

The Roots Awaken: Development and implementation of a root autotrophic respiration module for soil CO₂ flux partitioning in a cropping system process-based model

Mara Gabbrielli, Leonardo Vario^{*} , Marco Botta, Marco Perfetto, Marco Acutis, Alessia Perego, Giorgio Ragaglini

Department of Agricultural and Environmental Sciences, University of Milan, Via Celoria 2, 20133 Milan, Italy

ARTICLE INFO

Keywords:

Agroecosystem fluxes
Crop modeling
Soil respiration
Crop rotation
Accumulation chambers

ABSTRACT

As agricultural soils are both sources and sinks of C, evaluating their C balance by properly accounting for the individual components of the C fluxes and their environmental drivers is required. Soil CO₂ emissions (R_s) result from the combination of autotrophic respiration (R_a , from root growth and maintenance) and heterotrophic respiration (R_h , from soil organic matter decomposition). In this study, we developed a new module for the process-based ARMOSA (Analysis of cRopping systems for Management Optimization and Sustainable Agriculture) model to explicitly simulate root autotrophic respiration of wheat (*Triticum durum* Desf.) and processing tomato (*Lycopersicon esculentum* Mill.), with the aim of improving the quantification of soil C balance in cropping systems. Root respiration is simulated as influenced by the interactions between crop growth, root senescence and management practices. The new module was developed and tested using daily measured soil CO₂ fluxes collected in two Mediterranean sites (moist and dry) during multi-year crop rotations, using automated stations equipped with eight non-steady-state measurement chambers. According to the results, root respiration is a crop-specific process that is driven by soil conditions, as highlighted by the sensitivity analysis of the new module, which identified the crop maintenance respiration potential and the optimal soil temperature for growth and maintenance respiration as the top-ranked parameters. The new module application within the framework of ARMOSA model enabled the partitioning of soil CO₂ fluxes, allowing the estimation of the R_a/R_s ratio for wheat and tomato (ranging respectively from 9 to 90 % and from 1 to 87 % for wheat and tomato) as influenced by crop development. This improved the simulation of soil R_h throughout the entire crop rotations. The new module is able to quantify the actual contribution of a crop to the C balance under varying management and pedoclimatic conditions.

1. Introduction

Agricultural soils generate high CO₂ fluxes, but the balance between their sink and source capacity is subject to great uncertainty and high spatial and temporal variability (Delandmeter et al., 2023). Carbon (C) exchange fluxes between the atmosphere and soil are continuous and bidirectional: part of the atmospheric C, converted via photosynthesis into structural and non-structural carbohydrates, is either stored in soil organic matter (SOM) pools, or part is returned to the atmosphere through autotrophic and heterotrophic respiration or fermentation processes. As root and microbial respiration drive the C fluxes exiting the soil, the accumulation of non-structural carbohydrates (with short mean

residence time) in plant organs and crop residues in the soil may enhance substrate availability and thus potentially increase C losses (Savage et al., 2013). The total efflux of CO₂ into the atmosphere is known as total soil respiration (R_s) and is composed of: (i) a share produced by autotrophic organisms (autotrophic respiration, R_a) that originates from plant roots metabolism; (ii) a share developed by heterotrophic organisms (heterotrophic respiration, R_h) due to SOM decomposition and mineralisation processes (Zhang et al., 2013). Since crop residues are the main C input supporting agricultural soils sink capacity, it is essential to account for R_a losses when evaluating actual C sequestration.

Direct measurement of CO₂ fluxes from soils at field level can be

^{*} Corresponding author.

E-mail address: leonardo.vario@unimi.it (L. Vario).

<https://doi.org/10.1016/j.ijagro.2025.100044>

Received 21 January 2025; Received in revised form 18 June 2025; Accepted 19 June 2025

Available online 24 June 2025

1125-4718/© 2025 The Authors. Published by Elsevier B.V. on behalf of Società Italiana di Agronomia. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

carried out using accumulation chambers or micrometeorological methods (Butterbach-Bahl et al., 2013). The main limitation of these methods is the difficulty in differentiating CO_2 sources when a crop is present in the field, due to the diverse processes responsible for its production (Phillips et al., 2017), as measured fluxes reflect total R_g . Simulation models can help to identify baseline R_h under specific pedoclimatic and management conditions, while being also useful in situations where measurements are infrequent or absent (gap filling) or to extend point measurements to estimation across spatial scales (Grados et al., 2024). At the same time, the limitations of CO_2 measurement methods make the development and parameterisation of mechanistic modules for the simulation of these fluxes challenging.

Autotrophic respiration takes place at the mitochondrial level and consumes carbohydrates as a substrate to support all energy-demanding processes in the plant (Thornley and Cannell, 2000). However, given the complexity of measuring and quantifying the costs of each energy-demanding process, a simplified view is usually adopted (Thornley and Cannell, 2000) by grouping these costs into growth respiration (R_{ag}) and maintenance respiration (R_{am}). This growth-maintenance paradigm is applied within cropping systems modelling (Chen et al., 2008; Goudriaan, 1992; van Laar et al., 1997): R_{ag} is defined as the amount of C needed to increase the biomass by one C unit (Penning de Vries et al., 1983), and it is related to the overall plant biomass growth rate, while R_{am} is associated with the biomass of different plant organs.

Currently, the simulation of R_a is carried out with different approaches by dynamic cropping systems simulation models operating at daily time-step and at the field scale (Appendix A, Paragraph 1 A). In ARMOSA (Analysis of cRopping systems for Management Optimization and Sustainable Agriculture, Perego et al., 2013) original version (V.1), the crop growth module is based on a balance between gross CO_2 assimilation, R_{am} and R_{ag} , as implemented in SUCROS (van Laar et al., 1997) and WOFOST (van Keulen and Wolf, 1986). The R_a rates of the simulated plant organs (leaf, stem, root and storage) are considered as implicit variables, and calibration of their parameters employs crop total biomass accumulation as the objective variable (when the measured partitioning coefficients are unavailable). These models do not account for root senescence, which leads to a differentiation in the organ's

respiratory processes across crop growth stages. Furthermore, the respiratory components, due to their implicit formalisation, are not provided as model outputs, and therefore the total R_a attributed to the roots is not calculated based on their localisation along the soil profile. Despite the richness of processes represented by the ARMOSA model (Perego et al., 2013; Valkama et al., 2020; Tadiello et al., 2023), an integrated approach for explicit simulation of plant R_a is still lacking. Implementing a module for root R_a would enhance the ability of ARMOSA to represent C flows in cropping systems and improve the simulation of net C accumulation and its impacts on greenhouse gas (GHG) emissions mitigation.

The objectives of this work were: (i) to develop a new integrated module simulating soil emissions as a result of both R_h and R_a , thus overcoming the limitations of currently available models; (ii) to explore the new module output sensitivity to its input parameters; (iii) to assess the potential of the new module in improving the performance of the ARMOSA model in estimating total R_s compared with the original version.

2. Material and methods

2.1. The new roots autotrophic respiration module

The new ARMOSA module (V.2) draws inspiration from the approach adopted by DNDC model (DeNitrification-DeComposition, Li et al., 1994, Appendix A, Paragraph 1 A), while retaining the methodology derived from SUCROS and WOFOST (Appendix A, Paragraph 2 A), to explicitly simulate the individual contributions of R_{ag} and R_{am} (Fig. 1) to CO_2 emissions from soils.

Root growth respiration ($R_{ag}(\text{root}, z)$, $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$, Eq. (1)) of each z -th soil layer is simulated as a share of the total plant R_{ag} ($R_{ag}(\text{plant})$, $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$, Appendix A, Paragraph 3 A, Eq. (5A)) determined by the ratio between the root growth rate ($r\text{Biomass}(\text{root})$, $\text{kg DM ha}^{-1} \text{d}^{-1}$, Eq. (3A)) and the plant growth rate ($r\text{Biomass}(\text{plant})$, $\text{kg DM ha}^{-1} \text{d}^{-1}$).

$$R_{ag}(\text{root}, z) = R_{ag}(\text{plant}) \cdot \frac{r\text{Biomass}(\text{root})}{r\text{Biomass}(\text{plant})} \cdot F_{\text{root}}(z) \quad (1)$$

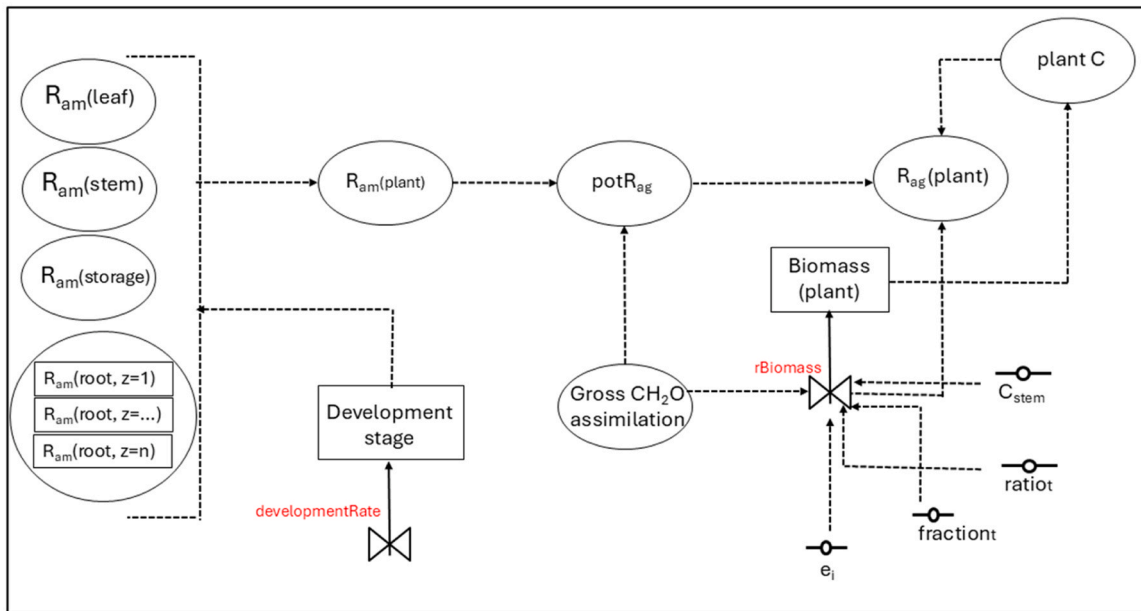


Fig. 1. Conceptual diagram of the new module implemented in the ARMOSA model (V.2). State, rate and auxiliary variables are indicated with a rectangle, a valve symbol and a circle, respectively. The most important parameters are indicated with a short segment (e_i , fraction , ratio , C_{stem}). The names of rate variables are in red. Continuous lines indicate inputs to and outputs from a state variable. Dotted lines indicate the dependence of a rate or auxiliary variable from another variable or parameter. Maintenance and growth autotrophic respiration are represented by R_{am} and R_{ag} , respectively.

The root maintenance respiration (R_{am} (root, z), Eq. (2)) of each z-th soil layer is calculated depending on root biomass ($Biomass(root)$, kg DM ha^{-1}) and on a maintenance coefficient (m_{root} , g CH_2O g DM^{-1} d $^{-1}$). Root senescence is incorporated by reducing R_{am} with a senescence exponential factor ($f_s(root)$, Eq. (8A)) when the BBCH (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie) scale value exceeds a threshold. This function is highly adaptable, as the threshold and senescence rate are implemented as crop- or variety-specific parameters. Additionally, the effect of temperature is simulated using the soil temperature ($T_{soil(z)}$, °C) as a reference, in relation to a base temperature (T_{base} , °C).

$$R_{am}(root, z) = m_{root} \cdot f_s(root) \cdot Biomass(root) \cdot 2^{\frac{T_{soil(z)} - T_{base}}{10}} \cdot F_{root}(z) \quad (2)$$

The total root R_a ($R_{ag} + R_{am}$) is distributed along the vertical soil profile explored by the roots by allocating a fraction ($F_{root}(z)$, Eq. (10A)) to each soil layer, using a function describing root density distribution (Eq. 9 A).

2.2. Case study for the new module assessment

The experimental data used for this study were collected within the LIFE project AGRESTIC– Reduction of Agricultural greenhouse gases Emissions Through Innovative Cropping systems (LIFE17 CCM/IT/000062). The data pertain to two experimental trials located at the Ca' Bosco farm (Ravenna, northern Italy, 44.48 N 12.17 E) and at the Caione farm (Foggia, southern Italy, 41.50 N 15.51 E).

Meteorological data used for the simulations were collected from weather stations located at the experimental sites, with daily records of precipitation, global radiation, air temperature, relative humidity, and wind speed (Supplementary Materials, Fig. S1). These sites are characterized by a temperate climate (Supplementary Materials, Fig. S1). At Ravenna (temperate humid climate), the average annual temperature was 14.8 °C, and annual rainfall recorded by the on-site meteorological station was 538 mm (2020), 513 mm (2021), 574 mm (2022), and 616 mm (January–October 2023). At Foggia (temperate dry climate), the average annual temperature was 16.5 °C, and annual rainfall was 231 mm (August–December 2019), 541 mm (2020), 514 mm (2021), and 569 mm (January–November 2022).

