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The ongoing journey of modelling intercropping systems: A conceptual resource sharing intercomparison from model developers and expert users

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ABSTRACT

Context: The global shift toward sustainable agriculture has increased interest in using process-based models to design and optimize intercropping systems. However, these models differ fundamentally in how they represent trade-offs (competition for light, water, and nutrients) and synergies (facilitation, complementarity) in resource sharing between species. This conceptual variation creates uncertainty in model selection and application, particularly since most models were originally developed for monoculture and subsequently adapted for intercropping.

Objective: In this study, we describe how current crop models represent interspecies resource-sharing mechanisms, analyse their structural differences, and synthesize findings from existing validation studies to understand how their structural differences affect model performance. The models examined include APSIM (APSIM-Canopy, APSIM-Micromet, APSIM-Strip, APSIM-Alternating, APSIM-APSwim, APSIM-SoilArbitrator), DayCent, DSSAT-Mixed, DSSAT-MPI, LandscapeDNDC, LUCIA, MONICA, SIMPLACE Lintul5-Intercrop, STICS-Big-Leaf, STICS-Multilayer, and WaNuLCAS.

Methods: Through the Agricultural Model Intercomparison and Improvement Project (AgMIP) platform, we engaged with model developers and expert users to collect detailed information on how crop models represent intercropping systems using structured interviews and questionnaires. We then developed a framework that groups models by their core conceptual approaches to simulating resource sharing. Finally, we synthesize findings from existing quantitative validation studies to connect conceptual intercomparison to predictive performance across different intercrop characteristics and environments.

Results and Conclusions: Our analysis identifies six distinct conceptual approaches for simulating light sharing and four for belowground resource (water and nutrient) competition. Intercrop models show greater structural divergence in canopy than in belowground representation. Furthermore, competitive trade-offs (light, water, and nutrients) are widely represented while facilitative and other complex processes like N_2-fixation, plasticity (shoot and root), microclimate effects or hydraulic lift are often simplified or omitted. Our analysis of model validation studies reveals a critical trade-off: structurally complex models often perform well in simulating intercropping when calibration is done on sole crops, whereas simpler models require extensive intercrop-specific calibration to achieve better prediction performance. This distinction is vital for model application in data-scarce environments, as more complex architectures can leverage existing sole-crop data to effectively simulate intercrop systems. The classification of the structural resource capture differences in combination with the evaluated model performance analysis allowed us to devise an evidence-based model selection criteria framework useful also for for non-specialist, while the unique detailed description provided are highly valuable for the model research community.

Significance: This study establishes a conceptual framework that provides the necessary foundation for a meaningful quantitative intercomparison of intercrop models, as structural understanding enables the interpretation of numerical differences in model outputs. It also guides hypothesis testing, model choice, priorities in model development and improvements.

1. Introduction

In recent decades, there has been a growing interest in intercropping systems driven by the push toward sustainable agriculture. This historical practice of growing two or more crops simultaneously in the same field has the potential to enhance soil health through improved organic matter cycling and microbial activity (Nyawade et al., 2020; Peng et al., 2024; Xiao et al., 2023), increase biodiversity (Huss et al., 2022), increase efficiency in the use of resources (Willey, 1990; Zhang and Li, 2003), provide potential for effective pest and weed management (Liebman and Dyck, 1993), build greater resilience to climate shocks and crop failure (Adam et al., 2025; Raseduzzaman and Jensen, 2017), and enhance nutritional quality in harvested crops (Nyagumbo et al., 2025). Despite mounting evidence of intercropping benefits, the complex ecological and management interactions inherent in these systems have limited their large-scale adoption across diverse environments globally.

An approach to address these complex interactions and support scaling of intercropping systems lies in the application of crop models. Crop models have been successfully used for decades to optimize production in conventional agricultural practices or monocultures (Basso et al., 2016; Boote et al., 1998; Hansen et al., 1991; Jones and Kiniry, 1986; Keating et al., 2003; Otter and Ritchie, 1985; van Diepen et al., 1989). When applied to intercropping (e.g., Corre-Hellou et al., 2009; Shili-Touzi et al., 2010), crop models can help researchers understand the complex interactions between different plant species, test several management scenarios, design new experiments, and explore the impact of intercropping systems under new environments or climate conditions. This supports developing a better understanding of when, where, and under which combinations the synergies gained by mixing crops outweigh the trade-offs.

The number of crop models capable of simulating intercropping has grown rapidly in recent years. For instance, established single-crop models like DSSAT (Hoogenboom et al., 2024; Jones et al., 2003), MONICA (Nendel et al., 2011), SIMPLACE Lintul5 (Enders et al., 2023) and STICS (Brisson et al., 2003) have been modified to expand their capabilities for simulating intercrops . Similarly, landscape models like LUCIA (Marohn et al., 2013a) and LandscapeDNDC (Haas et al., 2013) have been adapted to simulate intercropping. LUCIA was originally designed for sole-cropped annuals with simplified tree representation. However, this expansion reveals a core limitation: while the intercropping sub-routines are now integrated into these models, their capabilities to simulate different forms of intercropping such as mixed (random), row arrangements, strip or relay cropping are not well-documented in the literature.

Moreover, evidence from recent model evaluations reveals that intercropping models continue to struggle with intricate interactions across diverse geographies and farming systems. For example, the

APSIM-Canopy module inaccurately simulates Leaf Area Index (LAI) development because it assumes a sigmoidal relationship with thermal time, which is inconsistent with observed patterns that follow a power function form (Chimonyo et al., 2016). Similarly, challenges in simulating wheat-faba bean intercrops across European locations using APSIM-Canopy might be linked to limitations in capturing the dynamics of species with similar heights and handling the low solar angles characteristic of temperate regions (Berghuijs et al., 2021).

In a more recent evaluation, Demie et al. (2025) provided an insightful illustration of these challenges with a new intercrop model based on Lintul5 within the SIMPLACE framework. The model successfully simulated the overall effects on grain yield and biomass but not the key underlying processes such as the fraction of intercepted radiation, soil water content, and root biomass. This example directly illustrates a critical limitation: models may produce accurate final outcomes while fundamentally misrepresenting the biological and physical processes involved. This phenomenon is known as compensating errors (getting the right answers for the wrong reasons).

Adding to the structural problems identified in existing intercrop model evaluation studies, there are now different models available, each with its own approach and often overlapping capabilities. This makes choosing the right intercrop model harder, not easier. The question has shifted from simply asking "What can the model do?" to the much more challenging "Which of these many models is best suited for a particular intercropping system?" This creates a selection paradox, as each model has its own strengths and weaknesses that essentially make it a specialist, not a generalist.

The risk of comparing "apples and oranges" is amplified when users lack detailed descriptions of what the models can and cannot do and how different models address intercropping, particularly the specifics of aboveground versus belowground resource sharing. Therefore, the scientific community faces a dual challenge: not only to develop crop models that include more processes for interspecies interactions, but also to establish a rigorous benchmarking system to clearly define and communicate the specific type and degree of intercropping complexity each model can handle. Establishing such a framework is not merely an academic exercise; it is a prerequisite for understanding why models give different results based on their structural differences. Such an analysis can guide efforts to identify the weaknesses of existing intercrop models and to provide a foundation for developing more reliable intercrop models, particularly when using multiple models to inform agricultural policy.

Although previous review studies on intercropping modelling have provided overviews of how some models represent interspecies interactions (Chimonyo et al., 2015; Gaudio et al., 2019; Githui et al., 2023), they often fall short of giving detailed descriptions of how key processes are actually incorporated. This includes missing information about core concepts, assumptions, key equations, parameters, and conceptual similarities and differences. Without these details, the crop modelling community lacks a complete understanding of what existing models can do.

Therefore, understanding the conceptual basis of different modelling approaches is a prerequisite for meaningful quantitative model comparison. Before models can be compared empirically, we must understand what they represent, what assumptions they embody, and what processes they include or exclude. This enables interpretation of quantitative differences, diagnosis of why models differ, and identification of priorities for model improvement and development.

In this study, we provide a state-of-the-art overview of 16 crop models with intercropping capabilities through direct engagement with their developers and expert users. We analyse how each model represents aboveground and belowground resource sharing, identify key differences in modelling approaches and evaluate capabilities and limitations. Finally, we synthesize these findings with existing evidence from model validation studies to generate specific hypotheses that can guide future empirical quantitative model intercomparison.

2. Methodology

2.1. Model overview and classification

This study utilized the Agricultural Model Intercomparison and Improvement Project (AgMIP) platform (https://agmip.org) to engage with crop modelling teams, representing nine distinct crop models: APSIM (Keating et al., 2003), DayCent (Parton et al., 1998), DSSAT (Hoogenboom et al., 2024; Jones et al., 2003), LandscapeDNDC (Haas et al., 2013), LUCIA (Marohn et al., 2013a), MONICA (Nendel et al., 2011), SIMPLACE Lintul-Intercrop (Demie et al., 2025), STICS (Brisson et al., 2003), and WaNuLCAS (van Noordwijk and Lusiana, 1998).

For three models (APSIM, DSSAT, and STICS), multiple configurations were identified based on their approaches to simulating intercropping systems, resulting in 16 participating models (Table 1). APSIM accounts for five configurations: APSIM-Canopy, APSIM-Micromet, APSIM-Strip, APSIM-APSwim, and APSIM-SoilArbitrator. DSSAT includes two configurations: DSSAT-Mixed, which is part of the unreleased DSSAT v4.8.5, and DSSAT-MPI, which simulates competition externally between two crop modules using the Message Passing Interface (Pierre et al., 2023). STICS had two configurations: STICS-Big-Leaf and STICS-Multilayer (Vezy et al., 2023).

Each participating modelling group was asked to provide detailed and comprehensive explanations of interspecies representations in their entirety. This included descriptions of the core concepts and model structure, underlying assumptions, key equations, and driving variables influencing multispecies interactions. To facilitate this, an online survey questionnaire was used (see Supplementary Table S1 for details).

We developed a flexible framework for comparison, grounded in the concepts and assumptions underlying interspecies interactions. We examined how each model represents canopy structure, root architecture, and resource competition. For example, intercrop models that divide the canopy into vertical layers are grouped under the "layered canopy approach," while those focusing on how taller species shade shorter ones were classified as the "shading-centric" (Fig. 3). Similarly, for water and nutrient sharing, models using partial interspecies competition or empirical parameters were grouped as the "empirical or partial interspecies competition approach", whereas those partitioning resources based on root distribution were classified under the "resource allocation based on root growth approach". This framework forms the basis of our conceptual intercomparison in the results section, providing a clearer understanding of the fundamental similarities and differences between models.

