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M^3 model as a prototype tool for predicting performance of innovative plant teams (Report, Public)

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Executive Summary

This deliverable report describes the applicability of the Minimalist Mixture Model – M^3 – as a prototype tool for predicting performance of innovative plant teams. M^3 has been developed as part of the work conducted in DIVERSify within WP3. M^3, and its most recent further developments, are briefly described. The emphasis is on the general structure of the model, and the data needed for its calibration, running and validation. In addition, this report presents two applications of M^3 to predict the performance of existing and novel plant teams. In the first application, M^3 is used to determine the performance of plant teams differing from the existing ones for specific parameters, thus helping in the identification of key traits for superior performance, and hence potential innovative plant teams that should be prioritized in breeding. In the second application, M^3 is used to determine the stability of a plant team performance in the face of variable climatic conditions, including those projected for the future.

1. Introduction

Intercropping, i.e., growing more than one crop at the same time in the same field, often allows a better exploitation of resources (complementary) and some facilitation effects, which can support the reduction of the negative environmental impacts of agriculture. Intercrops can lead to higher (Li et al., 2020; Martin-Guay et al., 2018; Yu et al., 2016) and possibly more stable (Raseduzzaman and Jensen, 2017) yields. Cereal and legume intercrops are of particular interest because of the advantages stemming from the reduced competition with cereals for inorganic nitrogen, thanks to the ability of legumes to fix atmospheric nitrogen. The existence and extent of these advantages depends on the combination of functional traits of the two (or more) species in the intercrop, and their interactions with the growing conditions, as defined by management, soil type and weather.

By allowing the exploration of a large number of trait combinations and conditions, models facilitate investigating how plant features, management and pedoclimatic conditions interact in defining the provisioning of ecosystem services and in reducing the negative environmental effects of crop production. Exploration of these interactions is of particular relevance when aiming at defining the performance of yet-to-be-bred varieties to be grown in intercrops or in the face of future, still uncertain but likely more variable, climatic conditions. Relatively few existing crop growth models are capable of simulating intercropping (e.g., APSIM and DAISY: Abrahamsen and Hansen, 2000; Ghaley and Porter, 2014; Hansen et al., 1990; Keating et al., 2003). A further limitation of the use of these traditional crop growth models is their high parameter requirements, which are often difficult to determine from commonly available field observations (Berghuijs et al., under revision).

Minimalist models can offer an alternative approach for exploring a wide range of plant combinations and pedoclimatic conditions, as they rely on fewer parameters (Van der Werf et al., 2007). Previously existing minimalist models of intercrops (Gou et al., 2017b; Liu et al., 2017; Tan et al., 2020) were not able to account for nitrogen-limited conditions – a key mechanism in cereal-legume intercrops. Hence, as part of the work of DIVERSify, we developed M^3 – Minimalist Mixture Model – to include the effects of nitrogen availability on two crops growing in intercrop and most recently also the effects of water availability (Berghuijs et al., 2020; Berghuijs et al., 2021).

Here we briefly present M^3, its rationale, and its usability as a decision aid tool. To illustrate the use of M^3 to predict the performance of plant teams, we discuss two applications, one

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pertaining the identification of key plant characteristics defining yields, in existing and novel plant team combinations, and one considering the role of pedoclimatic conditions. In both cases, we use as an example wheat (*Triticum aestivum*) and faba bean (*Vicia faba*) grown in two locations, in northern and southern Europe.

2. Minimalist Mixture Model M^3

M^3 simulates the performance of crops in pure culture or intercrop, and how it is affected by crop management, environmental conditions and plant characteristics. The model state variables (**Figure 1**) are, for each crop, leaf area index, total above ground biomass, plant nitrogen amount, reproductive organ (grain) dry matter, temperature sum from sowing and, for the soil, soil water content and soil mineral nitrogen content in the rooting zone (red ellipses in **Figure 1**).

For each day, M^3 determines, among others, changes in plant nitrogen content, plant aboveground biomass, plant height, leaf area index, and grain weight for one crop (pure culture) or two crop species with overlapping growing seasons (intercrop). The model is based on the concept of radiation use efficiency to determine the potential aboveground biomass growth, which is then reduced when nitrogen or water availability or their combination are limiting factors (**Figure 1**, light blue boxes). The newly produced biomass is partitioned into leaf dry matter, grain dry matter, and remaining dry matter, in proportions depending on the phenological stage, in turn a function of accumulated temperature sums and base temperatures.

Biomass growth is coupled with water and nitrogen uptake. Soil water and soil mineral nitrogen availability to the crops is the result of inputs and losses to their respective balances. The soil water balance of the rooting zone accounts for inputs of water via precipitation and irrigation (if implemented) and losses via subsurface runoff, deep percolation below the rooting zone and evapotranspiration – all functions of soil texture. Potential evapotranspiration rate also depends on solar radiation, air temperature and humidity, while actual plant water uptake is reduced along with soil water availability. The soil nitrogen balance accounts for inputs via fertilization, if any, and soil nitrogen mineralization and losses via plant uptake.

The system responds to environmental conditions, chiefly solar radiation, air temperature and humidity, precipitation, and soil texture (green ellipses in **Figure 1**). It also responds to management choices: planting densities and geometry, sowing and harvesting dates, fertilization dates and amounts, implementation of irrigation (black rectangles in **Figure 1**); as well as key crop features.

