercrop model for capturing mixture effects with an extensive intercrop dataset

Dereje T. Demie [a,*], Daniel Wallach [a], Thomas F. Döring [b], Frank Ewert [a,c], Thomas Gaiser [a], Sofia Hadir [a], Gunther Krauss [a], Madhuri Paul [b], Ixchel M. Hernández-Ochoa [a], Rémi Vezy [d,e], Sabine J. Seidel [a]

[a] Crop Science Group, Institute of Crop Science and Resource Conservation, University of Bonn, Germany
[b] Agroecology and Organic Farming Group, Institute of Crop Science and Resource Conservation, University of Bonn, Germany
[c] Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany
[d] CIRAD, UMR AMAP, Montpellier F-34398, France
[e] AMAP, University Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

ARTICLE INFO

Keywords:
Cropping system
Cultivar choice
Diversification
Crop modeling
Crop mixtures

ABSTRACT

Cereal-legume intercrops have numerous advantages over monocultures. However, the intercrop's performance depends on the plant genotypes, management, and environment. Process-based agro-ecosystem models are important tools to evaluate the performance of intercrop systems as field experiments are limited in the number of treatments. The objective of this study was to calibrate and evaluate a new process-based intercrop model using an extensive experimental data set and to test whether the model is suitable for comparing intercrop management strategies. The data set includes all combinations of 12 different spring wheat entries (SW, *Triticum aestivum L.*) with two faba bean (FB, *Vicia faba L.*) cultivars, at two sowing densities, in three different environments. The results show that the intercrop model was capable of simulating the absolute mixture (intercrop) effects (AME) for grain yield, above-ground biomass, and topsoil root biomass, for both crops. However, the intercrop model does not perform better than a benchmark that ignores the intercrop effects when simulating plant height, fraction of intercepted radiation, volumetric soil water content, and subsoil root biomass. The intercrop model predicted reasonably well the differences between species and between SW cultivars for grain yield and aboveground plant biomass. Overall, the tested process-based model can be a useful tool for designing and pre-evaluation multiple combinations of crop management, species, and cultivars suitable for intercropping in diverse conditions.

1. Introduction

Intercropping is a cropping system where more than one species or cultivar is grown at the same time on the same field. Also referred to as 'crop mixtures', intercropping provides multiple advantages over monocultures, including on average higher yield on a given piece of land (Lithourgidis et al., 2011; Li et al., 2023), reduced production risk (Vandermeer, 1989), improved weed suppression (Lithourgidis et al., 2011), increased (sub) soil nitrogen (N) availability (Seidel et al., 2019), decreased nitrate leaching (Tribouillois et al., 2016), improved soil organic matter content, carbon sequestration (Lithourgidis et al., 2011; Shili-Touzi et al., 2010), and increased biodiversity (Kremen and Miles, 2012; Brandmeier et al., 2023). One of the prevalent intercrop systems is mixing cereals (such as wheat, barley, and maize) with grain legumes (such as bean, pea, and faba bean), which are often mixed within the row (Fischer et al., 2020; Malagoli et al., 2020). Research has shown that in comparison to their respective monoculture systems, wheat-faba bean intercrop significantly increases productivity and reduces nitrate leaching and runoff (Xu et al., 2019).

The numerous processes and mechanisms involved in intercrops highlight the need to deal with their complexity by combining concepts from diverse disciplines such as agronomy, physiology, and ecology. Additionally, there is a lack of information regarding intercropping management such as crop species, genotype selection and combination (Demie et al., 2022), spatial arrangement, and sowing proportion (Chimonyo et al., 2016). Several studies have shown that intercrop

* Corresponding author.
E-mail address: dereje.demie@uni-bonn.de (D.T. Demie).

https://doi.org/10.1016/j.agee.2024.109302
Received 6 May 2024; Received in revised form 2 September 2024; Accepted 17 September 2024
Available online 25 September 2024
0167-8809/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

performance depends on the genotype combination (Annicchiarico et al., 2019; Demie et al., 2022). However, evaluating a high number of genotypes and their traits under different environments and management under field conditions is costly and laborious. To address these challenges, process-based crop simulation models are widely recognized tools to examine cause-and-effect relationships in crop production. Virtual experiments using crop models can contribute to process understanding and cropping system design (Malézieux et al., 2009). They can be used to study the influence of climate variability, soil, or management options (Seidel et al., 2019; Asseng et al., 2019; Chenu et al., 2017), and for real-time simulation-based crop management (Seidel et al., 2016).

Currently, a handful of models simulate mixed cropping systems for yield and water use (Chimonyo et al., 2016; Miao et al., 2016; Pinto et al., 2019), light distribution (Munz et al., 2014; Tsubo et al., 2005), nitrogen transport and uptake (Shili-Touzi et al., 2010; Whitmore and Schröder, 2007), and weed suppression (Baumann et al., 2002). One approach to simulate intercrops is the light sharing in strip intercrop systems. Pierre et al. (2023) developed an approach to allow the model Decision Support System for Agro technology Transfer (DSSAT) to run two crop species in intercropping. Berghuijs et al. (2021) calibrated and tested The Agricultural Production Systems sIMulator (APSIM) for wheat-faba bean intercrops, and Vezy et al. (2023) proposed a set of generic formalisms for the simulation of intercrops, with an implementation in Simulateur mulTIdiscplinaire pour les Cultures Standard (STICS).

Nevertheless, the previously published studies on intercrop models have been limited by relatively small data sets, predominantly assessing aboveground plant growth and performance to evaluate the model. These studies often ignored different management strategies such as species and cultivar choice, or sowing densities. Therefore, the objectives of this study were 1) to evaluate a new intercrop model, based on the LINTUL5 model (Wolf, 2012) and (2) to assess the suitability of the model to compare intercrop management strategies concerning the interaction between the intercrop effect and the environment. The intercrop model is implemented within the modeling framework SIMPLACE (Scientific Impact Assessment and Modeling Platform for Advanced Crop and Ecosystem Management) by combining existing biomass, soil water, and nutrients components for monocultures with intercropping components for radiation and below-ground competition and distribution. The model framework has been developed during the last decade and allows the integration of climate change impact assessments, model uncertainty, and crop management (Enders et al., 2023).

An innovation in this study, compared to previous studies, is that the evaluation is based on a comparatively extensive experimental dataset. The experimental data are from spring wheat/faba bean (SW/FB) intercrops, for three environments, each with twelve SW entries, two FB cultivars, and two sowing densities (Paul et al., 2023). Measured variables are plant height, radiation interception, plant above-ground biomass, root biomass, soil moisture, and grain yield. The same measurements were also carried out on the monocultures in all cases. This data set allows us to evaluate the intercropping model more thoroughly in terms of above and below-ground dynamics, including roots, which is a major aspect of the interaction in the intercropping systems. A second innovation is the way the evaluation is performed. Evaluation concerns specifically the difference between the intercrop and the average of the monocultures. This is more pertinent than evaluating the error in simulating directly the results of the intercrop since it is specifically the effect of intercropping compared to the monoculture that is of major interest. Note also that no intercrop data are used here for calibration of the model. Thus, the evaluation is a measure of how well the model, integrating various mechanisms of interaction between the partner crops, simulates the intercrop effect, given information about the performance of the monocultures. We also introduce a new model skill measure (Wallach et al., 2019), which compares the error of the intercrop model with a benchmark. The benchmark is the error if one assumes that there is no intercrop effect so that the results of the intercrop are exactly equal to the average of the monocultures. The intercrop model has positive skill if the error is smaller than that of the benchmark.

2. Material and methods

2.1. Field experiments

2.1.1. Experimental site

The field experiments were conducted at two research facilities in one and two years, respectively. Experiments were conducted in 2020 and 2021 at the research facility Campus Klein-Altendorf (CKA) of the University of Bonn located in Rheinbach near Bonn, Germany (50° 37' N, 6° 59' E) at an altitude of 186 m a.s.l. The soil at the experimental station is classified as Haplic Luvisol (hypereutric, siltic) from loess (IUSS Working Group WRB, 2006) and characterized by a silty-loamy texture with clay accumulation in the subsoil between about 45 and 95 cm soil depth (Barej et al., 2014). The mean annual air temperature and precipitation (2008–2021) were 10.5 °C and 652 mm, respectively. In 2020, an experiment was also conducted at the organically managed research facility Wiesengut (WG) of the University of Bonn, which is located at 50° 47' N, 7°15' E at an altitude of 65 m a.s.l. The WG soil is characterized as a silt loam texture with Haplic Fluvisol (IUSS Working Group WRB, 2006) soil type. The average yearly temperature and annual rainfall at WG were 10.7°C and 733 mm (1991–2020), respectively. The mean monthly temperature and precipitation of the growth period are given in Fig S1: (A) CKA2020, (B) CKA2021, and (C) WG2020. A detailed description of these experiments is available in Paul et al. (2024, 2023).

2.1.2. Experimental setup and cultivars

The field experiments were performed as a randomized complete block design with four replicates except in CKA 2021 where a sowing error occurred, leading to less than four replications in most of the treatments. Some treatments were replicated three times, some two times, and some treatments were not replicated. Despite this, we proceeded to analyze the data from the treatments that adhered to the originally intended sowing ratio of spring wheat (SW) to faba bean (FB) (50:50) and respective monocultures. In CKA2021, the considered treatments included all monocultures crops and 50:50 intercrops of the twelve SW entries (ten cultivars and two mixtures of these SW cultivars), and two FB cultivars similar to the treatments in WG2020 and CKA2020 (Table S1). The plot size was 1.5 × 10 m with a 21 cm row distance, respectively (Table S2). The SW cultivars were selected based on their similarity regarding grain quality and maturity time, but divergence in terms of plant height, i.e. including shorter, medium, and taller genotypes. All combinations were each sown using two sowing densities, 80 % (low density, LD) and 120 % (high density, HD) of the crop density typically used by farmers in the region for monocultures (100 %, 400 seeds m^{-2} for SW and 45 seeds m^{-2} for FB). At both densities, SW and FB were mixed in a 1:1 ratio, i.e. in substitutive mixtures, which means 50 % of seeds of each species from the respective monocultures crops (high/low density) were mixed to obtain the respective density (high/low) in the intercrop (Paul et al., 2023). No fertilizer, pesticide, or irrigation was applied during the growth period. FB was sown at 6 cm soil depth by a seeding machine type Hege 95 B. Subsequently, SW was sown directly over FB with a Hege 80 seeder at 3 cm soil depth. Mechanical weeding was performed twice, about three and five weeks after sowing. For more details see Paul et al. (2023). However, due to the research site WG being organically managed, there was a higher weed infestation.