Within each identified modelling approach, we categorized the intercrop models as simple, intermediate, or complex based on their parameterization requirements and spatial resolution (Supplementary Table S2). For light competition, simple models are characterized by a low parameter demand and adopt a minimalist framework, assuming a single homogeneous canopy where species compete for a unified pool of light. Intermediate models, which have a moderate parameterization requirement, introduce greater spatial detail for instance, by resolving the canopy into discrete vertical or horizontal zones. In contrast, complex models feature the highest resolution of canopy architecture, a characteristic that allows for more detailed process simulation but is coupled with a need for intensive parameterization. A similar classification was applied to belowground competition models. Simple approaches simulate competition for water and nutrients via indirect methods, rather than by modelling direct root interactions. Intermediate models incorporate a greater degree of spatial realism, for example by accounting for the vertical distribution of roots within the soil profile. Complex models had the better resolutions for belowground representation for interspecies competition with high demand for parameterization.

Table 1
Overview of the process-based crop models included in this study, including model abbreviations, main references, and capabilities for simulating interspecies dynamics and competitive interactions.

Model	Model abbreviation	Main reference (s)	Diversified systems	Intercropping patterns	Interspecies competition	Row orientation	Multispecies N fixation	Plasticity effects	Hydraulic lift
APSIM	APSIM-Canopy	Carberry et al. (1996); Keating et al. (2003)	I	M	L	na	Y	na	na
APSIM	APSIM-Micromet	Snow and Huth (2004)	I	M	L/W	na	Y	na	na
APSIM	APSIM-Strip	Guo et al. (2024); Wu et al. (2021)	I	S	L/W/N	Y	Y	na	na
APSIM	APSIM-APSwim	Huth et al. (2012)	A/I	M/S	W/N	na	Y	na	Y
APSIM	APSIM-SoilArbitrator	Holzworth et al. (2014)	A/I	M/S	W/N	Y	Y	na	Y
APSIM	APSIM-Alternating	Carberry et al. (1996)	I	M	W/N	na	Y	na	na
DayCent	DayCent	Parton et al. (1998)	A/I	M/R/S	L/W/N	na	E	na	na
DSSAT	DSSAT-Mixed	Jones et al. (2003)	I	M	L/W/N	na	Y	na	na
DSSAT	DSSAT-MPI	Jones et al. (2003)	I	S	L	na	na	na	na
LandscapeDNDC	LandscapeDNDC	Haas et al. (2013)	A/I	M	L/W/N	na	Y	na	na
LUCIA	LUCIA	Marohn et al. (2013a)	A/I	M/R/S	L/W/N	Y	Y	SP/RP	na
MONICA	MONICA	Nendel et al. (2011)	I	R	L/W	na	na	na	na
STICS	STICS-Big-Leaf	Brisson et al. (2003)	I	M	L/W/N	Y	Y	na	na
STICS	STICS-Multilayer	Brisson et al. (2003)	I	R/S	L/W/N	Y	Y	na	na
SIMPLACE Lintul5	SIMPLACE Lintul5-Intercop	Enders et al. (2023)	I	M/R/S	L/W/N	Y	Y	SP	na
WaNuLCAS	WaNuLCAS	van Noordwijk and Lusiana, 1998	A/I	R/S	L/W/N	Y	Y	na	Y

Keys: A = agroforestry, I = intercropping, M = mixed planting geometry, R = alternate row arrangement, S = strip planting geometry, L = Interspecies light competition implemented, W = Interspecies water competition implemented, N = Interspecies nutrient(s) competition implemented, Y = process simulated, E = empirically simulated, na = not available (process not simulated), SP = shoot plasticity effect and RP = root plasticity effect. **Note:** APSIM Next Generation framework simulates agroforestry depending on the module plugins used (APSIM-APSwim/ APSIM-SoilArbitrator).

2.2. Analysis of intercrop model validation studies

To complement the conceptual intercomparison and provide quantitative insights into how structural differences among models affect intercropping simulation outputs, we explored and synthesized findings from peer-reviewed literature model validation studies. Our objectives were threefold: (1) to quantify the extent to which each model had been validated across different systems and environments; (2) to examine the relationship between a model's conceptual approach and its performance; and (3) to identify recurring patterns of success or failure that can inform model selection and future quantitative model comparison.

For each validation study, we extracted key information, including the intercrop system (species, spatial design, location), the biophysical processes evaluated (e.g., aboveground biomass, grain yield, leaf area index, soil water dynamics, and nitrogen uptake), and the reported performance statistics (e.g., RMSE, nRMSE, rRMSE, EF, D-index, bias) as listed in Supplementary Table 3. This information was compiled to identify the trade-offs between different modelling approaches and prediction performance.

3. Results

3.1. Overview of the 16 intercrop models

The number of crop models capable of simulating intercropping has grown significantly in recent years (Fig. 1), and these models have been applied globally across diverse species combinations and spatial arrangements (Fig. 2; Supplementary Table 3). The models differ considerably in the types of intercropping systems they can simulate (e.g., annual-annual, agroforestry), the spatial configurations they handle (e.g., mixed, row, strip), and the specific competition processes they include (e.g., light, water, nutrients).

Variation in process representation is evident among the models. For example, DSSAT-MPI simulates only interspecies light competition, whereas MONICA accounts for light and water dynamics (Fig. 1). Some models, such as LUCIA, SIMPLACE Lintul5-Intercrop, STICS-Multilayer, and WaNuLCAS, can additionally simulate the effects of row orientation (e.g., North-South versus East-West).

The APSIM framework exemplifies a particularly modular approach, allowing users to select different plugins for above- and belowground competition based on system characteristics and research objectives. In APSIM Classic (v7.10), users can choose between the APSIM-Canopy module (light competition only) or the APSIM-Micromet module (which adds microclimate effects). For belowground competition, APSIM Classic provides either the APSIM-Alternating module or the APSIM-APSwim module. In contrast, APSIM Next Generation integrates the MicroClimate module (a rebranding of Micromet) and APSIM-Strip for aboveground competition in both 1D and 2D systems, while using the APSIM-SoilArbitrator module for belowground resource sharing. Similarly, STICS-Multilayer (as adapted by Vezy et al., 2023) dynamically adapts its canopy representation, automatically shifting between the STICS-Multilayer and STICS-Big-Leaf approach depending on the

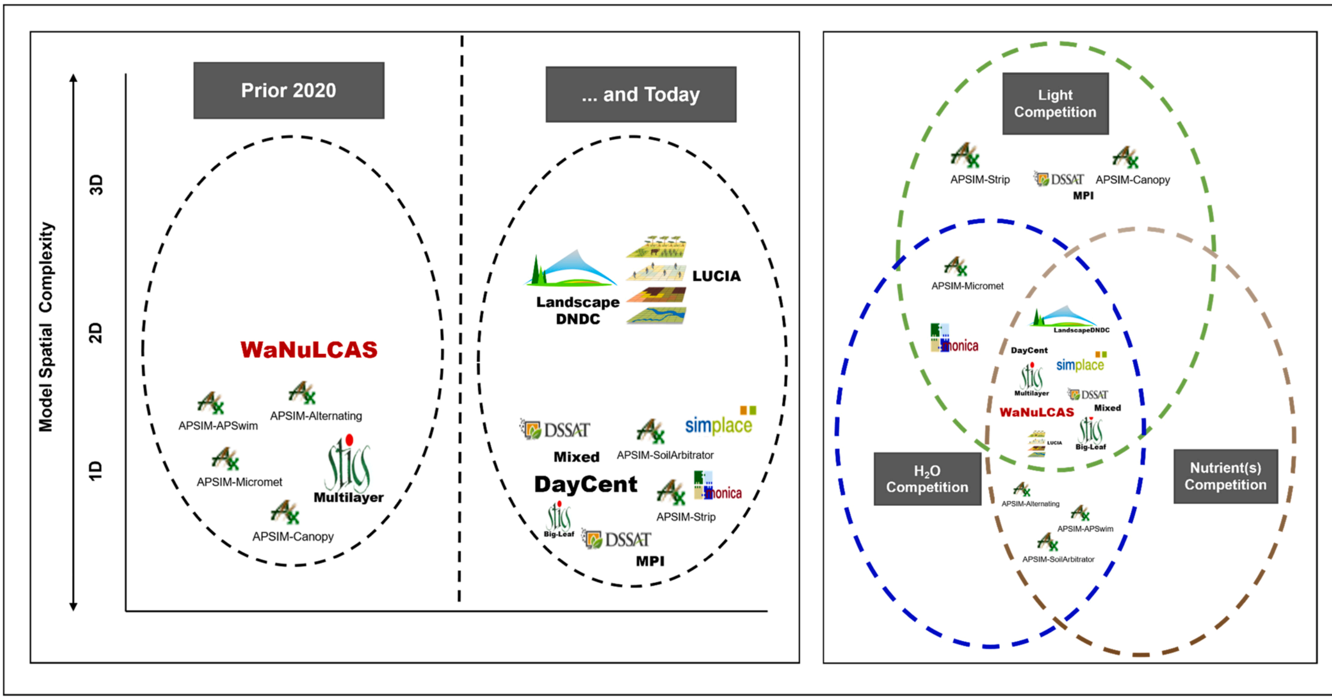

Fig. 1. Advances in modelling intercropping systems over time (left) and in complexity (right). The green dotted circle represents the incorporation of light competition routines, the blue dotted circle signifies water competition routines, and the brown dotted circle illustrates nutrient competition routines.

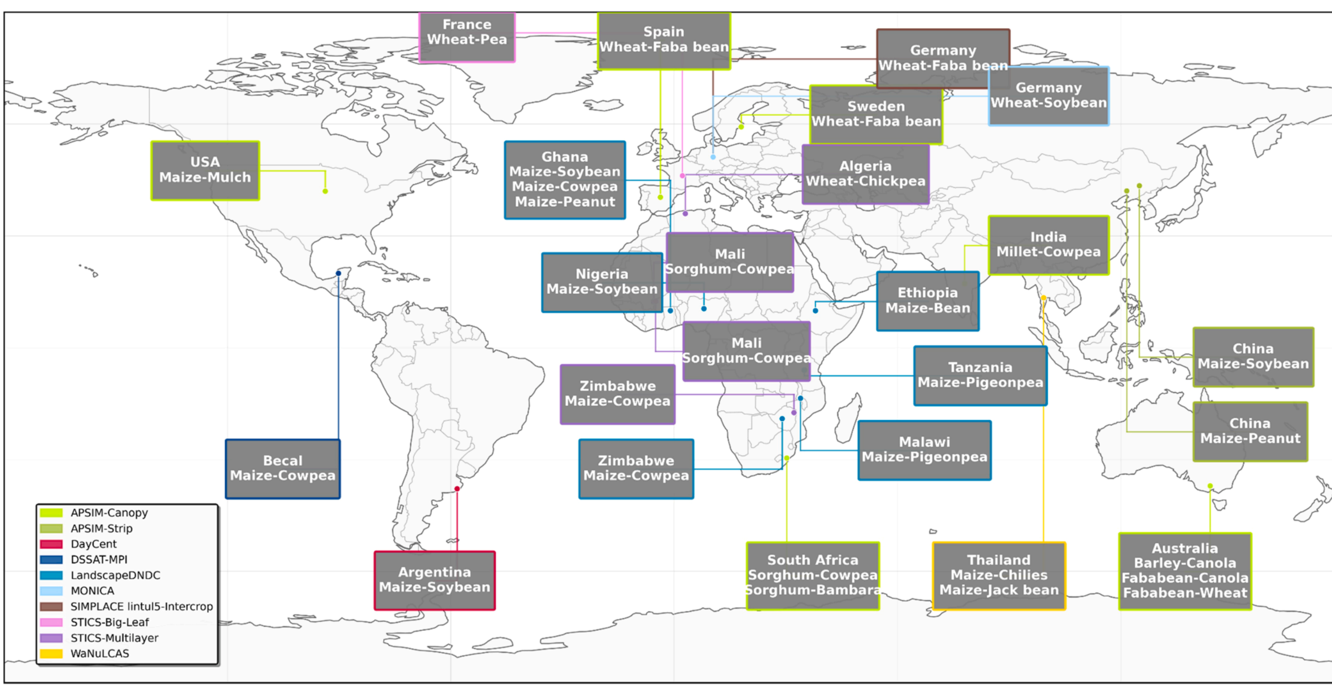

Fig. 2. Example applications of intercrop models across different geography and species combination globally (Supplementary Table 3). Note: DSSAT-Mixed and LUCIA were omitted because they have not yet been formally published in the peer-reviewed literature.

canopy structure. When there is clear dominance from one species canopy, light interception is computed using the multilayer approach. Conversely, when canopies are well mixed and height differences remain below a defined threshold, the model reverts to the Beer–Lambert formulation adapted for intercropping (Vezy et al., 2023).