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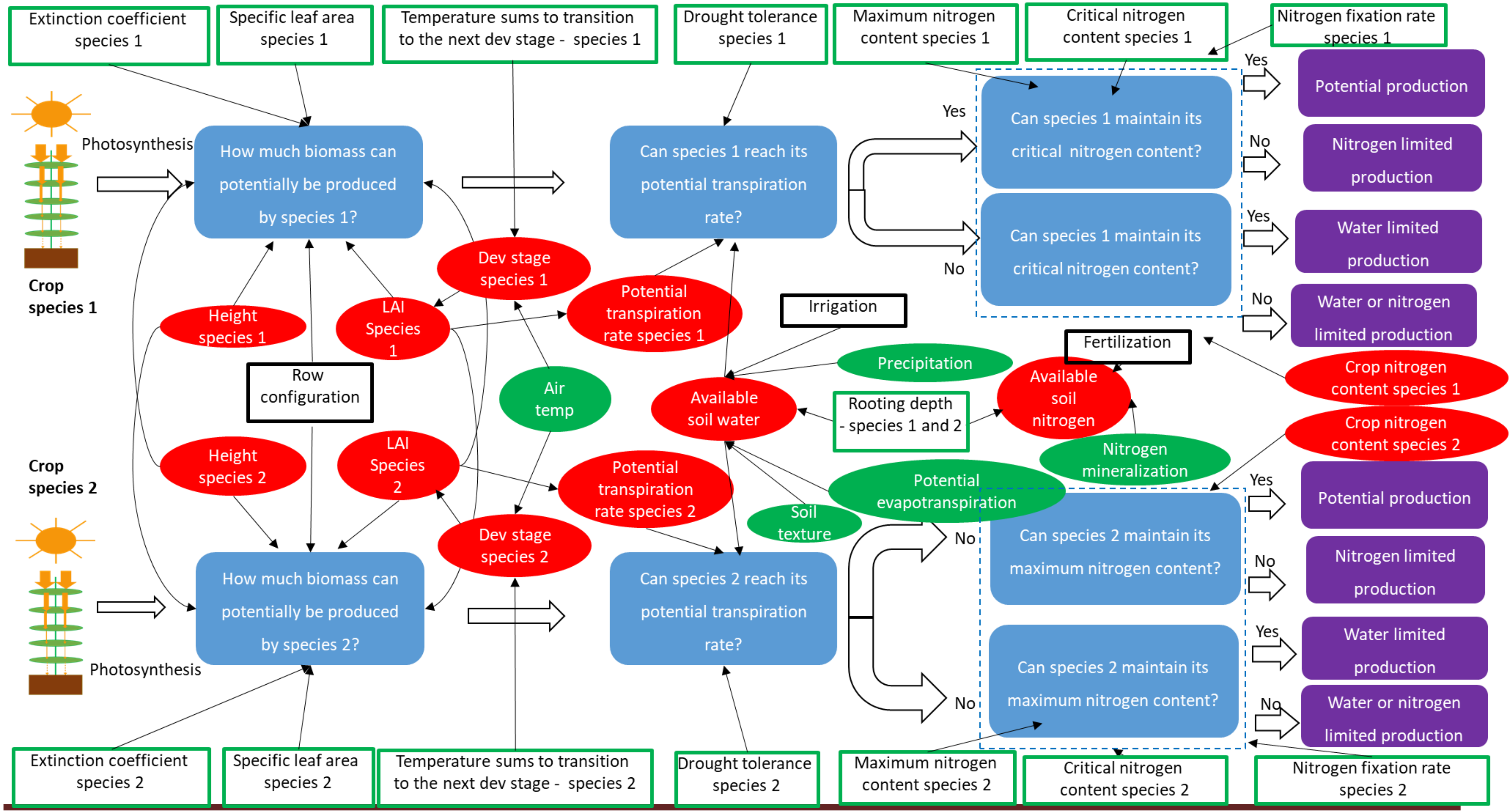
Extinction coefficient species 1
Specific leaf area species 1
Temperature sums to transition to the next dev stage - species 1
Drought tolerance species 1
Maximum nitrogen content species 1
Critical nitrogen content species 1
Nitrogen fixation rate species 1
Photosynthesis
Crop species 1
How much biomass can potentially be produced by species 1?
Can species 1 reach its potential transpiration rate?
Yes
No
Can species 1 maintain its critical nitrogen content?
Can species 1 maintain its critical nitrogen content?
Yes
No
Yes
No
Potential production
Nitrogen limited production
Water limited production
Water or nitrogen limited production
Dev stage species 1
Height species 1
LAI Species 1
Potential transpiration rate species 1
Irrigation
Row configuration
Air temp
Available soil water
Precipitation
Fertilization
Available soil nitrogen
Rooting depth - species 1 and 2
Crop nitrogen content species 1
Crop nitrogen content species 2
Nitrogen mineralization
Potential evapotranspiration
Soil texture
Crop species 2
Height species 2
LAI Species 2
Potential transpiration rate species 2
Dev stage species 2
How much biomass can potentially be produced by species 2?
Photosynthesis
Can species 2 reach its potential transpiration rate?
No
No
Can species 2 maintain its maximum nitrogen content?
Can species 2 maintain its maximum nitrogen content?
Yes
No
Yes
No
Potential production
Nitrogen limited production
Water limited production
Water or nitrogen limited production
Extinction coefficient species 2
Specific leaf area species 2
Temperature sums to transition to the next dev stage - species 2
Drought tolerance species 2
Maximum nitrogen content species 2
Critical nitrogen content species 2
Nitrogen fixation rate species 2

Figure 1 (previous page). *Structure of M^3. Crop biomass production (violet rectangles) is determined by the interaction of crop parameters (green rectangles), crop states and intermediate variables (red ellipses), with pedoclimatic conditions (green ellipses) and management practices (black rectangles). Figure modified after Berghuijs et al. (2021).*

To facilitate the model parametrization, and exploit commonly observed variables for which data are readily available from experimental trials (e.g., the 'core traits' in DIVERSify WP2; Kiær et al., 2020), the crops are described by high-level characteristics (green rectangles in **Figure 1**), corresponding to specific plant traits or to the outcomes of trait combinations. These crop characteristics are: specific leaf area, radiation use efficiency, nitrogen contents for unconstrained, reduced, and halted plant growth, leaf and grain partition fractions, and temperature sums needed for specific phenological development (including leaf senescence). More details of the M^3 model are reported in Berghuijs et al. (2020).

3. M^3 as decision support tool

3.1. Model structure

The code of M^3 is written in the programming language C#. To further facilitate its broad application, M^3 is also available in the form of an executable file, with intuitive input and output files, and supported by a thorough technical description. The model codes will be made available in a public code repository with a unique doi in January 2021.

The user must provide input data, summarizing the crop and environmental features. Specifically, the model requires six input files (**Figure 2**), containing a) a list of the simulations to be performed; b) management conditions (sowing and harvesting dates, fertilization and irrigation dates and amounts); c) weather conditions (daily minimum and maximum air temperature, average air relative humidity, air temperature, precipitation, average wind speed, cumulated daily solar radiation, and, if available, potential evapotranspiration); d) site location; e) soil parameters over the rooting zone (soil texture and related parameters, initial nitrogen content); f) the crop parameters for each simulated species. The model outputs are, amongst others, the daily simulated values of the state variables and their rates of change (**Figure 2** g, h). An example of temporal evolution of key model outputs is presented in **Figure 3**.

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3.2. Data needs for model parameterization and validation

M^3 was developed with the explicit aim to limit data requirements for its parameterization. The information necessary to construct the five input files can be obtained in different ways, depending on local data availability.

For each location, weather conditions are available through a local meteorological station, retrieved from data repositories (e.g. NASAPower, https://power.larc.nasa.gov/; or EObs, https://www.ecad.eu), or extracted from outputs of regional downscaling of climatological models, including future conditions (e.g., the Coordinated Regional Climate Downscaling Experiment, CORDEX, https://cordex.org/). If unavailable, the evapotranspiration rate is determined by an *ad hoc* module of the model, exploiting the Penman Monteith equation and the weather conditions.

Soil parameters, if not locally available, can be extracted from SoilGrids (Hengl et al., 2017).

Ideally, calibration of the crop parameters is based on within-season field observations of the state variables, phenology (dates of emergence, floral initiation, flowering dates, grain filling and physiological maturity dates) and direct measurements of parameters of M^3 under different fertilization treatments. Berghuijs *et al*. (2020a) parameterized M^3 using datasets for pure cultures of spring wheat (Gou et al., 2017a; Gou et al., 2016) and faba bean (Kropff, 1989) that contained many of the necessary data. Validation of the model was done with a dataset of pure cultures and strip intercrops of wheat and faba bean (Berghuijs et al., 2020). Despite the relatively low number of parameters of M^3 – markedly lower than many other crop growth models – many experiments do not report all the required information. A possible way to do a limited calibration and validation of M^3 is to partially adopt previously determined parameters, like the ones from Berghuijs et al. (2020), while determining as many as possible from the information that is available in the field trial. This is possible also in the presence of different planting designs (e.g., homogeneous mixture vs. strip intercrop), as long as planting densities are comparable, because the calibration is based on pure cultures. The most important parameters to adapt to the local conditions are the temperature sums, which drive the phenology.