2.1.3. Measurements

2.1.3.1. Crop phenology and above-ground biomass growth. Crop development was observed based on the BBCH-scale (Biologische Bundesanstalt, Bundessortenamt and CHemical industry), Meier (2001) which is a common system to monitor crop phenological development of mono- and dicotyledonous plant species. Agronomic data including plant above-ground biomass at three different plant growth stages, plant height at two distinct growth stages, root biomass, and grain yield, were collected. Results on grain yield (Paul et al., 2024) and partially on biomass have been already published (Paul et al., 2023). Table 1 shows a summary of the plant and soil-related data and measurement frequency for the data used in the current study. Treatments composed of two SW cultivars with both FB cultivars were selected as key treatments where the data collection was intensified.

2.1.3.2. Photosynthetically active radiation (PAR) interception and leaf area index. The PAR was measured two times in 2020 and three times in 2021 with an SS1 Sunscan canopy analysis system (Delta T- devices Cambridge, UK). The fraction of intercepted photosynthetically active radiation (fIPAR) was calculated as the difference between PAR measured below the canopy and global PAR, divided by global PAR. The LAI (leaf area index) was determined destructively by cutting plants 1 m long sections from the 3rd and 4th rows of the plots, scanned using the LI-3100 C Area Meter (Li-Cor, Biosciences GmbH, Bad Homburg, Germany), and calculated for one square meter.

2.1.3.3. Soil water content. FDR moisture sensors HH2 with ML3 Theta Probe, (ecoTech Umwelt-Meßsysteme GmbH, Bonn, Germany) were used to measure volumetric soil water content at different soil depths (30 cm, 45 cm, 60 cm, and 90 cm). The soil moisture content was measured four times on different days after sowing (DAS) during the growth period in 2020 (CKA2020: DAS ~55, ~ 73, ~ 97, ~ 114) and (WG2020: DAS ~ 57, ~ 77, ~ 104, ~ 119 DAS) and three times in 2021 (CKA2021: DAS ~ 67, ~98 and ~ 129).

2.1.3.4. Root biomass. Root samples were taken with a soil auger with an inner diameter of 9 cm down to 100 cm (divided every 10 cm) soil depth in the selected plots planted with two spring wheat cultivars, Anabele and SU Ahab, and one faba bean cultivar, Fanfare, on June 9th and on July 5th/6th 2021 at CKA. The root sampling in intercrops covered always one FB and one SW plant For a detailed description see Hadir et al. (2024). Soil cores were washed, sorted, oven-dried at 40 °C for 48 h, and weighed. An FTIR spectroscopy (Kemper et al., 2023) was used to quantify the root mass proportion per species and layer.

2.2. Model description

All crop models are simplifications of the complex dynamics of crop growth, and necessarily make a large number of assumptions. However, process-based dynamic models are still the best quantitative source of our knowledge of plant growth (Stöckle and Kemanian, 2020). Model complexity depends on the type of research question, data available, and efficiency in terms of demand for parametrization. This is particularly difficult for intercropping since multiple and complex interactions are known to occur between the intercrop components with their environment, but are difficult to quantify in the field. Our model makes several simplifying assumptions that help to make it more manageable. In particular, we assume that (a) there are no interactions with pests and diseases; (b) facilitation such as in-season N transfer from the legume crop to the cereals (as studied by Jensen, (1996) was not considered, and (c) the radiation interception model we used was developed for strip intercropping system (Gou et al., 2017b). However, the intercrop model considers various processes on a daily time step such as crop growth, soil water and N dynamics and water and N uptake by the roots, atmospheric N fixation of legumes, temporal and spatial niche competition for radiation, soil water and soil N, and grain yield production. The major processes will be explained in the following.

The simulations were conducted in the modeling platform SIMPLACE (Scientific Impact Assessment and Modelling Platform for Advanced Crop Ecosystem Management, Enders et al., 2023). The framework comprises a series of SimComponents, which are a set of functions that represent important crop and soil-related processes.

Selected SimComponents for the current study were LINTULPhenology, LINTUL5NPKDemand, SlimNitrogen, LINTUL5Biomass, SlimRoots, and SlimWater. An overview of key SimComponents is given by (Wolf, 2012) and Seidel et al. (2019).

The LINTULPhenology component calculates the crop developmental stages (DVS) based on the ratio between accumulated degree days and species-specific temperature sum requirement. Temperature sum starts to be accumulated at emergence, the crop reaches flowering at DVS 1, and physiological maturity at DVS 2. The DVS for each species in the intercrop is modeled separately. However, each species in the intercrop was simulated with the same crop parameters as the monocultures without re-parameterization. The radiation use efficiency (RUE) approach was implemented in the RadiationInterception SimComponent based on the approach of Monteith and Moss (1977), with a linear relationship between the accumulated crop biomass and intercepted radiation (IPAR). To calculate potential biomass, a linear regression between accumulated biomass and radiation interception is used. The LINTUL 5 default canopy extinction coefficient (k) value was

Table 1
Measured plant and soil variables used in the current study. Group 1 comprises the key treatments, namely the monocultures of two SW cultivars Lennox and SU Ahab, two FB monocultures, and intercrops of both wheat cultivars with the Mallory FB cultivar. Group 2 comprises the remaining 10 SW cultivars grown as monocultures and intercropping with two FB cultivars. Data was collected during field experiments (CKA, 2020 and 2021 ad (WG, 2020).

Measured variables	Group1[1] measurement frequency	Growth stage	Group2 measurement frequency	Growth stage	Measurements from
developmental stage	3	emergence, flowering, and maturity	3	emergence, flowering, and maturity	each species
grain yield	1	maturity	1	maturity	each species
above-ground biomass	3	vegetative, flowering, and maturity	1	flowering	each species
plant height	2	flowering and maturity	1	flowering	each species
leaf area index	2	vegetative and flowering	0	-	each species
root biomass	2	vegetative and flowering	0	-	each species
volumetric soil water content	3–4	vegetative and flowering, maturity	0	-	monocultures and intercrops
PAR	2–3		0	-	monocultures and intercrops

[1] key treatment. Volumetric soil water content and intercepted photosynthetically active radiation (PAR) were measured three times in 2021. Leaf area index and root biomass were measured only in 2021.

used to calculate daily radiation interception.

The SimComponent LINTUL5NPKDemand calculates the daily uptake rates of NPK (nitrogen, phosphorous, and potassium) depending on plant-available NPK in the rooted soil layers, root properties, and crop NPK demand (Wolf, 2012). In the case of FB, it is assumed that 80 % of the daily demand for nitrogen is fulfilled through biological fixation, while the remaining 20 % is sourced from soil N (Klippenstein et al., 2022). Faba bean in both monocultures and intercrops was simulated with the same assumption of biological nitrogen fixation (g m^{-2}) and soil nitrogen source.

The SimComponent LINTUL5Biomass calculates the biomass part from LINTUL5 taking the NPK stress factor NPKI into account. The daily increase in biomass may be reduced by reduction factors for transpiration (TRANRF, in case of drought stress) and nitrogen nutrition index (NNI), in case of N limitation. TRANRF is based on the ratio between actual and potential crop transpiration which are both calculated by the SimComponent SlimWater. The factors NNI and TRANRF range from 0 (full N or drought stress, no biomass increase) to 1 (no N or drought limitation).

The component SlimNitrogen calculates the plant N uptake, N turnover, and leaching of soil mineral N in layered soil (Addiscott and Whitmore, 1991). For each layer, the calculation considers the application of nitrate or ammonium fertilizer (if there is an application), leaching of nitrate and ammonium, supply from organic matter mineralization, nitrification, and crop N uptake to calculate the daily changes. The SlimWater SimComponent simulates soil water dynamics using a tipping bucket approach (Addiscott et al., 1986; Addiscott and Whitmore, 1991). Soil water movement is simulated by layer by considering plant water uptake, soil evaporation, surface runoff, and percolation.

The SlimRoot SimComponent (Addiscott and Whitmore, 1991) calculates the daily increase of seminal and lateral root biomass in different soil layers and converts it to root length per layer. Maximum rooting depth and maximum growth per day are crop-specific. At sowing, the initial biomass is provided via the seed parameters and used for the daily growth of the seminal roots which determine the vertical root penetration. Lateral roots are produced if the assimilates provided by the shoot are more than the assimilates needed by the seminal root. Root decay starts to occur at a user-defined DVS, in this case, at DVS 1.

2.2.1. Intercrop model description

The new intercrop model implemented in SIMPLACE[1] was assembled by using all crop-related SimComponents twice (one for each crop) and by using soil-related SimComponents once (one common soil) adding components to split radiation and water/nutrient uptake. The crop water demand per species was aggregated, potential transpiration of both crops was summed up and weighted by their area fraction to get field-scale data, and handed over to the root water uptake routine. The uptaken water was then disaggregated. For example, the actual transpiration was split up to calculate it per crop by using the below-ground allocation SimComponent (see below) while considering water uptake per layer and root length densities of both crops. The details of the equation were documented in Krauss, (2018).

2.2.1.1. Radiation interception in intercrop model. The radiation interception for intercrops is based on the proportion of each species and further species-specific plant characteristics. The radiation interception model is based on Gou et al. (2017b) in which two intercropped species share the incoming radiation based on their actual plant height, actual LAI, predefined proportion of each species in intercropping and a canopy extinction coefficient. The radiation interception model in intercropping was originally developed to simulate radiation interception in a strip intercropping system. Here we tested the model for in-row mixing of two species. The daily plant height increment was simulated by using the temperature-based approach of Gou et al. (2017b), but a stress effect was used in case of drought and/or nitrogen limitation. The equation is given as follows:

$$H_{d+1} = Fstress_d * r * (T_d - T_b) * H_d * \left(1 - \frac{H_d}{H_{\max}}\right) + H_d \quad (1)$$

Where H_{d+1} is plant height increment, r is a relative plant growth rate, d is day, T_d is the temperature (°C) at day d, T_b is the base temperature, H_d is the height at day d, Hmax is the maximal crop height, and $Fstress_d$ is a factor between 0 and 1 that reduces the daily potential growth due to drought (TRANRF) or N (NNI) stress at the day d. The model considers the minimum stress as a decision rule i.e. Fstress_d = min(TRANRF, NNI). The height growth stops when the temperature sum is higher than the maximum temperature sum. The relative plant growth rate is adapted from Berghuijs et al. (2020).