In these two sites, the following cropping systems (CS) were compared: (i) a Conventional Cropping System (CCS) aimed at maximizing productivity; (ii) an Efficient Cropping System (ECS) designed to achieve a more efficient use of agronomic inputs through the adoption of a Decision Support System (DSS), while allowing a significant mitigation of GHG emissions. In both farms, a GHG monitoring station was installed and connected to an IT infrastructure for data management. Each station consists of eight automatic flow-through non-steady-state chambers (four for each cropping system), a shelter, protecting the optical analysers, a multiplexer, a local processing unit (LPU) controlling the automation and the data transmission via GPRS (General Packet Radio Service) to a remote server. The two analysers measuring CO_2 concentration and N_2O concentration were a LI-850 (LI-COR, Lincoln, NE, USA) and GFC-7002TU (TELEDYNE TECHNOLOGIES, Thousand Oaks, CA, USA) respectively. During the measurement, each chamber closed hermetically according to a periodicity of 160 min, allowing 9 cycles per day per chamber, and a closure time of 15 min. Each chamber was equipped with 20 cm long soil probes to measure soil temperature and water content. Further details of the stations setup, operation, and data quality checks are described in Volpi et al. (2020) and in Gabbrielli et al. (2025). CO_2 soil fluxes were measured continuously for three to four years in the two pilot farms in 1 out of 4 plots, both for CCS and ECS (Table 1). Furthermore, additional field monitoring data was collected to calibrate and validate the process-based model ARMOSA V.2 to provide reliable daily predictions of CO_2 emissions due to R_s from topsoil layers as the sum of R_a and R_h .

In the monitored plots, for the trial in Ravenna, the CCS crop rotation

Table 1

Crop rotations simulated for each combination of site*cropping system*plot of the case studies. Alfalfa intercropping with durum wheat or barley is reported as “cereal + alfalfa”, while cover crops are highlighted with “(cc)”. The cover crop employed in plot 3 and 7 (Foggia ECS) is a mixture of phacelia (53 %, *Phacelia tanacetifolia* Benth.), tillage radish (11 %, *Raphanus sativus* L.) and Egyptian clover (36 %, *Trifolium alexandrinum* L.). * indicates the crops for which the new module was calibrated and validated.

Site	Cropping system	Plot	CO ₂ dataset	Crop rotation
Ravenna	CCS	2	Calibration	tomato, durum wheat, maize, durum wheat
		4		maize, durum wheat 1 *, tomato *, durum wheat 2 *
		6		durum wheat, maize, durum wheat, processing tomato
		8		durum wheat, processing tomato, durum wheat, maize
Ravenna	ECS	1	Validation	durum wheat+alfalfa, pea, durum wheat+alfalfa, processing tomato
		3		durum wheat+alfalfa, processing tomato, durum wheat+alfalfa, soybean
		5		pea, durum wheat+alfalfa 1 *, processing tomato *, durum wheat+alfalfa 2 *
		7		processing tomato, durum wheat+alfalfa, pea, durum wheat+alfalfa
Foggia	CCS	2	Calibration	durum wheat, barley, durum wheat
		4		sunflower, durum wheat *, barley
		6		barley, durum wheat, sunflower
		8		durum wheat, sunflower, durum wheat
Foggia	ECS	1	Validation	sunflower, barley+alfalfa, mustard (cc), lentil
		3		barley+alfalfa, mixture (cc), lentil, durum wheat + alfalfa
		5		lentil, durum wheat + alfalfa *, mustard (cc), sunflower
		7		durum wheat + alfalfa, mixture (cc), sunflower, barley+alfalfa

was maize (*Zea mays* L.), durum wheat (*Triticum durum* Desf.), processing tomato (*Lycopersicon esculentum* Mill.) and durum wheat, while the ECS was pea (*Pisum sativum* L.), durum wheat + alfalfa (*Medicago sativa* L.), processing tomato and durum wheat + alfalfa. In Foggia, the CCS crop rotation was sunflower (*Helianthus annuus* L.), durum wheat, barley (*Hordeum vulgare* L.) and durum wheat, while ECS included lentil (*Lens esculenta* Moench), durum wheat + alfalfa, mustard cover crop (*Brassica juncea* Coss.) followed by sunflower and barley. The details concerning crop and soil management in these plots are reported in the Supplementary Materials (Tables S1 and S2).

In all the experimental plots (Table 1), crop phenological stages were monitored during the cultivation period, while above-ground biomass (AGB, t DM ha^{-1}), yield (t DM ha^{-1}), and nitrogen uptake (kg N ha^{-1}) were measured for each crop at harvest. The soil analyses conducted at the two experimental sites (including sand and clay content, bulk density, and organic carbon content) at the beginning of the field trial were used to derive the necessary inputs for soil parameterization in the simulations. During the calibration and validation phases, the initial values of soil N pools (nitrate and ammonium content) for the topsoil layer (0 – 0.3 m) were obtained through laboratory analyses conducted after sampling at the beginning of the experimental period (Supplementary Materials, Table S3). The hydrological parameters of the soil are automatically recalculated by the model at each timestep, based on the initial values (Supplementary Materials, Table S3) using pedotransfer functions.

2.3. Sensitivity analysis of the new module

The screening method of [Morris \(1991\)](#) modified by [Campolongo et al. \(2007\)](#) was employed to assess the sensitivity of the new module by ranking the parameters based on the importance of their mean effect μ^* ([Supplementary Materials, Eq. \(S1\)](#)) on target outputs (R_{am} , R_{ag} and R_a). This method provides three sensitivity metrics for each input parameter: μ and μ^* reflect the overall significance of the parameter in influencing the variability of the model's outputs, while σ identifies the presence of non-linear effects and/or interactions between parameters. In this work, the sampling of the space of parameters is performed by setting 100 total trajectories (M), 4 levels (p) and 10 selected trajectories (r), obtaining $r(k+1) = 190$ different settings of the input parameters, where k represents the parameter number (18, [Table 2](#)). Each setting corresponds to one of the selected points in the k -dimensional hypercube and, for each one of the selected $r(k+1)$ points, the three above-mentioned tool outputs were calculated. The sensitivity test was performed on the simulations of both the calibration and the validation datasets. Results are presented separately for wheat and tomato.

Table 2

Crop-specific parameters of the new autotrophic respiration module: process (roots maintenance respiration, R_{am} ; root growth respiration, R_{ag} , heterotrophic respiration, R_h), definition, unit of measure, lower and upper bounds of parameters ranges for sensitivity analysis, default and calibrated values for the considered crops.

Parameter	Process	Definition	Unit of measure	Lower Bound	Upper Bound	Reference	Default	Calibrated	
								Wheat	Tomato
T_{base}	R_{am}	base temperature	°C	22.5	27.5	(Colombi et al., 2024 ; Goudriaan, 1992)	25	25	25
m_{leaf}	R_{am}	maintenance coefficient leaves	$g\ CH_2O\ g\ DM^{-1}$	0.01	0.05	(Colombi et al., 2024 ; Goudriaan, 1992)	0.03	0.03	0.03
m_{root}	R_{am}	maintenance coefficient root	$g\ CH_2O\ g\ DM^{-1}$	0.01	0.093	(Amthor J, 1984 ; Amthor, 1986 ; Gifford, 2003 ; Goudriaan, 1992 ; Penning de Vries, 1975)	0.05	0.075	0.085
m_{stem}	R_{am}	maintenance coefficient stem	$g\ CH_2O\ g\ DM^{-1}$	0.01	0.05	(Colombi et al., 2024 ; Goudriaan, 1992)	0.015	0.015	0.015
$m_{storage}$	R_{am}	maintenance coefficient storage	$g\ CH_2O\ g\ DM^{-1}$	0.01	0.05	(Colombi et al., 2024 ; Goudriaan, 1992)	0.005	0.005	0.005
e_{leaf}	R_{ag}	glucose efficiency for leaves growth	$g\ CH_2O\ g\ DM^{-1}$	1.0241	1.9019	(Goudriaan, 1992)	1.463	1.463	1.463
e_{root}	R_{ag}	glucose efficiency for roots growth	$g\ CH_2O\ g\ DM^{-1}$	1.0108	1.8772	(Goudriaan, 1992)	1.444	1.444	1.444
e_{stem}	R_{ag}	glucose efficiency for stem growth	$g\ CH_2O\ g\ DM^{-1}$	1.0591	1.9669	(Goudriaan, 1992)	1.513	1.513	1.513
$e_{storage}$	R_{ag}	glucose efficiency for storage growth	$g\ CH_2O\ g\ DM^{-1}$	1	1.8395	(Goudriaan, 1992)	1.415	1.415	1.415
$ratio_t$	biomass growth	stem translocation loss ratio	unitless	0.89965	0.99435	(Richter et al. (2010) ; (Goudriaan, 1992)	0.947	0.947	0.947
$BBCH_t$	biomass growth	stem translocation beginning BBCH stage	unitless	58	68	(Goudriaan, 1992)	60	60	60
$fraction_t$	biomass growth	stem translocation to storage organs fraction	unitless	0.14	0.26	(Goudriaan, 1992)	0.1	0.1	0.1
$BBCH_d$	R_{am}	roots senescence beginning BBCH stage	unitless	50	65	(Wang et al., 2021)	-	50	80
$slope_d$	R_{am}	roots senescence function slope	unitless	0.105	0.195	(Wang et al., 2021)	-	0.15	0.15
int_d	R_{am}	roots senescence function intercept	unitless	0.0525	0.5975	(Wang et al., 2021)	-	0.15	0.5
$fraction_e$	R_h	CO ₂ emission fraction from roots litter	unitless	0	1	(Wang et al., 2021)	-	0.035	0.035
c_{root}	R_{am}	roots distribution curvature	unitless	1	30	(Stöckle et al., 1994)	-	20	30
FDM_{shoot} (BBCH < 9)	biomass partitioning	shoot partition fraction	unitless	0.475	0.9975	(Goudriaan, 1992)	0.3 – 0.5	0.5	0.5
FDM_{shoot} (9 ≤ BBCH < 60)				(wheat) 0.475	(wheat) 0.8925	(Colombi et al., 2024)	0.3 – 0.5	0.6	0.5
FDM_{shoot} (BBCH ≥ 60)				(tomato) 0.475	(tomato) 0.8925	(Colombi et al., 2024)	0.7 – 0.9	1	0.85

2.4. Model calibration and evaluation

The new module was calibrated and validated for R_a simulation, while ARMOSA V.2 was evaluated for R_s under all conditions, and specifically for R_h during bare soil periods. As preparatory work for the calibration of the new root R_a module in ARMOSA V.2, the crop growth module parameters were calibrated (for the all the crops reported in [Table 1](#)) in two main steps: (i) calibration of the parameters involved in the algorithms for aboveground biomass (AGB) accumulation and N uptake; and (ii) calibration of the biomass partitioning coefficients for the various plant organs (stem, leaf, root, and storage). For steps (i) and (ii), the objective variables used were aboveground AGB, yield, crop N uptake, and Root to Shoot (R/S) ratio. Since direct measurements of root biomass were not performed, the R/S ratio values considered in this study were estimated from the AGB values measured at harvest using R/S ratios derived from the literature ([Amanullah, 2014](#); [Urbanaviči et al., 2022](#)).

2.4.1. New module calibration

The parameters involved in calculating R_{am} and R_{ag} ([Table 2](#)) were calibrated by a trial and error approach ([Mbonimpa et al., 2015](#)), starting from default values sourced from the literature. The calibration

was performed by employing soil CO₂ flux measurements collected from the CCS cropping systems at the Foggia and Ravenna sites (Table 1). The dataset included only crops that were also present in the ECS cropping systems, namely wheat and tomato. Indeed, the validation dataset, consisted of measurements taken from the ECS cropping systems at both sites. The objective variable was the cumulated R_a for each land use periods (LUPs), specifically: LUP wheat 1, LUP wheat 2 and LUP tomato for Ravenna; LUP wheat for Foggia (Supplementary materials, Tables S1 and S2). Indeed, for these LUPs, the measured daily CO₂ emissions (R_s) was employed to derive an estimated root R_a by subtracting from the measured R_s the simulated R_h, for which soil-specific parameters of the CN dynamics module had been previously calibrated using measured R_h during bare soil periods (Gabbrielli et al., 2025). The simulation performance during bare soil periods (average RRMSE of 20.26 % for cumulated R_h across the two sites, Gabbrielli et al., 2025) supported the use of these calibrated parameters. Furthermore, each LUP was subsequently subdivided into development stage (DVS) periods, based on the simulated BBCH values (BBCH ≤ 9, 9 < BBCH ≤ 49, 49 < BBCH ≤ 69, 69 < BBCH ≤ 89, BBCH > 89), to compare the cumulative R_a value of each DVS period in the simulation with the corresponding estimates.