3.2. Conceptual intercomparison of Intercrop models

In this section, we group the 16 intercrop models into distinct approaches based on their similarities and differences in fundamental assumptions and concepts for representing interspecies resource sharing for light, water, and nutrients. A detailed description of how each model represents intercropping systems, including its conceptual framework,

Table 2

Conceptual intercomparison of the different approaches and models for simulating light competition in an intercropping system, highlighting their key features, light uptake mechanisms, and underlying assumptions. Leaf area index (LAI), light extinction coefficient (k).

Model	Approach	Key features	Light sharing mechanisms	Assumptions
Uniform mixed canopy	STICS-Big-Leaf	Canopies of the two species are uniformly mixed and there is no clear dominance in height	Light interception is averaged across the canopy and shared between the species based on their combined LAI and k	Canopies of the two species are homogenous; uses Beer-Lambert law
Two-layer canopy	MONICA	Canopy divided into two layers based on species height ratio	Light penetrating to the lower layer is shared based on LAI and k	Canopy of species is uniform; uses Beer-Lambert law
Two-layer canopy	STICS-Multilayer	Canopy divided in two pseudo-3D layers (dominant and understorey); understorey divided into sunlit and shaded; direct and diffuse light; shoot plasticity	Light interception by the understorey parts (shaded and sunlit) determined by the fraction of total light intercepted by the dominant crop.	Light competition depends on row orientation, crop shape and inter-row distance; Beer-Lambert law
Three-layer canopy with four horizontal zones	WaNuLCAS	Divides canopy into four spatial zones and three vertical layers (top, middle (shared), lower) based on the relative heights of the species	Penetrating light in the middle-shared layer is proportional to species LAI and k across the four horizontal zones	Competition occurs only in the middle-shared layer; LAI evenly distributed in canopy, uses Beer-Lambert law
Multi layered canopy	APSIM-Canopy	Canopy divided into layers defined by the height of the species	Penetrating light shared proportional to species LAI and k in each canopy layer	LAI vertically distributed using a normalized height function; adapted Beer-Lambert law
Multi layered canopy	APSIM-Micromet	Canopy divided into layers defined by the height of the species; microclimate (canopy conductance, transpiration)	Penetrating light shared proportional to species LAI and k in each canopy layer;	Uniform LAI distribution within each component canopy; adapted Beer-Lambert law; integrates light competition with water demand
Multi layered canopy	DSSAT-Mixed	Divides canopy into fixed layers of 10 cm height	Penetrating light shared proportional to species LAI and k in each canopy layer	Homogenous vertical LAI distribution, Beer-Lambert law
Multi layered canopy	LandscapeDNDC	Divides the canopy into 40 discrete height layers; layer height starts at 2; layer dynamically rescaled when the canopy exceeds the maximum configured height.	Penetrating light shared proportional to species LAI and k in each canopy layer	Homogenous vertical LAI distribution; modified Beer-Lambert law
Shading-centric	DayCent	Simplified empirical shading modifier for the minor crop	Light interception between species adjusted by shading modifier.	Competition regulated by shading modifier based on canopy cover of dominant species
Shading-centric	LUCIA	Geometric shading principle based on daily sun angle and height difference and distance between species; species-specific shade tolerance	Light reaching shorter species is a function of sun shading angle, canopy shape, height and taller species LAI and k.	Canopy assumed to be half-elliptical; sun shading angle affected by row orientation; Beer-Lambert law
Strip-planted canopy	APSIM-Strip	Simplifies strip-planted systems by compressing LAI into rows; view factor quantifies shading between rows	Light interception by the taller and shorter species is a function of view factor to account for shading effects across five growth phases	Light competition is assumed to be regulated by strip width, path width and view factor.
Strip-planted canopy	DSSAT-MPI	Simplifies strip-planted systems by compressing LAI into rows; view factor quantifies shading between rows	Light interception by the taller and shorter species is a function of view factor to account for shading effects across five growth phases	Light competition is assumed to be regulated by strip width, path width and view factor.
Strip-planted canopy	SIMPLACE Lintul5-Intercrop	Simplifies strip-planted systems by compressing LAI into rows; view factor quantifies shading between rows; shoot plasticity	Light interception by the taller and shorter species is a function of view factor to account for shading effects across five growth phases	Light competition is assumed to be regulated by strip width, path width, view factor and canopy diameter.

Note: view factor refers to the reduction of radiation from the sky reaching the understorey species due to the architectural obstruction of the dominant species.

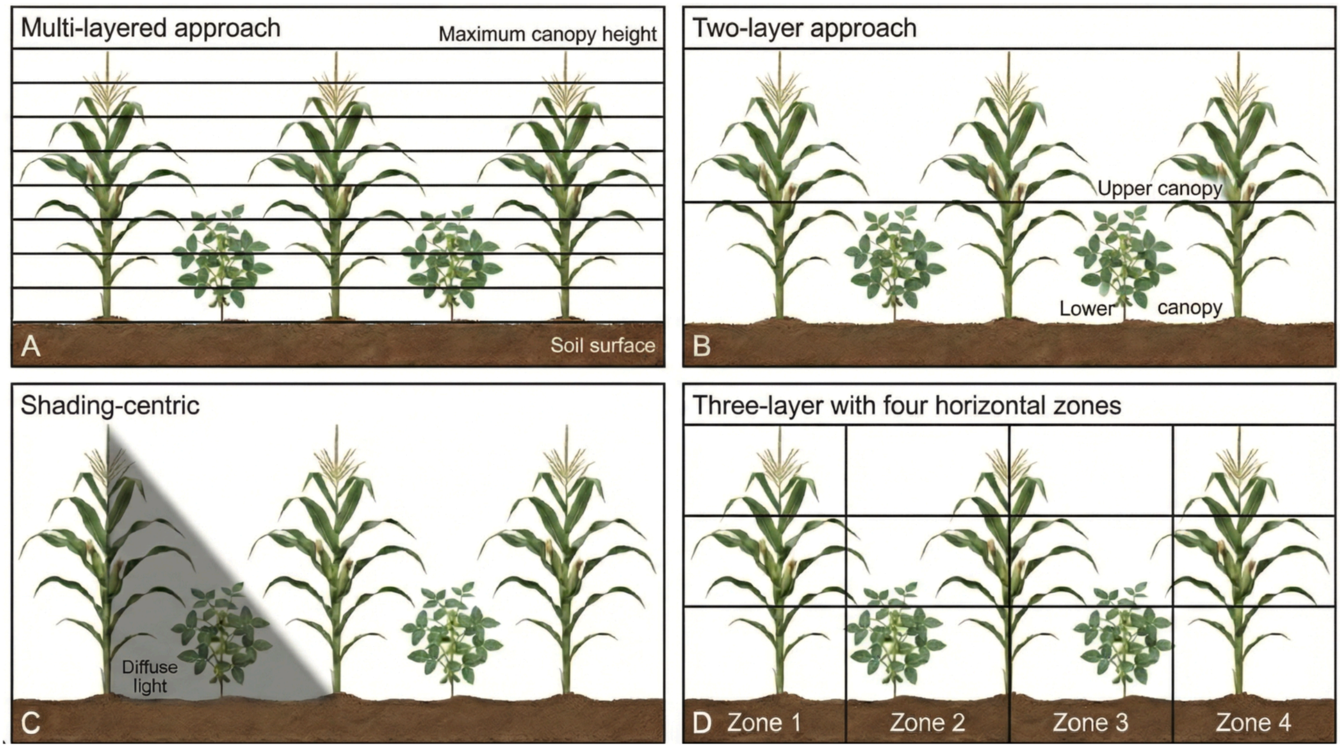

Fig. 3. Schematic representation of the examples modelling approaches for interspecies light competition among the current intercrop model generations. (A) Multi Layered canopy approach (APSIM-Canopy/APSIM-Micromet/DSSAT-Mixed/LandscapeDNDC), (B) Two-layer canopy approach (MONICA with 1D canopy /STICS-Multilayer with 2.5D); (C) Shading-centric approach (DayCent with 1D canopy based on empirical parameters/LUCIA uses 2D with geometric approach); and Three-layer canopy with four spatial zones approach (WaNuLCAS). Other approaches, including uniformly mixed canopy and strip-planted canopies, are also described in detail within Supplementary File 1.