2.2.1.2. Root growth, water, and N uptake in the intercrop model. The below-ground factor calculates the below-ground resource allocation according to the proportion of each species in intercrop and crop-specific root parameters. The below-ground allocation factor considers the root length density (RLD), the Root Restriction Factor (RRF), which is calculated by the SlimRoot SimComponent considering RLD and root age, and the proportion of each species in intercropping. The SplitWaterUptake SimComponent calculates the root water and N uptake of each species per soil layer from the mobile and the retained soil water. The details of the equation are documented in Krauss (2018). The potential transpiration for each crop is then scaled to the proportion of each species in intercropping, the demands of each crop in intercrops, and its root distribution. The below-ground allocation component calculates the water uptake and N as well as the root growth of each species from their root distribution and species-specific parameters. Further details can be found in Kraus, (2021). The RLD and RRF are scaled according to the proportion of each crop and the common RLD and RRF are the sum of the scaled RLDs and RRFs.

2.3. Model setup and inputs

The intercrop model was set up for the three environments. The required daily weather data minimum, mean, and maximum air temperature, wind speed, precipitation, and global solar radiation were available from the research facilities. Soil properties such as soil texture, bulk density, soil carbon, and hydraulic properties were collected as reported elsewhere (Seidel et. al. 2019). The crop proportion in intercropping (equiproportional substitutive mixture) and sowing dates were set according to the field experimental design and management (Table S2). The initial soil mineral nitrogen was set according to measurements conducted around sowing. The initial soil volumetric water content values were set to field capacity (Table S3). The maximum plant height (as observed in CKA2021, where it was assumed potential growth due to the good growth conditions) was set for each species and cultivar.

2.4. Model calibration

The model was calibrated with the data of the two SW cultivars Lennox and SU Ahab as we have the most measurements for them and for both FB cultivars (key treatments). The other SW cultivars were simulated with the same parameters calibrated for the selected two cultivars and kept the maximum measured plant height and initial biomasses respective for each cultivar. We compared the data from monocultures of all three experimental environments with the observation, minimized the deviation (calibration) and then applied the calibrated model to the intercrop data (validation). Firstly, the phenology parameters were calibrated to fit the observed emergence, anthesis, and maturity dates. For this, the temperature sum from sowing

[1] SIMPLACE Documentation. https://simplace.net/doc/simplace_modules/index.html

to emergence (parameter TSUMEM), temperature sum from emergence to anthesis (TSUM1), and temperature sum from anthesis to maturity (TSUM2) were adjusted for each species (Table S4). Following this, the parameter RUE and developmental stage at which leaf death starts (parameter DVSDLT) were estimated using the leaf area index and fIPAR. Furthermore, the proportion of dry matter translocated to leaf and stem was calibrated for FB comparing observed and simulated leaf area index and shoot biomass values. The daily root elongation rates per species (parameter MSRLD) were adjusted to simulate the maximum rooting depth measured on two dates at field experiment CKA2021. Estimated parameter values are shown in Supplementary (Table S4). Parameter estimation was done by trial and error, without optimization software, given that the number of parameters adjusted was few and field experiments were only three (Seidel et al., 2018). Since the aim of this study is to test how well the model can simulate the differences between monocultures and intercropping, the intercrop model was calibrated, using only the monocultures.

2.5. Model evaluation

2.5.1. Model evaluation in capturing the intercropping effect

The model evaluation in this study was focused on how well the intercrop model simulates the intercrop effects. The selected metric for this is the Absolute Mixture Effect (AME), defined as

$$AME_{total} = y_{intercrop} - 0.5(y_{SW,mono} + y_{FB,mono}) \tag{2}$$

where $y_{intercrop}$ is the value of the variable in question (e.g. grain yield) for the intercrop and $y_{SW,\ mono}$ and $y_{FB,\ mono}$ are the values for the SW and FB monocultures respectively. The factor 0.5 is appropriate here because all the intercrops are 50:50 intercrops (substitutive intercropping). If each species in the intercrop behaves simply like the monoculture (no intercrop effect) then $AME_{total} = 0$.

If there are separate measurements for each species in the intercrop (grain yield, biomass, root biomass, etc.), then one can evaluate an AME for SW and for FB separately:

$$AME_{SW} = y_{SW,intercrop} - 0.5(y_{SW,mono}) \tag{3}$$

$$AME_{FB} = y_{SW,intercrop} - 0.5(y_{FB,mono}) \tag{4}$$

Note that AME_{total} can be 0 while both AME_{SW} and AME_{FB} are not 0 if there is compensation of effects between the two species. For the case of plant height, Eqs. 4 and 5 are replaced by

$$AME_{SW} = y_{SW,intercrop} - \left(y_{SW,mono}\right) \tag{5}$$

$$AME_{FB} = y_{SW,intercrop} - y_{FB,mono}\Big) \tag{6}$$

For those variables where species-specific values were not available separately (i.e soil water content and fIPAR), the AME was calculated according to the following equations:

$$AME_{SWC} = SWC_{intercrop} - 0.5(SWC_{SW} + SWC_{FB}) \tag{7}$$

$$AME_{fiPAR} = fiPAR_{intercrop} - 0.5(fiPAR_{SW} + fiPAR_{FB}) \tag{8}$$

Where AME_{SWC} is AME of soil water content; $SWC_{intercrop}$ is soil water content in intercropping; SWC_{SW} is soil water content in SW monocultures and SWC_{FB} soil water content in FB monocultures. AME_{PAR} is AME of fIPAR; $fIPAR_{intercrop}$ is fIPAR in intercropping; PAR_{SW} is fIPAR in SW monocultures and PAR_{FB} is fIPAR in FB monocultures.

To improve the statistical robustness when evaluating a model, Yang et al. (2014) suggested the use of more than one performance measure; therefore, to evaluate how well the intercrop model simulates AME, we used the metric of mean squared error (MSE, to calculate the model skill) and relative mean squared error (RMSE) defined as:

$$MSE = \left(\frac{1}{n}\right)\sum_{i=1}^{n}\left(AME_i^{obs} - AME_i^{sim}\right)^2 \text{ and } RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(AME_i^{obs} - AME_i^{sim}\right)^2} \tag{9}$$

where $AME_{i,}^{obs}$ (treatment mean of the replication) and $AME_{i,}^{sim}$ are the observed and simulated values of AME for situation i, respectively. The above equation can be applied to AME_{total} or AME_{SW} and AME_{FB}, for any of the measured variables.

The simplest assumption about AME is that AME is 0 (no intercrop effect). In the case of mixture effects, we assume that the process-based intercrop model agrees better with the measurements than that simple assumption (observed AME=0). Thus, the latter is used as a benchmark. We introduced the skill score (Wallach et al., 2019) in model evaluation, which is measured in terms of the likelihood ratio of a model concerning some reference (benchmark). Therefore, we define the model skill measure:

$$model\ skill = 1 - \frac{MSE\ of\ intercrop\ model}{MSE\ of\ benchmark} \tag{10}$$

A positive skill value indicates that the intercrop model has a smaller MSE than if one assumes no intercrop effect. A value of 1 indicates that the intercrop model is perfectly simulating these values (e.g. observed is equal to simulated yield). This skill measure can be thought of as the fraction of the intercrop effect that is explained by the intercrop model.

2.5.2. Model evaluation in capturing management effects

To evaluate how well the model simulates management effects (choice of species, cultivar, sowing density) we look at differences in AME between two different management (mgt) decisions, mgt1 and mgt2 for both simulated and observed values. For example, mgt1 could involve SW cultivar1, while mgt2 could involve SW cultivar2. Given that multiple cultivars of SW were used in the field experiment, we selected two cultivars that showed very low and high observed AME of grain yield from each of the three environments. We then compared the simulated AME differences between selected cultivars with the observed differences (simulated differences vs. observed differences between the two cultivars). Similarly, for sowing density, we considered high sowing density for mgt1 and low sowing density for mgt2. Then we assessed how much these differences can be explained by the intercrop model compared to the benchmark that assumes no intercrop effect. The measure of the management effect is then expressed as:

$$\Delta AME = AME_{mgt2} - AME_{mgt1} \tag{11}$$

Where ΔAME is the difference between AME of management2 and AME of management 1; AME_{mgt2} is AME of trait in question, for example grain yield for management2; AME_{mgt1} is AME of trait in question for example grain yield for management1.

3. Results

3.1. Model calibration with monoculture data

The fit of the calibrated model to the observations of the monoculture treatments in all three environments was generally good with RMSE of 0.6 t ha^{-1}, 2.1 t ha^{-1}, 0.15 m, 0.08 for grain yield, shoot biomass, plant height, and fraction of intercepted radiation respectively (Fig.S2 - S6). Exceptions were biomass at flowering and harvest at WG2020, where the simulated values were strongly overestimated compared to the measured values.

3.2. Model evaluation with intercrop data

3.2.1. Grain yield and absolute mixture effect

The intercrop model performed well in simulating the absolute grain yield (Fig. 1) and AME (Table 2 and Fig. 2). The experimental data consistently showed positive AME for SW grain yield, though with a substantial range between 0.56 and 0.84 t ha^{-1} (Table 2). In contrast, the AME for FB grain yield ranged from −0.79 ha^{-1} to +0.41 ha^{-1}, depending on the environmental conditions. In both observed and simulated AME of SW grain yield was consistently larger than AME of FB. In most cases, the skill of the intercrop model was substantial, ranging from 0.29 to 0.84 (Table 2). The skill was negative, i.e. MSE was larger than for the benchmark, in the two cases with the smallest AME values, which favored the benchmark model since it assumes AME=0. RMSE for the intercrop model was not particularly large for those two cases, but those were the two cases with the smallest values of RMSE for the benchmark.