To compare simulated and estimated R_a, due to differences in climate, management, crops, and especially soil characteristics affecting gas diffusivity, simulated values were extracted from different soil layers for the two sites since higher diffusivity corresponds to a deeper emitting soil layer, due to increased gas mobility (Button et al., 2023). The effective diffusivity of CO₂ within the soils was calculated following Hutchinson and Livingston (2001), using daily simulated bulk density and soil water content for the whole simulated period. In Ravenna the diffusivity of soil was three times higher (0.002316 cm² s⁻¹) than in Foggia (0.000778 cm² s⁻¹). Accordingly, R_a was simulated over the 0–0.3 m soil layer for Ravenna and the 0–0.1 m layer for Foggia.

Since the ARMOSA model (V.1 and V2) does not simulate intercropping, in the validation datasets, the R_a component associated with alfalfa (intercropped with wheat) was simulated independently and then added to that of wheat during the period following the interseeding. The simulation of alfalfa R_a was performed by limiting the available solar radiation for alfalfa due to shading caused by intercropping with wheat.

2.4.2. Model evaluation

The ARMOSA model V.2 performance was evaluated using both the cumulated R_s from the entire available datasets and the cumulated R_h of the bare soil periods (BS) following wheat and tomato harvest (BS wheat 1, BS wheat 2 and BS tomato for Ravenna; BS wheat for Foggia), during which R_a contribution to R_s was equal to zero and thus measured CO₂ fluxes were caused only by R_h. Finally, the behaviour of ARMOSA V.2 was assessed by analysing the daily trend of the R_a/R_s ratio in contrast with R_s during the considered LUPs, as simulated by the model. The ratio trends were analysed starting from full emergence (first true leaf, BBCH 11), marking the onset of autotrophic activity. To compare the simulated ratio trends with literature-derived values for specific development stages, non-linear regression curves were fitted, by applying an asymptotic growth model (Bates and Chambers, 1992) separately to R_a/R_s ratios corresponding to BBCH stages between emergence and BBCH_d (BBCH stages lower than 51, beginning of heading, and 81, beginning of fruit ripening, respectively for wheat and tomato) and to BBCH values comprised between BBCH_d and BBCH at crop harvest. Moreover, to evaluate the impact of the additional R_a module in the ARMOSA model, CO₂ emissions and ancillary variables from the original version (V.1) were compared to those from version V.2.

2.4.3. Performance indices

The following performance indices were employed as objective functions for calibration and as evaluation metrics: root mean square error (RMSE, g CO₂ m⁻², Supplementary materials, Eq. (S2)), relative root mean square error (RRMSE, %, Eq. 3S), and modelling efficiency (EF, dimensionless, Nash and Sutcliffe, 1970, Eq. (S4)). Cumulated

emissions of CO₂, and ancillary variables (AGB, yield, and N uptake), were also evaluated by graphically analysing the decomposition of RMSE into two components representing systematic error (RMSE_S, Eq. (3)) and random error (RMSE_U, Eq. (4)), as reported in Coucheney et al. (2015), where $\hat{S}_i$ derives from the linear regression between the observed (O_i) and simulated (S_i) values: $\hat{S}_i = a + b \cdot O_i$.

$$RMSE_S = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{S}_i - O_i)^2} \quad (3)$$

$$RMSE_U = \sqrt{\frac{1}{n} \sum_{i=1}^n (S_i - \hat{S}_i)^2} \quad (4)$$

3. Results

3.1. Sensitivity analysis

The results of the sensitivity analysis vary depending on the process and the crop being considered. The interaction effects are minimal for the R_{ag} process parameters, both for wheat and tomato, as well as for the parameter m_{root} of R_{am}. In other cases, many of the considered parameters align along the bisector, indicating limited interaction effects between them (Fig. 2).

For the R_{ag} output, it was observed that growth efficiency parameters exhibit higher sensitivity. Specifically, for wheat, e_{leaf} , e_{stem} , and e_{root} are the parameters that, in this order, have the greatest influence on the output within their range of variation. For tomato, these parameters remain among the most important for the R_{ag} output, but with a different order: e_{stem} ranks first, followed by e_{root} and e_{leaf} . The influence of parameters not directly related to the root system is due to their role in calculating the output in the model framework, i.e., an increase in a specific parameter for one organ can lead to a decrease in the growth of another organ and, consequently, a reduction in the R_{ag} output.

The parameter m_{root} exerts a dominant influence on R_{am} for all crops and sites, showing notably higher μ^* values compared to other parameters and reduced σ values, thus deviating from the 1:1 line dividing the quadrant as well as from other parameters in the process. With a less pronounced but still significant effect across all crops, the int_d is noteworthy. For wheat the slope_d parameter shows a significant effect similar to that of T_{base}. However in tomato, the sensitivity of the output to the parameters slope_d is slightly greater than that of T_{base}.

Analysing the sensitivity of total R_a output reveals that the highest sensitivity is associated with parameters governing R_{am}, compared to those governing R_{ag}. This is because, while R_{ag} is performed by the root system only for a limited period, the processes driving R_{am} persist over a longer duration. Consequently, the primary influence on root R_a stems from parameters that most strongly affect R_{am}. Notably, parameters governing downward root growth, root distribution along the soil profile, and root R_{ag} occupy an intermediate role, exhibiting relatively modest influence. Parameters associated with biomass allocation between above-ground and root portions, and those affecting the respiration of other plant organs, display negligible effects, effectively yielding zero on the sensitivity scale.

3.2. Daily and seasonal trends of partitioned soil respiration

The new module for root autotrophic respiration simulation effectively captures field-measured daily total R_s (as the sum of R_h and R_a), particularly for the calibration datasets, while during validation the simulated patterns slightly diverge from the observed ones (Fig. 3). Indeed, for the Ravenna calibration dataset, during the LUP wheat 2 and during the LUP tomato in particular, R_s predictions closely align with the measured flux trends thanks to an adequate simulation of the increase and subsequent decrease in R_a. Similarly, for the Foggia calibration

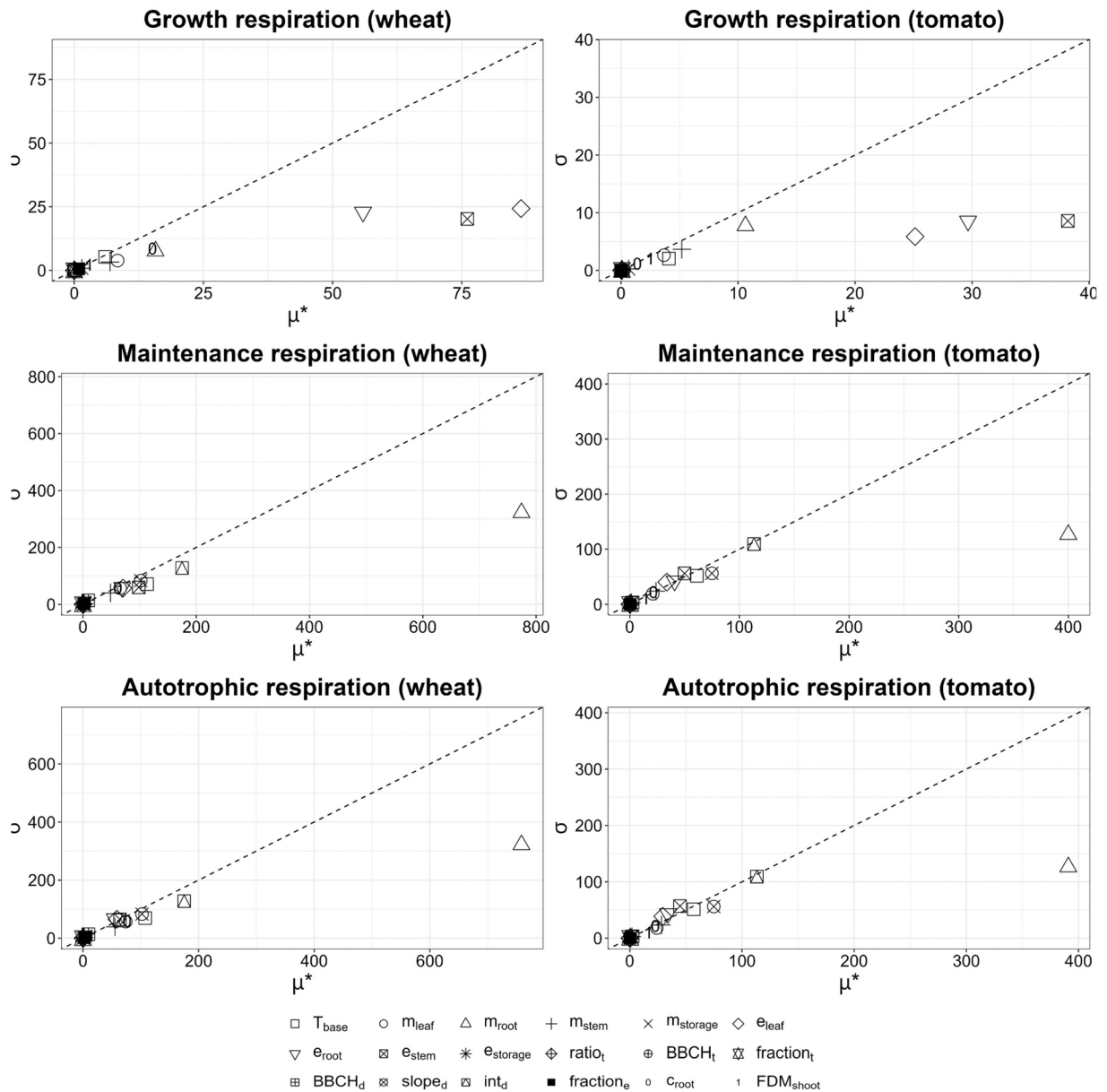


Fig. 2. Plots of the Morris sensitivity measures (μ^* , σ , g CO₂ m₂) indicating the sensitivity of the new model outputs (growth, maintenance and total autotrophic respirations) to the input parameters (Table 2) for each of the investigated crop (wheat and tomato). In each panel, the dashed line denotes the threshold $\sigma = \mu^*$.

dataset, the simulated R_s align well with measured fluxes during LUP wheat, though R_h tends to be underestimated during the subsequent bare soil period (BS wheat), with the initial peak from soil tillage accurately captured and the second peak slightly underestimated (Fig. 3). A consistent model performance during validation was demonstrated by the tomato cultivation (LUP tomato) simulation in Ravenna, while during LUP wheat 1 a slight R_s overestimation is reported for the validation dataset. On the other hand, in the validation dataset, the simulated R_s tends to be underestimated during the final stages of the crop development, coinciding with the growth of the intercropped alfalfa, as observed in LUP wheat 2 in Ravenna and LUP wheat in Foggia (Fig. 3).

The V.2 model effectively reproduced the overall R_s trend measured in field conditions during crop development. Simulated R_s followed an increasing trend until it reached its peak at full canopy and flowering development stages, then reproduced the decrease observed during more advanced development stages (Fig. 4). This trend was mainly caused by the R_a component. Indeed, the V.2 model simulates the

increase of R_a/R_s ratio that occurred from the early stages of the crop cycle following the growth of roots and the overall increase of R_s . The maximum R_a/R_s , above 80%, preceded the onset of root senescence ($BBCH < BBCH_d$, Eq. (8A)) and subsequent R_a/R_s decrease due to the reduction of root activity. The relative positioning of the two asymptotic growth curves, fitted respectively for early and late development stages ($BBCH < BBCH_d$ and $BBCH > BBCH_d$, Fig. 4), reversed between the two analysed crops. Specifically, during early stages, the R_a/R_s ratio tended to be higher during late stages for tomato, while the opposite was simulated for wheat. Late-stage R_a/R_s values were higher for tomato and lower for wheat compared to the early-stage ratios.