Finally, management conditions are generally known, or can be assumed, for sensitivity analyses, e.g., on the role of an earlier or delayed sowing date, and the application of fertilization, irrigation or both.

Comparisons of the model outputs, for example grain dry matter at harvest, with field observations, allows the ability of the model to simulate crop growth to be determined.

a) Example of file listing the simulations to be performed, with one sample simulation line.

RunID	Output FileDirectory	OutputFileName	Farmer file directory	Farmer file name	Soil file directory	Soil file name	Weather station ID	Weather station file directory	Weather station file name	Weather file directory	Weather file name	Water limited growth
1		output_run2019WheatFababean.csv		farmer_parameters_intercrop2019WheatFababean_6_6.csv		soil_parameters.csv	1		wageningen_station.csv		wageningen_test.csv	TRUE

b) Example of management parameter file.

Symbol	Meaning	Value	Unit	Symbol	Meaning	Value	Unit	Symbol	Meaning	Value	Unit	Symbol	Meaning	Value	Unit	CropParameterFile Directory	CropParameterF
date_sow	Date at which the crop is sown	2019-04-01	yyyy-mm-dd	sow_dens	Sowing density	184.5	seeds per m2	date_har	Date at which the crop is harvested	2019-08-08	yyyy-mm-dd	strip_width	Width of the strip	1.5	m		wheat.csv
date_sow	Date at which the crop is sown	2019-04-01	yyyy-mm-dd	sow_dens	Sowing density	2.20E+01	seeds per m2	date_har	Date at which the crop is harvested	2019-08-14	yyyy-mm-dd	strip_width	Width of the strip	1.5	m		fababean_em.cs
date_nfert	Date at which fertilizer is applied	2019-04-01	yyyy-mm-dd	nfert	Amount of nitrogen applied	5.00E-03	kg N/m2										
date_nfert	Date at which fertilizer is applied	2019-05-15	yyyy-mm-dd	nfert	Amount of nitrogen applied	2.25E-03	kg N/m2										
date_irr	Date at which irrigation is applied	2019-06-27	yyyy-mm-dd	nirr	Amount of water that was applied	1.80E-02	m3 H2O / m2										

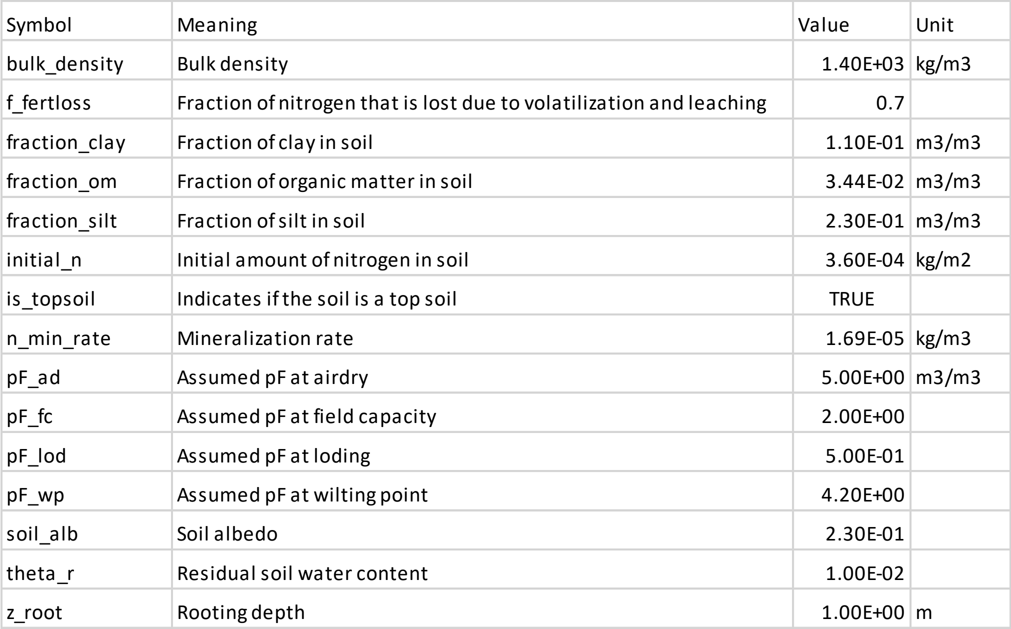
c) Sample lines of weather data input file.

stn	date	doy	day	month	year	tmin	tmax	precipitat	irradiatio	vap	vwind	pet	remark
…													
3	2019-07-01	182	1	7	2019	14.67	21.93	1.41	21.9	2116.71	0.97		
3	2019-07-02	183	2	7	2019	11.11	15.72	6.08	12.92	1546.22	0.79		
3	2019-07-03	184	3	7	2019	9.77	15.31	3.31	18.71	1459.76	0.55		

d) Sample lines of input file for site properties.

WeatherStationID	Country	City	Latitude	Longitude	Elevation
…					
7	SE	Uppsala	59.835	17.7	32
8	NL	Wageningen	51.99	5.65	0

e) Example of input file for soil properties.



Symbol	Meaning	Value	Unit
bulk_density	Bulk density	1.40E+03	kg/m3
f_fertloss	Fraction of nitrogen that is lost due to volatilization and leaching	0.7	
fraction_clay	Fraction of clay in soil	1.10E-01	m3/m3
fraction_om	Fraction of organic matter in soil	3.44E-02	m3/m3
fraction_silt	Fraction of silt in soil	2.30E-01	m3/m3
initial_n	Initial amount of nitrogen in soil	3.60E-04	kg/m2
is_topsoil	Indicates if the soil is a top soil	TRUE	
n_min_rate	Mineralization rate	1.69E-05	kg/m3
pF_ad	Assumed pF at airdry	5.00E+00	m3/m3
pF_fc	Assumed pF at field capacity	2.00E+00	
pF_lod	Assumed pF at loding	5.00E-01	
pF_wp	Assumed pF at wilting point	4.20E+00	
soil_alb	Soil albedo	2.30E-01	
theta_r	Residual soil water content	1.00E-02	
z_root	Rooting depth	1.00E+00	m

f) Example of input file for crop parameters, here for the case of wheat.