3.2.2. Above-ground biomass

The observed and simulated above-ground biomass AME of SW was consistently positive. However, the AME for FB was negative in many cases (Fig. 3). The skill was 0.37 for FB, 0.46 for SW, and 0.33 for the total of both species, based on squared error averaged over the environments, growth stages, cultivars, and sowing densities. In CKA2020 and CKA2021, skill varied between 0 and 0.91, while in WG2020 many of the skill measures were negative (Table S5).

3.2.3. Plant height

The observed AME for plant height was low for both species (Fig. 4 and Table S6). As a result, the skill was negative in most cases, showing the benchmark performed slightly better than the intercrop model (Table S6). However, the RMSE was 0.05 m and 0.08 m which is quite low for SW and FB, respectively highlighting the low impact of intercropping on plant height.

3.2.4. Fraction of intercepted radiation

Observations showed that intercropping had a minor effect on the fraction of intercepted radiation for both crop species (fIPAR, Fig. 5). The measurements are shown only for the two species together since it was not possible to measure radiation interception of SW and FB separately in in-row intercropping. The intercrop model performed reasonably well (RMSE 0.04–0.05), but the benchmark performed slightly better (Table S7).

3.2.5. Root biomass

Observations showed that there was a root mass advantage in intercropping for SW at both observed dates compared to monocultures, especially in the topsoil layers (0–20 cm) (Fig. S8-9). However, the model underestimated the root biomass in the upper 10 cm (Fig. S8, S9). The AME values for both species were much larger in the top layer (0–30 cm) than in the lower layers. For the 0–30 cm layer, the model skill was large, in the range of 0.46–0.86 depending on the development stage and species (Table S8). For the lower soil layers, the AME was small, and skill was often negative.

3.2.6. Volumetric soil water content

The effect of intercropping on soil moisture was small, with values of RMSE ranging from 0.01 to 0.042 volumetric soil water content (VSWC). The skill scores here are all close to 0, indicating the similar performance of the intercropping model with the benchmark (Table S9).

3.3. Intercrop model capability to simulate management effects

3.3.1. Effect of species and environment

In general, both observed and simulated AME values were substantially larger for SW than for FB. The skill for simulating ΔAME of grain yield ranged between 0.12 and 0.92. For above-ground biomass, the model effectively represented the differences between species at CKA2020 and CKA2021, with skill values between 0.24 and 0.81. However, model performance at WG2020 showed that the model was not able to capture species differences (Table 3).

3.3.2. Effect of cultivars

We considered here only two SW cultivars in each environment, the

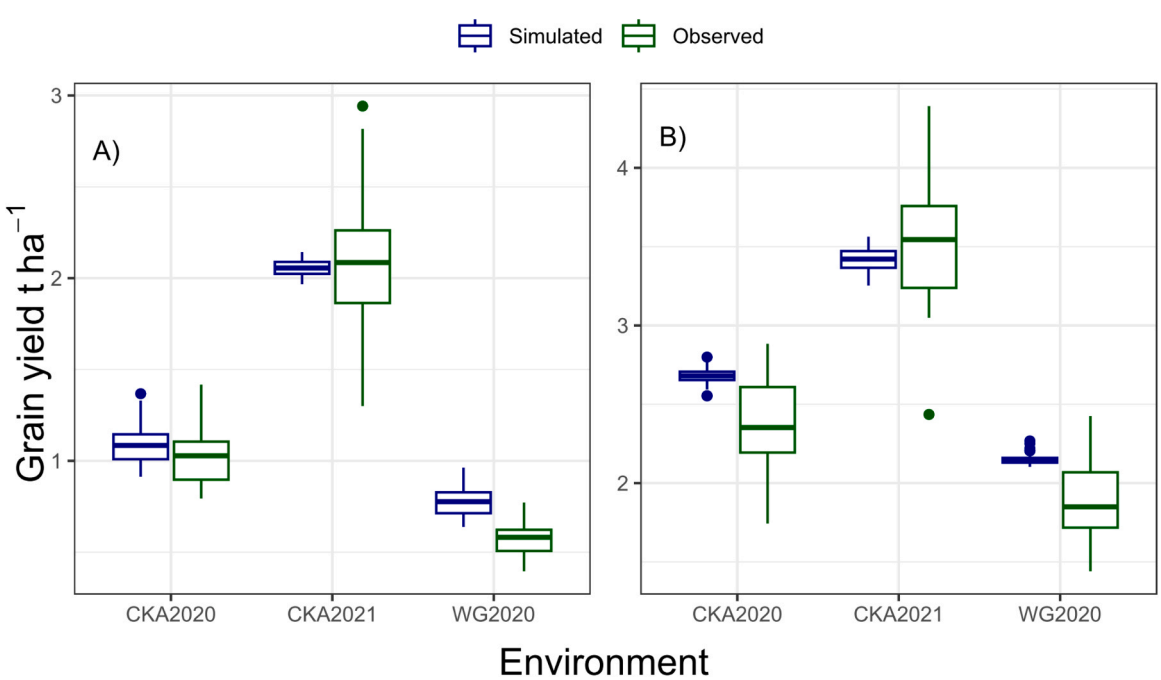

Fig. 1. Simulated and observed absolute dry matter grain yield (t ha^{-1}) of faba bean (left panel) and spring wheat (right panel) grown under an intercropping system (average for all intercropping treatments), across three environments. Observations per site were 48 per species for CKA2020 and WG2020 and 38 per species for CKA2021.

Table 2
Model evaluation of absolute mixture effect (AME) of grain yield (t ha^{-1}[a]) in both monocultures and intercrops. Results are averages over cultivars of faba bean (FB) and spring wheat (SW) and sowing densities for three environments.

Environment	AME[a]	Observed	Simulated	Model skill[b]	RMSE IM[c]	RMSE[e] B[d]
CKA2020	AME_{total}	−0.13	0.33	−3.00	0.50	0.20
	AME_{FB}	−0.79	−0.46	0.77	0.38	0.82
	AME_{SW}	0.66	0.79	0.84	0.27	0.69
CKA2021	AME_{total}	1.25	0.57	0.60	0.80	1.30
	AME_{FB}	0.41	0.15	0.29	0.48	0.58
	AME_{SW}	0.84	0.42	0.59	0.59	0.93
WG2020	AME_{total}	0.55	0.35	0.74	0.20	0.50
	AME_{FB}	−0.01	−0.37	−18.00	0.38	0.08
	AME_{SW}	0.56	0.72	0.84	0.22	0.58

[a] Absolute mixture effect;
[b] Model skill is the skill measure compared to the no-mixture effect (benchmark),
[c] Intercrop model;
[d] Benchmark model and
[e] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

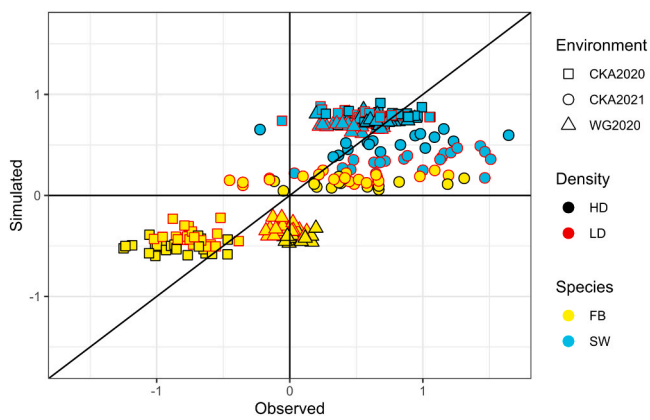

Fig. 2. Simulated and observed absolute mixture effect (AME) of dry matter grain yield (t ha^{-1}) for faba bean (FB) and spring wheat (SW) grown under three environments (CKA 2020 and 2021, WG2002) and two plant densities (HD- high sowing density, LD- low sowing density). Overall R^2 is 0.59.

cultivars with the smallest and largest observed AME values averaged over sowing densities. The two SW cultivars for each environment were: CKA2020- KWS starlight vs Anabel; CKA2021: Lennox vs Sonett and WG2020: Lennox vs mix_group 1. The two FB cultivars were Mallory and Fanfare. The intercrop model was capable of simulating the cultivar differences between the two SW cultivars AME of grain yield though consistently underestimating the size of the difference, with a skill range of 0.21–0.24. For faba bean, the intercrop model performed similarly to the benchmark that considers no intercrop effects, with a skill that approached zero (Table 4).

3.3.3. *Effect of sowing density*

Observations showed that the sowing density had a significant effect on the AME of grain yield for both crop species. However, this effect i.e. the difference between the AME of two densities was not captured by the intercrop model, except in very few cases (Table 5).

4. Discussion

The current study specifically focused on evaluating the capability of a process-based intercrop model to simulate the intercropping effects of a spring wheat/faba bean intercropping under different management conditions. In this study, the crop parameters were calibrated for monoculture using the data from monoculture treatments without recalibration for intercrops. Therefore, this is not a test of how well the model simulates the effect of the environment on a monoculture. It is however a rigorous test of how well the model can simulate the differences between monocultures and intercropping. This approach differs from previous studies that have evaluated intercrop models. Past studies typically looked at errors in the model, but not at the errors from the difference between monocultures and intercrop, focusing mostly on the model's capability to simulate environmental effects on the monocultures and the effects of intercropping (Berghuijs et al., 2021; Gou

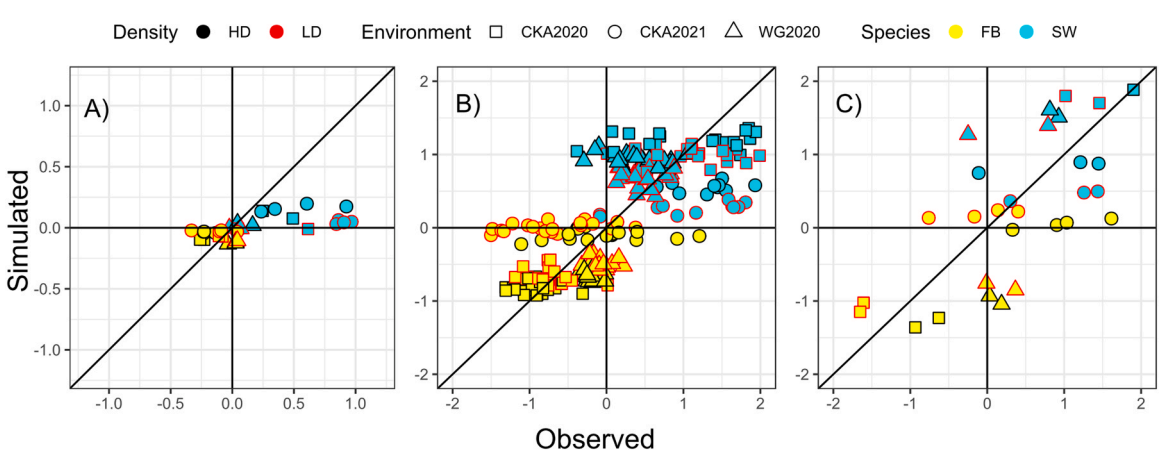

Fig. 3. Simulated and observed absolute mixture effect (AME) for above-ground biomass during A) the vegetative stage, B) around flowering, and C) at maturity, for faba bean (FB) and spring wheat (SW) grown under three environments (CKA 2020 and 2021, WG2020) and two planting densities (HD- high sowing density, LD- low sowing density). The distance of a point from the vertical line is the error of the benchmark. Overall R^2 for AME is 0.42.

