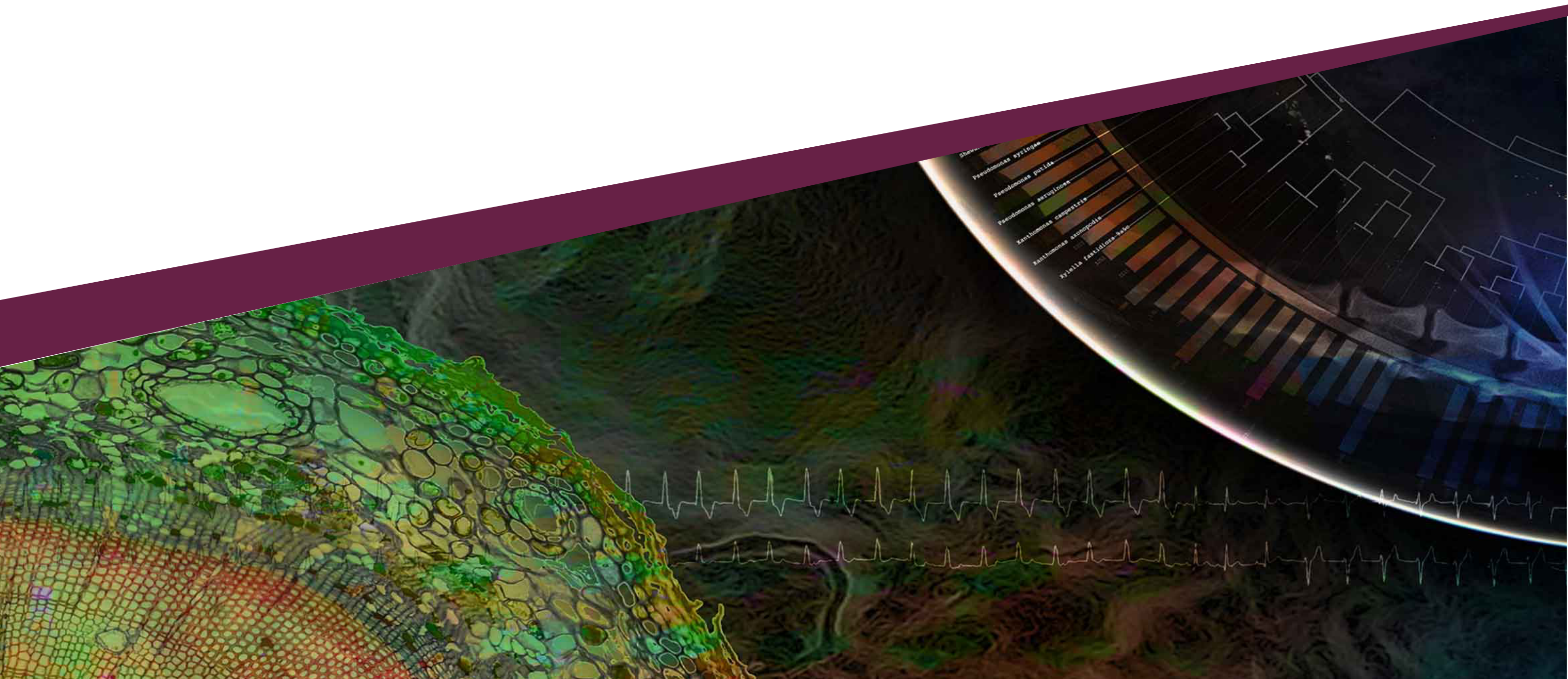
Towards modelling perennial grain intercrops: a review of current approaches and future needs

Lang Wang

Introductory Research Essay
Swedish University of Agricultural Sciences, SLU
Department of Ecology
2026



Towards modelling perennial grain intercrops: a review of current approaches and future needs

Lang Wang, Swedish University of Agricultural Sciences, Department of Ecology,
https://orcid.org/0009-0008-3797-1077

Publisher: Swedish University of Agricultural Sciences,
Department of Ecology
Year of publication: 2026
Place of publication: Uppsala
ISBN (electronic) 978-91-8124-299-7
DOI: https://doi.org/10.54612/a.4prn1cj1ab
Keywords: perennial grain crops, intercropping systems, crop model

Abstract

Modern agriculture must sustain high productivity while reducing its environmental footprint. Two promising strategies are the use of perennial grain crops, which provide ecosystem benefits such as deep roots and reduced soil erosion compared with annual crops, and intercropping, which can enhance resource-use efficiency through species complementarity. Their combination, perennial grain intercrops, has strong potential for sustainable intensification, although possibly at the cost of reduced yields. This potential tradeoff between sustainability gains and yield penalties, as well as the performance of such systems under climatic conditions, remain largely unexplored. Process-based crop models offer a way to assess the benefits and drawbacks of such cropping systems under varying climatic and management conditions, yet no existing model fully captures their unique dynamics. This essay reviews 15 modeling studies on mixed cropping systems, including intercropping, that involve perennials, although not necessarily grain crops, and identify which models include descriptions of the key components necessary to describe perennial grain intercrops: light and soil resource competition, rooting depth, soil carbon–nitrogen cycling, overwintering, and regrowth after winter. I show that, while most models include the core mechanisms needed for perennial intercropping, their implementations fall short for perennial grains. In particular, root dynamics, deep-soil resource feedbacks, survival over winter, and the dual-use allocation trade-off between grain and biomass remain poorly represented. Addressing these limitations requires integrating dynamic sink functions and multi-year root dynamics into existing process-based frameworks. Overcoming the current data bottleneck through a targeted, iterative experimental and modeling approach will unlock the full potential of these tools to design resilient, sustainable perennial grain intercropping systems.

Keywords: perennial grain crops, intercropping systems, crop model

Table of contents

List of tables

1. Introduction

Global food production is under increasing pressure to change. While modern agriculture has achieved remarkable productivity gains, this progress has often come at high environmental costs. Intensive farming practices are major contributors to greenhouse gas emissions, soil degradation, biodiversity loss, and water pollution (Foley et al., 2011; Steffen et al., 2015). In addition, climate change is increasing the frequency of extreme temperatures, prolonged dry spells, and intense precipitation events, making it ineffective for farmers to only rely on past experience to manage their fields (Calvin et al., 2023). In this context, there is a need to redesign cropping systems to support their sustainability and resilience (Bommarco et al., 2013; Stone et al., 2025).