3.3. Cumulated soil CO₂ emissions

For the calibration dataset (Fig. 5), the LUPs cumulative R_s did not deviate significantly from the 1:1 line, indicating no substantial over- or underestimation for either of the two sites, while the simulations conducted on the validation dataset showed greater deviation from the 1:1

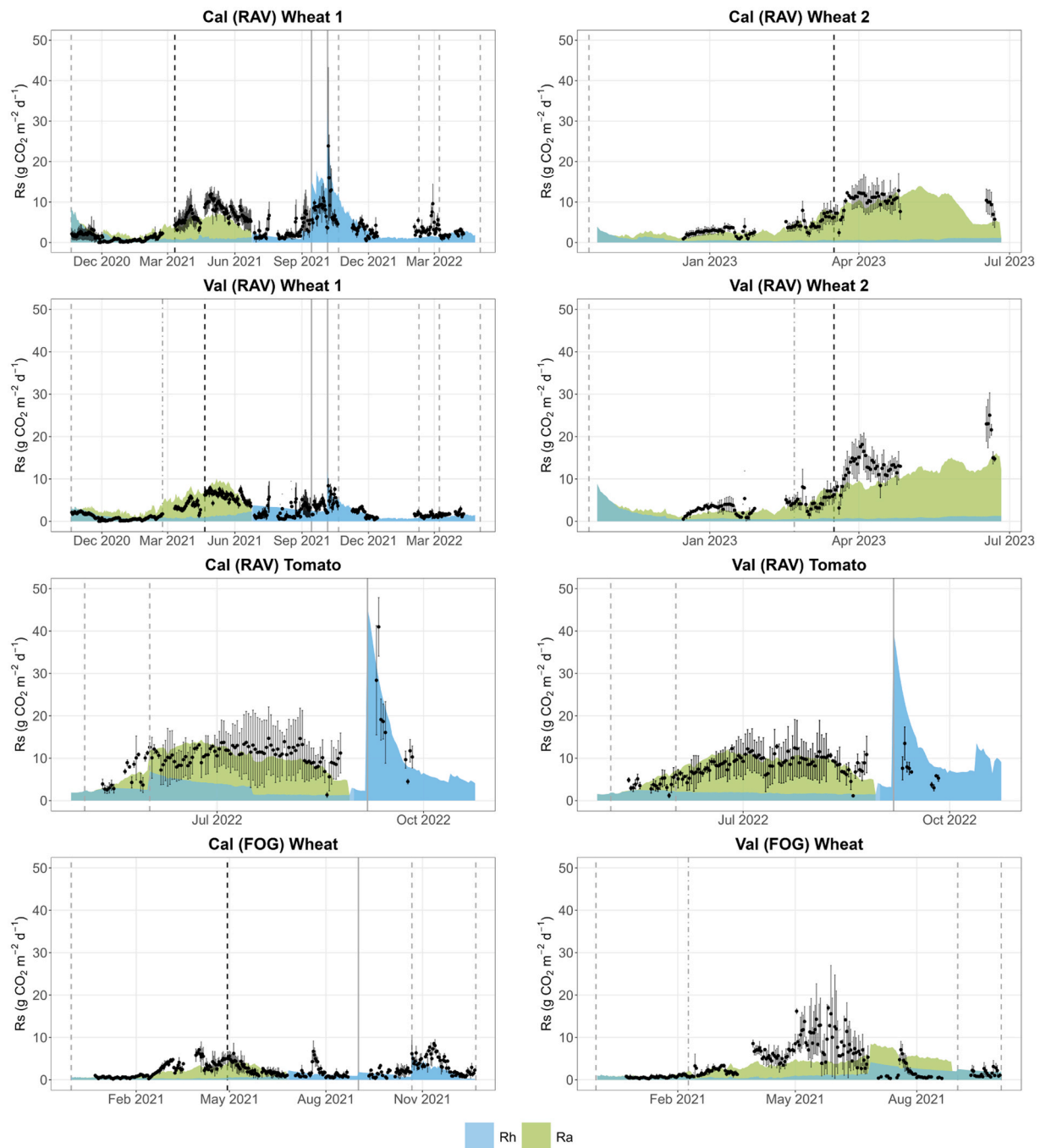


Fig. 3. Time-series of daily CO_2 (R_s , $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) emissions in the calibration (Cal) and validation (Val) datasets of the two sites (Ravenna, RAV; Foggia, FOG): observed values (black) and ARMOSA V.2 simulated values (heterotrophic respiration, R_h , $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, light blue; roots autotrophic respiration, R_a , $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, green). Error bars represent the standard deviation of the daily observed value. Tillage events are reported as dashed (harrowing) and solid (plowing) grey lines, while the dash-dotted grey line signals alfalfa inter-sowing. The dashed black lines represent herbicide applications.

line, as expected. Overall, the model's performance was satisfactory during the calibration phase, with an average RRMSE of 10.9% and a EF of 0.95. Validation results showed larger deviations (average RRMSE increased to 45.1%, with a EF of 0.51), particularly during the LUPs of wheat cultivation, where intercropping periods with alfalfa were consistently underestimated, as previously noted. During BS periods, emissions were generally well simulated, even in the validation phase.

During calibration for the Ravenna site, R_s tended to be overestimated for the LUP wheat 1 during the vegetative DVS period ($9 < \text{BBCH} < 49$, Fig. 5) while final DVS periods aligned well with observations. This overestimation was presumably due to an inaccurate

simulation of the tillage effect, which impacted measured R_s for a longer period of time as can be seen from the analysis of the daily trends (Fig. 3). However, for the other crop growth LUPs in the calibration dataset, the simulated values showed no significant deviations from observations (EF 0.9) while model efficiency decreased for the validation datasets (EF 0.65). At the Foggia site, the calibration dataset showed no substantial discrepancies between simulated and observed R_s (EF 0.65) while during validation, as highlighted by daily trends and LUPs cumulative emissions analysis, notable discrepancies emerged between measured and simulated emissions (EF -0.52).

Soil respiration simulation quality in the validation dataset, when

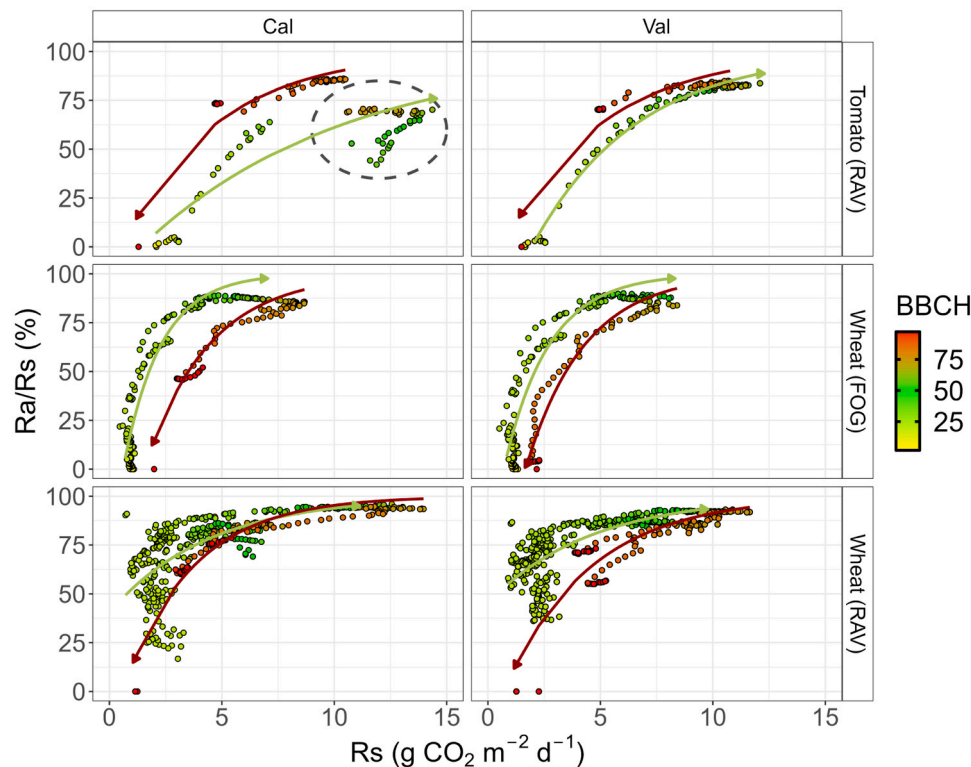


Fig. 4. Ratio of root autotrophic respiration to total soil respiration (R_a/R_s , %) as a function of daily total soil respiration (R_s , $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) simulated for the surface soil layer (0–0.3 m). The colour of the points represents the BBCH growth stage of the crop. The non-linear regression lines were obtained, by applying an asymptotic growth model, separately to R_a/R_s ratios corresponding to BBCH stages below BBCH_d (green lines) and to BBCH values comprised between BBCH_d and crop harvests BBCH_h (red lines). BBCH_d is the stage at which root senescence starts (BBCH 50 and 80 for wheat and tomato respectively). In the top-left panel (Tomato RAV Cal) points within the circle represent the effect of increased soil moisture in the inter-row caused by irrigation on R_a/R_s .

evaluated for the DVS periods following the interseeding of alfalfa (BBCH >49) depended on alfalfa growth conditions (Fig. 5). In Ravenna during LUP wheat 1, alfalfa growth was severely limited, therefore its contribution was efficiently reproduced by the model, while it was underestimated during LUP wheat 2 in Ravenna and LUP wheat in Foggia (with the latter LUP showing the highest underestimate) due to less limiting conditions for the growth of the intercropped crop. Indeed, no weeding treatments were applied during wheat cultivation at the Foggia site to preserve alfalfa growth (Table S2, Supplementary materials), while at the Ravenna site, the treatment was carried out during LUP wheat 2, but at a reduced dosage compared to the one applied earlier during LUP wheat 1 (Table S1 and Fig. 3). Presumably, the reduced weed control resulted in increased weed species and alfalfa plant densities, leading to a rise in measured R_a .

3.4. Comparison between the original model version (V.1) and version V.2

A high simulation accuracy is observed across all datasets by applying ARMOSA V.2, allowing the simulation results to be classified as good or satisfactory during the validation phase. The analysis of the ancillary variables (AGB, yield, and N uptake) indicated a generally satisfactory predictive accuracy of the model, particularly for N uptake. All the crop related variables fall below the 1:1 line (Fig. 6), indicating that the random error (RMSE_u) exceeded the systematic error (RMSE_s), which suggests that the simulation inaccuracies are mainly driven by high variability in the measurements (Gabrielli et al., 2025) rather than by the model's systematic biases. On the other hand, soil related variables, as simulated by the new model version (V.2), are equally subject to the prevalence of systematic error, as in the V.1 simulations.

The version V.2 predominantly exhibits random error, whereas V.1

displayed significant systematic error (Fig. 6). The version V.1 showed higher systematic error for the Ravenna (moist site) than for the Foggia (dry site) dataset, due to the higher magnitude of the measured (and thus simulated) emissions at the first site, as both RMSE components were tendentially proportional to the value of the variable for which they are calculated. The best results were obtained for the calibration dataset of Ravenna with the newly implemented module V.2. The calibration dataset from Foggia had the highest systematic error but ranked very well in terms of overall performance, largely due to the fact that most emissions from the Foggia datasets were relative to BS periods. Indeed, V.2 application demonstrates a marked improvement in the model fitting during crop growth LUPs, along with an enhanced simulation of R_h during the subsequent BS periods (Fig. 3). In all cases, it was observed that immediately after crop harvest, V.2 correctly simulated lower emissions compared to those obtained with V.1, while emissions levels in the two versions tended to converge following the first soil tillage after harvest (returning to the original calibration level).

4. Discussion

4.1. Soil respiration partitioning with ARMOSA V.2: strengths and limitations

The developed module, as illustrated in Fig. 3, significantly enhances the simulation of soil CO_2 emissions, primarily during periods when the soil is covered by crops (crop growth LUPs, R_s) and even during the subsequent fallow periods (BS, R_h), following the harvest. The ARMOSA V.2 performance is consistent with previously reported results for DNDC simulation of daily R_s during crop growth, which showed R^2 values ranging from 0.36 to 0.6 and EF values from −0.26 to 0.58 during calibration and validation based on non-continuous R_s measurements (Li

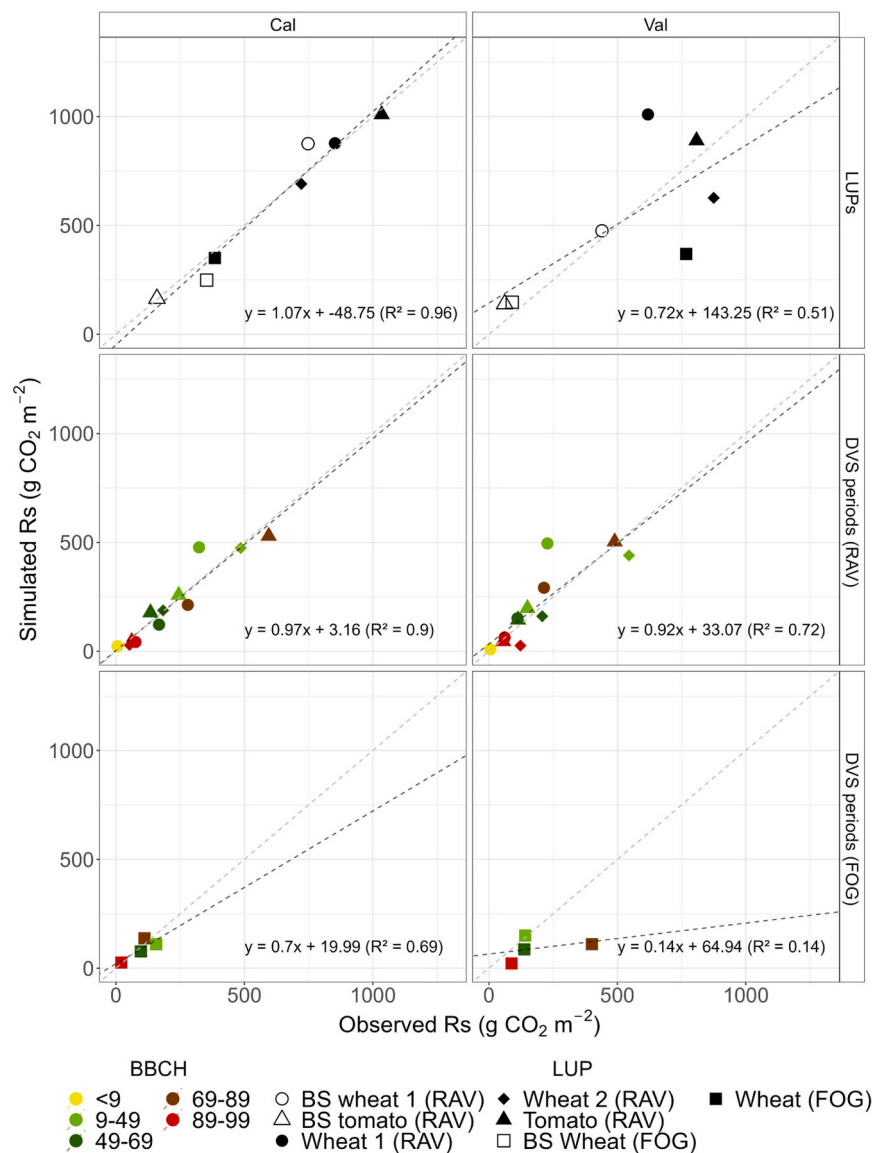


Fig. 5. Cumulative CO₂ emissions (R_s) based on the Land Use Periods (LUPs, top panels) and on the Development Stage (DVS) periods in Ravenna (RAV, middle panels) and Foggia (FOG, bottom panels). The panels on the left represent cumulative emissions for the calibration (Cal) datasets, while those on the right depict cumulative emissions for the validation (Val) datasets. Bare soil (BS) periods are labelled based on the name of the crop that precedes them. The grey line represents the 1:1 line, while the black line shows the regression line between observed and simulated data.