Symbol	Meaning	Value	Unit
A_lv0	Initial leaf area per plant	2.10E-05	m2 leaf per pl
f_emer	Fraction of seeds emerged	1	seedlings per
rue	Radiation use efficiency	3.16E-09	kg J-1
s_la	Specific leaf area	21.5	m2 leaf per kg
t_b	Base temperature	0	degC
tsum_em_flo	Temperature sum from emergence to flowering	905	degC
tsum_so_em	Temperature sum from sowing to emergence	112	degC day
tsum_flo_mat	Temperature sum from flowering to maturity	700	degC day
dev_1	Development rate from which the fraction of biomass partitioned to the leaves decreases.	0.25	-
dev_2	Development rate at which no biomass is partitioned to the leaves.	0.95	-
f_lv_0	Fraction of newly produced biomass assigned to the leaves from emergence to the moment it decreases.	0.65	-
t_min_sen	Maximum temperature at which no senescence takes place	-10	degC day
s_sen_t	Slope of the senescence to daily temperature plot	2.38E-03	
k	Extinction coefficient	0.6	
h_max	Maximum crop height	0.85	m
rgrh	Intial relative growth rate of height	0.00567	(degC day)-1
h_0	Initial plant height	0.02	m
dev_y1	Development rate from which the fraction of biomass partitioned to the storage organs starts to increase	0.88	
dev_y2	Development rate from which all biomass is assigned to the storage organs	1	
f_NFix	Fraction of nitrogen demand that is fullfilled by N2 fixation	0	
Nmax0	Maximum nitrogen concentration at early growth	0.05	
coeffAMax	Biomass at which the maximum nitrogen concentration of the crop is 1 in a pure culture; in absence of a maximum nitrogen content.	0.14	
coeffACrit	Biomass at which the critical nitrogen concentration of the crop is 1 in a pure culture; in absence of a maximum nitrogen content.	0.1	
coeffAMin	Biomass at which the minimum nitrogen concentration of the crop is 1 in a pure culture; in absence of a maximum nitrogen content.	0.02	
coeffB	Coefficient in nitrogen dilution curve	0.35	
coeffBMax	Coefficient in nitrogen dilution curve maximum nitrogen concentration	0.56	
coeffBCrit	Coefficient in nitrogen dilution curve critical nitrogen concentration	0.57	
coeffBMin	Coefficient in nitrogen dilution curve minimum nitrogen concentration	0.46	
fNCrit	Fraction critical nitrogen content at early growth to total nitrogen content	0.76	
fNMin	Fraction minimal nitrogen content at early growth to total nitrogen content	0.75	
rint_max	Maximum rain interception per unit of leaf area.	0.00025	
tranco	Transpiration coefficient	0.009	
f_int_cr	Fraction of light interception above which mortality due to self shading occurs	0.91	
rdrsh	Maximum relative rate of leaf senescence due to self shading	0.03	

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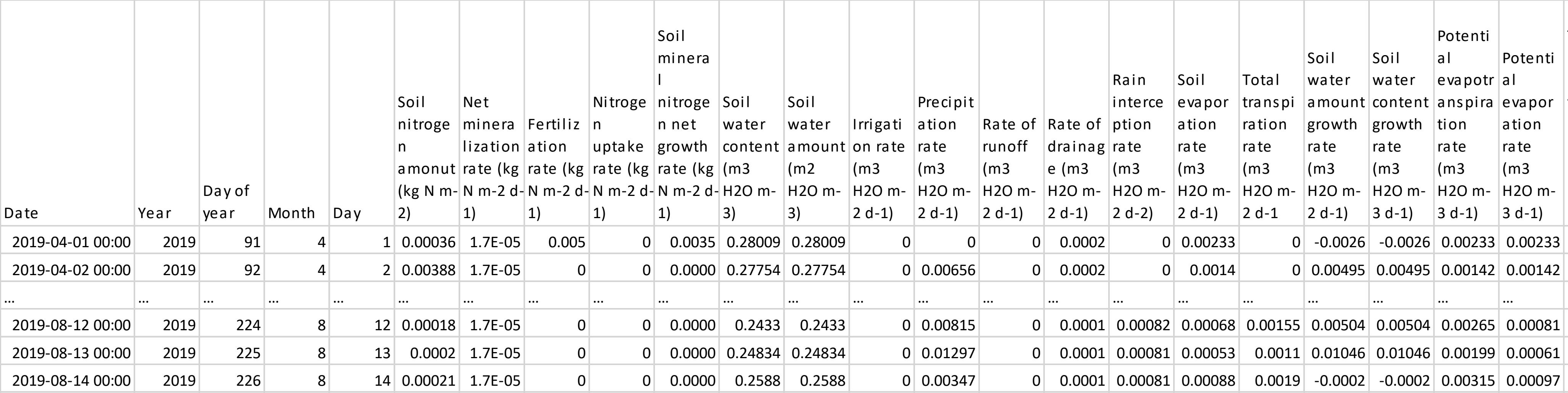
g) Sample of output file, including the header row, and the first two and last three rows of the simulated growing season. For visual clarity, this image shows only the first 24 columns of an 80-column file, reporting conditions relevant for both crops.



Date	Year	Day of year	Month	Day	Soil nitrogen amonut (kg N m-2)	Net mineralization rate (kg N m-2 d-1)	Fertilization rate (kg N m-2 d-1)	Nitrogen uptake rate (kg N m-2 d-1)	Soil mineral nitrogen net growth rate (kg N m-2 d-1)	Soil water content (m3 H2O m-3)	Soil water amount (m2 H2O m-3)	Irrigation rate (m3 H2O m-2 d-1)	Precipitation rate (m3 H2O m-2 d-1)	Rate of runoff (m3 H2O m-2 d-1)	Rate of drainage (m3 H2O m-2 d-1)	Rain interception rate (m3 H2O m-2 d-2)	Soil evaporation rate (m3 H2O m-2 d-1)	Total transpiration rate (m3 H2O m-2 d-1	Soil water amount growth rate (m3 H2O m-2 d-1)	Soil water content growth rate (m3 H2O m-3 d-1)	Potential evapotranspiration rate (m3 H2O m-3 d-1)	Potential evaporation rate (m3 H2O m-3 d-1)
2019-04-01 00:00	2019	91	4	1	0.00036	1.7E-05	0.005	0	0.0035	0.28009	0.28009	0	0	0	0.0002	0	0.00233	0	-0.0026	-0.0026	0.00233	0.00233
2019-04-02 00:00	2019	92	4	2	0.00388	1.7E-05	0	0	0.0000	0.27754	0.27754	0	0.00656	0	0.0002	0	0.0014	0	0.00495	0.00495	0.00142	0.00142
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
2019-08-12 00:00	2019	224	8	12	0.00018	1.7E-05	0	0	0.0000	0.2433	0.2433	0	0.00815	0	0.0001	0.00082	0.00068	0.00155	0.00504	0.00504	0.00265	0.00081
2019-08-13 00:00	2019	225	8	13	0.0002	1.7E-05	0	0	0.0000	0.24834	0.24834	0	0.01297	0	0.0001	0.00081	0.00053	0.0011	0.01046	0.01046	0.00199	0.00061
2019-08-14 00:00	2019	226	8	14	0.00021	1.7E-05	0	0	0.0000	0.2588	0.2588	0	0.00347	0	0.0001	0.00081	0.00088	0.0019	-0.0002	-0.0002	0.00315	0.00097

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h) Columns 25 to 52 of the output file, reporting the status of crop 1. In the case of simulations with intercrop, an additional 28 columns are filled, with the status of crop 2 for the same variables of crop 1.