An approach to address the environmental challenges is designing cropping systems that rely more on ecosystem services and less on fossil fuel-based inputs such as synthetic fertilizers and pesticides (Bommarco et al., 2013). Ecosystem services like nutrient cycling, pest regulation, soil structure maintenance, and water retention can help sustain crop productivity while reducing environmental impacts (Creamer et al., 2022; Power, 2010). However, how effectively these services support production depends on the crop(s), their functional traits, and the pedoclimatic conditions (Brooker et al., 2015). Not all combinations lead to desirable outcomes, and there are often trade-offs between different goals such as marketable yield, its year-to-year stability, and ecological functions (e.g., pest regulation and nutrient cycling) (Weiner et al., 2017). Such trade-offs can be seen in cereal–legume intercrops, which often excel in pest suppression but might lead to reduced grain yields compared with pure crops (Brooker et al., 2015). These context-dependent trade-offs make redesigning cropping systems challenging.

Arable crops are currently mostly annual crops, with the exception of some forage crops, such as leys. An alternative to annual grains are perennial grain crops, which remain in the field for multiple years without being resown. The perennial growth habit results in continuous ground cover and development of deeper root systems. These features can contribute to a variety of ecosystem benefits, such as reduced soil erosion and improved water and carbon retention (Crews & Cattani, 2018). For example, field trials with intermediate wheatgrass (Thinopyrum intermedium, Kernza), a perennial grain, showed increased soil carbon and reduced nitrate leaching compared with annual grain crops (Jungers et al., 2019). Deeper rooting also helps perennials access resources from deeper soil layers, compared with annual crops. This can be particularly valuable under dry or variable climatic conditions (Culman et al., 2013), if such advantage is not offset by its larger canopy size and hence higher transpiration demands (Vico et al., 2023). These benefits can support agricultural systems towards resilience and sustainability. However, despite the ongoing breeding efforts, perennial grain crops often result in lower yields than their annual counterparts, because they allocate more resources to root and vegetative growth instead of reproductive organs, which in most cases constitute the marketable yields (Glover et al., 2010). While this could reduce grain yield, the greater vegetative biomass could also allow forage use in perennial grains managed as dual-use systems (Gutknecht et al., 2026).

Another possible approach to improve agricultural sustainability is increasing crop diversity in the field. This can be done in time, via rotating functionally different crops, or space, via intercropping, i.e., growing two or more crop species with partially overlapping seasons. In both cases, combining different functional traits and resource use patterns of different species can improve overall productivity and ecosystem services, if species are effectively matched (Brooker et al., 2015; Tamburini et al., 2020). Interactions among species, and hence potentially benefits and tradeoffs, are strongest in intercropping, with outcomes depending on how the functional traits of the selected species interact with each other and with their environment (Brooker et al., 2015). Compared with pure crops, intercropping can enhance temporal and spatial resource-use efficiency and resilience to environmental disturbances such as drought or pest outbreak (Lithourgidis et al., 2011). Intercropping a fast-growing cereal with a nitrogen-fixing legume could reduce the need for synthetic nitrogen fertilizers while also suppressing weeds through rapid canopy closure (Jensen et al., 2020). Intercropping could also increase land-use efficiency (Lithourgidis et al., 2011), reduce pest outbreaks (Letourneau et al., 2011), and improve soil nutrient cycling (Power, 2010). However, poorly matched mixtures can result in strong interspecific competition, reducing both yield and its stability (Brooker et al., 2015). Moreover, the management of intercrops is typically more complex than monocultures, requiring careful planning of sowing dates, spatial arrangements, and harvest timing (Meirelles et al., 2024). This complexity can create practical barriers to adoption and increase the knowledge and management demands placed on farmers (Brannan et al., 2023). Consequently, there is a growing need for approaches that support the design and evaluation of such complex cropping systems.

Combining perennial grain crops with other perennial species through intercropping could allow to reap the benefits of both approaches: the ecosystem service advantages of perennials and the functional complementarity of intercrops. Indeed, this possibility is borne out in practice. For example, alfalfa–Kernza intercrops sustained grain yields over five years while unfertilized Kernza pure crops declined, illustrating how nitrogen-fixing legumes can enhance the long-term productivity of perennial grains (Crews et al., 2022). Kernza mixtures with red clover or alfalfa increased forage production and suppressed weeds, demonstrating the added value of intercrops for forage production and weed management, though grain harvests were sometimes reduced. By contrast, Kernza intercropped with kura and berseem clover helped maintain grain yields while still providing legume forage, balancing productivity and ecological services (Pinto et al., 2024). Other legumes, such as white clover or Canada milkvetch, have even facilitated Kernza productivity more effectively than highly competitive species, underscoring the potential to fine-tune species choice for synergistic outcomes (Reilly et al., 2022).

Perennial intercropping systems are inherently more complex than either perennial pure cultures or intercropping of annual crops. In intercropping, species interactions can shift over seasons or years in the presence of perennial species. Interactions among plant growth, soil and climatic conditions can lead to outcomes that are difficult to predict. For example, initial facilitation between species might turn into competition later in the growing season or in subsequent years, as root systems expand or nutrient availability changes (Brooker et al., 2015; Jensen et al., 2020; Weiner et al., 2017). Similarly, long-term benefits like improved soil carbon and water retention often appear only after several years, and their effects can vary depending on environmental conditions (Brooker et al., 2015; Crews & Cattani, 2018; Jungers et al., 2019). Relying solely on empirical assessments is unlikely to capture the full potential or limitations of perennial intercrops. To effectively design perennial intercropping systems, we need tools that can account for changes over time and test cropping system outcomes across a variety of scenarios.

Process-based crop models are well suited to assess the performance of perennial intercropping. They represent the biophysical processes that drive crop growth and resource cycling, allowing to explore how cropping systems behave under different environmental and management scenarios (van Ittersum et al., 2003). This ability is especially important in the context of climate change, which adds uncertainty through greater variability and more frequent extremes (Calvin et al., 2023). Models can be used to test how perennial intercrops might perform under such different climatic and management scenarios, offering insights into their resilience and long-term viability.