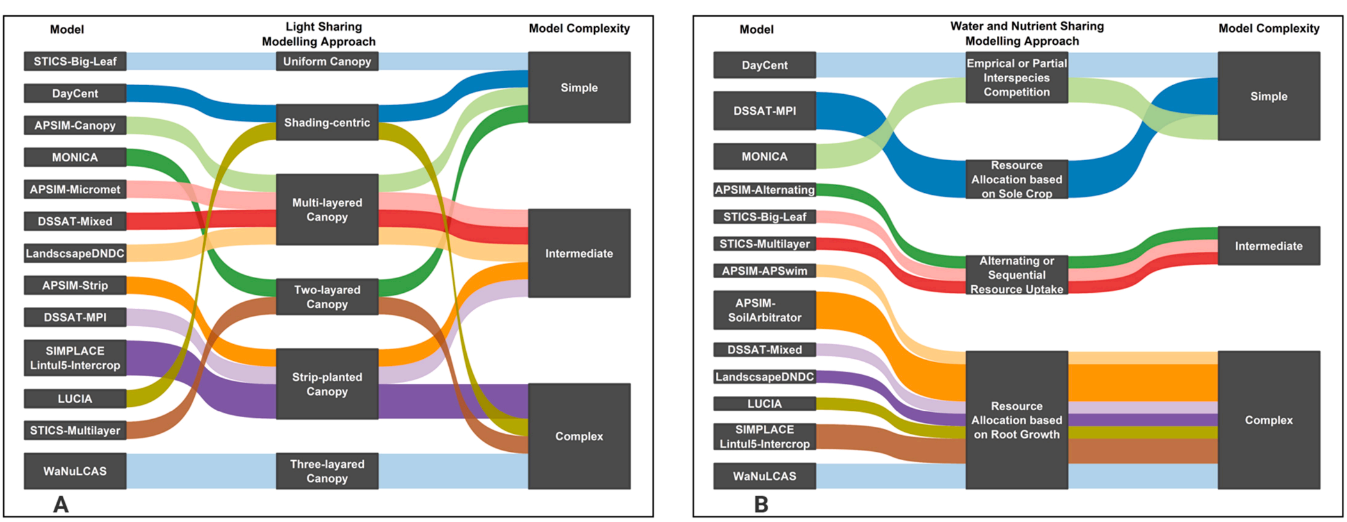

Fig. 4. Conceptual comparison of intercropping models based on thier resource-sharing approaches. (A) illustrates the varying approaches to modelling above-ground light sharing. (B) compares the modelling concepts for below-ground sharing for water and nutrients. **Note:** The intercomparison highlights the differences in complexity among the participating models. **Note:** DSSAT-MP has rooting depth differences among species for water and N uptake, but interspecies competition is yet to be incorporated (relying on sole-crop approach based on RLD per soil layer).

core assumptions, and mathematical equations, is provided in Supplementary File 1.

3.2.1. Approaches to interspecies light competition

Our analysis identified six major conceptual approaches that crop models use to simulate light competition (Table 2). These approaches range from simple, one-dimensional (1D) representations to more complex pseudo-3D canopy structure.

3.2.1.1. Uniform mixed canopy. The uniformly mixed canopy approach simplifies complex canopies by aggregating them into a single, homogenous "big leaf" layer. This approach is best suited for randomly mixed intercrops where species have similar heights and canopy structures, such as wheat-pea mixture (Table 2; Supplementary Table 3). Among the models, only STICS implements this approach through its STICS-Big-Leaf formalism. The core assumption is that light is shared between species based on their relative light-capturing capacities;

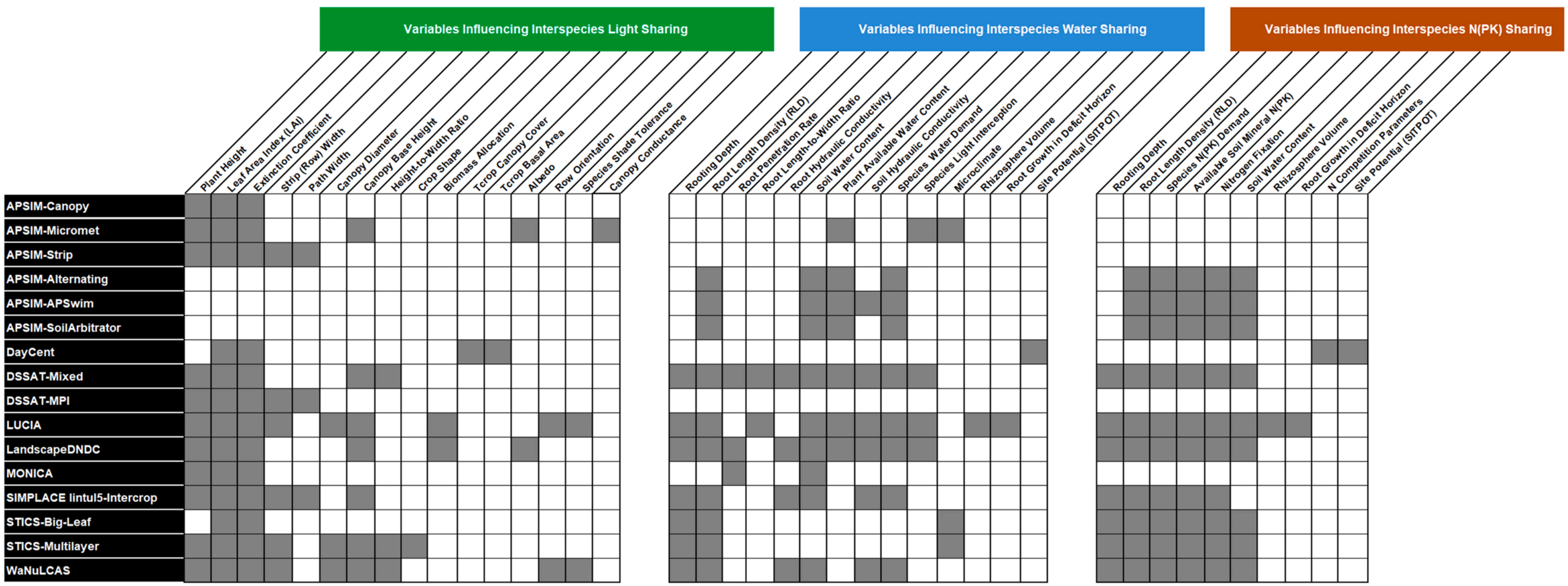

Fig. 5. Key variables influencing interspecies competition in intercrop models. Filled blocks indicate the presence of parameters, while white blocks denote parameters not implemented in the models. **Note:** For the DayCent model, competition parameters include the basal area competition factor 2 (BASFC2) and basal area adjustment factor (BASF).

specifically, a species with a greater leaf area and a higher extinction coefficient will intercept a proportionally larger share of the available light (Table 2).

3.2.1.2. Two-layer canopy approach. The two-layer canopy approach divides the canopy into two distinct vertical layers: an upper layer occupied by the taller species, and a lower layer containing both the shorter species and the lower portions of the taller one (Table 2; Fig. 3). Both MONICA and STICS-Multilayer implement this approach, though they differ substantially in their underlying canopy structural representation. MONICA uses a one-dimensional canopy structure in which the layers are defined by the height ratio between the two species. The model assumes that the upper canopy layer intercepts most of the incoming radiation. The residual light reaching the lower layer is then partitioned between the shorter species and the lower portion of the taller species based on their respective leaf area index (LAI) and extinction coefficients (Table 2).

In contrast, STICS-Multilayer adopts a highly parameterized, pseudo-3D (also known as 2.5D) canopy structure to simulate interspecies light sharing (Fig. 4). This detailed representation enables STICS-Multilayer to handle both row and narrow strip planting configurations, whereas MONICA was designed specifically for row arrangements (Table 1).

3.2.1.3. Three-layer canopy with four horizontal zones. The three-layer canopy with four horizontal zones is among the most spatially explicit approaches for simulating interspecies light sharing and is implemented exclusively in the WaNuLCAS model (Table 2). This approach divides the canopy into three vertical layers and four horizontal zones, capturing both vertical and horizontal heterogeneity in canopy structure (Fig. 3).

The vertical stratification consists of an upper layer dominated by the taller species (e.g., maize, tree), a mixed layer containing leaves from both species, and a lower layer dominated by the shorter species (e.g., soybean). Horizontally, the entire plot is divided into four zones to account for spatial variation in light availability across the intercrop arrangement. This enables the explicit representation of edge effects and gradients in shading intensity. The multi-strata canopy structure, combined with detailed parameterization (Fig. 5), makes WaNuLCAS particularly well-suited for simulating complex systems such as tree-crop interactions in agroforestry and other row or strip configurations in annual-annual systems (Table 1).

3.2.1.4. Multi-layered canopy approach. The multi-layered canopy approach divides the canopy into multiple discrete vertical layers based on plant height, with light transmission calculated sequentially through each layer using the Beer-Lambert law (Fig. 3A; Table 2). This approach assumes horizontal homogeneity within each layer while explicitly accounting for vertical gradients in light availability. Four crop models implement this approach: APSIM-Canopy, APSIM-Micromet, DSSAT-Mixed, and LandscapeDNDC. Despite sharing this conceptual basis, the models differ substantially in their layer resolution, parameterization details, and processes they simulate (Fig. 5).

These differences are apparent in their implementation. APSIM-Canopy offers the simplest approach, focusing exclusively on light competition with layers defined by dynamically adjusting crop heights. In contrast, APSIM-Micromet extends this by calculating canopy conductance and potential transpiration for each species, accounting for mutual shading effects on both radiation and conductance. This creates a linkage between light competition and water balance, positioning APSIM-Micromet as the most process-integrated model within this category.

Layer definition also varies significantly between the models. DSSAT-Mixed uses fixed 10 cm layers from the soil surface to the maximum canopy height, with the leaf area index in each layer varying according to the differential height growth of each species. In contrast, LandscapeDNDC divides the canopy into 40 vertical layers regardless of species height. Notably, LandscapeDNDC uses an initial layer height of 2 cm that is dynamically rescaled when the canopy grows beyond the maximum configured height, ensuring a constant number of layers by adjusting their thickness.

3.2.1.5. Shading-centric approach. The shading-centric approach focuses on quantifying the reduction in light availability for understorey species caused by shading from taller species (Table 2). Rather than simulating light transmission through discrete canopy layers, this approach estimates shading effects based on the geometry or canopy characteristics of the taller species. Two models implement this approach, LUCIA and DayCENT, though they differ substantially in their level of mechanistic detail and spatial representation (Fig. 3C; Fig. 5).

LUCIA uses a geometric approach to simulate light reaching the shorter plant based on the daily varying sun angles and the canopy architecture of the taller species. Specifically, the model calculates the total light reaching the shorter species throughout the day as the sum of three distinct components: (1) lateral light, which occurs during morning and evening hours and is typically considered negligible; (2) diffuse light passing through the taller canopy and (3) direct light that reaches the shorter crop when the taller crop does not obstruct the sun's direct path (Table 2). LUCIA dynamically accounts for species height changes, allowing the initially shorter species to overgrow the taller one. Notably, the STICS-Multilayer model also uses a geometric principle similar to that of LUCIA to determine interspecies light sharing.

In contrast, DayCENT adopts a more simplified method, using a "shading modifier" derived from the canopy cover and leaf biomass of the taller species (designated as the "T-crop"). This modifier is not explicitly process-based but instead represents an aggregated, empirically calibrated effect of multiple plant traits. This distinction extends to their spatial representation: DayCENT uses a 1D canopy structure with minimal parameterization, making it suitable for applications where spatial detail is not critical, whereas LUCIA employs a 2D representation. Despite these differences, the core shading mechanism in both models provides the flexibility to simulate various planting configurations, including mixed, row, and strip arrangements (Table 1).