et al., 2017; Abdalla et al., 2011). The employment of the new module correctly reduced post-harvest R_h rates, in comparison with the previous model version, thanks to the introduction of the root senescence simulation that allocates root biomass to SOM pools, within specific layers, already during crop cultivation. By simulating gradual root senescence over time, this function ensures that dead root biomass is transferred to the SOM pools as it decomposes, preventing its instantaneous transfer at harvest, thus avoiding an excessive increase in R_h rates post-harvest. This effect is clearly evident in Delandmeter et al. (2023), whose simulations show an overestimation of emissions after crop harvest, particularly for wheat.

Choosing the correct emitting soil layer depth is a critical point when simulating root R_a that is sometimes overlooked, as common practice typically relies on the use of reference depths. The emissions measured from the soil in Foggia are approximately one-third of those at the Ravenna site. This difference is related to the dry climate and lower effective gas diffusivity at Foggia, compared to the moist climate and higher diffusivity at Ravenna. These results illustrate how the interplay between climate, soil C pools, and gas diffusivity in silty-clay-loam soils

drives R_s measurements, and emphasize the need for accurate evaluation of this soil property before calibrating parameters for R_a . Furthermore, although root presence can impact soil diffusivity, the impact of cereal fasciculate root system is relatively small (Pulido-Moncada et al., 2024), while the potentially greater influence of the taproot system is minimised by chamber placement in the inter-row areas where roots presence is reduced. Therefore, the decision to assign a site-specific emitting layer for R_s simulation and to consistently apply it across both bare soil and cropping periods within each site appears appropriate.

Carbon dioxide fluxes were measured using the automatic chambers method to assess GHG soil emission under two management conditions. Therefore, for an in-depth analysis of root growth and R_a , which would allow for further validation of the new module, it would be necessary to acquire a dedicated dataset that provides measurements of CO₂ fluxes in root exclusion and ancillary measurements (including partitioned root biomass per soil layer and litter fractions). Furthermore, since most process-based cropping system models lack routines for simulating weed growth, their performance during periods of intercropping and high weed pressure is inherently limited. Indeed, for the wheat LUPs

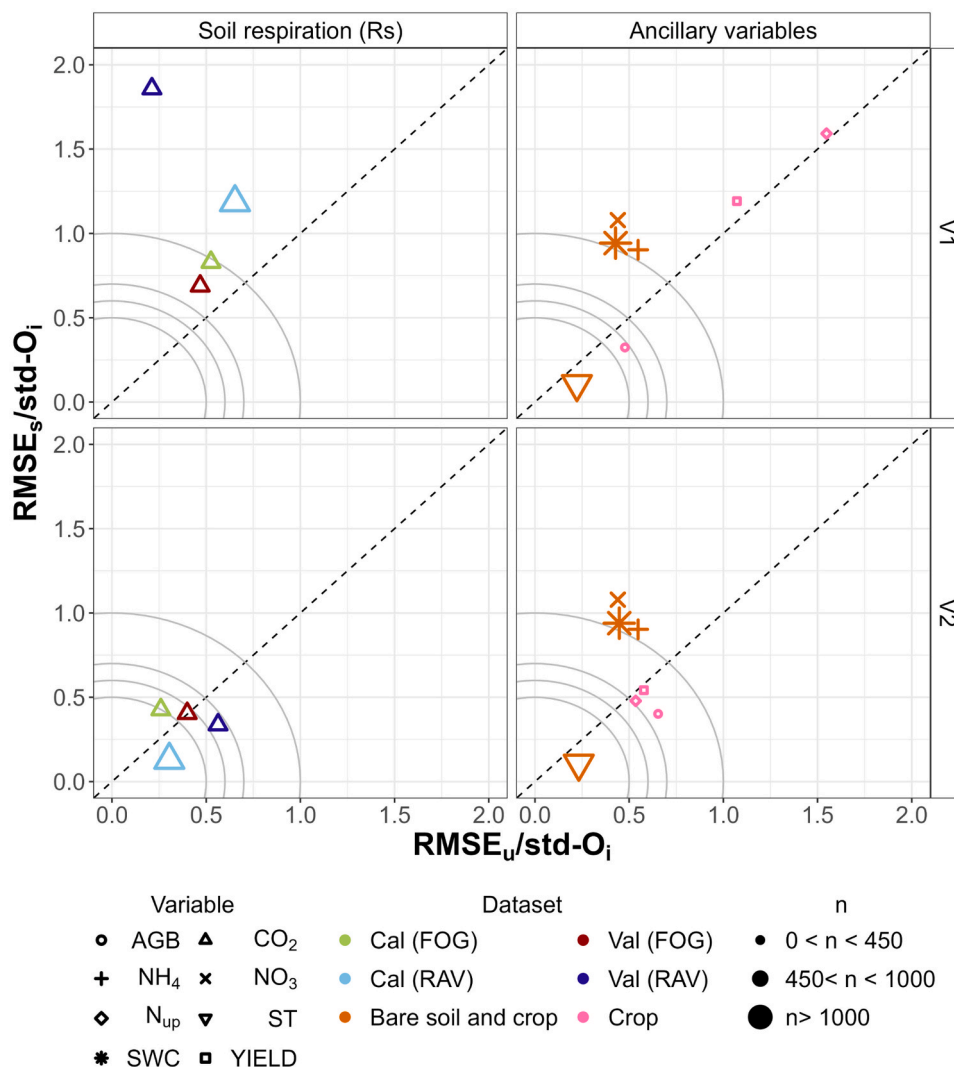


Fig. 6. RMSE corresponds to the distance between the origin and the coordinates of the point. To allow the comparison of model performance across variables with different units of measure (total CO₂ emissions, panels on the left, and ancillary variables, panels on the right), RMSE_s and RMSE_u were normalized by the standard deviation of observed values (std-O_i). The model performance was evaluated in the two datasets (Ravenna, RAV; Foggia, FOG; calibration, Cal; validation, Val) with the original model version (V.1) and with the implemented module (V.2). The represented ancillary variables are the following: above-ground biomass (AGB, kg DM ha⁻¹), yield (YIELD, kg DM ha⁻¹), N_{up} (Nup, kg N ha⁻¹), soil temperature (ST, °C) and moisture (SWC, %), soil ammonium (NH₄, kg N-NH₄⁺ ha⁻¹) and nitrate (NO₃, kg N-NO₃⁻ ha⁻¹) content. The dotted line represents the bisector of the first quadrant. The datasets used for CO₂ include land use periods (LUPs) with wheat, tomato, and bare soil (BS). For crop-related variables, the datasets refer exclusively to wheat and tomato. The datasets used for soil-related variables cover the entire simulation period (crop LUPs and BS). Point size is proportional to the total number of observations per dataset (n).

validation, the increase in measured R_s is not solely attributed to alfalfa, but rather to the presence of weeds. During intercropping periods, in addition to alfalfa, a significant presence of weeds was induced by reduced or absent weeding interventions. Given the lack of detailed information on the quantity of weeds present, directly estimating the emissions attributable to their R_a is not feasible. However, the magnitude of the underestimation of R_s reported for the validation dataset is aligned with the increase in R_s associated with the presence of weed species that ranged between 10% and 15% (Oyeogbe et al., 2017).

4.2. R_a/R_s variability and its simulation

The contribution of root R_a to R_s, and therefore the R_a/R_s ratio, displays a high variability being dependent on crop species, their development stage, crop status, pedoclimatic and environmental conditions and direct measurement or estimate method. Indeed, mean measured R_a/R_s ratios are reported to range from 10% to 95% (Hanson et al., 2000) for agricultural ecosystems across climate zones and

measurement method (i.e., isotopic approaches, roots exclusion, component integration). Specifically, for temperate and tropical agricultural systems, the literature reported range is comprised between 14% to 73% (Subke et al., 2006). In the current case study, conducted at the experimental sites of Ravenna and Foggia—located in Köppen climatic zones Cfa (humid) and Csa (dry), respectively—the mean R_a/R_s ratios for wheat in the calibration dataset were 62% (simulated range 17–91%) and 70% (1–89%), and 68% (1–87%) for tomato (Fig. 4). Studies on wheat grown in silt-loam soils under a temperate climate with warm summers (Cfb) confirmed the R_a/R_s ratio trends simulated in the presented case studies, with the literature showing that higher measurement frequency tends to yield higher average R_a/R_s values—a pattern that aligns with the elevated ratios observed at our daily resolution. Indeed, R_a/R_s averaged 28% with 19 non-continuous measurements, ranging from 59% in late April to 1% in August (Prolingheuer et al., 2014). Weekly measurements from April to July yielded a 40% average, varying between 15% in early April and 66% in early May (Suleau et al., 2011), while daily monitoring showed a 56% average

(Moureaux et al., 2008).

The effects on R_a/R_s of the interaction between seasonal weather variability and management practices (harvest timing, irrigation, fertilisation soil tillage) were successfully reproduced by the model. The observed reversal in the simulated R_a/R_s ratios between early and late BBCH stages reflects the seasonal timing of crop maturity: tomato reaches its late developmental stages in late summer, when R_h contribution to R_s declines and harvest occurs while the plant is still green, whereas wheat reaches these stages from early spring, with rising R_h contribution and the harvest occurs during summer when soil temperature is rising and the crop is senescing. This resulted in a more pronounced decline of late-stage R_a and R_a/R_s ratio for wheat than for tomato. Furthermore, the effect of irrigation strategies on R_s partitioning is demonstrated in the simulated R_a/R_s patterns during tomato cultivation. In the calibration dataset (conventional irrigation), a reduction in R_a/R_s ratios was observed to correspond with high R_s values, where R_a/R_s would typically be the highest due to its asymptotic growth behaviour (Fig. 4). The reduction in R_a/R_s was driven by the application of larger irrigation volumes compared to those used for the DSS-managed tomato (validation dataset) during summer (early June to early August). This resulted in higher R_h emissions due to the rewetting of dry soil (Jarvis et al., 2007), as soil moisture was the main limiting factor of this process (Burger et al., 2005; Zhang et al., 2021). The smaller irrigation volumes applied following the DSS led to lower microbial biomass activity, and thus to a reduced contribution of R_h to R_s . This confirms the model's ability to simulate how soil moisture variations, driven by irrigation practices, modulate the upper limit of R_a/R_s by affecting R_h responses.

5. Conclusion

In this study, a new module was developed to explicitly incorporate the autotrophic component of R_s into the ARMOSA model, to specifically simulate the CO_2 produced by crop roots in each soil layer. While the previous model version included equations for the implicit calculation of root R_a , this study explicitly modelled these emissions, by simulating the effect of the interactions between crop growth and development, root senescence and environmental conditions.

The new module sensitivity analysis results revealed that root R_a is mainly influenced by the crop-specific parameter regulating maintenance respiration (m_{Root}), which accounts for the largest share of CO_2 emissions during crop development. This is followed by the parameter T_{base} , which drives the effect of temperature on growth and maintenance respiration processes.

The simulation of daily total and cumulated R_s for wheat and tomato at each site was found to be satisfactory. However, further model

development is required to account for intercropping (of interseeded crops and weed species) in the estimate of soil CO_2 fluxes and their partitioning, so that, together with the acquisition of datasets dedicated to monitoring root growth, these estimates could be further refined. Despite these limitations, the newly developed module serves as an additional tool to partition the components of total R_s , thereby facilitating progress in the estimation of C exchange within the soil-crop-atmosphere continuum and enabling an improved assessment of C balance in cropping systems as influenced by management practices.