Several models have been developed for intercropping, with most of them targeting annual crops and often relying on limited calibration or validation with intercrop field data (Weih et al., 2022). To the best of our knowledge, no models currently exist for perennial grain intercrops. These models simulate competition for light, water, and nutrients, incorporating functional trait differences (Berghuijs et al., 2020; Vezy et al., 2023). Similarly, models of perennial pure crops have been proposed, often focusing on biomass accumulation, root growth, and long-term soil carbon dynamics (Salis, 2017; Tang et al., 2024; Wu et al., 2007). However, most of these models were developed for forage-based systems (e.g., leys) and do not explicitly represent grain allocation processes required to assess grain-harvest systems such as perennial grain crops (Faverjon et al., 2019b; Maire et al., 2013; Snow et al., 2013).

This essay assesses how modelling can support the design and evaluation of perennial grain intercropping systems. I review existing models that include both mixtures (including intercropping) and perennials, and identify challenges that need to be addressed to develop them for perennial grain intercropping systems. Here, to capture transferable mechanisms of species interaction and resource competition in a broader sense, I include a broad set of models that simulate coexisting plant species, such as pasture or forage-mixture models, rather than restricting the review to classical intercropping models. This broader scope helps capture general mechanisms of species interaction and resource competition. My overarching questions are:

1.Which existing models include both mixtures (including intercropping) and perennials?

2.What mechanisms have been included in these models? And which of these mechanisms could support the development of perennial grain intercropping models?

3.What are the key challenges in adapting existing modelling approaches to perennial grain intercropping?

By addressing these questions, I aim to identify what developments in modelling tools can support the transition to sustainable, resilient, and climate-adaptive perennial grain intercropping systems.

2. Methodology

To identify relevant literature on modelling perennial intercropping systems, I conducted a structured search in the Web of Science Core Collection. The search combined terms related to intercropping, perennial systems, and modelling, while excluding tree- or forest-based systems that fall outside the scope of this essay. Specifically, the Boolean string applied was

Abstract: polycultur* OR intercrop* OR mix* OR strip*

AND Abstract: perennial* OR permaculture* OR rye* OR ley* OR forage* OR pasture* OR fescue*

AND Title: model*

NOT Title: tree* OR forest* OR wood* OR agroforest* OR coffee*

The search was limited to publications from 2010 to 2025. After applying these filters, 329 articles remained (as of 19th September 2025). I screened all the abstracts to further assess their relevance, selected 15 articles that are relevant for the abovementioned questions (Table A1), and read them in full.

3. Results

3.1 Models applied to simulate mixtures including perennial species

The systematic review of the 15 selected studies shows that different types of models have been applied to simulate mixtures (including intercropping) that involve perennials. These models fall broadly into two categories. On the one hand, the detailed process-based models explicitly describe key biophysical fluxes such as radiation interception, soil water and nitrogen uptake, soil organic carbon and nutrient turnover, species-specific rooting, regrowth (i.e., biomass recovery after cutting or grazing) and overwintering (i.e., survival through winter dormancy into the next growing season). On the other hand, the simplified models, including minimalist and phenomenological approaches, approximate interactions without simulating the physiological mechanisms in full. Table 1 summarizes the identified models and their applications.

Table 1. Overview of models that simulate crop mixtures involving perennial crops.

Model type	Model (and module) name (key reference)	Application
Detailed process-based models	DAISY (Manevski et al., 2015)	Maize–red fescue intercrops
	STICS intercrop module (Shili-Touzi et al., 2010)	Winter wheat–red fescue intercrops
	APSIM–AgPasture (Snow et al., 2013)	Perennial ryegrass–clover grazed pastures
	Extended APSIM (Bartel et al., 2020)	Maize–perennial groundcover intercrops
	IFSM (Jégo et al., 2015; Payant et al., 2021)	Alfalfa–grass mixtures
	VGL (Faverjon et al., 2019a; Louarn & Faverjon, 2018)	Perennial grass–legume mixtures

	Gemini (Maire et al., 2013; Soussana et al., 2012)	Perennial grassland mixtures
	CoSMo + CropSyst (Movedi et al., 2024)	Perennial forage-alfalfa mixtures
Simplified models with minimalist and phenomenological approaches	Eckersten RUE-based model (Eckersten et al., 2011)	Perennial sow-thistle–spring barley intercrops
	GLV models (Fort et al., 2017; Halty et al., 2017)	Perennial forage mixtures
	Allometric biomass models (Demie et al., 2024)	Native perennial mixtures

None of the models were applied to perennial grain intercrops. Accordingly, they are not directly applicable without extensions. Yet, we can draw on the strengths of both detailed process-based and simplified models to develop such a tool to adequately represent resource dynamics, species interactions, and long-term system performance in the perennial intercrop systems. I identify the following functional mechanisms already included in the models and relevant to perennial grain performance:

- Light competition

Light competition is well represented in all models reviewed. DAISY, STICS, APSIM, and IFSM all include canopy modules that simulate radiation interception and partitioning among coexisting species, making them suitable to capture aboveground interactions in intercrops.

- Soil resource competition

Competition for soil water and nitrogen is often included in these models. DAISY and STICS include detailed soil–plant N uptake and water balance modules, while APSIM–AgPasture and extended APSIM extend this to perennial pasture or perennial groundcover systems. IFSM likewise integrates soil nutrient and water dynamics at a whole-farm scale.

- Rooting depth differentiation

Rooting depth is included in most models, though the level of detail varies. DAISY, STICS, APSIM–AgPasture and extended APSIM allow layered rooting profiles by species, which enables simulation of vertical complementarity. In contrast, IFSM parameterizes rooting as a single, species-specific maximum depth (e.g., 100 cm for alfalfa; 80 cm for timothy), providing a coarse representation of belowground complementarity and uptake distribution.

•Long-term soil process

The level of detail of capturing long-term changes in soil processes depends on the model. DAISY and APSIM include modules for soil organic matter turnover and nutrient cycling, and IFSM explicitly tracks long-term changes in soil carbon and nitrogen pools. STICS represents nitrogen cycling reasonably well but provides only a simplified representation of soil carbon turnover.

•Overwintering and regrowth

Overwintering and regrowth are only included in models allowing multi-year simulations such as APSIM–AgPasture and extended APSIM, as well as in forage-oriented models like IFSM, VGL, and GEMINI. By contrast, the single-season applications of DAISY and STICS do not include these processes. However, none of these models represent the allocation strategy characteristic of perennial grain crops, where reproductive yield and vegetative reserve formation must be balanced within the same plant.