3.2.1.6. Strip-planted canopy approach. The strip-planted canopy approach is specifically designed for intercropping systems where species are arranged in distinct alternating strips or rows (Table 2). This approach simplifies the spatial heterogeneity of such systems by compressing the leaf area of each species into rows while neglecting the bare paths between them. Three models implement this framework: APSIM-Strip, DSSAT-MPI, and SIMPLACE Lintul5-Intercrop. All three models use a "view factor" (specific reduction of solar radiation reaching the understorey species due to the architectural obstruction of the dominant species) to quantify shading effects between different species in adjacent rows.

APSIM-Strip and DSSAT-MPI share a core set of parameters including LAI, plant height, extinction coefficient, strip width, and path width to define both the vertical structure of individual strips and the horizontal geometry of the arrangement (Fig. 5). These parameters are then used to calculate the view factor, which quantifies the degree of mutual shading. In contrast, SIMPLACE Lintul5-Intercrop extends this approach by additionally incorporating canopy diameter, which provides a more detailed representation of canopy shape and its influence on light interception. This expanded parameterization enables SIMPLACE Lintul5-Intercrop to simulate both strip and row arrangements with greater fidelity, a flexibility not explicitly detailed in the other two models (Table 1; Fig. 5).

3.2.2. Approaches to interspecies water and nutrient competition

Our analysis identified four main approaches for simulating belowground resource competition between intercropped species (Table 3).

Table 3
Conceptual intercomparison of process-based crop models with intercropping capabilities, highlighting their key features, below-ground resources uptake mechanisms, and assumptions to simulating water and nutrient(s) competition in an intercropping system.

Approach	Model	Key features	Water and nutrient(s) uptake/sharing mechanisms	Assumptions
Empirical or partial interspecies competition	DayCent	Indirect modelling of competition using empirical parameters	Water and N shared proportional to basal area competition factor (BASFC)	BASFC values > 1.0 favour competitiveness of understory species for all resources while < 1.0 favour dominant species
Empirical or partial interspecies competition	MONICA	Prioritized water uptake for the major crop; no interspecies nitrogen competition	Dominant crop accesses water first in shared soil layers.	Dominant crop's water demand is prioritized; excess goes to the second crop; non-limiting N conditions.
Alternating or sequential resource uptake	APSIM-Alternating	Alternating-day resource access by species; N_2 fixation	Water and nitrogen uptake for species based on its proportional RLD within individual soil layers.	Alternating-day access introduces a lag in resource stress for the non-dominant crop; N_2 fixation reduces N demand
Alternating or sequential resource uptake	STICS-Big-Leaf/STICS-Multilayer	Sequential daily uptake, with dominant crop accessing resources first while the understory crop takes the remaining	Water and N uptake proportional to RLD in each soil layer	Sequential daily uptake prioritizes the dominant crop, introducing a one-day lag for the subordinate crop
Resource allocation approach based on root growth	APSIM-APSwim	Simultaneously solves Richards' equation for water flows; convection-dispersion equations for N fluxes; N_2 fixation; hydraulic lift; 2D spatial capability	Water and N shared proportional to RLD × demand at each depth; simultaneous solution of flows into roots	Physically based hydraulic approach; bidirectional uptake enables hydraulic lift; N_2 fixation reduces N demand
Resource allocation approach based on root growth	APSIM-SoilArbitrator	Simultaneously solves uptake equations using Runge-Kutta integration across layers, crops, and zones; N_2 fixation; hydraulic lift; dynamic feedbacks	Water and nutrients shared based on crop model-defined uptake functions incorporating RLD; four-point integration captures dynamic depletion	Simultaneous competition without order-dependence; bidirectional uptake enables hydraulic lift; demand driven N**2** fixation; spatial redistribution of uptake as resources deplete
Resource allocation approach based on root growth	DSSAT-Mixed	Partitioning water and nitrogen between competing species based on RLD, N_2 fixation	Water and N shared proportional to their RLD in each soil layer	Fractional radiation interceptions determine water demand, while N_2 fixation reduces N demand
Resource allocation approach based on root growth	LandscapeDNDC	Competition regulated by root biomass and spatial root overlap; flexible soil discretization	Water and N shared proportionally to their RLD in each soil layer	Assumes that spatial overlap of roots intensifies competition in shared soil layers
Resource allocation approach based on root growth	LUCIA	Competition only in soil layers where the cylindrical root systems of species overlap; roots growth preferentially into resource-rich horizons; N_2 fixation; flexible soil discretization	Water and nutrients (NPK) shared proportionally to species specific rhizosphere volume in overlapping zones per soil layer	Rhizosphere overlap and proportional fine root biomass distribution and preferential root growth regulate species competition; fixed or demand driven N_2 fixation reduces N demand
Resource allocation approach based on root growth	SIMPLACE Lintul5-Intercrop	Competition focusses on allocation factors and root restriction factors (RRFs); N_2 fixation	Water and N shared proportional to their RLD and RRFs in each soil layer; surplus redistribution in shared layers.	Area fractions and RRFs determine competitiveness in shared layers, while N_2 fixation reduces N demand
Resource allocation approach based on root growth	WaNuLCAS	Resource sharing based on relative root length density and demand of each species; 4 soil layers and 4 zones with overlapping root options; N_2 fixation; hydraulic lift	Water and nutrients (N, P) shared proportional to their combined RLD x demand factor in each soil layer and zone.	Combined RLD and resource demand in root overlapping zones accounts also for the sink strength of the different species; N_2 fixation reduces N demand while hydraulic lift enhances surface water for companion species
Sole-crop approach based on root growth allocation	DSSAT-MPI	Each species simulated independently as sole crop; intercropping simulations only when N and water are not limiting resource conditions	No explicit interspecies competition or partitioning; competition occurs only implicitly through resource depletion	Each species calculates uptake independently based on its RLD; assumes excess resource availability (high input/fertility system); no competitive partitioning between species

3.2.2.1. Sole-crop approach based on root growth allocation. The sole-crop approach is the simplest approach for modelling belowground interactions, calculating each species' resource uptake as if it were in a monoculture. This approach, which includes no explicit competition function, is used when belowground competition is assumed to be negligible. The DSSAT-MPI model exemplifies this, as it does not explicitly account for interspecies competition for soil water and nitrogen (Table 3). Instead, it utilizes the sole-crop routines from the CROPGRO and CERES-Maize models within the DSSAT framework. However, this approach may still yield plausible results because the underlying CROPGRO and CERES models have different root profile depths, root length densities (RLD), and mechanisms for water and N uptake, which introduces an implicit element of differential resource capture.

3.2.2.2. Empirical or partial interspecies competition approach. The empirical or partial competition approach, implemented in DayCent and MONICA, relies on simplified assumptions or empirical parameters rather than a detailed mechanistic representation of belowground interactions (Table 3; Fig. 5).

MONICA uses a priority-based water allocation where the dominant crop accesses water first, with any remainder allocated to the secondary crop. The model does not, however, explicitly account for interspecies nitrogen competition, instead relying on sole-crop nitrogen uptake routines. To address this limitation, a new conceptual approach, MONICoSMo, is under development. This future module will simulate competition for both water and nitrogen using suitability functions while maintaining compatibility with MONICA's existing sole-cropping parameterizations (Confalonieri, 2014; Triacca et al., in prep).

In contrast, DayCent incorporates empirical parameters to modulate both water and nitrogen competition. The model adjusts these competitive dynamics through indirect mechanisms based on two key parameters: the basal area competition factor (BASFC) and site potential (SITPOT) (Fig. 5).

3.2.2.3. Alternating or priority to access resources. The alternating or sequential uptake approach, implemented in the APSIM-Alternating module and the STICS models (STICS-Big-Leaf and STICS-Multilayer), partitions resource access between species either temporally or hierarchically (Table 3).

The APSIM-Alternating module manages resource competition by reversing the daily calculation sequence between species, ensuring that neither species consistently has priority access to soil resources. Water uptake from each soil layer is calculated as a function of an extraction coefficient proportional to the species' root length density (RLD). Although a species with higher RLD has greater extraction capacity, the species calculated first on any given day has priority access to available water. Nitrogen uptake follows a similar sequential process, where the first species meets its demand (constrained by soil supply) before the second accesses any remaining nitrogen. This alternating priority provides approximately equal opportunity for both species to acquire resources over time.

In contrast, STICS uses a fixed sequential uptake approach in which a designated dominant crop accesses resources first, followed by the second crop. In STICS, water competition is determined by soil water availability, species-specific root characteristics, and potential transpiration, while nitrogen uptake is influenced by crop biomass and nitrogen dilution dynamics (Table 3; Fig. 5).

3.2.2.4. Resource allocation approach based on root growth. The resource allocation approach based on root growth is the most mechanistic approach for simulating interspecies belowground competition. Seven models implement this approach: APSIM-APSwim, APSIM-SoilArbitrator, DSSAT-Mixed, LandscapeDNDC, LUCIA, SIMPLACE Lintul5-Intercrop, and WaNuLCAS. These models distribute water and nitrogen among competing species based on factors such as root distribution, root biomass, and resource demand (Table 3; Fig. 4). Although root length density (RLD) and rooting depth are common variables across most of these models, their implementation details vary substantially (Table 3; Fig. 5).

Several models use RLD as the primary driver for resource partitioning. DSSAT-Mixed, for instance, partitions water and nitrogen in direct proportion to the RLD of each species in each soil layer. LandscapeDNDC further expands on this by using both RLD and species-specific root biomass to partition belowground water and nitrogen. Similarly, SIMPLACE Lintul5-Intercrop uses RLD in combination with root restriction factors (RRFs) to allocate resources proportionally among competing crops.

Other models in this category, particularly within the APSIM framework, focus on achieving a simultaneous solution to resource competition. APSIM-APSwim simulates interspecies competition for water and nitrogen based on hydraulic gradients, RLD, and resource demand rather than calculation order, ensuring that species with higher RLD and demand capture proportionally more resources. Notably, it uses Richards' equation for water flow and convection-dispersion equations for nitrogen fluxes to resolve this competition simultaneously. APSIM-SoilArbitrator also provides a simultaneous solution but uses Runge-Kutta integration to do so. Within a single daily timestep, this approach calculates four estimates of uptake rates across different layers, crops, and zones to accurately integrate uptake as resource availability changes. In this model, the uptake functions also incorporate RLD as a key determinant of resource acquisition.

WaNuLCAS calculates water, nitrogen, and phosphorus sharing proportionally, based on a combination of RLD and resource demand, thereby accounting for the sink strength of different species. It also uses horizontal zones to spatially represent up to four competing species, considers hydraulic potentials in water uptake, and uses Runge-Kutta integration to simulate the competition mechanisms.

LUCIA takes a slightly different mechanistic approach by focusing on fine root biomass and the associated root system volume of each species. This allows the model to restrict resource competition to the overlapping rhizosphere zones of the two root cylinders within a soil layer. In the non-overlapping zones, each species has full access to the available water, nitrogen, phosphorus, and potassium resources within its reach (Fig. 3).