Development rate of species 1	Emergence status of species 1	Aboveground dry matter weight of species 1 (kg m-2)	Aboveground dry matter production of species 1 (kg m-2 d-1)	Aboveground dry mortality of species 1 (kg m-2 d-1)	Leaf area index of species 1 (-)	Leaf area index of species 1 production (d-1)	Leaf area index of species 1 mortality (d-1)	Fraction of light intercepted	Shoot height of species 1 (m)	Shoot height growth of species 1 (m d-1)	Storage organ dry matter weight 1 (kg m-2)	Storage organ dry matter production 1 (kg m-2 d-1)	Crop nitrogen amount of species 1 (kg N m-2)	Crop nitrogen total demand 1 (kg N m-2)	Crop nitrogen demand from soil 1 (kg N m-2)	Crop nitrogen uptake rate of species 1 (kg N m-2 d-1)	Crop nitrogen fixation rate of species 1 (kg N m-2 d-1)	Crop nitrogen loss by senescence of species 1 (kg N m-2 d-1)	Crop nitrogen net growth of species 1 (kg N m-2 d-1)	Crop nitrogen content of species 1 (kg N kg-1)	Maximum nitrogen content of species 1 (kg kg-1)	Critical nitrogen content of species 1 (kg kg-1)	Minimum nitrogen content of species 1 (kg kg-1)	Crop growth reduction factor of species due to nitrogen shortage 1 (-)	Potential transpiration rate of species 1 (m3 H2O m-2 d-1)	Ac tra ra ra sp 1 (H2 2 (
0	FALSE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.038	0.0375	1	0	
0	FALSE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.038	0.0375	1	0	
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
2	TRUE	0	0	0	0	0	0	0	0	0	0	0	0.00605	0	0	0	0	0	0	0	0.05	0.038	0.0375	1	0	
2	TRUE	0	0	0	0	0	0	0	0	0	0	0	0.00605	0	0	0	0	0	0	0	0.05	0.038	0.0375	1	0	
2	TRUE	0	0	0	0	0	0	0	0	0	0	0	0.00605	0	0	0	0	0	0	0	0.05	0.038	0.0375	1	0	

Figure 2. *Example of input (a-f) and output (g-h) files for the M*^{3} *model. All the files are in the comma-delimited format but are reported here as tables for enhanced readability.*

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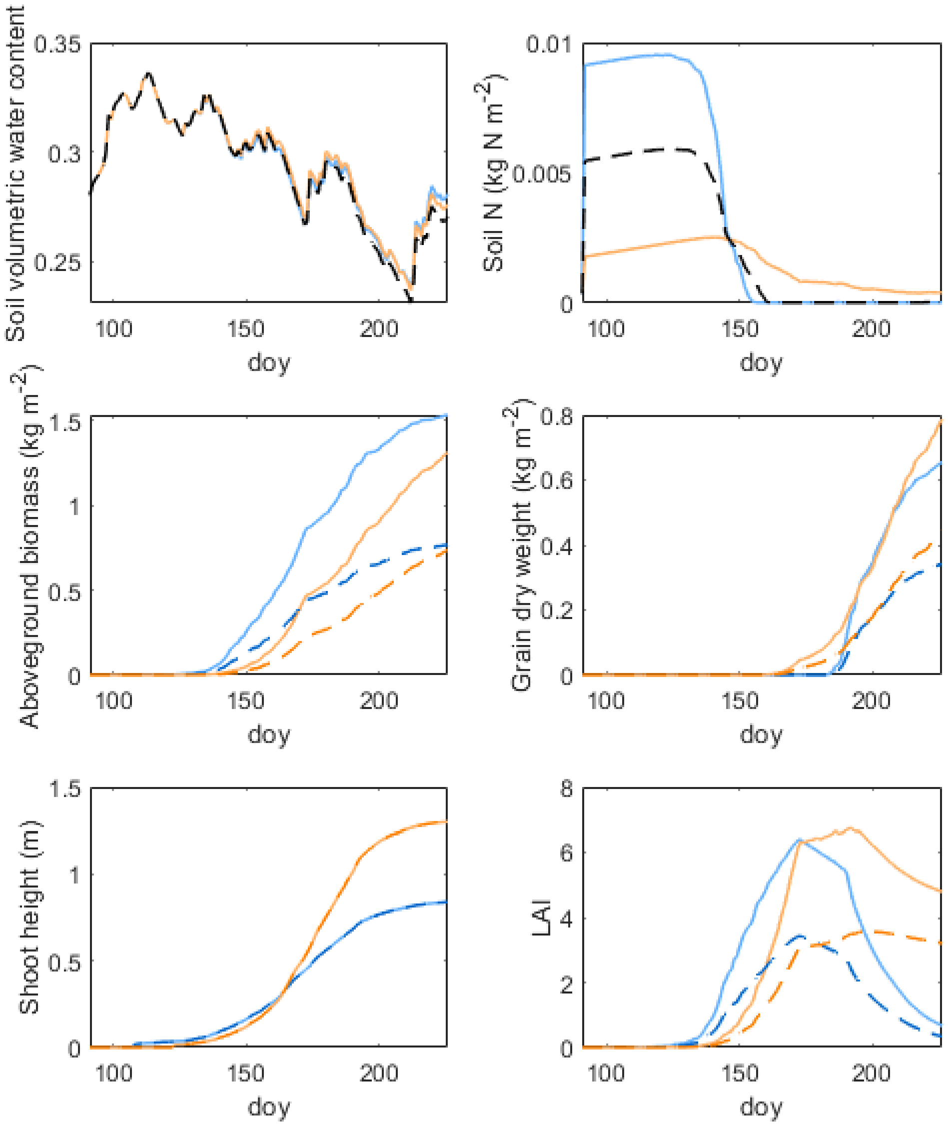

Figure 3. *Example of model output for Wageningen under current climatic conditions. First row, soil volumetric water content and soil nitrogen content; middle row, above ground biomass and grain dry weight; bottom row, shoot height and leaf area index (LAI). Blue lines refer to wheat, orange ones to faba bean; solid lines to pure cultures and dashed to strip intercrops. For soil conditions, only one value is available in intercrops, and it is reported as a black dashed line.*

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4. Examples of model applications

Once calibrated, M^3 can be used to simulate the effects of different plant teams (by altering the crop parameters), management approaches (by altering the management parameters), and pedoclimatic conditions (by considering different soil types and observed or modelled climatic forcing). Here we present two examples of applications, one aiming at determining the most relevant plant characteristics for yields in pure culture and intercrop for fixed climatic conditions (Section 4.1), and one elucidating the role of variability in the climatic conditions on crop yields, and the stabilizing effects of intercropping (Section 4.2).

4.1. Application 1: Evaluation of the role of plant characteristics on plant team performance

As an example of model application to determine the key crop characteristics for intercrop performance, we performed a local sensitivity analysis, i.e., we varied all crop parameters around their calibrated values for each site and determined those with the largest effect on the single crop yield and that in intercrop. For technical details about the analysis, see Berghuijs et al. (2020).