3.2 Models applied to simulate mixtures including perennial species Key challenges in adapting existing modelling approaches to perennial grain intercropping

Although many of the core mechanisms required for simulating perennial intercrops are already represented in the models above, these models mostly capture plant-plant interactions through resource competition routines or simplified approximations. Important challenges therefore remain when adapting them to perennial grain intercrop systems, where interspecific interactions must be represented together with perennial grain-specific processes. This limitation arises because most reviewed models were originally designed for either annual crops or perennial forages, and therefore certain elements are missing or oversimplified when transferred to perennial grain intercrops.

First, while several models simulate regrowth after cutting or grazing in forage or groundcover contexts (e.g., APSIM–AgPasture, IFSM, VGL, GEMINI), none of the reviewed applications couple grain formation with reserve accumulation within the perennial species. Grain production is represented only for annual components, whereas perennial biomass is handled as forage or groundcover, meaning that reproductive sinks and survival reserves are treated separately in different plant types rather than as competing sinks within a single perennial grain plant.

Related to this, simulating perennial grain intercrops requires representing root system dynamics across multiple years, including deep nutrient capture, vertical root plasticity and root turnover linked to the plant ability to survive winter and resume growth in subsequent seasons. In the reviewed models, rooting is generally specified as a fixed depth profile for uptake within a single season (in DAISY, STICS or APSIM) or as a single maximum rooting depth parameter at whole-farm scale (in IFSM). This description is sufficient for estimating the soil nutrient balance but does not capture changes in rooting distribution over time. Even in individual-based community models such as VGL, root morphogenesis is represented within seasons but not coupled with the multi-year deep resource acquisition typical of perennial grain ideotypes.

Moreover, coexistence and management rules in these mixture models are formulated with objectives typical of pasture or perennial groundcover systems. These objectives focus on maintaining forage productivity or continuous soil cover (e.g., suppression windows in extended APSIM or floristic turnover in CoSMo+CropSyst), rather than maintaining a grain-harvest perennial alongside the companion species. As a result, the coexistence focuses on sward stability or cover retention, not on preserving perennial grain yield while sustaining the perennial plant across successive harvests.

Furthermore, modelling perennial grain intercrops requires that overwinter survival and reserve status carry over mechanistically into the next season reproductive allocation, since perennial grains must balance survival and grain production across years. In the reviewed models, overwintering and regrowth are included only in forage-oriented, multi-cut configurations, and carryover is generally handled through fixed survival thresholds or biomass reset rules, without linking reserve levels or stress exposure to subsequent grain sink formation. In IFSM and community-oriented models such as CoSMo+CropSyst, seasonal transitions modify biomass pools or species composition, but this is implemented at stand level rather than through plant-level allocation feedbacks relevant to perennial grain physiology.

4. Discussion

This review confirms that, while existing process-based models like APSIM (Bartel et al., 2020; Snow et al., 2013), STICS (Shili-Touzi et al., 2010), and DAISY (Manevski et al., 2015) provide a robust foundation for intercropping, none are currently equipped to simulate the unique, multi-year dynamics of perennial grain intercrops, as they lack processes key for these crops. The results highlight a critical gap between the tools available and the systems we aim to explore and ultimately design.

4.1 The key modeling challenges

The challenges identified in this review are not isolated technical constraints, rather biologically interconnected. These connections form a cascading hierarchy of effects: the plant's internal resource allocation (Section 4.1.1) drives its physical root architecture (Section 4.1.2), which in turn determines its capacity for overwintering and seasonal carryover (Section 4.1.3). This biological complexity ultimately demands dynamic management rules (Section 4.1.4).

4.1.1 The dual-allocation dilemma: balancing grain production and survival

The fundamental challenge in the use of perennial grains, and consequently in modelling them, is the trade-off between reproductive effort (grain yield) and vegetative persistence (survival), though in practical applications this tension is partly mitigated in some dual-use perennial grain systems (Gutknecht et al., 2026). Biologically, this trade-off is a non-linear competition for resources. Unlike annual crops that direct all assimilates to the grain during filling, perennials must allocate a significant portion of carbon and nitrogen to the crown and rhizomes to survive winter and regrow the following spring (DeHaan et al., 2005; Glover et al., 2010). Modeling this trade-off is crucial to assess the marketable yield of perennial grain crops, as prioritizing grain yield often comes at the physiological cost of reduced root biomass and stand longevity (Bell et al., 2008).

Current process-based models often rely on modified annual crop templates that struggle to capture this tension between reproductive effort and survival, and how that plays out throughout the growing seasons. A pertinent example is the recent intermediate wheatgrass module in APSIM Next Generation, which utilizes photosynthesis parameters and senescence rates initially adapted from the wheat module (Innes et al., 2026). While this approach successfully simulates biomass accumulation in intermediate wheatgrass by adjusting radiation use efficiency, it treats the crop dynamics largely as a sequence of seasonal growth cycles rather than a continuous problem of resource allocation. To improve accuracy, future models must incorporate dynamic sink strength functions where the demand for storage reserves competes directly with grain filling late in the growing season, moving away from fixed partitioning rules derived from annual cereals.

4.1.2 Root system architecture and deep soil feedbacks in perennial grain crops

The internal allocation logic of the plant directly dictates its physical structure, most notably the root system. The ability of perennial grains to provide ecosystem services, such as nitrate capture and carbon sequestration, often relies on deep, dense root systems that differ fundamentally from annual species (Crews & Cattani, 2018). Empirical observations on Thinopyrum intermedium demonstrate that its roots can extend deeper and maintain higher density than annual wheat, facilitating access to subsoil water (Duchene et al., 2020). In an intercropping context, adequately simulating this vertical root distribution is essential to capture "niche complementarity," where the perennial grain accesses deep resources while a companion legume utilizes the shallow soil layers (Thorup-Kristensen et al., 2020).

However, representing this root system architecture remains a weakness, as most grain models utilize static rooting depth parameters or simple descent rates suited for annuals. Even the most recent APSIM Next Generation Intermediate Wheatgrass model has this limitation, as it currently employs the standard wheat root organ without modification. As a result, the model does not represent intermediate wheatgrass deeper and denser roots, despite the developers explicitly acknowledging these characteristics (Innes et al., 2026). This simplification means that critical dynamics, such as the retention of nitrogen in living roots versus the decomposition observed in annuals, are not fully captured yet. By relying on annual root templates, current models likely underestimate the deep soil feedbacks and the competitive dominance of perennials in mixed systems. This necessitates a shift toward multi-layer resource uptake routines that account for root turnover and legacy effects (Tang et al., 2024).