Funding

This research was funded by the EU LIFE programme within the framework of the AGREStIC project (Reduction of Agricultural gReenhouse gases EmiSsions Through Innovative Cropping systems— LIFE17 CCM/IT/000062 – www.agrestic.eu).

CRediT authorship contribution statement

Leonardo Vario: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Mara Gabbrielli:** Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Giorgio Ragaglini:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Alessia Perego:** Writing – review & editing, Conceptualization. **Marco Acutis:** Writing – review & editing, Conceptualization. **Marco Perfetto:** Writing – review & editing, Investigation. **Marco Botta:** Writing – review & editing, Software.

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.

Acknowledgement

We gratefully thank Horta s.r.l. for managing the field trials in Ravenna and Foggia. This study was carried out within the framework of the AGRIENERCARBON (CUP E17F23000010009) Operational Group, co-funded by FEARS under Operation 16.1.01 of the 2014–2020 Rural Development Programme of the Lombardy Region. The authors acknowledge support from the University of Milan through the APC initiative.

Appendix A

1A. Existing approaches for autotrophic respiration simulation.

STICS (Beaudoin et al., 2023), DayCent (Parton et al., 1994) and APSIM (Holzworth et al., 2014), except for the Oryza2000 module, simulate a share of implicit autotrophic respiration, which is taken into account through a reduction of the value of the radiation use efficiency (RUE) parameter.

Among the models based on gross C assimilation, a distinction can be made according to the estimated order of growth respiration versus maintenance respiration. DNDC (Chen et al., 2008; Li et al., 1994) simulates daily CO_2 produced by roots autotrophic respiration ($ROOTCO_2$, mg C $ha^{-1} d^{-1}$, Eq. 1a) based on three independent coefficients: growth respiration coefficient (R_{rg} , mg C $g^{-1} DM$), maintenance respiration coefficient (R_{rb} , mg C $g^{-1} DM$), and a third coefficient expressing the dependence of the total roots autotrophic respiration on N uptake (R_{nu} , mg C $meq N^{-1}$). The potential respiration is obtained by multiplying the corresponding coefficients respectively for the daily roots biomass increase (RG, g DM $ha^{-1} d^{-1}$), the living roots biomass (RB, g DM $ha^{-1} d^{-1}$) and the N uptake (NU, $meq N ha^{-1} d^{-1}$) at the considered time step. The potential respiration is regulated by a temperature function (that employs a Q_{10} factor of 2.5, an optimal temperature of 20) that considers soil temperature (T , °C) at a depth of 15 cm; and by a soil moisture factor (MF, unitless) that evaluates oxygen availability for the roots. Furthermore, root senescence is represented by employing a root age factor ($ROOTAGE$, unitless) which decreases linearly from one to zero while going from crop emergence to harvest (Li et al., 1994).

$$ROOTCO_2 = (R_{nu} \bullet NU + R_{rg} \bullet RG + R_{rb} \bullet RB) \bullet 2.5^{\frac{(T-20)}{10}} \bullet MF \bullet ROOTAGE \quad (1A)$$

A second category of models is based on the assumptions of McCree and Thornley (Thornley and Cannell, 2000), according to which maintenance respiration subtracts a portion of the carbohydrates assimilated from the plant's growth and thus from growth respiration. Models using this approach

include SUCROS (Goudriaan, 1992) and ORYZA (Bouman, 2001). In these models, respiration is divided into growth and maintenance respiration. In general, the plant's total autotrophic respiration (R , kg C, Eq. 2a) is simulated as the sum of growth respiration, $(1 - Y_g) \bullet (P - k_m \bullet M)$, and maintenance respiration, $(k_m \bullet M)$. The total respiration is proportional to the complement of the growth yield (Y_g , unitless), i.e., the amount of C that is added to the dry matter (M , kg DM) per unit of C used and to the growth rate (P , kg C d^{-1}). In the complete formulation of this approach, the maintenance respiration rate coefficient (k_m , kg C d^{-1}) is limited by a Q_{10} factor with a base of 2 (Thornley and Cannell, 2000). This total respiration estimate can be divided among the different plant organs considering their dry matter amount. Moreover, to account for senescence process, that led biomass to stop respiring as defined developmental stages are reached, a reduction factor is introduced for maintenance respiration. This factor is calculated using the ratio of green leaf biomass (i.e., not subject to senescence) to total biomass, assuming that leaf senescence can accurately represent the reduction in respiration of other organs (Goudriaan, 1992).

$$R = (1 - Y_g)(P - k_m \bullet M) + k_m \bullet M \quad (2A)$$

2A. ARMOSA V.1 crop growth module.

In the following sections, variables and parameters indicated respectively as *variable(i)* and *parameter_i* refer to organ-specific values, where *i* indicates the following organs: leaf, root, stem, and storage. The notation *variable(plant)* indicates the sum of all the four organ-specific values. The algorithm originally implemented in the ARMOSA model for simulating plant autotrophic respiration ($R_a(\text{plant})$, g $\text{CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) is derived from the function implemented in SUCROS (Goudriaan and van Laar, 1994). The algorithm estimates daily biomass accumulation rate, also referred to as growth rate ($r\text{Biomass}(i)$, kg DM $\text{ha}^{-1} \text{ d}^{-1}$, Eq. 3 A), and growth respiration ($R_{ag}(i)$, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$, Eq. 6A) as limited by maintenance respiration ($R_{am}(i)$, kg $\text{CO}_2 \text{ ha}^{-1} \text{ d}^{-1}$, Eq. 7A), with the latter following the same dynamic to that of leaf senescence, meaning that the maintenance respiration of all organs decreases in response to the temporal pattern of leaf senescence.

$$r\text{Biomass}(i) = \frac{[\text{GPHOT} - R_{am}(\text{plant}) + \text{ratio}_t \bullet \text{fraction}_t \bullet C_{\text{stem}}] \bullet 2.5}{e_i} \quad (3A)$$

The daily biomass accumulation depends on the sum of the amount of carbohydrates produced by the photosynthesis process (GPHOT, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$) with the ones that are translocated from the stem to the considered organ. Indeed, in this approach there is no distinction between carbohydrates deriving from photosynthesis and those deriving from translocation. This sum is reduced by the maintenance respiration of all the organs (multiplied by a conversion factor of 0.27 to convert its value from CH_2O to C). Translocation contribution to biomass accumulation is simulated, for crop BBCH>BBCH_t (stem translocation beginning stage), by assuming a fixed translocation coefficient (*ratio_t*, unitless, default value equal to 0.947, Penning de Vries et al., 1989) that is multiplied by the C fraction of the stem (C_{stem} , kg C kg DM⁻¹) regulated by a factor (*fraction_t*, unitless) that limits translocation on the base of the crop development stage. The net C assimilation (Eq. 3a numerator) is converted in carbohydrates by using the conversion factor given by the ratio between the molecular mass of CH_2O and that of C (equal to 2.5). Finally, biomass accumulation is allocated to each organ by using their organ-specific growth glucose efficiency (e_i , kg $\text{CH}_2\text{O g DM}^{-1} \text{ d}^{-1}$).

The calculation of the specific growth respiration of each organ ($R_{ag}(i)$, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$) occurs in three successive steps (Eqs. (4A), (5A) and (6A)). Growth respiration is higher than zero if the amount of absorbed CH_2O (GPHOT) is greater than 0, and the biomass growth rate ($r\text{Biomass}(\text{plant})$) is different from 0. These conditions allow growth respiration estimate in the algorithm only in the case of actual biomass growth.

$$\text{pot}R_{ag}(\text{plant}) = \text{GPHOT} - R_{am}(\text{plant}) \quad (4A)$$

$$R_{ag}(\text{plant}) = \text{pot}R_{ag}(\text{plant}) \bullet \sum [r\text{Biomass}(i) \bullet C_i \bullet 2.5] \quad (5A)$$

$$R_{ag}(i) = R_{ag}(\text{plant}) \bullet \frac{r\text{Biomass}(i)}{r\text{Biomass}(\text{plant})} \quad (6A)$$

The first step consists of simulating the total potential respiration share ($\text{pot}R_{ag}(\text{plant})$, kg $\text{CH}_2\text{O ha}^{-1}$), that is used in the second step to obtain the total growth respiration ($R_{ag}(\text{plant})$, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$) as the product between the potential respiration and the sum of all the organs biomass accumulation rates, that are converted in carbohydrates using their specific C fraction (C_i , kg C kg DM⁻¹) and the 2.5 conversion factor. The third step uses the total growth respiration to assign a fraction to each organ ($R_{ag}(i)$, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$) based on the ratio between the growth rate of the organ itself and the total growth rate.

Therefore, maintenance respiration is calculated for each plant organ ($R_{am}(i)$, kg $\text{CH}_2\text{O ha}^{-1} \text{ d}^{-1}$, Eq. (7A)) as directly proportional to an organ-specific maintenance coefficient (m_i , g $\text{CH}_2\text{O g DM}^{-1} \text{ d}^{-1}$) and to the biomass of the considered organ ($\text{Biomass}(i)$, kg DM ha^{-1}). When simulating maintenance respiration for leaves, only green leaves biomass is considered in the equation. The maintenance respiration of all the organs is limited, as soon as leaf senescence starts, by a multiplicative reduction coefficient (f_s , unitless) that is calculated as the ratio between green leaf biomass and total leaf biomass (Fig. 1A). A temperature reduction factor is also employed: it is based on a Q_{10} factor of 2 and employs the daily mean air temperature (T_{air} , °C), and a reference temperature for maintenance respiration (T_{base} , °C, default equal to 25 °C).

$$R_{am}(i) = m_i \bullet f_s \bullet \text{Biomass}(i) \bullet 2^{\frac{T_{\text{air}} - T_{\text{base}}}{10}} \quad (7A)$$

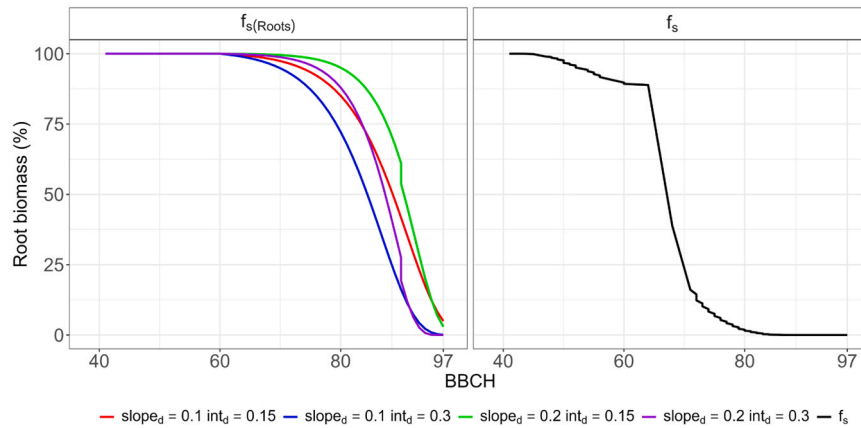


Fig. 1A. Root biomass senescence trend as a function of BBCH, according to the original function (f_s), and the modified function (Eq. 6a) with variations in its main parameters: $slope_d$ (rate at which roots biomass loses its biological activity), and int_d (fraction of roots that remain viable upon reaching physiological maturity).

3A. The new ARMOSA algorithm (V.2) for roots autotrophic respiration simulation.

The parameters and variables of the original and new modules are listed in Table 1A. Growth respiration, being defined as the cost of building new biomass (i.e., the amount of C required to increase biomass by one unit of C), is strictly linked to the magnitude of gross C assimilation: their formalization is based on stoichiometric ratios and therefore presents less differences across the most widely used modelling approaches, which largely converge on its estimation method. Therefore, in the new algorithm, the formalization of growth respiration was retained as in the original approach (Eqs. (4A), (5A) and (6A)) and has been directly converted to an output variable.

On the other hand, maintenance respiration is the component of total autotrophic respiration for which various simulation approaches (Bouman, 2001; Goudriaan, 1992; Li et al., 1994) and direct measurement findings (Penning de Vries et al., 1979; Penning de Vries and van Laar, 1982) are reported in the literature. Therefore, this component was modified in the new module to achieve a higher level of detail, particularly for the root organ.

The soil temperature of the layer where the roots are located is simulated by the model (Appendix A, Eq. 9 A) following Parton et al. (1994) for the superficial soil layer (from 0 to 5 cm depth) and following SWAT approach for the other layers (Neitsch et al., 2009).

The multiplicative factor f_s in the original version V.1 is used to estimate the maintenance respiration of all the organs. Root and leaf senescence are unsynchronized processes (Schneider and Lynch, 2018), therefore the use of a single factor to simulate them both might lead to a temporal mismatch between simulated and observed CO_2 fluxes. Since leaf senescence precedes root senescence, in the original version of the algorithm the implicit root autotrophic respiration values could be severely underestimated at phenological stages during which the root biomass reaches its maximum growth rate.