We focused on wheat and faba bean grown in pure culture and homogeneous intercrop in two locations, differing in pedoclimatic conditions: Uppsala (Central Sweden; 59.84° N, 15.70° E) and Ancona (Central Italy; 43.55° N, 13.36° E). The weather conditions correspond to those observed at the sites during the 2017 DIVERSify field trials and were obtained from NASAPower. The management conditions correspond to those of the DIVERSify "conventional management" field trials in 2017 in each site. The crops were parameterized as described in Berghuijs et al. (2020). But, to match the local conditions, we adjusted the phenological parameters (temperature sum from emergence to flowering and from flowering to maturity) and the maximum crop height, assumed to be the same in both sites but different across species. The values of the parameters are reported in Berghuijs et al. (2021).

The local sensitivity analysis returns the relative change and direction of change of crop yield resulting from a small change of the parameter value. This relative change in yields is normalized with respect to the relative change of the parameter, to obtain the relative sensitivity (also called elasticity). For example, a relative sensitivity of 2 means that a 0.1% change in the parameter value results in a 0.2% change in the yield. Wheat and faba bean characteristics can thus be ranked based on how large a change in yield is caused by a set change in the parameter value.

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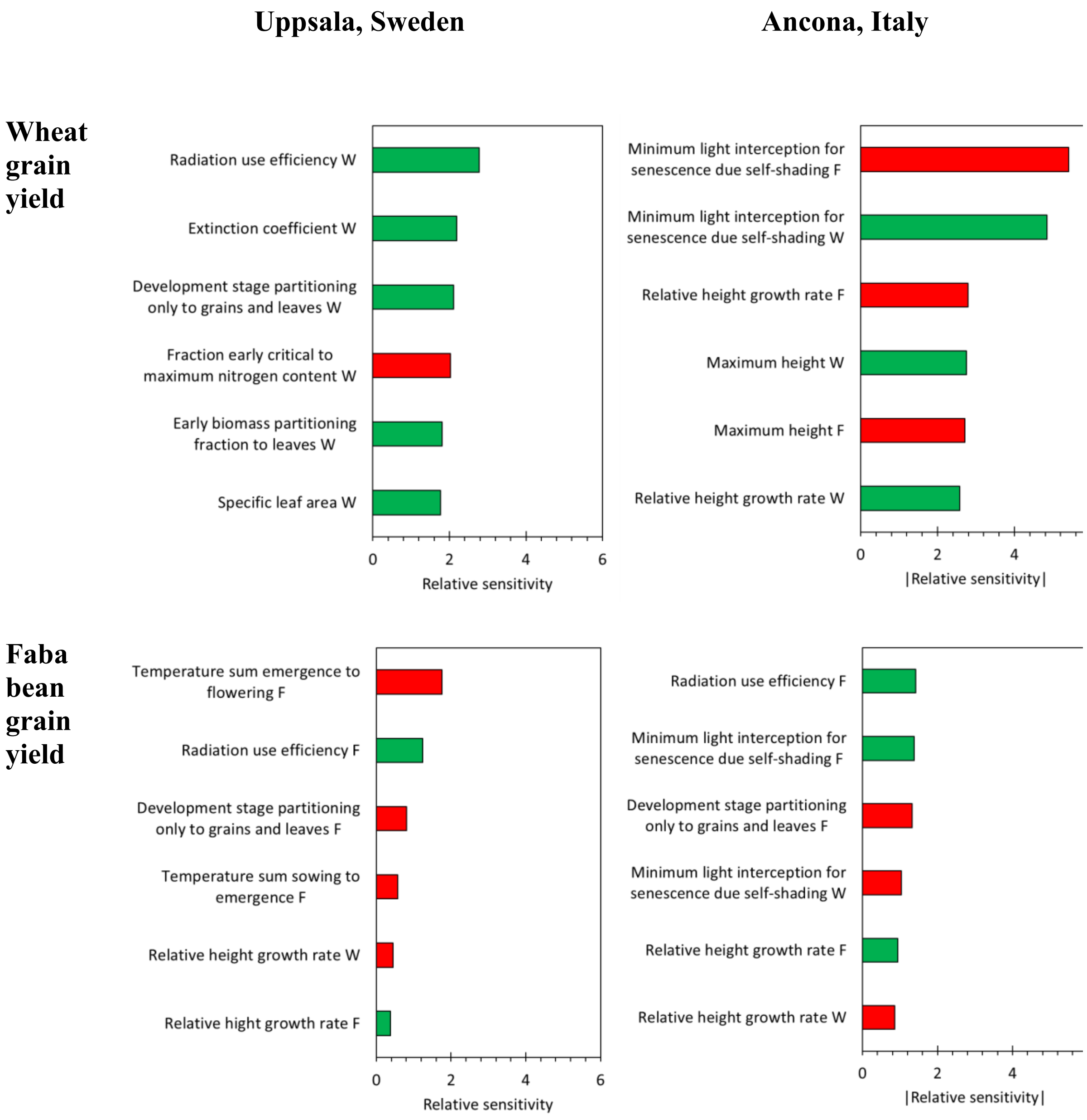

Figure 4. *Relative sensitivity of the individual grain yields of wheat (W) and faba bean (F) in wheat-faba bean intercrops grown in Uppsala and Ancona in 2017 (under conventional management) to various plant characteristics (redrawn after Berghuijs et al., 2021). For graphical clarity, only the six characteristics to which the total yields are most sensitive are shown. The x-axis reports the absolute value of the relative sensitivity: green bars indicate a positive effect of increasing the value of the parameter on the yield; red bars indicate a negative effect.*