3.3. Representation of synergistic and other complex processes

Current intercrop models represent competitive processes with varying degrees of mechanistic detail, but synergistic and facilitative processes are often simplified or omitted entirely (Table 1). Nitrogen fixation is the most frequently incorporated facilitative process among the studied models; however, as DSSAT-MPI and MONICA do not account for interspecies nitrogen sharing, their N_2-fixation simulations rely on existing sole-crop frameworks. Additionally, only a few models (e.g., APSIM-Micromet) explicitly simulate changes in temperature, humidity, and wind speed within the canopy, which can significantly affect crop growth and water use. Hydraulic lift, the process by which deep-rooted plants redistribute water to shallower soil layers, benefiting neighboring shallow-rooted species, is implemented in only three models: APSIM-APSwim, APSIM-SoilArbitrator, and WaNuLCAS. Other key processes, such as shoot and root plasticity, are generally represented in few models like LUCIA, and SIMPLACE Lintul5-Intercrop (Table 1).

Furthermore, many complex ecological interactions, including pest and disease dynamics, allelopathy, and changes in soil microbial communities, are generally absent from the current generation of intercrop models, although recent progress has been made in modelling brown rust epidemics in wheat-pea mixtures (Deheinzelin et al., 2026). This fundamental asymmetry in process representation, which prioritizes competition over facilitation, limits the utility of current models for a comprehensive assessment of intercropping performance and its potential benefits. It is important to acknowledge that models are inherently simplifications of reality and cannot capture all processes in full, they remain powerful tools when their scope is clearly defined and their limitations are explicitly acknowledged. Many ecological and socio-economic processes such as labour constraints, market access, and land tenure are inevitably omitted. This limitation is particularly consequential in smallholder farming systems in sub-Saharan Africa and other low-income regions, where socio-economic constraints are often the primary determinants of intercropping adoption and performance, yet remain largely absent from current models. Emerging efforts to couple process-based crop models with agent-based socioeconomic frameworks such as the LUCIA-MP-MAS linkage represent a promising direction (Marohn et al., 2013b, 2022), but broader validation across diverse smallholder contexts are needed before such approaches can inform policy at scale.

3.4. Overview of intercrop model validation studies

Our analysis reveals that the extent of model validation is highly uneven across the intercrop models reviewed (Supplementary Table 3). Established models such as APSIM (e.g., APSIM-Canopy, APSIM-Strip, APSIM-Alternating) and STICS (e.g., STICS-Big-Leaf, STICS-Multilayer) have been validated across a wide range of systems. In contrast, others have been tested in only a few specific contexts. Furthermore, most validation studies have focused on cereal-legume intercrops, with significant gaps remaining for systems involving root and tuber crops.

A direct comparison of performance metrics between models is inherently challenging due to disparities in experimental datasets, calibration methodologies, and reporting standards. Our approach, therefore, avoids direct model-to-model comparisons and instead synthesizes the validation literature to identify general patterns in performance across different processes and conditions. This synthesis reveals a clear and consistent hierarchy of predictive accuracy across most models and approaches (Supplementary Table 3). Phenology is typically simulated with good accuracy (normalized root mean square error [nRMSE] $< 10\%$; modeling efficiency [EF] > 0.90), followed by aboveground biomass and grain yield (nRMSE: 15–50%; EF: 0.40–0.90), and then leaf area index (LAI) and plant height (nRMSE: 20–70%; EF: 0.20–0.70). The greatest predictive uncertainty is associated with soil processes and nitrogen dynamics, where performance frequently deteriorates (nRMSE: 30–100%; EF: -1.0–0.70).

Furthermore, we have seen that model performance is also highly sensitive to the physical architecture of the intercropping system. This sensitivity is particularly evident in how models handle vertical structure; while they generally perform well in height-differentiated systems (nRMSE: 16–22%), they can fail dramatically in similar-height systems, where inaccurate canopy representation leads to large offsetting errors in biomass and yield predictions (mean bias error [MBE]: -3.9 to $+7.9$ t ha^{-1}). Beyond vertical structure, model accuracy also varies significantly with the horizontal arrangement. For example, one study evaluating the STICS model across three spatial designs found that performance was best for alternate row systems (LER nRMSE = 1–18%), deteriorated for mixed within-row systems (nRMSE = 19%), and was lowest for narrow strip systems (nRMSE = 30%) (Vezy et al., 2023; Supplementary Table 3).

Furthermore, recent research suggests that STICS-Multilayer can accurately simulate interspecies light sharing in cereal–legume hill planting systems typical of West Africa intercropping systems, despite these configurations not being explicitly supported by the model structure (De Freitas et al., 2026)). In this case, two seeds of two different crops sown within a single planting hole are represented as mixed along the row, with inter-row spacing adjusted to approximate the observed spatial arrangement. This results highlights the flexibility of the STICS-Multilayer intercrop light interception formalisms in representing spatial patterns of intercropping systems with highly contrasted canopy heights within the mixture.

The greatest predictive uncertainty among the evaluated models is associated with belowground processes (Supplementary Table 3). A critical finding from the validation literature is that models can sometimes reproduce state variables like soil water content with low absolute error (root mean square error [RMSE]: 0.02–0.05), they often exhibit poor predictive skill (EF < 0.1), indicating a failure to capture the underlying dynamics. This issue is more frequent for nitrogen dynamics, where performance frequently deteriorates (nRMSE: 30–100%; EF: -1.0–0.70). Specific validation studies report N uptake errors reaching as high as 83% and systematic biases in N acquisition ranging from -10.1 to $+23.4$ kg ha$^{-1.}$ This consistent pattern suggests that the observed discrepancies are not merely due to the limitations of any single model structure, but rather reflect fundamental challenges, including the complexity of simulating simultaneous resource competition, accounting for inherent soil heterogeneity, and addressing the high variability of validation data.

4. Discussion

4.1. Divergence in light modelling approaches and its consequences

Our analysis identified six major approaches that intercrop models use to simulate how species share light: uniform mixed canopy, two-layer canopy, three-layer canopy with four spatial horizontal zones, multi-layered canopy, strip-planted canopy, and shading-centric methods (Table 2). Most of these models are built on the basic idea of applying the Beer-Lambert law to plant canopies, which treats the canopy as a series of horizontal uniform layers, a principle that Monsi and Saeki (2005) established. Some of the intercrop models incorporate geometric shading principles to simulate interspecies light sharing, a methodological advancement that builds on the work of Tournebize and Sinoquet (1995).

Existing model validation studies indicate that the performance of different light competition modelling approaches depends heavily on species canopy height characteristics and spatial configuration (Supplementary Table 3). The multi-layered canopy approach, as implemented in APSIM-Canopy, has shown robust performance in tropical systems with distinct height differences between species. In Sri Lankan rice-maize-mungbean systems, Amarasingha et al. (2017) reported high accuracy, with maize grain yield RMSE of 0.353 t ha^{-1} and mungbean yield RMSE of 0.075 t ha^{-1} across multiple sites. Similarly, in South African sorghum-cowpea intercrops, Chimonyo et al. (2016) found low RMSE values for aboveground biomass (AGB) under both full (0.036 t ha^{-1}) and deficit (0.037 t ha^{-1}) irrigation. Nelson et al. (2022) further supported the robustness of this approach in Indian pearl millet-cowpea systems, where APSIM-Canopy achieved an overall Index of Agreement (IA) of 0.87 for grain yield and an IA of 0.91 for total biomass, alongside IA values of 0.75 for LAI, 0.94 for millet height, and 0.75 for cowpea height.

However, the performance of the same APSIM-Canopy model deteriorates when applied to intercrops of similar-height species in temperate zones. In a study of European wheat-faba bean intercrops, Berghuijs et al. (2021) found that APSIM-Canopy failed to capture the vertical canopy structure, underestimating wheat height (MBE: -0.54 m) while overestimating faba bean height (MBE: 0.45 m). This structural failure led to a significant underestimation of spring wheat biomass (MBE: -3.87 t ha^{-1}) and grain yield (MBE: -3.90 t ha^{-1}), while simultaneously overestimating faba bean biomass (MBE: $+7.30$ t ha^{-1}) and yield (MBE: $+7.90$ t ha^{-1}).

The strip-planted canopy approach yielded mixed results, with performance varying by system and the specific variable being assessed. For instance, in Chinese maize-peanut strip systems, APSIM-Strip achieved low nRMSE values for maize biomass (16%) and yield (18%), as well as for peanut biomass (22%) and yield (21%), indicating its effectiveness in height-differentiated subtropical strip configurations (Guo et al., 2024).

Similarly, SIMPLACE-Lintul5 demonstrated high model skill score (0.59–0.84) for biomass and yield in spring wheat-faba bean systems. The skill score measures the performance of intercrop model against sole crop model (specifically a skill score value of 1 indicates that the intercrop model is simulating the output variable perfectly). However, the same study revealed significant limitations for the fraction of intercepted photosynthetically active radiation (fIPAR). When the intercropping effect on light capture was small, the model's skill scores were often near or below zero, indicating it failed to outperform a simple benchmark for this specific process (Demie et al., 2025).

The STICS-Multilayer model, with its two-layer canopy, has demonstrated consistently strong performance across diverse temperate systems, even when calibrated on sole-crop data. An evaluation by Vezy et al. (2023) reported strong performance without intercrop-specific recalibration, achieving nRMSE values of 18% for grain yield (EF = 0.87), 23% for biomass, and approximately 9% for maximum height (EF = 0.92). This robustness is further supported by findings from other studies, including low RMSE for plant height (0.14 m) and biomass (1.51 t ha^{-1}) in pea-barley systems (Launay et al., 2009), and high accuracy for LAI (nRMSE: 19–27%; EF: 0.93–0.99) in durum wheat-chickpea systems (Kherif et al., 2022).

In contrast, simplified 1D approaches with two-layer canopies show variable performance that is highly dependent on the calibration strategy. The MONICA model, for instance, achieved a low biomass RMSE (0.54–1.07 t ha^{-1}) and a high Index of Agreement (IA) of 0.98–0.99 for German wheat-soybean relay intercrops when calibrated with intercrop-specific data (Yu et al., 2024). However, when calibrated using only sole-crop data, performance for the soybean component deteriorated dramatically, with the biomass RMSE increasing to 2.48–2.65 t ha^{-1} . This represents an average performance decrease of 219% compared to the intercrop-calibrated model, highlighting the critical role of calibration for this type of approach with simpler canopy representation (Supplementary Table 3).

The performance variability observed across different modelling approaches above suggests that model failures are primarily attributable to two key factors: the alignment between a model's structural assumptions and the physical characteristics of the intercropping system, and the influence of external environmental factors, such as solar angle and the proportion of diffuse light.

The first factor is evident in how models handle different canopy structures. Models generally achieve high predictive accuracy in tropical, height-stratified systems where one species forms a distinct overstorey, as this physical structure conforms to the core assumption of horizontally uniform canopy layers. However, this framework often fails when applied to temperate systems with similar-height species. In these contexts, the canopies of both species overlap extensively, creating a horizontally heterogeneous light environment that violates the one-dimensional (1D) logic inherent in many multi-layered canopy approaches. This may explain why models with pseudo-3D (2.5D) canopy representations, such as STICS-Multilayer, tend to perform more consistently across different species combinations.