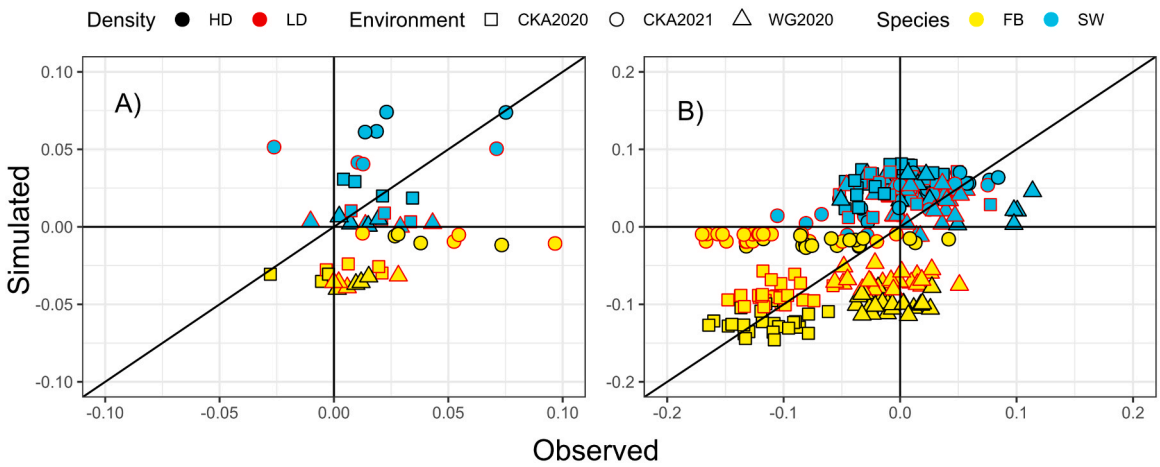

Fig. 4. Simulated and observed absolute mixture effect (AME) for plant height at A) vegetative and B) flowering stage for faba bean (FB) and spring wheat (SW) for three environments (CKA 2020 and 2021, WG2020) and two planting densities (HD- high sowing density, LD- low sowing density). Overall R^2 for AME is 0.30.

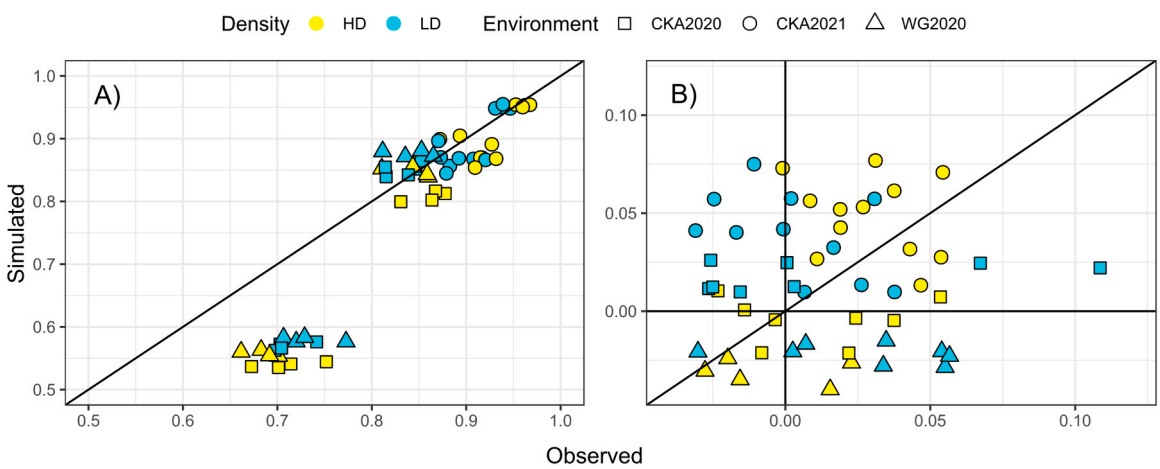

Fig. 5. Simulated and observed A) fraction of intercepted photosynthetically active radiation (fPAR) and B) absolute mixture effect (AME) of the fraction of intercepted photosynthetically active radiation (fIPAR) at different measurement dates. Overall R^2 is 0.88 for fPAR and 0.05 for AME of fPAR. Three environments (CKA 2020 and 2021, WG2020), HD- high sowing density, LD- low sowing density.

Table 3
Evaluation of the intercrop model simulating species interaction in intercropping (all cultivars and both densities) in grain yield in (t ha^{-a}) and shoot biomass (t ha^{-a}) for both monocultures and intercrops at different growth stages.

Environ-ment	Traits	Develop-ment Stage	Faba bean AME[a]		Spring wheat AME		ΔAME[d]		Model skill	RMSE[g]	
			obs[b]	sim[c]	obs	sim	obs	sim		IM[e]	B[f]
CKA2020	Grain	Maturity	−0.79	−0.46	0.66	0.79	1.45	1.25	0.92	0.41	1.40
CKA2021	yield		0.41	0.15	0.84	0.42	0.43	0.27	0.27	0.70	0.83
WG2020			−0.01	−0.37	0.56	0.72	0.57	1.09	0.12	0.55	0.59
CKA2020	Biomass	vegetative	−0.17	−0.08	0.35	0.05	0.52	0.13	0.39	0.44	0.56
		flowering	−0.84	−0.75	1.42	1.09	2.26	1.84	0.81	1.02	2.44
		maturity	−1.21	−1.19	1.50	1.86	2.71	3.05	0.95	0.55	2.77
CKA2021		vegetative	−0.16	−0.03	0.71	0.11	0.88	0.14	0.24	0.70	0.90
		flowering	−0.41	−0.04	1.88	0.41	2.29	0.45	0.25	2.27	2.63
		maturity	0.44	0.12	1.36	0.69	0.92	0.57	0.25	1.40	1.70
WG2020		vegetative	0.02	−0.12	0.06	0.01	0.05	0.13	−0.2	0.11	0.10
		flowering	−0.14	−0.58	0.42	0.81	0.56	1.39	−1.0	0.90	0.60
		maturity	0.14	−0.90	0.57	1.45	0.43	2.34	−9.0	1.90	0.50

[a] Absolute mixture effect;
[b] observed;
[c] simulated;
[d] the difference between the AME of two species;
[e] Intercrop model;
[f] Benchmark and
[g] RMSE IM and RMSE B are root mean squared errors of the intercrop model and the benchmark respectively.

Table 4
Evaluation of the intercrop model in regards to the effect of spring wheat (SW) and faba bean (FB) cultivars on AME of grain yield at three environments. The two SW cultivars for each environment were: CKA2020- KWS starlight vs Anabel; CKA2021: Lennox vs Sonett and WG2020: Lennox vs mix_group 1. The two FB cultivars are Mallory and Fanfare. See Table S1 for the details about the cultivars.

Environment	AME	Cultivar 1		Cultivar 2		ΔAME[d]		Model skill	RMSE[g]	
		AME[a] obs[b]	AME sim[c]	AME obs	AME sim	obs	sim		IM[e]	B[f]
CKA2020	AME_{SW}	0.38	0.72	0.75	0.78	0.37	0.06	0.24	0.34	0.39
CKA2021		0.55	0.39	0.96	0.48	0.41	0.09	0.21	0.45	0.51
WG2020		0.45	0.71	0.66	0.73	0.20	0.02	0.21	0.19	0.21
CKA2020	AME_{FB}	−0.89	−0.46	−0.69	−0.47	0.08	−0.18	−0.02	0.28	0.28
CKA2021		0.1	0.12	0.69	0.16	0.17	−0.05	0.07	0.72	0.75
WG2020		−0.04	−0.37	0.03	−0.37	0.11	−0.01	−0.06	0.12	0.12

[a] Absolute mixture effect;
[b] observed;
[c] simulated;
[d] the difference between the AME of the two cultivars;
[e] Intercrop model;
[f] Benchmark and
[g] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

Table 5
Evaluation of intercrop model in simulating the effect of sowing density of faba bean (FB) and spring wheat (SW) on absolute mixture effect (AME) of grain yield t ha^{-1}[a].

Environment	AME	Low density		High density		ΔAME[d]		Model skill	RMSE[g]	
		AME[a] Obs[b]	AME Sim[c]	AME obs	AME sim	obs	sim		IM[e]	B[f]
CKA2020	AME_{FB}	−0.73	−0.41	−0.85	−0.51	0.12	0.10	0.25	0.18	0.21
CKA2021		0.34	0.17	0.48	0.12	−0.14	0.05	−0.04	0.58	0.57
WG2020		−0.04	−0.34	0.02	−0.41	−0.06	0.07	−1.30	0.16	0.10
CKA2020	AME_{SW}	0.58	0.79	0.73	0.79	−0.15	0.00	0.04	0.26	0.27
CKA2021		0.89	0.34	0.71	0.52	0.18	−0.18	−0.32	0.65	0.56
WG2020		0.48	0.69	0.65	0.74	−0.17	−0.05	0.14	0.24	0.26
CKA2020	AME_{total}	−0.07	0.38	−0.12	0.28	−0.03	0.10	−30.0	0.27	0.23
CKA2021		0.6	0.51	1.19	0.64	0.04	−0.13	−0.09	0.71	0.68
WG2020		0.22	0.36	0.67	0.33	−0.23	0.02	−0.13	0.33	0.31

[a] Absolute mixture effect;
[b] observed;
[c] simulated;
[d] the difference between the AME of two densities;
[e] Intercrop model;
[f] Benchmark and
[g] RMSE IM and RMSE B are respectively root mean squared errors of the intercrop model and the benchmark.

et al., 2017a; Munz et al., 2014a; Githui et al., 2023; Version et al., 2023). To evaluate the model, we introduce an original measure of intercrop model performance, namely a model skill measure that measures model MSE compared to MSE assuming that there is no intercrop effect.