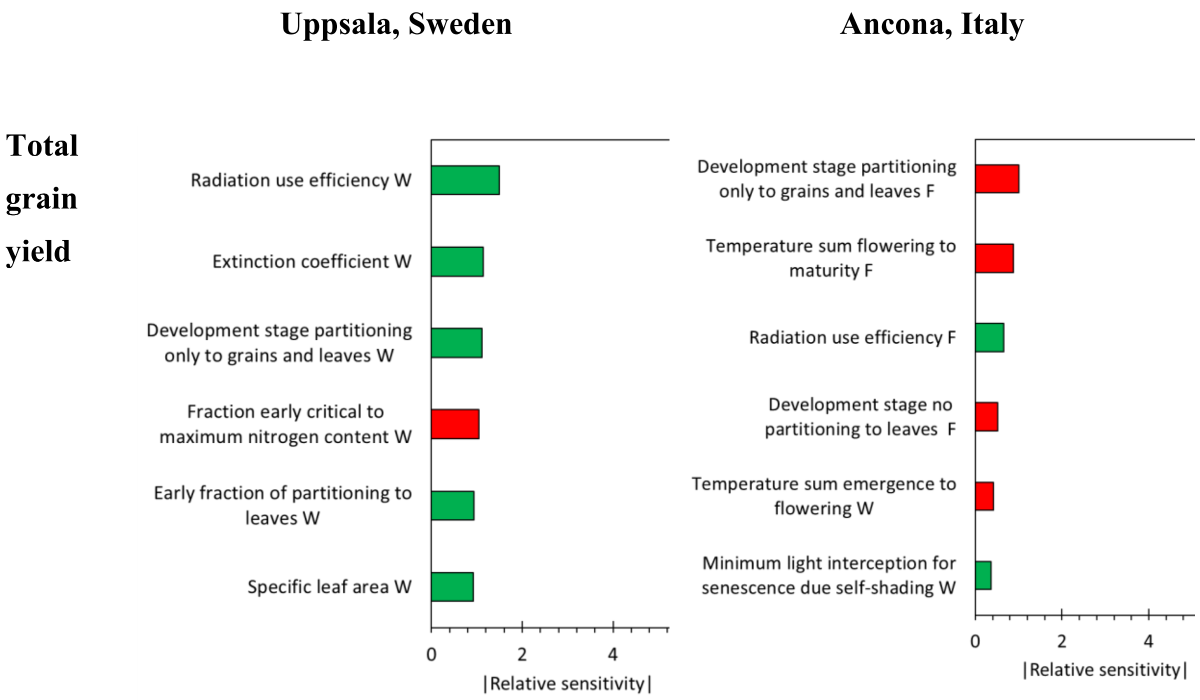

Figure 5. *Relative sensitivity of the sum of the wheat (W) and faba bean (F) yields in wheat-faba bean intercrops grown in Uppsala and Ancona in 2017 (conventional management) to various plant traits (redrawn after Berghuijs et al., 2021). Only the six traits to which the total yields are most sensitive are shown. The x-axis reports the absolute value of the relative sensitivity: green bars indicate an increase in yield and red bar a decrease in yield in the face of increasing the parameter value.*

The relative sensitivity of the individual yields of wheat in wheat-faba bean intercrops to crop parameters is higher than the relative sensitivity of individual yields of faba bean (**Figure 4**). The individual yields of either species in the wheat-faba bean intercrops are mainly affected by the characteristics of that species in Uppsala, while they are more affected by those of the second species in Ancona (**Figure 4**). All the plant characteristics of one species that affect the local sensitivity of the yield of the second species represent aspects of competition for light (relative height growth rate, maximum and minimum light interception for senescence), underlining the importance of accessing light to ensure biomass growth and ultimately grain yield. All the most important plant characteristics for the total wheat-faba bean intercrop yield relate to wheat in Uppsala, while the four most important characteristics that affect the total intercrop yield in Ancona relate to faba bean (**Figure 5**). In contrast to the individual yield of faba bean in Uppsala and the individual yields of both wheat and faba bean in Ancona, the top six plant characteristics that affect the total intercrop yield include almost no parameters that are directly related to light competition between the species, because if one crop exploits more light, the other crop exploits less light (and vice versa) so improvement in yield of one crop is balanced by a drop in yield of the other. This suggests that individual yields could be affected by changing characteristics related to crop height, but that this effect is much smaller when considering the total yield of the intercrop.

4.2. Application 2: Effect of climatic conditions on intercrop yield and its stability

The effects of climatic conditions and their variability on yields in wheat and faba bean pure cultures and strip-intercrops were examined by forcing M^3 by climatic model outputs relative to Wageningen (the Netherlands, 51.99° N, 5.65° E). The model parameterization procedure and the parameter values for this site are reported in Berghuijs et al. (2020). The climatic forcing was obtained from CORDEX, so as to include future (projected) climatic conditions. Specifically, gridded daily maximum and minimum air temperatures, relative humidity, precipitation, surface down-welling shortwave radiation, and wind speed were obtained for the EU-44 domain from CORDEX. As an example, we chose the outputs of the NOAA GFDL ESM2M global climate model and the SMHI RCA4 regional climate model (ensemble r1ip1, version 1), for the periods 1951-2000 (historic data) and 2051-2100, assuming the Representative Concentration Pathway (RCP) 8.5. This scenario corresponds to a continued increase in greenhouse gas emissions, and the worst-case scenario in the AR5 IPCC report. All the other parameters were as in Berghuijs et al. (2020), the same crop and the same management of the field trials were assumed. In other words, no adaptation of crop parameters or management (including sowing date) to climatic conditions was considered.

There was a substantial interannual variability in yields both on a per unit area and per plant basis (shown by the box-and-whisker ranges in **Figure 6** left and **Figure 7**, respectively) and consequently in the land equivalent ratio (**Figure 6** right). Such a large variability is due to the interannual variability in weather conditions, with solar radiation affecting the potential biomass growth, precipitation affecting the actual biomass growth, and temperature affecting the phenological evolution, and hence the allocation of new biomass to different organs. On a per unit area basis, historical vs. future climatic conditions do not alter the general pattern of yield differences between crops and cropping systems (**Figure 6**). Conversely, when considering the yields per plant, future climatic conditions resulted in lower yields in faba bean, but not in wheat (**Figure 7**, **Table 1**). Cropping system and climatic conditions weakly interacted in defining wheat yields, but not faba bean yields, with pure

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cultures benefitting from the expected change in climatic conditions, while intercrops are negatively affected.

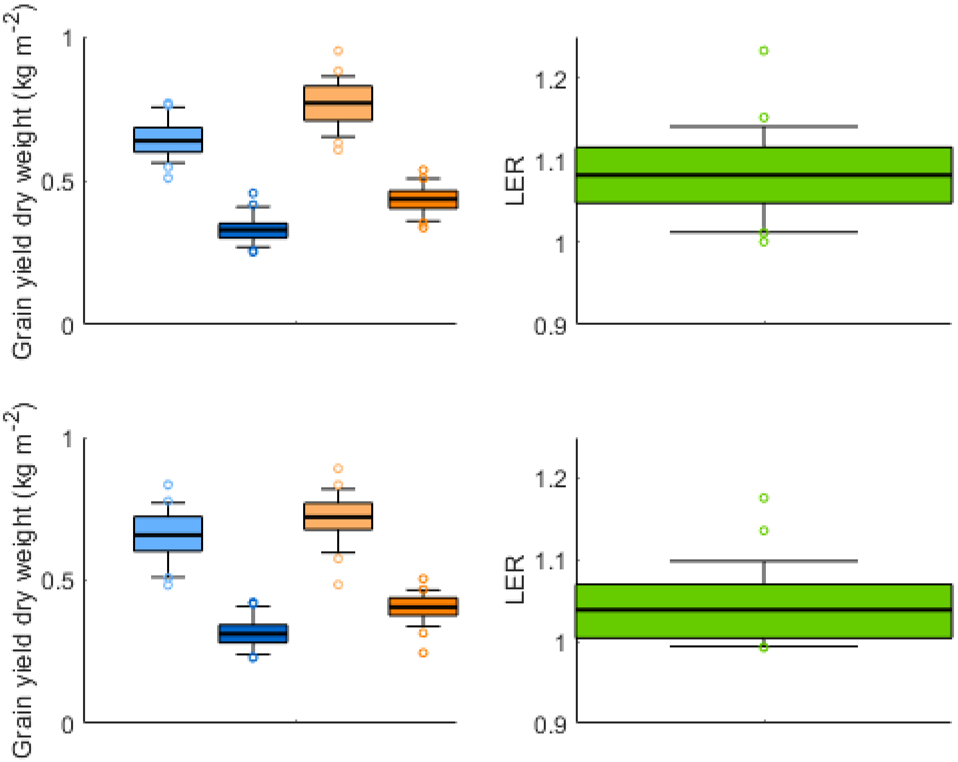

Figure 6. *Boxplot showing grain dry weight per unit ground area (left) and land equivalent ratio (right) for wheat and faba bean grown under historical (top) and future climates (bottom), in Wageningen. Grain dry weights are compared for wheat (blue) and faba bean (orange), grown in pure cultures (lighter shades) and strip intercropping (darker shades). Historical and future climate simulations each cover 50 years, 1951-2000 and 2051-2100 respectively. The thick horizontal line indicates the mean, the boxes extend from the first to the fourth quartile, and the whiskers from the 5th to the 95th percentiles; symbols are outliers outside this range.*