Beyond structural mismatch, the second major factor appears to be latitudinal gradients in light quality. Tropical regions, with high solar angles and predominantly direct radiation, are well-suited to the assumptions of the Beer-Lambert law used by many models. In contrast, temperate regions experience lower solar angles and a higher proportion of diffuse light, where scattering and lateral penetration become significant drivers of light interception. This could explain why a model like SIMPLACE-Lintul5 Intercrop can simulate biomass and yield reasonably well, yet exhibits poor predictive skill for the fraction of intercepted light. Based on these observations, we propose two key hypotheses for future investigation:

Hypothesis 1. We hypothesize that in intercropping systems with significant height disparities (e.g., tall cereals with short legumes), multi-layered canopy and shading-centric models will significantly outperform uniform canopy models in predicting species-level light interception. Conversely, under conditions of crop height equality or in wide strip-cropping configurations, simpler uniform canopy models will yield comparable accuracy to complex architectural models, as the spatial separation reduces the need for mechanistic shading simulations.

Hypothesis 2. We hypothesize that intercrop models with simplified one-dimensional light-sharing assumptions are more likely to produce compensating species-level errors in temperate climates, where diffuse radiation constitutes a substantially higher proportion of total incoming radiation, than in tropical environments where direct beam radiation typically dominates. This is because diffuse light penetrates canopies more uniformly and from multiple angles, violating the Beer-Lambert law assumption of unidirectional beam radiation, and causing these models to simultaneously underestimate light capture by the shorter species and overestimate it for the taller species. However, we acknowledge that this compensation effect at the whole-system level (e.g., acceptable LER predictions) may not be exclusively attributable to diffuse radiation, as parameter compensation and calibration artefacts may also contribute.

4.2. Challenges in modelling belowground interactions

Current intercrop models use four main approaches for simulating water and nutrient competition: sole crop approach relying on root growth allocation, alternating or sequential uptake, partial interspecific competition, and interspecies resource allocation based on root growth. Notably, the divergence among models is far less pronounced for belowground processes than for light sharing. This reflects the fact that most current intercrop models were adapted from monoculture frameworks, and modelling belowground competition for water and nutrients is inherently more difficult than simulating aboveground light competition, a fact widely recognized in the literature (Hodge, 2004; Lynch, 1995; Schenk, 2006; Tilman, 2020). This difficulty is compounded by a relative scarcity of empirical data on root dynamics (e.g., root biomass) and soil processes (Yu et al., 2024).

The validation evidence consistently highlights that the performance of current modelling approaches is uneven across the resource gradient from low- to high-input conditions. The alternating-day approach in APSIM, for example, effectively simulates water-sharing under severe stress in low-input systems. This was shown by Chimonyo et al. (2016) in South African sorghum-cowpea systems, where the model captured crop water use (RMSE: 8.1–24.1 mm) and water use efficiency (WUE) with RMSE values of 1.66, 1.97, and 3.06 kg mm^{-1} ha^{-1} under full irrigation, deficit irrigation, and rainfed conditions, respectively. However, this approach is less reliable under adequate moisture; Nelson et al. (2022) reported that it often simulated premature senescence despite ample water availability, resulting in a low modelling efficiency (EF) of 0.22 and an nRMSE of 28% (Supplementary Table 3).

A similar discrepancy between absolute error and predictive skill was observed in the SIMPLACE-Lintul5 model, which uses a resource allocation approach based on root growth. In a study of German spring wheat-faba bean intercrops, Demie et al. (2025) reported high precision in simulating volumetric soil water content (RMSE: 0.018–0.048); however, the corresponding model skill scores (-0.34–0.07) indicated a lack of predictive power despite the low absolute error. This pattern extended to root biomass, where the model achieved a low RMSE for wheat (0.09–0.14 t ha^{-1}) and faba bean (0.33–13 t ha^{-1}), yet yielded extremely poor skill scores ranging from −1.3–0.70 and −16.5–0.78, respectively (Supplementary Table 3). These results highlight that a low absolute error does not inherently signify robust model performance; rather, the divergence between RMSE and skill scores suggests that traditional error metrics may be insufficient for capturing model reliability in complex intercropping systems.

The performance of the STICS-Multilayer sequential uptake approach in simulating nitrogen dynamics is highly context-dependent.

The model has shown success in some temperate systems, for instance, by capturing facilitation processes in low-N European organic systems (Launay et al., 2009) and achieving high predictive skill for wheat nitrogen acquisition (EF: 0.91–0.94) in wheat-fescue intercrops (Shili-Touzi et al., 2010). However, this accuracy often does not extend to the secondary crop (EF for fescue N acquisition: 0.46–0.49) and deteriorates significantly for soil processes, with soil inorganic nitrogen yielding EF values as low as −0.34 in the same study. This pattern of high uncertainty is consistent across other studies. Traoré et al. (2022) reported a high nRMSE of 38% for nitrogen uptake in tropical sorghum-cowpea systems. Similarly, Kherif et al. (2022) found high error rates for N uptake in durum wheat-chickpea intercrops (nRMSE: 54% for wheat, 83% for chickpea) and poor performance for soil nitrogen content (nRMSE: 49%; EF: 0.44). Vezy et al. (2023) confirmed this trend, reporting a high nitrogen acquisition nRMSE of 54% (EF = 0.71), although the model performed better for the ratio of nitrogen derived from the atmosphere (NDFA), with an nRMSE of 20% (EF = 0.71) (Supplementary Table 3).

The LandscapeDNDC model, which also uses a root-growth-based allocation, exhibits significant predictive uncertainty in simulating nitrogen dynamics. Validation studies reveal high error rates for nitrogen acquisition in aboveground biomass, with rRMSE values ranging from 30% for peanut to 69% for maize (Fuchs et al., 2024). Systematic biases are also evident; the model underestimated nitrogen uptake for cowpea (bias: −10.1 kg ha^{-1}) and peanut (bias: −4 kg ha^{-1}), while substantially overestimating it for soybean (bias: +23.4 kg ha^{-1}).

The poor simulation of belowground processes across multiple models from the syntheses above points to a limitation in our current understanding and mathematical representation of interspecific interactions, rather than deficiencies in any particular modelling approach. The consistently high error rates for soil nitrogen and water dynamics suggest that current models may be 'right for the wrong reasons,' accurately predicting aboveground outcomes without correctly simulating the underlying soil processes.

While current models mostly simulate baseline nitrogen uptake, the dynamic nature of N_2-fixation in legume-based intercrops remains a critical challenge. In intercropping, the presence of a competitive non-fixing companion crop like cereals, root crops, and tuber crops often stimulates the legume to increase its reliance on atmospheric N_2-fixation compared to sole stands, due to the rapid depletion of soil mineral nitrogen. Most models currently lack the mechanistic feedback loops required to dynamically upregulate N_2-fixation rates in response to this interspecific competition (Table 1). A critical underlying knowledge gap compounds this modelling limitation: the sensitivity of N_2-fixation to soil mineral N availability varies substantially between legume species and varieties, and remains poorly characterised across the diversity of species and intercrop configurations used in practice. Without robust parameterisation of this sensitivity, even models that incorporate dynamic fixation feedback loops cannot be reliably applied or validated across contrasting intercrop systems.

Based on these observations from the validation studies, we propose several hypotheses for future investigation:

Hypothesis 3. Current intercrop models are significantly more accurate at predicting aboveground variables (e.g., LAI, biomass, and yield) than belowground processes (e.g., soil nitrogen, water content, and nutrient uptake). This is because light-interception models are more established than those for complex root-zone interactions; consequently, low absolute errors in belowground data often hide a model's inability to predict how species share resources.

Hypothesis 4. We hypothesize that in environments with severe water or nutrient limitations, models incorporating more mechanistic representations of root distribution and interspecies resource partitioning will predict resource uptake more accurately than models relying on fixed or empirical root parameters, as the spatial dynamics of root competition become the primary determinant of differential resource capture under scarcity. However, under high-input conditions with adequate water and nutrients, the performance advantage of mechanistic approaches will be similar to that of simpler models not because belowground competition is absent, but because aboveground interactions are the primary limiting factor for yield.

Hypothesis 5. We hypothesize that models explicitly linking soil mineral nitrogen depletion to the upregulation of legume nodulation and N_2-fixation will more accurately simulate the nitrogen-yielding benefits of legume-based intercrops than models using static N_2-fixation rates derived from sole-crop calibrations.

Hypothesis 6. We further hypothesize that predictive error for soil nitrogen dynamics is primarily driven by the inadequate representation of soil nitrogen transformation processes (e.g., mineralization, immobilization, nitrification) rather than inaccuracies in simulating plant nitrogen uptake mechanisms. This implies that improving soil submodels is also critical for capturing interspecies nutrient competition.

4.3. Practical guide to intercrop model selection

Our conceptual analysis reveals that the selection of an intercrop model is not a matter of preference but a critical decision that must align the model's structural assumptions with the user's specific intercropping system, research objectives, and data availability. The significant performance variability observed in validation studies highlights that there is no universally "best" model; instead, there are appropriate models for specific contexts. This section translates our findings into a practical guide to help users navigate this complex landscape, with specific recommendations illustrated in Fig. 6. Based on the evidence from our analysis, users can identify the most suitable modelling approach by considering the following contexts:

1. **For systems with clear height stratification (e.g., tropical maize-legume):** These systems align well with the one-dimensional (1D) assumptions of layered canopies. The choice of model depends on both the spatial arrangement and the level of detail required. For mixed (random mixture) arrangements, multi-layered canopy approaches (e.g., APSIM-Canopy, DSSAT-Mixed, LandscapeDNDC) are essential to capture the complex, overlapping canopy structure. For row or strip arrangements with height stratification, either multi-layered models or simpler two-layer approaches (e.g., MONICA, STICS-Multilayer) may suffice, depending on the research objectives. Shading-centric models (e.g., DayCent, LUCIA) are particularly appropriate for these systems where geometric shading effects dominate.
2. **For row or strip intercrops with similar-height species (e.g., temperate wheat-pea):** In these systems, which violate the 1D assumption of horizontal uniformity, a model with a pseudo-3D or 2D spatial representation of the canopy is the most suitable choice (e.g., STICS-Multilayer, APSIM-Strip, SIMPLACE-Lintul5 Intercrop). Users should be aware that model performance in these temperate environments may be compromised by a higher proportion of diffuse light, which is not explicitly accounted for in most radiation schemes. **Note:** STICS-Big-Leaf approach has been shown to work for mixed systems under non height dominance between species.
3. **For resource-limited versus high-input systems:** The predictive accuracy of belowground models is highly contingent on the resource environment. In water-limited or nitrogen-stressed systems, complex approaches are more desirable, even though simpler concepts utilizing priority-based or sequential uptake routines may yield acceptable performance due to the more straightforward competition dynamics under scarcity. Conversely, in high-input systems with abundant resources, these simplified approaches often fail; in such environments, direct competition effects are more subtle, and other processes may become dominant. Thus, the selection of a modelling framework must be dictated by the resource intensity of the target