A major objective of the simulation of intercrops is to improve process understanding and to develop a rapid screening tool for possible management strategies. It is therefore important to evaluate how accurately the model can evaluate differences between different management strategies. This has not been done in previous studies but is done here for three major management decisions, namely choice of species, choice of cultivars, and choice of sowing density.

The calibrated and evaluated model, despite its simplifications, is a promising tool to simulate the effects of intercropping systems and, thus, to support their design. This should be of particular interest as experimental capacities are limited to studying the large range of factors and treatments to optimize intercropping systems. Such models can also help to interpret experimental results in terms of crop growth dynamics and resource acquisition. Though only calibrated based on sole crop treatments, the presented intercrop model was able to simulate in-row mixture effects on grain yield, shoot, and root biomass, while considering species and cultivars differences. The relatively simplistic assumptions in the model to account for above and below-ground competition of considered species for resources may be of use for other intercropping systems including other species combinations, but this awaits further testing.

4.1. Capability of the model to simulate intercropping effects

Considering the aboveground plant growth, the intercrop model captured the intercropping effect on most of the variables. The model skill was large for grain yield and above-ground biomass when intercrop effects were large. When intercrop effects were small, which was, in general, the case for plant height and light interception, the benchmark was quite good and the intercrop model often did not perform better. Additionally, we evaluated the model capabilities in terms of simulating the crop species individually, as well as the model performance of the SW and FB under an intercropping system and for different plant densities in terms of above and below-ground biomass production and soil moisture. The field experiment dataset offered substantial opportunities, as data on key variables were collected separately for each species including root biomass, facilitating a comprehensive evaluation of the model. It was assumed that there are no substantial effects of one crop on a given process of another crop, for instance, radiation use efficiency, therefore the model explicitly simulates species interactions and traits' plasticity such as grain yield and biomass due to competition. Evaluating

the intercrop model based on how well the model simulates the intercrop effect on each species in intercropping enables to ensure that the model could be employed for in silico analysis of different species intercropping and management effects as it was used by Launay et al. (2009) and (Githui et al., 2023).

Modeling below-ground resource (water, N) competition is an important element for designing optimal field arrangements for intercropping systems (Gaudio et al., 2019). We have found that the intercrop model has reasonable skill in simulating the effect of intercropping on the topsoil root biomass of each species. As below-ground competition depends strongly on root biomass, the good performance of the intercrop model shows the potential to reasonably capture belowground dynamics in terms of water and nutrient uptake (Table S8). To our knowledge, this is one of the first studies that specifically address below-ground dynamics of root growth and resource uptake of row intercropping systems, which can further help to elucidate competition and complementary effects of intercropping systems.

The intercrop model performance in simulating the AME of soil water content was similar to the benchmark. Both, the measured and the simulated data showed low AME values, meaning that soil water content in intercropping is similar to the average of the two monocultures (SW and FB). There is limited research on water use of intercropping, particularly in row mixed intercropping. Our results suggest that the total water consumption of the intercrop is perhaps similar to the average water consumption of the monocultures. However, the study by Mao. et al. (2012) highlights that actual water use in intercropping from expected use ranged from −13.7 % to +19.8 %. However, since the study is based on a relay intercrop experiment of maize/pea intercrop it is not directly comparable with our design of mixing within the row. Few modeling studies have been published on evaluating competition for soil water in strip intercropping systems (Tan et al., 2020; Miao et al., 2016), but no studies have looked into the competition for soil water in row intercropping.

In the current study, the intercrop model successfully simulated the intercrop effects on key variables such as grain yield, above-ground biomass, and root biomass without re-parametrization for intercropping. This highlights the ability of the intercrop model to simulate interspecific interactions and plant plasticity due to competition (Ajal et al., 2022). In this model, the daily increment in plant growth was regulated by water (TRANRF) and nitrogen availability (nitrogen-limited, NNI). Thus, under limited resources, the competition of one species affects the growth of the other species (Justes et al., 2021). For instance, cereals are highly competitive (Miao et al., 2016) for soil water, resulting in drought stress for intercropped legumes, hence, the plant growth of legumes is limited while that of cereals increases, allowing them to capture more resources. Likewise, under limited nitrogen availability, the growth of cereals can be limited, however, since the legumes fix atmospheric nitrogen and fulfill most of its demand (Klippenstein et al., 2022) they grow faster. Therefore, the ability of the model to capture the traits of plasticity due to intercropping is important because it is relevant for understanding the productivity of species grown in intercrops as compared to sole crops (Ajal et al., 2022).

4.2. Intercrop model performance on simulating management strategies

It was often reported that the performance of intercropping depends on the genotypes and their traits, the environment, and the management (Demie et al., 2022; Paul et. al., 2024). Optimizing species and cultivar combinations allows for maximizing the overall performance of intercropping (Berghuijs et al., 2020). However, the complexity of the interactions in intercropping makes it a challenging task to understand the drivers for high productivity in intercropping.

The intercrop model demonstrated a high skill level, indicating the capability to simulate species differences and intercropping regarding the AME of above-ground biomass and grain yield. The SW cultivar differences observed in the field experiment (lowest and highest observed AME of grain yields) were also reasonably predicted by the intercrop model. Consequently, the model can assist in making informed choices in selecting SW cultivars, optimizing their suitability for intercropping scenarios, and potentially enhancing overall grain yields (Brooker et al., 2015).

Understanding species-interspecific interactions is important in the decision of species choice for intercropping (Cheriere et al., 2020). SW in intercropping exhibited a higher degree of competitiveness than FB hence SW in intercropping was more productive than SW in monoculture, resulting in a consistently positive AME of grain yield and above-ground biomass. A similar response was reported in the literature, where cereals are considered strong competitors in cereal/legumes intercropping (Yu et al., 2016; Paul et al., 2023). On the contrary, FB tended to exhibit a negative AME at CKA2020 and WG2020 which are characterized by drought stress environment, and a positive AME, at CKA2021 which is characterized as a relatively moist environment. This trend is particularly observed in key plant traits such as grain yield and above-ground biomass. The crops grown in 2020 (CKA2020 and WG2020) suffered from drought stress. Under these conditions, SW with its deeper root system (Fig. S7) accessing subsoil water tends to suppress FB. This phenomenon of vigorous rooting system of cereals suppressing legume intercropping was demonstrated in Corre-Hellou and Crozat., (2005), and early rapid growth hence resulted in early dominance and legacy effect at a later stage of SW (Paul et al., 2023). Consequently, FB in mixtures faces a disadvantage compared to FB in monocultures, while SW in mixtures takes an advantage over SW monocultures. However, in 2021 (CKA2021), there was an adequate amount of precipitation and thus plant available water, allowing both species to grow almost as well as they do in respective monoculture. Site-specific partner combinations of cereals and legumes together with appropriate management practices are a key element in enhancing total productivity in intercropping (Paul et. al.,2024; Nelson et al., 2021; Zhu et al., 2023). Launay et al. (2009) reported that the relative productivity depended on the selected species and cultivars and environment.

Planting density significantly affects the growth dynamics and overall productivity of intercropping (Hadir et al., 2024). According to Yu et al. (2016) and Paul et al. (2024), higher grain yields in mixed cropping systems are observed at increased sowing densities compared to lower sowing densities. The management strategy sowing density was poorly simulated compared to the benchmark. The model's approach, which relies on considering only initial crop dry weight (seed weight) and the number of plants that emerged per m^2 (model parameter RINPOP) which mainly affects root growth as a proxy for sowing density effects, may be overly simplistic and inadequate in capturing the true complexity of density-dependent processes in plant growth. Consequently, poor simulation results are plausible given these limitations. Therefore, improved equations need to be implemented in the model to simulate the sowing density effect in intercropping. A similar approach is used in the STICS model as mentioned in Brisson et al. (2003) in which plant density introduced as an input parameter corresponds to the density of emerged plants. However, it was not tested if the approach captures the density effect in intercropping.

4.3. Specifications and limitations

Compared to the crop model applied in monocultures, the only new mechanism in the intercrop model is the shading of one species by another, which determines the radiation interception by each species. The model was able to simulate the competition for and complementary use of water and N by the two intercropped species. Each species takes up water and N as in the monocultures models depending on the demand, root biomass, root length density, and available soil N and water, but by doing so depletes the amount available for the other species. Biological nitrogen fixation (kg N ha^{-1}) by the legume in the intercrop follows the same equation as for the monoculture but is increased because the cereal reduces available soil N. Thus competition and

complementarity are a consequence of modeling the two species together, without any new mechanisms being required other than competition for light.

A limitation of this study was that the model was evaluated only for the spring wheat-faba bean intercropping dataset, even though this allowed a thorough model evaluation. Expanding the scope by including simulations of intercrops with various other cereals/legumes would enhance the model's applicability. In addition, the field experimental data exhibited high variability among different replicates, with only a few treatments showing significant differences. The preselected SW cultivars used for calibration (key treatments with higher intensity of data collection) had similar characteristics and differed only slightly in plant height and initial biomass. This consequently led to minor differences in simulated values. Additionally, the experiment at the organically managed research station (WG), was partly affected by weed infestation. The weed infestation varied between monocultures and intercrops, leading to high data variability. In the simulation, no component accounted for weed competition, resulting in a disparity between the simulated and observed mixture effects in this specific environment. Additionally, at CKA2021 there was no replication in most of the treatments leading to further uncertainties.