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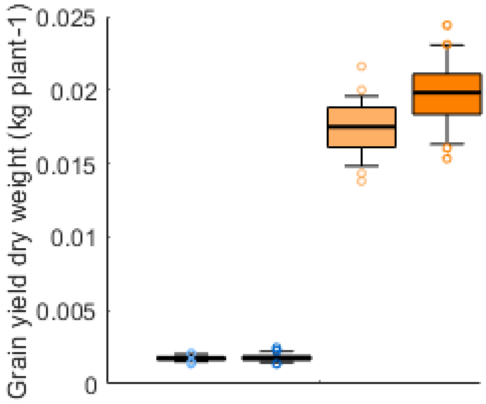

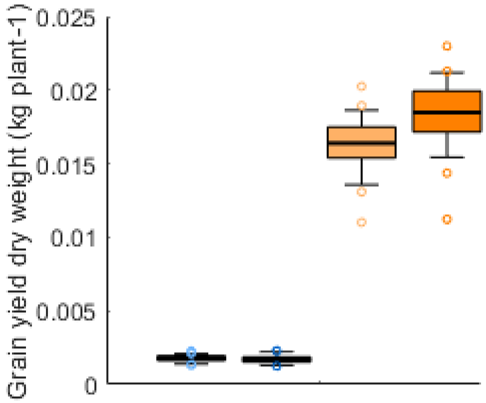

Figure 7. *Boxplot showing grain dry weight per plant for wheat (blue) and faba bean (orange) grown under historical (top) and future climates (bottom), in Wageningen, in pure cultures (first box in each pair) and in intercrop (second box in each pair). The thick horizontal line indicates the mean, the boxes extend from the first to the fourth quartile, and the whiskers from the 5th to the 95th percentiles; symbols are outliers outside this range.*

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Table 1. *Summary of the results of the ANOVA testing the role of period (historical vs. future), and management (pure culture vs intercrop) on grain yields per plant of wheat and faba bean.*

	Wheat		Faba bean	
	F	*p*	*F*	*p*
Scenario (1951-2000 vs. 2051-2100 for RCP8.5)	0.339	0.56	22.17	**<0.001**
Management (pure culture vs. intercropping)	0.289	0.59	72.13	**<0.001**
Scenario x management	5.33	**0.02**	0.20	0.65

Table 2. *Summary of the coefficients of variation (CV) of grain dry weight per plant and their 95% bootstrap confidence intervals (ci), based on 10^4 bootstraps, for wheat and faba bean growing as pure culture and intercrop, under the two climatic scenarios.*

	Historical			Future – RCP 8.5		
	CV	CV ci - lower	CV ci - upper	CV	CV ci - lower	CV ci - upper
Wheat – pure	0.093	0.079	0.111	0.112	0.099	0.143
Wheat - intercrop	0.133	0.111	0.165	0.147	0.123	0.178
Faba bean - pure	0.093	0.079	0.112	0.100	0.081	0.136
Faba bean - intercrop	0.101	0.086	0.122	0.110	0.088	0.161

Considering the grain yields of each crop separately and on a per plant basis, intercropping increased yield variability, as summarized by the coefficient of variation (**Table 2**). Also climate change increased yield variability in both crops and cropping systems. This result is in contrast to the general expectation that intercropping, regardless of climatic conditions, should reduce the yield variability in the face of variable weather patterns (Raseduzzaman and Jensen,

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2017), but in line with observations across the DIVERSify WP2 field trials, when comparing 2017 and 2018 (Weih et al., 2021; Weih M, personal communication, December 2020).

5. M^3 as tool for predicting the performance of innovative plant teams

Intercropping is one strategy, among others, for potentially enhancing and stabilizing yields, and reducing yield variability and the negative environmental effects of agriculture. Yet, to achieve these goals, the plant team and management approaches must be suitable to the local pedoclimatic conditions. It is thus necessary to determine which crops and crop varieties, and management practices, allow the benefits of intercropping to be achieved for each set of soil features, climates and even weather conditions.

Models allow the effective exploration of a range of plant characteristics and pedoclimatic conditions, including yet-to-be-bred varieties to be grown in future climates. But for their results to be robust, they need to be adequately parameterized and validated. Even the few traditional crop growth models developed to simulate intercropping are difficult to use, because of their large number of parameters and the corresponding data requirements.

Here, we briefly described the Minimalist Mixture Model, M^3, developed as part of the DIVERSify project and designed to limit data requirements for its parameterization. We discussed the data needs for M^3 calibration, running, and validation, in terms of frequently available soil and management parameters and meteorological data, and the relatively low number of within-season crop phenological and height observations, and final biomass and yield.

To exemplify the potential use of M^3 for predicting the performance of innovative plant teams, two applications were discussed, using wheat and faba bean as example. With the appropriate calibration, other combinations of field crop species could be explored.

Application 1 aimed at showing how M^3 can help in identifying the characteristics of the plant team members that have the largest effect on grain yields, and how their alteration can improve or reduce the team performance. This type of analysis allows the performance of plant teams differing from the existing ones (in the example the varieties sown in Ancona and Uppsala) to be determined for specific crop characteristics. Considering that these characteristics relate to single or combinations of plant traits, it provides insight into how existing varieties could be modified to improve their performance as plant team members and in pure culture, and highlights which traits or combinations of traits should be prioritized in breeding programs for the maximum (positive) impact when the corresponding varieties are grown in plant teams (intercropping).

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Application 2 aimed at showing how M^3 can support the investigation of the effects of climatic conditions on yield and its stability, in pure cultures and intercrops, including how they can change under future conditions. This type of analysis answers the question whether a specific plant team (in this case wheat and faba bean varieties used in the WP2 field trials in Wageningen) lead to consistent performance year after year, beyond a field experiment of limited duration, and including projections for future climatic conditions. A specific plant team can thus be assessed based on whether its performance is robust to the vagaries of weather, and even to the expected changes in climatic conditions. This is an important step, because the performance depends on the interaction of plant and climate features, which are often nonlinear. It is thus difficult to predict a priori which set of plant characteristics can lead to the largest benefit under the (variable) climatic conditions.

As such, M^3 supports the identification of the most promising plant characteristics for breeding for intercrops and varieties for further field testing, including aspects of climate adaptation.

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