To obtain the decoupling between roots maintenance respiration and leaf senescence, a new function was implemented in the new module to independently simulate root senescence that, as with the leaf senescence process, causes the death of part of the root biomass as a function of crop development (expressed as the BBCH stage, in accordance with the ARMOSA crop development simulation).

This function simulates the portion of root biomass that has a biological function during the considered time step ($f_s(\text{roots})$, unitless, Eq. (8A), Fig. 1A), and that therefore consumes carbohydrates through maintenance respiration ($R_{am}(i)$ higher than zero). The BBCH value for which the onset of the senescence simulation begins is implemented as a parameter ($BBCH_d$, unitless) and can be calibrated as a crop or variety-specific parameter, as well as the portion (int_d , unitless) of the roots that remains alive upon reaching physiological maturity (BBCH equal to 97). Dead root biomass is transferred to the labile organic matter pool of the soil (*litter*) and it decomposes accordingly (with an efficiency of $1 - fraction_e$, unitless), using a specific decomposition rate that is also species-specific.

$$f_s(\text{roots}) = \begin{cases} 1 - \left(\left(1 - slope_d^{(30 - DAS)} \right) \bullet int_d \right) & \text{when } BBCH \geq BBCH_d \\ 1 & \text{else} \end{cases} \quad (8A)$$

The implemented function is an exponential of the time step (DAS, d, i.e. Days after Senescence onset), ensuring that the proportion of viable root biomass decreases more rapidly as crop development progresses through the stages, with the exponential base being a modifiable parameter ($slope_d$, unitless) that determines the rate at which root biomass loses its biological activity.

In the new module, total root autotrophic respiration was distributed along the vertical soil profile explored by the roots following the approach by CropSyst (Stöckle et al., 1994), by developing a function describing root density distribution ($D_{\text{roots}}(z, t)$, unitless, Eq. 9 A) along the soil profile. The function estimates the root fraction allocated the z th soil layer during the t th time step ($F_{\text{roots}}(z, t)$, unitless, Eq. (10A), Fig. 2A), that serves to allocate root biomass, and consequently respiration, to the different soil layers. Root density distribution is simulated, through an exponential function, depending on: the curvature of the roots distribution (c_{roots} , unitless, ranging from 0 to 30), the root length at the considered time step ($RootsDepth(t)$, m), and the depth of the deepest soil layer reached by the roots ($LayerDepth(t)$, m).

$$D_{\text{roots}}(z, t) = \max \left\{ 0; -2 \bullet \left[1 - e^{\frac{c_{\text{roots}} \bullet (RootsDepth(t) - LayerDepth(t))}{4}} \right] \right\} \quad (9A)$$

$$F_{\text{roots}}(z, t) = \frac{D_{\text{roots}}(z, t)}{\sum D_{\text{roots}}(z, t)} \quad (10A)$$

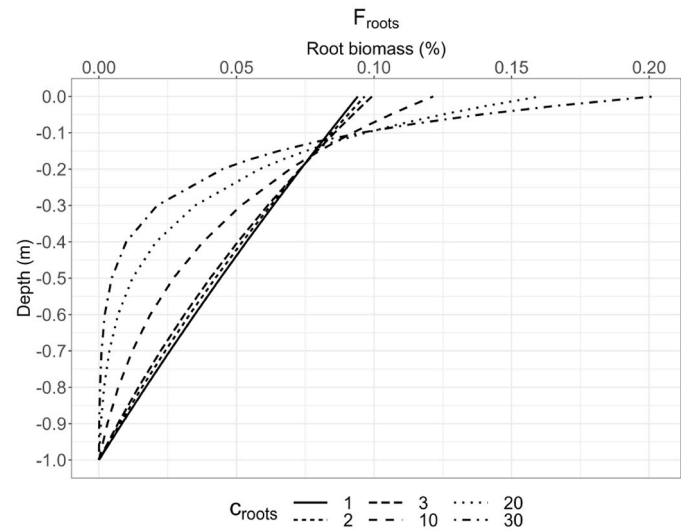


Fig. 2A. Percentage distribution of root biomass along the soil profile, according to different curvatures of the root distribution function (c_{root} , dimensionless).

In the new autotrophic respiration module (Fig. 3A), the maintenance component is calculated separately for the aboveground organs: stem and storage maintained the same formalisation of the original model version (R_{am} (i), Eq. (7A)), while leaf respiration ($R_{\text{am}}(\text{leaf})$, Eq. (11A)) is calculated without using the multiplicative coefficient representing the ratio between green leaf biomass and total leaf biomass.

$$R_{\text{am}}(\text{leaf}) = m_{\text{leaf}} \bullet \text{Biomass}(\text{leaf}) \bullet 2^{\frac{T_{\text{air}} - T_{\text{base}}}{10}}$$

(11A)

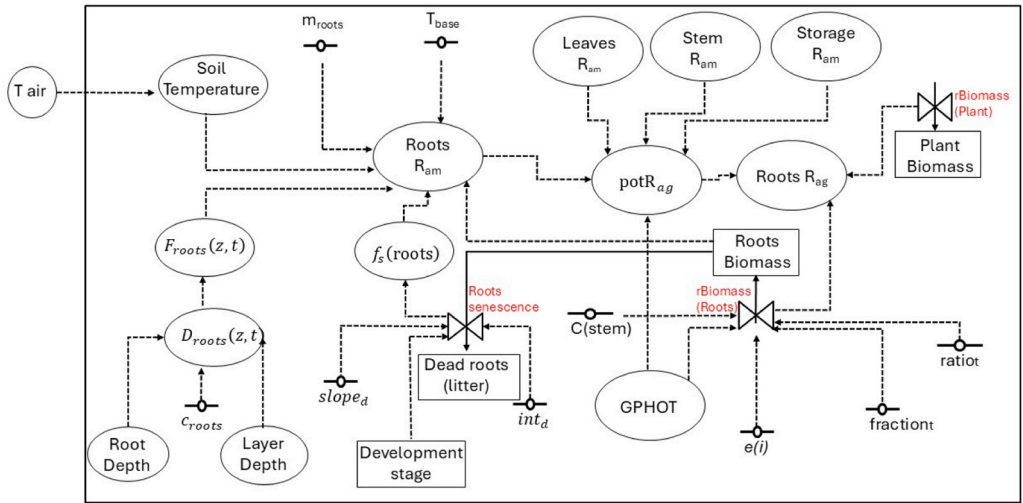


Fig. 3A. Conceptual diagram of the new module implemented in ARMOSA. State, rate and auxiliary variables are indicated with a rectangle, a valve symbol and a circle, respectively. The names of rate variables are in red. Continuous lines indicate inputs to and outputs from a state variable. Dotted lines indicate the dependence of a rate or auxiliary variable from another variable or parameter.

Table 1A
Parameters and variable of the original model version (V.1) and of the autotrophic respiration module (V.2).

Symbol	Definition	Unit of measure	Version	Eq.
e_{leaf}	leaves growth respiration glucose efficiency	$\text{g CH}_2\text{O g DM}^{-1}$	V.1 & V.2	3 A
e_{root}	roots growth respiration glucose efficiency	$\text{g CH}_2\text{O g DM}^{-1}$	V.1 & V.2	3 A
e_{stem}	stem growth respiration glucose efficiency	$\text{g CH}_2\text{O g DM}^{-1}$	V.1 & V.2	3 A
e_{storage}	storage growth respiration glucose efficiency	$\text{g CH}_2\text{O g DM}^{-1}$	V.1 & V.2	3 A
ratio_t	stem translocation loss ratio	unitless	V.1 & V.2	3 A
BBCH_t	stem translocation beginning BBCH stage	unitless	V.1 & V.2	3 A
fraction_t	stem translocation to storage organs fraction	unitless	V.1 & V.2	3 A

(continued on next page)

Table 1A (continued)

Symbol	Definition	Unit of measure	Version	Eq.
GPHOT	daily total gross assimilation (CH ₂ O)	kg CH ₂ O g DM ⁻¹ d ⁻¹	V.1 & V.2	3 A, 4 A
rBiomass	biomass growth rate	kg DM ha ⁻¹ d ⁻¹	V.1 & V.2	3 A, 5 A, 6 A
C _{leaf}	leaves dry matter C fraction	kg C kg DM ⁻¹	V.1 & V.2	5 A
C _{root}	roots dry matter C fraction	kg C kg DM ⁻¹	V.1 & V.2	5 A
C _{stem}	stem dry matter C fraction	kg C kg DM ⁻¹	V.1 & V.2	3 A, 5 A
C _{storage}	storage dry matter C fraction	kg C kg DM ⁻¹	V.1 & V.2	5 A
R _{am}	maintenance respiration rate	kg CH ₂ O g DM ⁻¹ d ⁻¹	V.1 & V.2	2, 3 A, 4 A, 7 A, 11 A
potR _{ag}	potential growth respiration	kg CH ₂ O g DM ⁻¹ d ⁻¹	V.1 & V.2	4 A, 5 A
R _{ag}	growth respiration rate	kg CH ₂ O g DM ⁻¹ d ⁻¹	V.1 & V.2	1, 5 A, 6 A
m _{stem}	stem maintenance respiration coefficient	g CH ₂ O g DM ⁻¹	V.1 & V.2	7 A
m _{storage}	storage maintenance respiration coefficient	g CH ₂ O g DM ⁻¹	V.1 & V.2	7 A
f _s	maintenance respiration reduction factor	unitless	V.1	7 A
T _{air}	air temperature	°C	V.1 & V.2	7 A, 11 A
m _{leaf}	leaves maintenance respiration coefficient	g CH ₂ O g DM ⁻¹	V.1 & V.2	7 A, 11 A
T _{base}	base temperature for maintenance respiration	°C	V.1 & V.2	2, 7 A, 11 A
Biomass	crop biomass	kg DM ha ⁻¹	V.1 & V.2	2, 7 A, 11 A
m _{root}	roots maintenance respiration coefficient	g CH ₂ O g DM ⁻¹	V.1 & V.2	2, 7 A
BBCH _d	roots senescence beginning BBCH stage	unitless	V.2	8 A
slope _d	roots senescence function slope	unitless	V.2	8 A
int _d	roots senescence function intercept	unitless	V.2	8 A
DAS	days after senescence onset	d	V.2	8 A
f _s (roots)	roots maintenance respiration reduction factor	unitless	V.2	2, 8 A
C _{root}	root distribution curvature	unitless	V.2	9 A
z	soil layer depth	m	V.2	1, 2, 9 A, 10 A
t	time-step	d	V.2	9 A, 10 A
D _{roots} (z,t)	roots density distribution function	unitless	V.2	9 A, 10 A
LayerDepth (t)	deepest soil layer reached by the roots	m	V.2	9 A
RootDepth(t)	roots length	m	V.2	9 A
F _{roots} (z,t)	roots fraction allocated to each soil layer	unitless	V.2	1, 2, 9 A, 10 A
T _{soil}	soil temperature	°C	V.2	2
fraction _e	CO ₂ emission fraction from roots litter	unitless	V.2	-
FDM _{shoot}	shoot partition fraction	unitless	V.1 & V.2	-

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ijagro.2025.100044](https://doi.org/10.1016/j.ijagro.2025.100044).

References

Abdalla, M., Kumar, S., Jones, M., Burke, J., Williams, M., 2011. Testing DNDC model for simulating soil respiration and assessing the effects of climate change on the CO₂ gas flux from Irish agriculture. *Glob. Planet. Change* 78, 106–115. <https://doi.org/10.1016/j.gloplacha.2011.05.011>.

Amanullah, 2014. Wheat and Rye Differ in Drymatter Partitioning, Shoot-Root Ratio and Water Use Efficiency Under Organic and Inorganic Soils. *J. Plant Nutr.* 37 (11), 1885–1897. <https://doi.org/10.1080/01904167.2014.911888>.

Amthor, J., 1984. The role of maintenance respiration in plant growth. *Plant, Cell and Environ.* 7, 561–569.

Amthor, J.S., 1986. Evolution and applicability of a whole plant respiration model. *J. Theor. Biol.* 122.

Bates, D.M., Chambers, J.M., 1992 (Eds.). *Nonlinear models. Chapter 10 of Statistical Models in S.* Wadsworth & Brooks/Cole.

Beaudoin, N., Lecharpentier, P., Ripoche-Wachter, D., Strullu, L., Mary, B., Léonard, J., 2023. In: Launay, M., Justes, E. (Eds.), *STICS soil-crop model: Conceptual framework, equations and uses.* éditions Quae. *Erscheinungsort nicht ermittelbar*, p. 519.

Bouman, B.A.M., 2001. *ORYZA2000: Modeling Lowland Rice.* IRRI., p. 235.

Burger, M., Jackson, L.E., Lundquist, E.J., Louie, D.T., Miller, R.L., Rolston, D.E., Scow, K.M., 2005. Microbial responses and nitrous oxide emissions during wetting and drying of organically and conventionally managed soil under tomatoes. *Biol. Fertil. Soils* 42, 109–118. <https://doi.org/10.1007/s00374-005-0007-z>.