5. Conclusions

The intercropping model based on the soil-crop model LINTUL5 is found to be a promising tool for designing intercropping systems, despite its simplifications. Experiments are limited in the number of treatments but models can help to interpret experimental results in terms of crop growth dynamics and resource acquisition. Calibrated using only data for sole crop treatments, the intercrop model was able to simulate in-row mixture effects on grain yield, shoot, and root biomass, while considering species and cultivar differences. The intercrop model demonstrated a high skill level, underlining the capability to simulate species differences and intercrop performance regarding the AME of above-ground biomass and grain yield. The effect of SW cultivar choice was also reasonably predicted by the intercrop model. The limitations of using a soil-crop model to design intercropping systems must however be kept in mind. It must also be considered that many of the hoped-for benefits of intercropping, such as increased biodiversity or reduced weed populations, are not simulated by crop models. Crop models can be an important aid in intercrop design, but will need to be coupled with other considerations.

Funding

The presented study has been funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy-EXC 2070-390732324 (PhenoRob) as well as by the European Union (EU horizon project IntercropVALUES, grant agreement No 101081973).

CRediT authorship contribution statement

Daniel Wallach: Writing – review & editing, Methodology. **Thomas F. Döring:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization. **Frank Ewert:** Methodology, Funding acquisition, Conceptualization. **Thomas Gaiser:** Writing – review & editing, Methodology. **Ixchel M. Hernández-Ochoa:** Writing – review & editing. **Rémi Vezy:** Writing – review & editing. **Sabine J. Seidel:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization. **Dereje T. Demie:** Writing – original draft, Visualization, Formal analysis, Data curation. **Sofia Hadir:** Writing – review & editing, Data curation. **Gunther Krauss:** Writing – review & editing, Software, Methodology. **Madhuri Paul:** Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109302.

References

Addiscott, T.M., Heys, P.J., Whitmore, A.P., 1986. Application of simple leaching models in heterogeneous soils. Geoderma 38, 185–194. https://doi.org/10.1016/0016-7061(86)90014-5.

Addiscott, T.M., Whitmore, A.P., 1991. Simulation of solute leaching in soils of differing permeabilities. Soil Use Manag 7, 94–102. https://doi.org/10.1111/j.14752743.1991.tb00856.x.

Ajal, J., Kiær, L.P., Pakeman, R.J., Scherber, C., Weih, M., 2022. Intercropping drives plant phenotypic plasticity and changes in functional trait space. Basic Appl. Ecol. 61, 41–52. https://doi.org/10.1016/j.baae.2022.03.009.

Annicchiarico, P., Collins, R.P., De Ron, A.M., Firmat, C., Litrico, I., Hauggaard-Nielsen, H., 2019. Do we need specific breeding for legume-based mixtures? Advances in Agronomy, 1st ed. Elsevier Inc. https://doi.org/10.1016/bs.agron.2019.04.001.

Asseng, S., Martre, P., Ewert, F., Dreccer, M.F., Beres, B.L., Reynolds, M., Braun, H.J., Langridge, P., Le Gouis, J., Salse, J., Baenziger, P.S., 2019. Model-driven multidisciplinary global research to meet future needs: The case for "improving radiation use efficiency to increase yield.". Crop Sci. 59, 843–849. https://doi.org/10.2135/cropsci2018.09.0562.

Barej, J.A.M., Pätzold, S., Perkons, U., Amelung, W., 2014. Phosphorus fractions in bulk subsoil and its biopore systems. Eur. J. Soil Sci. 65, 553–561 https://doi.org/10.1111/ejss.12124.

Baumann, D.T., Bastiaans, L., Goudriaan, J., Van Laar, H.H., Kropff, M.J., 2002. Analysing crop yield and plant quality in an intercropping system using an eco-physiological model for interplant competition. Agric. Syst. 73, 173–203. https://doi.org/10.1016/S0308-521X(01)00084-1.

Berghuijs, H.N.C., Wang, Z., Stomph, T.J., Weih, M., Van der Werf, W., Vico, G., 2020. Identification of species traits enhancing yield in wheat-faba bean intercropping: development and sensitivity analysis of a minimalist mixture model. Plant Soil 455, 203–226. https://doi.org/10.1007/s11104-020-04668-0.

Berghuijs, H.N.C., Weih, M., van der Werf, W., Karley, A.J., Adam, E., Villegas-Fernández, Á.M., Kiær, L.P., Newton, A.C., Scherber, C., Tavoletti, S., Vico, G., 2021. Calibrating and testing APSIM for wheat-faba bean pure cultures and intercrops across Europe. F. Crop. Res. 264. https://doi.org/10.1016/j.fcr.2021.108088.

Brandmeier, J., Reininghaus, H., Scherber, C., 2023. Multispecies crop mixtures increase insect biodiversity in an intercropping experiment. Ecol. Solut. Evid. 4, 1–12. https://doi.org/10.1002/2688-8319.12267.

Brisson, N., Gary, C., Justes, E., Roche, R., Mary, B., Ripoche, D., Zimmer, D., Sierra, J., Bertuzzi, P., Burger, P., Bussière, F., Cabidoche, Y.M., Cellier, P., Debaeke, P., Gaudillère, J.P., Hénault, C., Maraux, F., Seguin, B., Sinoquet, H., 2003. An overview of the crop model stics. Eur. J. Agron. 18, 309–332. https://doi.org/10.1016/S1161-0301(02)00110-7.

Brooker, R.W., Bennett, A.E., Cong, W.F., Daniell, T.J., George, T.S., Hallett, P.D., Hawes, C., Iannetta, P.P.M., Jones, H.G., Karley, A.J., Li, L., Mckenzie, B.M., Pakeman, R.J., Paterson, E., Schöb, C., Shen, J., Squire, G., Watson, C.A., Zhang, C., Zhang, F., Zhang, J., White, P.J., 2015. Improving intercropping: A synthesis of research in agronomy, plant physiology and ecology. New Phytol 206, 107–117. https://doi.org/10.1111/nph.13132.

Chenu, K., Porter, J.R., Martre, P., Basso, B., Chapman, S.C., Ewert, F., Bindi, M., Asseng, S., 2017. Contribution of Crop Models to Adaptation in Wheat. Trends Plant Sci. 22, 472–490. https://doi.org/10.1016/j.tplants.2017.02.003.

Cheriere, T., Lorin, M., Corre-Hellou, G., 2020. Species choice and spatial arrangement in soybean-based intercropping: Levers that drive yield and weed control. F. Crop. Res. 256, 107923. https://doi.org/10.1016/j.fcr.2020.107923.

Chimonyo, V.G.P., Modi, A.T., Mabhaudhi, T., 2016. Water use and productivity of a sorghum-cowpea-bottle gourd intercrop system. Agric. Water Manag. 165, 82–96. https://doi.org/10.1016/j.agwat.2015.11.014.

Corre-Hellou, G., Crozat, Y., 2005. Assessment of root system dynamics of species grown in mixtures under field conditions using herbicide injection and 15N natural abundance methods: A case study with pea, barley and mustard. Plant Soil 276, 177–192 https://doi.org/10.1007/s11104005-4275-z.

Demie, D.T., Döring, T.F., Finckh, M.R., van der Werf, W., Enjalbert, J., Seidel, S.J., 2022. Mixture × Genotype Effects in Cereal/Legume Intercropping. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.846720.

Enders, A., Vianna, M., Gaiser, T., Krauss, G., Webber, H., Srivastava, A.K., Seidel, S.J., Tewes, A., Rezaei, E.E., Ewert, F., 2023. Spec. Issue.: Integr. multiscale Model. SIMPLACE — a versatile Model. Simul. Framew. Sustain. Crops agroecosystems 1–18. https://doi.org/10.1093/insilicoplants/diad006.

Fischer, J., Böhm, H., Heβ, J., 2020. Maize-bean intercropping yields in Northern Germany are comparable to those of pure silage maize. Eur. J. Agron. 112, 125947 https://doi.org/10.1016/j.eja.2019.125947.

Gaudio, N., Escobar-Gutiérrez, A.J., Casadebaig, P., Evers, J.B., Gérard, F., Louarn, G., Colbach, N., Munz, S., Launay, M., Marrou, H., Barillot, R., Hinsinger, P., Bergez, J. E., Combes, D., Durand, J.L., Frak, E., Pagès, L., Pradal, C., Saint-Jean, S., Van Der Werf, W., Justes, E., 2019. Current knowledge and future research opportunities for modeling annual crop mixtures. A review. Agron. Sustain. Dev. 39 https://doi.org/10.1007/s13593-019-0562-6.

Githui, F., Jha, V., Thayalakumaran, T., Christy, B.P., Leary, G.J.O., 2023. Resource sharing in intercropping models and a case study with APSIM in southern Australia. Eur. J. Agron. 142, 126680. https://doi.org/10.1016/j.eja.2022.126680.

Gou, F., van Ittersum, M.K., van der Werf, W., 2017b. Simulating potential growth in a relay-strip intercropping system: Model description, calibration and testing. F. Crop. Res. 200, 122–142. https://doi.org/10.1016/j.fcr.2016.09.015.

Gou, F., van Ittersum, M.K., Simon, E., Leffelaar, P.A., van der Putten, P.E.L., Zhang, L., van der Werf, W., 2017a. Intercropping wheat and maize increases total radiation interception and wheat RUE but lowers maize RUE. Eur. J. Agron. 84, 125–139. https://doi.org/10.1016/j.eja.2016.10.014.

Krauss, G., 2018 SplitWaterUptake ⟨https://simplace.net/doc/5.0/simplace_modules/net/simplace/sim/components/experimental/intercropping/SplitWaterUptake.html⟩.

Hadir, S., Döring, T.F., Justes, E., Demie, D.T., Paul, M., Legner, N., Kemper, R., Gaiser, T., Weedon, O., Ewert, F., Seidel, S.J., 2024. Root growth and belowground interactions in spring wheat - faba bean intercrops. Plant Soil https://doi.org/10.1007/s11104-024-06742-3.

IUSS Working Group WRB 2006. World Reference Base for Soil Resources 2006. World Soil Resources Report No 103, FAO, Rome.

Jensen, E.S., 1996. Grain yield, symbiotic N2 fixation and interspecific competition for inorganic N in pea-barley intercrops. Plant Soil 182, 25–38. https://doi.org/10.1007/BF00010992.