4.1.3 Seasonal carryover

In perennial systems, the physiological state at the end of one season determines the potential of the next, creating a "system memory" that models of annual crops do not need and hence possess. The system memory pertains plant size and resource allocation and how that is affected by previous management choices. For example, legacy effects where management choices in one year (e.g., high N fertilization) cause lodging or yield penalties in subsequent years, as observed in field trials (Jungers et al., 2017), are not yet simulated, limiting the ability to predict long-term performance.

Another aspect to consider is the need to accurately predicting phenology. This requires modeling "dual induction", where plants must be exposed to specific vernalization (cold) and photoperiod (day length) cues to transition from vegetative to reproductive stages (Heide, 1994). If these requirements are not met, the crop remains vegetative, with no grain yield. Recent modeling work has made significant strides in predicting the timing of these phases, yet the depletion of belowground carbon and nitrogen reserves required for survival remains simplified (Innes et al., 2026). Simulations can now correctly predict that grain yield of intermediate wheatgrass fails in sub-tropical latitudes due to insufficient vernalization, but the physiological cost of winter survival is often handled by resetting the crop back to an early vegetative state rather than mechanistically depleting reserves. This approach might miss the link between winter reserve depletion and spring vigor (Höglind et al., 2016; Yoshida et al., 1998).

4.1.4 The management complexity in mixed systems

The interaction of these physiological and temporal factors creates a management landscape that is far more complex than in monocultures. While annual and perennial crop models already include many management practices such as fertilization timing, harvest height, and even repeated defoliation in forage or ley systems, the challenge in mixed perennial grain intercrops is the added layer of inter–specific interactions. In perennial intercrops, the competitive balance between species is not static across both seasons and years, as perennial plants accumulate biomass and reserves that alter their future competitive ability. Consequently, modelling the effects of management practices, such as defoliation, fertilization timing, and harvest height, must account for both these temporal and competitive dynamics, rather than fixed schedules. Such an approach could help towards capturing the typical highly context-dependent interactions of intercrops and the role of nutrient and water competition (Brooker et al., 2015).

Current grain crop models, however, are largely designed for fixed schedules and simplified effects of management operations, which can obscure intercropping benefits. For instance, recent validation efforts of crop models for perennial intercrops typically assume distinct crop rows with no inter-row recruitment and treat harvesting as simple biomass removal, missing the complexities of rhizome spread and nutrient cycling from grazing or residue return (Innes et al., 2026). These simplifications limit the model's ability to simulate "creeping" competition or weed suppression dynamics. To support the design of resilient intercropping systems, models must be developed to include adaptive management rules and the consequences of management actions. Although forage models already adjust harvest timing to optimize biomass yield and forage quality, perennial grain intercrops require adaptive harvest rules designed specifically to maintain species coexistence and balance competitive interactions (Bybee-Finley & Ryan, 2018).

4.2 The data bottleneck

Addressing these conceptual challenges in modeling is contingent on sufficient data availability, in particular from field experiments. However, perennial grains are still in the early stages of domestication and breeding (Crews & Cattani, 2018). There is still limited basic agronomic data from a wide range of environments simply because the crop is not globally available or widely cultivated. We lack the specific physiological data needed for the modules described above, such as the precise C/N allocation trade-offs between grain and rhizomes, multi-year root dynamics, and the impact of intercrop management on reserve accumulation. A tight, iterative feedback loop where modeling highlights key data gaps and hypotheses to guide experiments, and new data in turn refines the models (Hammer et al., 2020). This data scarcity also reinforces the need for minimalist models, such as the one used for annual intercrops by Berghuijs et al. (2020), which allow us to explore key trade-offs while we slowly gather additional data.

4.3 Towards a comprehensive assessment and design tool

If we can navigate these challenges, the resulting models will be far more than simple yield predictors. They will be comprehensive tools for both assessment and design of cropping systems. As assessment tools, they can quantify the ecosystem functioning of these systems, for example, by running multi-decade simulations to provide robust estimates of soil organic carbon sequestration (Tang et al., 2024) or reduced nitrate leaching (Jungers et al., 2019). They can also link biophysical outputs to farm-scale economic models, similar to how IFSM is used to evaluate the whole-farm performance of forage-based systems (Rotz, 2018).

Perhaps most powerfully, these models can serve as tools for variety design. By simulating "virtual cultivars" with different traits (e.g., "more allocation to grain" vs. "deeper roots"), these models can guide plant breeding (Rötter et al., 2015; Weih et al., 2022). This in silico ideotype design would allow researchers to test the potential performance of new traits across many climates before investing a decade in breeding for them in the field (Hammer et al., 2020), thereby accelerating the development of resilient, locally-adapted perennial grains.

5. Conclusion

This introductory essay highlights that, although perennial grain intercropping offers a promising strategy for sustainable agriculture, current simulation models are not yet fully equipped to guide their design. Although current models successfully capture how plants compete for basic resources like light and water, they do not represent the unique life history strategies of perennial grains, specifically the critical physiological trade-off between producing seeds for harvest and storing energy in roots to survive the winter. Bridging this gap requires developing current models to account for dynamic feedbacks and multi-year processes, such as the functioning of deep root systems and the cumulative effects of seasonal carryover on subsequent-year performance. By integrating these long-term ecological dynamics into agricultural simulations, models can be transformed into powerful design tools, allowing scientists to virtually test and optimize these complex ecosystems for climate resilience and environmental benefits without relying solely on time-consuming field trials.