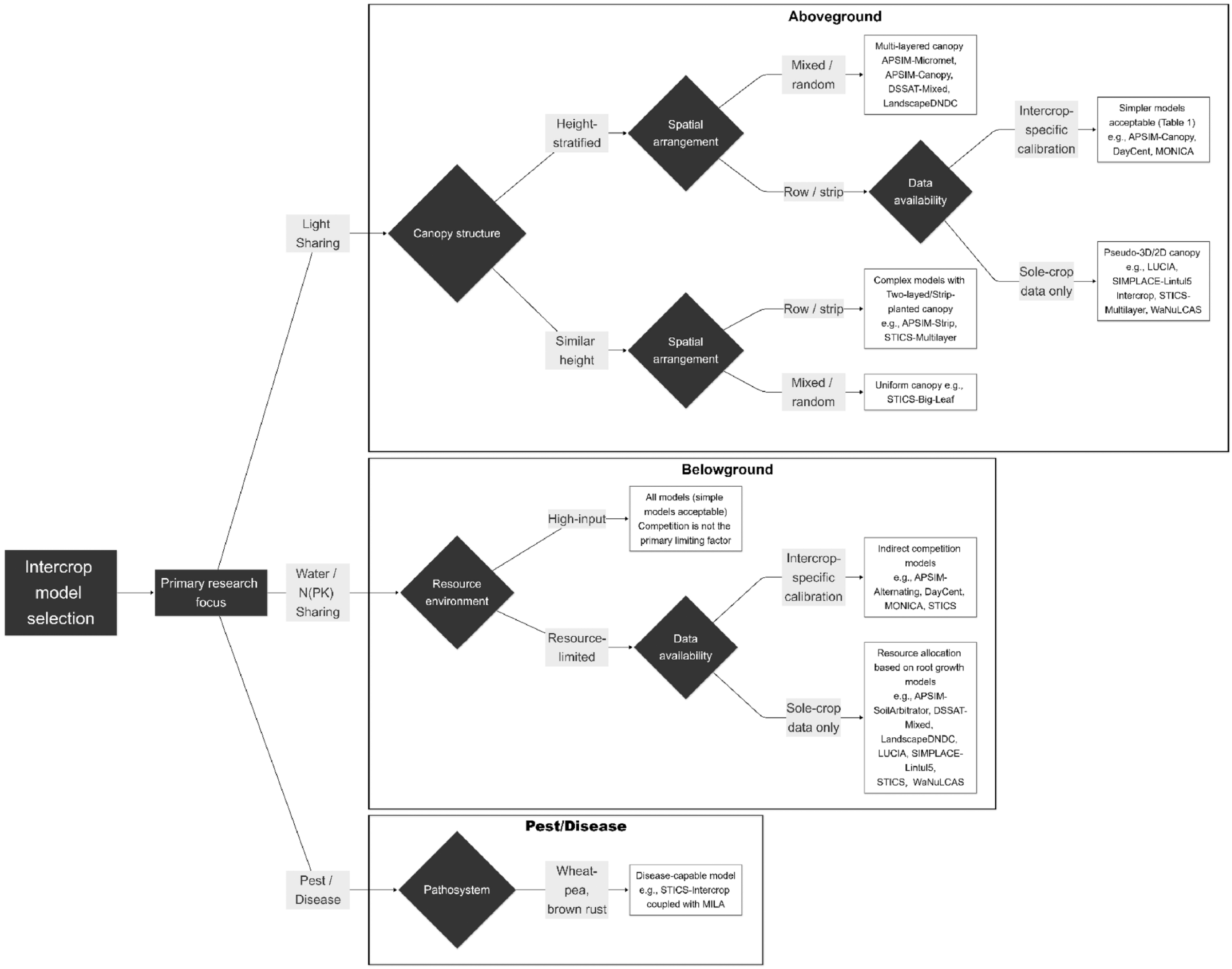

Fig. 6. A schematic decision flowchart to guide the selection of an appropriate intercrop model. The framework incorporates critical considerations from the validation studies of various modelling approaches identified in this study.

environment; however, users must remain cognizant of the generally poor performance of all current models regarding belowground processes (Supplementary Table 3), regardless of their structural complexity.

4. **When the research focus is on belowground processes:** Users must proceed with significant caution. Our analysis indicates that no current model reliably simulates soil water and nitrogen dynamics, with normalized RMSE for N-uptake commonly ranging from 30 to 83%. If investigating these processes is the primary goal, models featuring more mechanistic soil sub-modules (e.g., DSSAT-Mixed, LandscapeDNDC, LUCIA, WaNuLCAS) are theoretically preferable. However, their predictions should be treated as hypotheses to be tested rather than as reliable forecasts as no validation studies exist for most of the models.
5. **When only sole-crop parameterization data is available:** Were rich datasets from intercrop experiments are available, a simpler, well-calibrated model may be sufficient. But if working in a data-limited context, one must prioritize models with greater structural complexity. Validation studies highlight that structurally simpler models, like MONICA, can achieve high predictive accuracy, but only when they are carefully calibrated with data from the specific intercrop system they intend to simulate. In contrast, structurally complex models, particularly those with pseudo-3D canopy representations like STICS-Multilayer, have demonstrated a remarkable ability to provide acceptable predictions using parameters calibrated only on sole crops.

4.4. Research priorities for intercrop model improvement

To move forward, our analysis points to three interconnected research priorities for the intercropping modelling community: First, a shift from traditional agronomic trials to targeted, “model-guided” experiments. This approach involves comprehensive "golden experiments" designed to simultaneously measure critical data identified from this study including plant structural development (height, branching, canopy shape, canopy radius) and LAI development, micro-climate, root expansion and overlap, soil water content, soil mineral nitrogen, plant nitrogen uptake, and biological N_2-fixation at high spatial and temporal resolution in addition to aboveground biomass and grain yield across diverse intercropping configurations and environmental conditions. Such datasets are essential for improving both competitive and facilitative process representation, ultimately enhancing model reliability and utility for designing sustainable intercropping systems.

Second, there is a stronger need for a follow-up study on quantitative multi-model intercomparison of the various approaches identified from this study. Follow-up studies should leverage existing (if imperfect) intercropping datasets or *in-silico* intercomparison to quantify whether the structural uncertainties in current intercrop models are acceptable for capturing intricate intercropping dynamics. This is essential for evaluating predictive capabilities, strengths, limitations, model suitability for specific contexts, and will help in testing hypotheses identified from this study on why models succeed or fail under specific intercrop physical structures and growing environments.

Third, the community should develop and adopt standardized protocols for intercrop model calibration, evaluation, and uncertainty quantification. Without clear standards for reporting performance and assessing model skill, it remains difficult to compare findings across studies and build a collective understanding of model reliability for policy and farmer recommendations.

5. Conclusion

Our analysis identified six distinct approaches to modelling interspecies light competition and four for belowground competition within the current generation of intercrop models. It reveals that facilitative and other complex processes that govern the performance of intercropping systems are often simplified or omitted entirely. The synthesis of validation studies demonstrates that model performance is highly context-dependent; certain approaches perform well in systems with clear canopy stratification or in tropical environments, where physical structure aligns with model assumptions. Conversely, the underlying assumptions of many models break down in temperate, similar-height systems, where complex canopy overlap and higher proportions of diffuse light lead to deteriorating performance especially in approaches with one-dimensional canopy architecture.

Furthermore, a more fundamental limitation identified across all models is the systemic failure to reliably simulate belowground water and nitrogen dynamics. The study also highlights a critical trade-off between structural complexity and calibration dependency, as more complex models can often simulate intercrop performance using only sole-crop parameterization, a task at which simpler models typically fail. Based on these findings, we propose a series of testable hypotheses regarding the influence of light quality, vertical niche differentiation, and the representation of soil processes on model accuracy. Ultimately, this research culminates in a decision-support framework designed to optimize model selection for diverse intercropping systems, tailored to specific spatial arrangements, resource environments, and data constraints. By identifying these selection criteria and outlining future modelling priorities, this work establishes a foundation for more robust and reliable simulations of interspecific interactions.

CRediT authorship contribution statement

Adam Muhammad Adam: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Myriam Adam:** Writing – review & editing. **Folkard Asch:** Writing – review & editing, Supervision, Conceptualization. **Kenneth J Boote:** Writing – review & editing. **Vimbayi Grace Petrova Chimonyo:** Writing – review & editing. **Mathias Christina:** Writing – review & editing. **Marc Corbeels:** Writing – review & editing. **Antoine Couëdel:** Writing – review & editing, Data curation. **Mathilde De Freitas:** Writing – review & editing, Data curation. **Tomas Della Chiesa:** Writing – review & editing. **Frank Ewert:** Writing – review & editing. **Gatien N Falconnier:** Writing – review & editing, Conceptualization. **Kathrin Fuchs:** Writing – review & editing, Data curation. **Thomas Gaiser:** Writing – review & editing. **Ken E Giller:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Gerrit Hoogenboom:** Writing – review & editing, Data curation. **Neil Huth:** Writing – review & editing, Data curation. **Jibrin Mohammed Jibrin:** Writing – review & editing. **Eric Justes:** Writing – review & editing. **Alpha Y Kamara:** Writing – review & editing. **Michael Kermah:** Writing – review & editing. **Nuttapon Khongdee:** Writing – review & editing **Eric Koomson:** Writing – review & editing. **David Kraus:** Writing – review & editing. **Marcos Lana:** Writing – review & editing, Funding acquisition, Conceptualization. **Moritz Laub:** Writing – review & editing, Data curation. **Betha Lusiana:** Writing – review & editing, Data curation. **Carsten Marohn:** Writing – review & editing, Data curation, Conceptualization. **Patricia Moreno-Cadena:** Writing – review & editing. **Claas Nendel:** Writing – review & editing. **Wanwisa Pansak:** Writing – review & editing. **Willingthon Pavan:** Writing – review & editing. **Jacques Fils Pierre:** Writing – review & editing, Data curation. **Hanna J Poffenbarger:** Writing – review & editing. **Ehsan Eyshi Rezaie:** Writing – review & editing. **Alex C Ruane:** Writing – review & editing, Methodology. **Montserrat Salmeron:** Writing – review & editing, Data curation. **Clemens Scheer:** Writing – review & editing. **Sabine J Seidel:** Writing – review & editing, Data curation. **Pacsu Simwaka:** Writing – review & editing, Data curation. **Upendra Singh:** Writing – review & editing. **Johan Six:** Writing – review & editing. **Amit Kumar Srivastava:** Writing – review & editing. **Meine van Noordwijk:** Writing – review & editing. **Johanna Volk:** Writing – review & editing, Methodology. **Jing Yu:** Writing – review & editing, Data curation. **Georg Cadisch:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary information associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110491.

Data availability

No data was used for the research described in the article.

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