Justes, E., Bedoussac, L., Dordas, C., Frak, E., Louarn, G., Boudsocq, S., Journet, E.P., Lithourgidis, A., Pankou, C., Zhang, C., Carlsson, G., Jensen, E.S., Watson, C., Li, L., 2021. the 4C Approach As a Way To Understand Species Interactions Determining Intercropping Productivity. Front. Agric. Sci. Eng. 8. https://doi.org/10.15302/J-FASE-2021414.

Kemper, R., Döring, T.F., Legner, N., Meinen, C., Athmann, M., 2023. Oil radish, winter rye and crimson clover: root and shoot performance in cover crop mixtures. Plant Soil. https://doi.org/10.1007/s11104-023-06240-y.

Klippenstein, S.R., Khazaei, H., Vandenberg, A., Schoenau, J., 2022. Nitrogen and phosphorus uptake and nitrogen fixation estimation of faba bean in western Canada. Agron. J. 114, 811–824 https://doi.org/10.1002/agj2.20945.

Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. Ecol. Soc. 17 https://doi.org/10.5751/ES-05035-170440.

Launay, M., Brisson, N., Satger, S., Hauggaard-Nielsen, H., Corre-Hellou, G., Kasynova, E., Ruske, R., Jensen, E.S., Gooding, M.J., 2009. Exploring options for managing strategies for pea-barley intercropping using a modeling approach. Eur. J. Agron. 31, 85–98 https://doi.org/10.1016/j.eja.2009.04.002.

Li, Chunjie, Stomph, T.J., Makowski, David, Li, Haigang, Zhang, Chaochun, Zhang, Fusuo, Wopke Van der Werf, 2023. The productive performance of intercropping. Proc. Natl. Acad. Sci. 120. https://doi.org/10.1073/pnas.2201886120.

Lithourgidis, A.S., Dordas, C.A., Damalas, C.A., Vlachostergios, D.N., 2011. Annual intercrops: An alternative pathway for sustainable agriculture. Aust. J. Crop Sci. 5, 396–410 https://search.informit.org/doi/10.3316/informit.281409060336481.

Malagoli, P., Naudin, C., Vrignon-Brenas, S., Sester, M., Jeuffroy, M.H., Corre-Hellou, G., 2020. Modelling nitrogen and light sharing in pea-wheat intercrops to design decision rules for N fertilisation according to farmers' expectations. F. Crop. Res. 255. https://doi.org/10.1016/j.fcr.2020.107865.

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., De Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: Concepts, tools and models. A review. Agron. Sustain. Dev. 29, 43–62. https://doi.org/10.1051/agro:2007057.

2021 Krauss. G., 2021. BelowGroundAllocation ⟨https://simplace.net/doc/5.0/simplace_modules/net/simplace/sim/components/experimental/intercropping/BelowgroundAllocationFactor.html⟩.

Mao, L., Zhang, L., Li, W., van der Werf, W., Sun, J., Spiertz, H., Li, L., 2012. Yield advantage and water saving in maize/pea intercrop. F. Crop. Res. 138, 11–20. https://doi.org/10.1016/j.fcr.2012.09.019.

Meier, U., 2001. Growth stages of mono-and dicotyledonous plants: BBCH Monograph In: Fed. Biol. Res. Cent. Agric. For., 2nd ed., 49, pp. 66–70. https://doi.org/10.5073/20180906-074619

Miao, Q., Rosa, R.D., Shi, H., Paredes, P., Zhu, L., Dai, J., Gonçalves, J.M., Pereira, L.S., 2016. Modeling water use, transpiration and soil evaporation of spring wheat-maize and spring wheat-sunflower relay intercropping using the dual crop coefficient approach. Agric. Water Manag. 165, 211–229. https://doi.org/10.1016/j.agwat.2015.10.024.

Monteith, J.L., and Moss C.J. 1977. Climate and the Efficiency of Crop Production in Britain. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, Vol. 281, No. 980, The Ma. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 281, 277–294. http://www.jstor.org/stable/2417832.

Munz, S., Feike, T., Chen, Q., Claupein, W., Graeff-Hönninger, S., 2014. Understanding interactions between cropping pattern, maize cultivar and the local environment in strip-intercropping systems. Agric. For. Meteorol. 195–196, 152–164. https://doi.org/10.1016/j.agrformet.2014.05.009.

Nelson, W.C.D., Siebrecht-Schöll, D.J., Hoffmann, M.P., Rötter, R.P., Whitbread, A.M., Link, W., 2021. What determines a productive winter bean-wheat genotype combination for intercropping in central Germany? Eur. J. Agron. 128. https://doi.org/10.1016/j.eja.2021.126294.

Paul, M.R., Demie, D.T., Seidel, S.J., Döring, T.F., 2023. Effects of spring wheat / faba bean mixtures on early crop development. Plant Soil. https://doi.org/10.1007/s11104-023-06111-6.

Paul, M.R., Demie, D.T., Seidel, S.J., Döring, T.F., 2024. Evaluation of multiple spring wheat cultivars in diverse intercropping systems. Eur. J. Agron. 152. https://doi.org/10.1016/j.eja.2023.127024.

Pierre, J.F., Singh, U., Ruiz-Sánchez, E., Pavan, W., 2023. Development of a Cereal–Legume Intercrop Model for DSSAT Version 4.8. Agric 13. https://doi.org/10.3390/agriculture13040845.

Pinto, V.M., van Dam, J.C., de Jong van Lier, Q., Reichardt, K., 2019. Intercropping simulation using the SWAP model: Development of a 2x1D algorithm. Agric 9. https://doi.org/10.3390/agriculture9060126.

Seidel, S.J., Gaiser, T., Kautz, T., Bauke, S.L., Amelung, W., Barfus, K., Ewert, F., Athmann, M., 2019. Estimation of the impact of precrops and climate variability on soil depth-differentiated spring wheat growth and water, nitrogen and phosphorus uptake. Soil Tillage Res 195, 104427. https://doi.org/10.1016/j.still.2019.104427.

Seidel, S.J., Palosuo, T., Thorburn, P., Wallach, D., 2018. Towards improved calibration of crop models – Where are we now and where should we go? Eur. J. Agron. 94, 25–35. https://doi.org/10.1016/j.eja.2018.01.006.

Seidel, S.J., Rachmilevitch, S., Schütze, N., Lazarovitch, N., 2016. Modelling the impact of drought and heat stress on common bean with two different photosynthesis model approaches. Environ. Model. Softw 81, 111–121. https://doi.org/10.1016/j.envsoft.2016.04.001.

Shili-Touzi, I., De Tourdonnet, S., Launay, M., Dore, T., 2010. Does intercropping winter wheat (Triticum aestivum) with red fescue (Festuca rubra) as a cover crop improve agronomic and environmental performance? A modeling approach. F. Crop. Res. 116, 218–229. https://doi.org/10.1016/j.fcr.2009.11.007.

Stöckle, C.O., Kemanian, A.R., 2020. Can Crop Models Identify Critical Gaps in Genetics, Environment, and Management Interactions? Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00737.

Tan, M., Gou, F., Stomph, T.J., Wang, J., Yin, W., Zhang, L., Chai, Q., van der Werf, W., 2020. Dynamic process-based modelling of crop growth and competitive water extraction in relay strip intercropping: Model development and application to wheat-maize intercropping. F. Crop. Res. 246. https://doi.org/10.1016/j.fcr.2019.107613.

Tribouillois, H., Cohan, J.P., Justes, E., 2016. Cover crop mixtures including legume produce ecosystem services of nitrate capture and green manuring: assessment combining experimentation and modelling. Plant Soil 401, 347–364. https://doi.org/10.1007/s11104-015-2734-8.

Tsubo, M., Walker, S., Ogindo, H.O., 2005. A simulation model of cereal-legume intercropping systems for semi-arid regions: I. Model development. F. Crop. Res. 93, 10–22. https://doi.org/10.1016/j.fcr.2004.09.002.

Version, D., Pierre, J.F., Singh, U., 2023. Development of a Cereal–Legume Intercrop Model for DSSAT Version 4.8. Agriculture. https://www.mdpi.com/2077-0472/13/4/845.

Vandermeer, JH., 1989. Introduction. The Ecology of Intercropping. Cambridge University Press, Cambridge, pp. 1–14. https://doi.org/10.1017/CBO9780511623523.

Vezy, R., Munz, S., Gaudio, N., Launay, M., Lecharpentier, P., Ripoche, D., Justes, E., 2023. Modeling soil-plant functioning of intercrops using comprehensive and generic formalisms implemented in the STICS model. Agron. Sustain. Dev. 43. https://doi.org/10.1007/s13593-023-00917-5.

Wallach, D., Makowski, D., Jones, J.W., Brun, F. (Eds.), 2019. Working with dynamics crop models. Academic Press.

Whitmore, A.P., Schröder, J.J., 2007. Intercropping reduces nitrate leaching from under field crops without loss of yield: A modelling study. Eur. J. Agron. 27, 81–88. https://doi.org/10.1016/j.eja.2007.02.004.

Xu, Y., Qiu, W., Sun, J., Müller, C., Lei, B., 2019. Effects of wheat/faba bean intercropping on soil nitrogen transformation processes. J. Soils Sediment. 19, 1724–1734. https://doi.org/10.1007/s11368-018-2164-3.

Wolf, 2012. User guide for Lintul5: Simple generic model for simulation of crop growth under potential, water limited and nitrogen, phosphorus and potassium limited conditions.

Yang, J.M., Yang, J.Y., Liu, S., Hoogenboom, G., 2014. An evaluation of the statistical methods for testing the performance of crop models with observed data. Agric. Syst. 127, 81–89. https://doi.org/10.1016/j.agsy.2014.01.008.

Yu, Y., Stomph, T.J., Makowski, D., Zhang, L., van der Werf, W., 2016. A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management. F. Crop. Res. 198, 269–279. https://doi.org/10.1016/j.fcr.2016.08.001.

Zhu, S.G., Zhu, H., Zhou, R., Zhang, W., Wang, W., Zhou, Y.N., Wang, B.Z., Yang, Y.M., Wang, J., Tao, H.Y., Xiong, Y.C., 2023. Intercrop overyielding weakened by high inputs: Global meta-analysis with experimental validation. Agric. Ecosyst. Environ. 342, 108239. https://doi.org/10.1016/j.agee.2022.108239.