References

Bartel, C. A., Archontoulis, S. V., Lenssen, A. W., Moore, K. J., Huber, I. L., Laird, D. A., & Dixon, P. M. (2020). Modeling perennial groundcover effects on annual maize grain crop growth with the Agricultural Production Systems sIMulator. *Agronomy Journal*, *112*(3), 1895–1910. https://doi.org/10.1002/agj2.20108

Bell, L. W., Byrne (nee Flugge), F., Ewing, M. A., & Wade, L. J. (2008). A preliminary whole-farm economic analysis of perennial wheat in an Australian dryland farming system. *Agricultural Systems*, *96*(1), 166–174. https://doi.org/10.1016/j.agsy.2007.07.007

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 and Soil*, *455*(1–2), 203–226. https://doi.org/10.1007/s11104-020-04668-0

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Brannan, T., Bickler, C., Hansson, H., Karley, A., Weih, M., & Manevska-Tasevska, G. (2023). Overcoming barriers to crop diversification uptake in Europe: A mini review. *Frontiers in Sustainable Food Systems*, *7*. https://doi.org/10.3389/fsufs.2023.1107700

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., … White, P. J. (2015). Improving intercropping: A synthesis of research in agronomy, plant physiology and ecology. *New Phytologist*, *206*(1), 107–117. https://doi.org/10.1111/nph.13132

Bybee-Finley, K. A., & Ryan, M. R. (2018). Advancing Intercropping Research and Practices in Industrialized Agricultural Landscapes. *Agriculture*, *8*(6), 80. https://doi.org/10.3390/agriculture8060080

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P. W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W. W. L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., … Péan, C. (with Lee, H.). (2023). *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.* (First). Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647

Creamer, R. E., Barel, J. M., Bongiorno, G., & Zwetsloot, M. J. (2022). The life of soils: Integrating the who and how of multifunctionality. *Soil Biology and Biochemistry*, *166*, 108561. https://doi.org/10.1016/j.soilbio.2022.108561

Crews, T. E., & Cattani, D. J. (2018). Strategies, Advances, and Challenges in Breeding Perennial Grain Crops. *Sustainability*, *10*(7), 2192. https://doi.org/10.3390/su10072192

Crews, T. E., Kemp, L., Bowden, J. H., & Murrell, E. G. (2022). How the Nitrogen Economy of a Perennial Cereal-Legume Intercrop Affects Productivity: Can Synchrony Be Achieved? *Frontiers in Sustainable Food Systems*, *6*. https://doi.org/10.3389/fsufs.2022.755548

Culman, S. W., Snapp, S. S., Ollenburger, M., Basso, B., & DeHaan, L. R. (2013). Soil and Water Quality Rapidly Responds to the Perennial Grain Kernza Wheatgrass. *Agronomy Journal*, *105*(3), 735–744. https://doi.org/10.2134/agronj2012.0273

DeHaan, L. R., Tassel, D. L. V., & Cox, T. S. (2005). Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems*, *20*(1), 5–14. https://doi.org/10.1079/RAF200496

Demie, G., Negash, M., Asrat, Z., & Bohdan, L. (2024). Species specific and multi-species allometric models for estimating aboveground biomass of native perennial plant species grown in the agricultural landscape of Central Ethiopia. *Agroforestry Systems*, *98*(1), 179–196. https://doi.org/10.1007/s10457-023-00898-0

Duchene, O., Celette, F., Barreiro, A., Dimitrova Mårtensson, L.-M., Freschet, G. T., & David, C. (2020). Introducing Perennial Grain in Grain Crops Rotation: The Role of Rooting Pattern in Soil Quality Management. *Agronomy*, *10*(9), 1254. https://doi.org/10.3390/agronomy10091254

Eckersten, H., Lundkvist, A., Torssell, B., & Verwijst, T. (2011). Modelling species competition in mixtures of perennial sow-thistle and spring barley based on shoot radiation use efficiency. *Acta Agriculturae Scandinavica, Section B — Soil & Plant Science*, *61*(8), 739–746. https://doi.org/10.1080/09064710.2011.555778

Faverjon, L., Escobar-Gutiérrez, A., Litrico, I., Julier, B., & Louarn, G. (2019a). A generic individual-based model can predict yield, nitrogen content, and species abundance in experimental grassland communities. *JOURNAL OF EXPERIMENTAL BOTANY*, *70*(9), 2491–2504. (WOS:000469784900013). https://doi.org/10.1093/jxb/ery323

Faverjon, L., Escobar-Gutiérrez, A., Litrico, I., Julier, B., & Louarn, G. (2019b). A generic individual-based model can predict yield, nitrogen content, and species abundance in experimental grassland communities. *Journal of Experimental Botany*, *70*(9), 2491–2504. https://doi.org/10.1093/jxb/ery323

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., … Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337–342. https://doi.org/10.1038/nature10452

Fort, H., Dieguez, F., Halty, V., & Lima, J. M. S. (2017). Two examples of application of ecological modeling to agricultural production: Extensive livestock farming and overyielding in grassland mixtures. *Ecological Modelling*, *357*, 23–34. https://doi.org/10.1016/j.ecolmodel.2017.03.023

Glover, J. D., Reganold, J. P., Bell, L. W., Borevitz, J., Brummer, E. C., Buckler, E. S., Cox, C. M., Cox, T. S., Crews, T. E., Culman, S. W., DeHaan, L. R., Eriksson, D., Gill, B. S., Holland, J., Hu, F., Hulke, B. S., Ibrahim, A. M. H., Jackson, W., Jones, S. S., … Xu, Y. (2010). Increased Food and Ecosystem Security via Perennial Grains. *Science*, *328*(5986), 1638–1639. https://doi.org/10.1126/science.1188761

Gutknecht, J. L., Anderson, J. A., Annor, G., Bajgain, P., Crews, T. E., Cureton, C., DeHaan, L., Meier, E., Peters, T., Picasso, V., Reilly, E. C., Reser, A., Ritter, T., Krug, A. S., Tautges, N., & Jungers, J. M. (2026). Development and adoption of Kernza—A perennial grain crop for sustainable agriculture. *PLANTS, PEOPLE, PLANET*, *n/a*(n/a). https://doi.org/10.1002/ppp3.70164

Halty, V., Valdés, M., Tejera, M., Picasso, V., & Fort, H. (2017). Modeling plant interspecific interactions from experiments with perennial crop mixtures to predict optimal combinations. *Ecological Applications*, *27*(8), 2277–2289. https://doi.org/10.1002/eap.1605

Hammer, Graeme. L., McLean, G., van Oosterom, E., Chapman, S., Zheng, B., Wu, A., Doherty, A., & Jordan, D. (2020). Designing crops for adaptation to the drought and high-temperature risks anticipated in future climates. *Crop Science*, *60*(2), 605–621. https://doi.org/10.1002/csc2.20110

Heide, O. M. (1994). Control of flowering and reproduction in temperate grasses. *New Phytologist*, *128*(2), 347–362. https://doi.org/10.1111/j.1469-8137.1994.tb04019.x