Butterbach-Bahl, K., Baggs, E.M., Dannenmann, M., Kiese, R., Zechmeister-Boltenstern, S., 2013. Nitrous oxide emissions from soils: How well do we understand the processes and their controls? *Philos. Trans. R. Soc. B: Biol. Sci.* 368. <https://doi.org/10.1098/rstb.2013.0122>.

Button, E.S., Marshall, M., Sánchez-Rodríguez, A.R., Blaud, A., Abadie, M., Chadwick, D. R., Jones, D.L., 2023. Greenhouse gas production, diffusion and consumption in a soil profile under maize and wheat production. *Geoderma* 430. <https://doi.org/10.1016/j.geoderma.2022.116310>.

Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. *Environ. Model. Softw.* 22, 1509–1518. <https://doi.org/10.1016/j.envsoft.2006.10.004>.

Chen, D., Li, Y., Grace, P., Mosier, A., 2008. N₂O emissions from agricultural lands: a synthesis of simulation approaches. *Plant Soil* 309, 169–189.

Colombi, A., Bancheri, M., Acutis, M., Basile, A., Botta, M., Perego, A., 2024. A sound understanding of a cropping system model with the global sensitivity analysis. *Environ. Model. Softw.* 173. <https://doi.org/10.1016/j.envsoft.2023.105932>.

Coucheney, E., Buis, S., Launay, M., Constantin, J., Mary, B., de Cortázar-Atauri, I.G., Ripoche, D., Beaudoin, N., Ruget, F., Sitiraka Andrianarisoa, K., Le Bas, C., Justes, E., Léonard, J., 2015. Accuracy, robustness and behavior of the STICS soil-crop model for plant, water and nitrogen outputs: evaluation over a wide range of agro-environmental conditions in France. *Environ. Model. Softw.* 64, 177–190. <https://doi.org/10.1016/j.envsoft.2014.11.024>.

Delandmeter, M., Léonard, J., Ferchaud, F., Heinesch, B., Manise, T., Faurès, A., Bindelle, J., Dumont, B., 2023. A comprehensive analysis of CO₂ exchanges in agro-ecosystems based on a generic soil-crop model-derived methodology. *Agric. For. Meteorol.* 340. <https://doi.org/10.1016/j.agrformet.2023.109621>.

Gabbrielli, M., Perfetto, M., Botta, M., Volpi, I., Castellucci, A., Ruggeri, M., Allegrezza, M., Alessi, N., Vario, L., Acutis, M., Perego, A., Ragaglia, G., 2025. Optimization of agronomic management positively affects soil GHG emission: Viable solutions of mitigation in moist and dry Mediterranean climate zones. *Eur. J. Agron.* 168, 127668. <https://doi.org/10.1016/j.eja.2025.127668>.

Gifford, R.M., 2003. Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Funct. Plant Biol.* 30, 171–186. <https://doi.org/10.1071/FP02083>.

Goudriaan, J., 1992. Crop growth model for water-limited conditions (SUCROS2).

Goudriaan, J., van Laar, H.H., 1994. Modelling potential crop growth processes.

Grados, D., Kraus, D., Haas, E., Butterbach-Bahl, K., Olesen, J.E., Abalos, D., 2024. Common agronomic adaptation strategies to climate change may increase soil greenhouse gas emission in Northern Europe. *Agric. For. Meteorol.* 349, 109966. <https://doi.org/10.1016/j.agrformet.2024.109966>.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.

Holzworth, D., Huth, N., deVoil, P., Zurcher, E., Herrmann, N., McLean, G., Chenu, K., van Oosterom, E., Snow, V., 2014. APSIM—Evolution towards a new generation of agricultural systems simulation. *Environ. Model. Softw.* 62, 327–350.

Hutchinson, G.L., Livingston, G.P., 2001. Vents and seals in non-steady-state chambers used for measuring gas exchange between soil and the atmosphere. *Eur. J. Soil Sci.* 52, 675–682. <https://doi.org/10.1046/j.1365-2389.2001.00415.x>.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of

- Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect. *Tree Physiol.* 27, 929–940.
- van Keulen, H., Wolf, J., 1986. Modelling of agricultural production: weather soils and crops. *Simul. Monogr.* 479.
- van Laar, H.H., Goudriaan, J., van Keulen, H., 1997. SUCROS97: Simulation of crop growth for potential and water-limited production situations. *Appl. Spring Wheat. AB-DLO* 14.
- Li, C., Frolking, S., Harris, R., 1994. Modelling carbon biogeochemistry in agricultural soils. *Glob. Biogeochem. Cycles* 8, 237–254.
- Li, Z., Yang, J.Y., Drury, C.F., Yang, X.M., Reynolds, W.D., Li, X., Hu, C., 2017. Evaluation of the DNDC model for simulating soil temperature, moisture and respiration from monoculture and rotational corn, soybean and winter wheat in Canada. *Ecol. Model.* 360, 230–243. <https://doi.org/10.1016/j.ecolmodel.2017.07.013>.
- Mbonimpa, E.G., Gautam, S., Lai, L., Kumar, S., Bonta, J.V., Wang, X., Rafique, R., 2015. Combined PEST and Trial-Error approach to improve APEX calibration. *Comput. Electron. Agric.* 114, 296–303. <https://doi.org/10.1016/j.compag.2015.04.014>.
- Morris, M.D., 1991. Factorial sampling plans for preliminary computational experiments. *Technometrics* 33.
- Moureaux, C., Debacq, A., Hoyaux, J., Suleau, M., Tourneur, D., Vancutsem, F., Bodson, B., Aubinet, M., 2008. Carbon balance assessment of a Belgian winter wheat crop (*Triticum aestivum* L.). *Glob. Change Biol.* 14, 1353–1366. <https://doi.org/10.1111/j.1365-2486.2008.01560.x>.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models part I — a discussion of principles. *J. Hydrol.* 10, 282–290.
- Neitsch, S., Arnold, J., Kiniry, J., Williams, J., 2009. Soil and water assessment tool theoretical documentation version 2009.
- Oyeogbe, A.I., Das, T.K., Bhatia, A., Singh, S.B., 2017. Adaptive nitrogen and integrated weed management in conservation agriculture: impacts on agronomic productivity, greenhouse gas emissions, and herbicide residues. *Environ. Monit. Assess.* 189. <https://doi.org/10.1007/s10661-017-5917-3>.
- Parton, W.J., Ojima, D.S., Cole, C.V., Schimel, D.S., 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Bryant, R.B., Arnold, R.W. (Eds.), *Quantitative Modeling of Soil Forming Processes*. Soil Science Society of America, Madison, WI, USA, pp. 147–167.
- Penning de Vries, F., 1975. The cost of maintenance processes in plant cells. *Ann. Bot.* 39.
- Penning de Vries, F., van Laar, H.H., 1982. Simulation of plant growth and crop production.
- Penning de Vries, F., Witlage, J.M., Kremer, D., 1979. Rates of respiration and of increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress and to their sugar content. *Ann. Bot.* 44, 595–609.
- Penning de Vries, F., van Laar, H.H., Chardon, M.C.M., 1983. Bioenergetics of growth of seeds, fruits, and storage organs.
- Penning de Vries, F., Jansen, D., ten Berge, H., Bakema, A., 1989. Simulation of ecophysiological processes of growth of several annual crops. In: *Simulation of Ecophysiological Processes of Growth of Several Annual Crops*. Springer, Netherlands.
- Perego, A., Giussani, A., Sanna, M., Fumagalli, M., 2013. The ARMOSA simulation crop model: overall features, calibration and validation results. *Ital. J. Agrometeorol.* 42.
- Phillips, C.L., Bond-Lamberty, B., Desai, A.R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K., Vargas, R., 2017. The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling. *Springer International Publishing. Plant Soil* 413, 1–25. <https://doi.org/10.1007/s11104-016-3084-x>.
- Prolingheuer, N., Scharnagl, B., Graf, A., Vereecken, H., Herbst, M., 2014. On the spatial variation of soil rhizospheric and heterotrophic respiration in a winter wheat stand. *Agric. For. Meteorol.* 195–196, 24–31. <https://doi.org/10.1016/j.agrformet.2014.04.016>.
- Pulido-Moncada, M., Petersen, S.O., Clough, T.J., Munkholm, L.J., Squartini, A., Longo, M., Dal Ferro, N., Morari, F., 2024. Soil pore network effects on the fate of nitrous oxide as influenced by soil compaction, depth and water potential. *Soil Biol. Biochem.* 197. <https://doi.org/10.1016/j.soilbio.2024.109536>.
- Richter, G.M., Acutis, M., Trevisiol, P., Latiri, K., Confalonieri, R., 2010. Sensitivity analysis for a complex crop model applied to Durum wheat in the Mediterranean. *Eur. J. Agron.* 32, 127–136. <https://doi.org/10.1016/j.eja.2009.09.002>.
- Savage, K., Davidson, E.A., Tang, J., 2013. Diel patterns of autotrophic and heterotrophic respiration among phenological stages. *Glob. Change Biol.* 19, 1151–1159. <https://doi.org/10.1111/gcb.12108>.
- Schneider, H.M., Lynch, J.P., 2018. Functional implications of root cortical senescence for soil resource capture. *Plant Soil* 423, 13–26. <https://doi.org/10.1007/s11104-017-3533-1>.
- Stöckle, C.O., Nelson, R., Donatelli, M., Yan, Y., Ferrer, F., Van Evert, F., McCool, D., Martin, S., Mulla, D., Bechini, L., Deabaek, P., 1994. Cropping Systems Simulation Model User's Manual. (https://modeling.bsyse.wsu.edu/CS_Suite_4/CropSyst/documentation/articles/description.html).
- Subke, J.A., Inglima, I., Cotrufo, M.F., 2006. Trends and methodological impacts in soil CO₂ efflux partitioning: a metaanalytical review. *Glob. Change Biol.* 12, 921–943. <https://doi.org/10.1111/j.1365-2486.2006.01117.x>.
- Suleau, M., Moureaux, C., Dufranne, D., Buysse, P., Bodson, B., Destain, J.P., Heinesch, B., Debacq, A., Aubinet, M., 2011. Respiration of three Belgian crops: partitioning of total ecosystem respiration in its heterotrophic, above- and below-ground autotrophic components. *Agric. For. Meteorol.* 151, 633–643. <https://doi.org/10.1016/j.agrformet.2011.01.012>.
- Tadiello, T., Gabbrielli, M., Botta, M., Acutis, M., Bechini, L., Ragaglini, G., Fiorini, A., Tabaglio, V., Perego, A., 2023. A new module to simulate surface crop residue decomposition: description and sensitivity analysis. *Ecol. Model.* 480, 110327. <https://doi.org/10.1016/j.ecolmodel.2023.110327>.
- Thornley, J.H.M., Cannell, M.G.R., 2000. Modelling the components of plant respiration: representation and realism. *Ann. Bot.* 85, 55–67.
- Urbanaviči, I., Bonfiglioli L., Bonfiglioli M. A. Pagnotta Diversity in Root Architecture of Durum Wheat at Stem Elongation under Drought Stress 2022. <https://doi.org/10.3390/agronomy12061329>.
- Valkama, E., Kunyipiayeva, G., Zhapayev, R., Karabayev, M., Zhusupbekov, E., Perego, A., Schillaci, C., Sacco, D., Moretti, B., Grignani, C., Acutis, M., 2020. Can conservation agriculture increase soil carbon sequestration? A modelling approach. *Geoderma* 369, 114298. <https://doi.org/10.1016/J.GEODERMA.2020.114298>.
- Volpi, I., Bosco, S., Guidotti, D., Mammini, M., Neri, S., Virgili, G., Meriggi, P., Mantino, A., Laville, P., Ragaglini, G., 2020. Improving GHG flux monitoring in agricultural soil through the AGRESTIC prototype: a focus on the assessment of data quality. In: *2020 IEEE International Workshop on Metrology for Agriculture and Forestry, MetroAgriFor 2020 - Proceedings*. Institute of Electrical and Electronics Engineers Inc, pp. 139–143.
- Wang, C., Amon, B., Schulz, K., Mehdi, B., 2021. Factors that influence nitrous oxide emissions from agricultural soils as well as their representation in simulation models: a review. *agronomy* 11, 770. <https://doi.org/10.3390/agronomy11040770>.
- Zhang, M., Yan, X., Lu, Z., Bai, Q., Zhang, Y., Wang, D., Zhou, Y., Yin, Y., 2021. Effects of micropore group spacing and irrigation amount on soil respiration and yield of tomato with microsprinkler irrigation under plastic film in greenhouse. *J. Sens.* 2021. <https://doi.org/10.1155/2021/6658059>.
- Zhang, Q., Lei, H.M., Yang, D.W., 2013. Seasonal variations in soil respiration, heterotrophic respiration and autotrophic respiration of a wheat and maize rotation cropland in the North China Plain. *Agric. For. Meteorol.* 180, 34–43. <https://doi.org/10.1016/j.agrformet.2013.04.028>.