Höglind, M., Van Oijen, M., Cameron, D., & Persson, T. (2016). Process-based simulation of growth and overwintering of grassland using the BASGRA model. *Ecological Modelling*, *335*, 1–15. https://doi.org/10.1016/j.ecolmodel.2016.04.024

Innes, P. J., Newell, M. T., Pembleton, K. G., Hayes, R. C., & Radanielson, A. M. (2026). An Intermediate Wheatgrass model for APSIM Next Generation. *European Journal of Agronomy*, *172*, 127858. https://doi.org/10.1016/j.eja.2025.127858

Jégo, G., Rotz, C., Bélanger, G., Tremblay, G., Charbonneau, É., & Pellerin, D. (2015). Simulating forage crop production in a northern climate with the Integrated Farm System Model. *CANADIAN JOURNAL OF PLANT SCIENCE*, *95*(4), 745–757. (WOS:000360994100015). https://doi.org/10.4141/CJPS-2014-375

Jensen, E. S., Carlsson, G., & Hauggaard-Nielsen, H. (2020). Intercropping of grain legumes and cereals improves the use of soil N resources and reduces the requirement for synthetic fertilizer N: A global-scale analysis. *Agronomy for Sustainable Development*, *40*(1), 5. https://doi.org/10.1007/s13593-020-0607-x

Jungers, J. M., DeHaan, L. H., Mulla, D. J., Sheaffer, C. C., & Wyse, D. L. (2019). Reduced nitrate leaching in a perennial grain crop compared to maize in the Upper Midwest, USA. *Agriculture, Ecosystems & Environment*, *272*, 63–73. https://doi.org/10.1016/j.agee.2018.11.007

Jungers, J. M., DeHaan, L. R., Betts, K. J., Sheaffer, C. C., & Wyse, D. L. (2017). Intermediate Wheatgrass Grain and Forage Yield Responses to Nitrogen Fertilization. *Agronomy Journal*, *109*(2), 462–472. https://doi.org/10.2134/agronj2016.07.0438

Letourneau, D. K., Armbrecht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., Escobar, S., Galindo, V., Gutiérrez, C., López, S. D., Mejía, J. L., Rangel, A. M. A., Rangel, J. H., Rivera, L., Saavedra, C. A., Torres, A. M., & Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, *21*(1), 9–21. https://doi.org/10.1890/09-2026.1

Lithourgidis, A. S., Dordas, C. A., Damalas, C. A., & Vlachostergios, D. N. (2011). Annual intercrops: An alternative pathway for sustainable agriculture. *Australian Journal of Crop Science*, *5*(4), 396–410.

Louarn, G., & Faverjon, L. (2018). A generic individual-based model to simulate morphogenesis, C-N acquisition and population dynamics in contrasting forage legumes. *ANNALS OF BOTANY*, *121*(5), 875–896. (WOS:000430676600009). https://doi.org/10.1093/aob/mcx154

Maire, V., Soussana, J.-F., Gross, N., Bachelet, B., Pagès, L., Martin, R., Reinhold, T., Wirth, C., & Hill, D. (2013). Plasticity of plant form and function sustains productivity and dominance along environment and competition gradients. A modeling experiment with Gemini. *Ecological Modelling*, *254*, 80–91. https://doi.org/10.1016/j.ecolmodel.2012.03.039

Manevski, K., Borgesen, C., Andersen, M., & Kristensen, I. (2015). Reduced nitrogen leaching by intercropping maize with red fescue on sandy soils in North Europe: A combined field and modeling study. *PLANT AND SOIL*, *388*(1–2), 67–85. (WOS:000350571500008). https://doi.org/10.1007/s11104-014-2311-6

Meirelles, F. C., Cavalcante, A. G., Gonzaga, A. R., Coelho, A. P., van der Werf, W., Bastiaans, L., Arf, O., & Lemos, L. B. (2024). Relative Sowing Time and Spatial Arrangement in Upland Rice/Legume Intercropping Systems. *International Journal of Plant Production*, *18*(2), 161–174. https://doi.org/10.1007/s42106-024-00294-3

Movedi, E., Paleari, L., Argenti, G., Vesely, F. M., Stagliano, N., Parrini, S., & Confalonieri, R. (2024). The application of a plant community model to evaluate adaptation strategies for alleviating climate change impacts on grassland productivity, biodiversity and forage quality. *ECOLOGICAL MODELLING*, *488*, 110596. https://doi.org/10.1016/j.ecolmodel.2023.110596

Payant, C., Jégo, G., Ouellet, V., Grenier, P., Tremblay, G., Bélanger, G., & Charbonneau, É. (2021). Modeled performance of forage mixtures and annual crops grown in eastern Canada under climate change. *AGRONOMY JOURNAL*, *113*(6), 4945–4964. (WOS:000725543300001). https://doi.org/10.1002/agj2.20894

Pinto, P., Cartoni-Casamitjana, S., Stoltenberg, D. E., & Picasso, V. D. (2024). Forage boost or grain blues? Legume choices shape Kernza intermediate wheatgrass dual-purpose crop performance. *Field Crops Research*, *316*, 109522. https://doi.org/10.1016/j.fcr.2024.109522

Power, A. G. (2010). Ecosystem services and agriculture: Tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1554), 2959–2971. https://doi.org/10.1098/rstb.2010.0143

Reilly, E. C., Gutknecht, J. L., Tautges, N. E., Sheaffer, C. C., & Jungers, J. M. (2022). Nitrogen transfer and yield effects of legumes intercropped with the perennial grain crop intermediate wheatgrass. *Field Crops Research*, *286*, 108627. https://doi.org/10.1016/j.fcr.2022.108627

Rötter, R. P., Tao, F., Höhn, J. G., & Palosuo, T. (2015). Use of crop simulation modelling to aid ideotype design of future cereal cultivars. *Journal of Experimental Botany*, *66*(12), 3463–3476. https://doi.org/10.1093/jxb/erv098

Rotz, C. A. (2018). Modeling greenhouse gas emissions from dairy farms. *Journal of Dairy Science*, *101*(7), 6675–6690. https://doi.org/10.3168/jds.2017-13272

Salis, L. (2017). Modelling pasture production and soil temperature, water and carbon fluxes in Mediterranean grassland systems with the Pasture Simulation model. *Grass and Forage Science*. https://doi.org/10.1111/GFS.12310

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. *Field Crops Research*, *116*(3), 218–229. https://doi.org/10.1016/j.fcr.2009.11.007

Snow, V. O., Smale, P. N., & Dodd, M. B. (2013). Process-based modelling to understand the impact of ryegrass diversity on production and leaching from grazed grass-clover dairy pastures. *Crop and Pasture Science*, *64*(10), 1020. https://doi.org/10.1071/CP13263

Soussana, J.-F., Maire, V., Gross, N., Bachelet, B., Pagès, L., Martin, R., Hill, D., & Wirth, C. (2012). Gemini: A grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation. *Ecological Modelling*, *231*, 134–145. https://doi.org/10.1016/j.ecolmodel.2012.02.002

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, *347*(6223), 1259855. https://doi.org/10.1126/science.1259855

Stone, T. F., Alford, J., Bečvářová, P. H., Eisa, M. A. M., El-Naggar, A. H., Carpio Espinosa, M. J., Frąc, M., Álvaro-Fuentes, J., García-Gil, J. C., Krabbe, K., Martins, J. T., Pathan, S. I., Plaza, C., Rasmussen, J., Righini, C., & Thorsøe, M. H. (2025). Food system strategies to increase grain legume-cereal intercropping in Europe. *Agroecology and Sustainable Food Systems*, *49*(4), 518–542. https://doi.org/10.1080/21683565.2024.2427783

Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*(45), eaba1715. https://doi.org/10.1126/sciadv.aba1715

Tang, F. H. M., Crews, T. E., Brunsell, N. A., & Vico, G. (2024). Perennial intermediate wheatgrass accumulates more soil organic carbon than annual winter wheat – a model assessment. *Plant and Soil*, *494*(1), 509–528. https://doi.org/10.1007/s11104-023-06298-8

Thorup-Kristensen, K., Halberg, N., Nicolaisen, M., Olesen, J. E., Crews, T. E., Hinsinger, P., Kirkegaard, J., Pierret, A., & Dresbøll, D. B. (2020). Digging Deeper for Agricultural Resources, the Value of Deep Rooting. *Trends in Plant Science*, *25*(4), 406–417. https://doi.org/10.1016/j.tplants.2019.12.007

van Ittersum, M. K., Leffelaar, P. A., van Keulen, H., Kropff, M. J., Bastiaans, L., & Goudriaan, J. (2003). On approaches and applications of the Wageningen crop models. *European Journal of Agronomy, Modelling Cropping Systems: Science, Software and Applications*, *18*(3), 201–234. https://doi.org/10.1016/S1161-0301(02)00106-5

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. *Agronomy for Sustainable Development*, *43*(5), 61. https://doi.org/10.1007/s13593-023-00917-5

Vico, G., Tang, F. H. M., Brunsell, N. A., Crews, T. E., & Katul, G. G. (2023). Photosynthetic capacity, canopy size and rooting depth mediate response to heat and water stress of annual and perennial grain crops. *Agricultural and Forest Meteorology*, *341*, 109666. https://doi.org/10.1016/j.agrformet.2023.109666

Weih, M., Adam, E., Vico, G., & Rubiales, D. (2022). Application of Crop Growth Models to Assist Breeding for Intercropping: Opportunities and Challenges. *Frontiers in Plant Science*, *13*. https://doi.org/10.3389/fpls.2022.720486

Weiner, J., Du, Y.-L., Zhang, C., Qin, X.-L., & Li, F.-M. (2017). Evolutionary agroecology: Individual fitness and population yield in wheat (Triticum aestivum). *Ecology*, *98*(9), 2261–2266. https://doi.org/10.1002/ecy.1934

Wu, L., McGechan, M. B., McRoberts, N., Baddeley, J. A., & Watson, C. A. (2007). SPACSYS: Integration of a 3D root architecture component to carbon, nitrogen and water cycling—Model description. *Ecological Modelling*, *200*(3), 343–359. https://doi.org/10.1016/j.ecolmodel.2006.08.010

Yoshida, M., Abe, J., Moriyama, M., & Kuwabara, T. (1998). Carbohydrate levels among winter wheat cultivars varying in freezing tolerance and snow mold resistance during autumn and winter. *Physiologia Plantarum*, *103*(1), 8–16. https://doi.org/10.1034/j.1399-3054.1998.1030102.x

Appendix 1

Table A2. Reference list of the 15 studies assessed in detail.

Title	**Reference**
Modeling perennial groundcover effects on annual maize grain crop growth with the Agricultural Production Systems sIMulator	Bartel et al., 2020
Species specific and multi-species allometric models for estimating aboveground biomass of native perennial plant species grown in the agricultural landscape of Central Ethiopia	Demie et al., 2024
Modelling species competition in mixtures of perennial sow-thistle and spring barley based on shoot radiation use efficiency	Eckersten et al., 2011
A generic individual-based model can predict yield, nitrogen content, and species abundance in experimental grassland communities	Faverjon et al., 2019
Two examples of application of ecological modeling to agricultural production: Extensive livestock farming and overyielding in grassland mixtures	Fort et al., 2017
Modeling plant interspecific interactions from experiments with perennial crop mixtures to predict optimal combinations	Halty et al., 2017
Simulating forage crop production in a northern climate with the Integrated Farm System Model	Jégo et al., 2015
A generic individual-based model to simulate morphogenesis, C–N acquisition and population dynamics of forage legumes	Louarn & Faverjon, 2018
Plasticity of plant form and function sustains productivity and dominance along environment and competition gradients. A modeling experiment with Gemini	Maire et al., 2013

Reduced nitrogen leaching by intercropping maize with red fescue on sandy soils in North Europe: a combined field and modeling study	Manevski et al., 2015
The application of a plant community model to evaluate adaptation strategies for alleviating climate change impacts on grassland productivity, biodiversity and forage quality	Movedi et al., 2024
Modeled performance of forage mixtures and annual crops grown in eastern Canada under climate change	Payant et al., 2021
Does intercropping winter wheat (*Triticum aestivum*) with red fescue (*Festuca rubra*) as a cover crop improve agronomic and environmental performance? A modeling approach	Shili-Touzi et al., 2010
Process-based modelling to understand the impact of ryegrass diversity on production and leaching from grazed grass-clover dairy pastures	Snow et al., 2013
Gemini: A grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation	Soussana et al., 2012