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Model evaluation of cover crops, application to eleven species for banana cropping systems

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ABSTRACT

Cover crops are increasingly used for weed management. But selecting the most suitable species of cover crop to be associated with a main crop requires long-term trials. We present a model-based method that uses a reduced number of parameters to help select cover crops in the context of banana cover-cropping systems. We developed the SIMBA-CC model to focus on radiation interception. The model was calibrated for 11 cover crop species by measuring their growth in 4 m^2 plots with three levels of shade (0, 50, and 75%). The SIMBA-CC model served to predict the long term growth potential of the 11 cover crop species in function of the radiation under the banana crop canopy. The model was validated using three species in association with banana plants. We defined three indicators based on outputs of the model to assess the ability of each of the 11 species (i) to compete with weeds and (ii) to be maintained in the long-term under the canopy of the main crop, and (iii) to evaluate competition with the main crop for nitrogen resource. This *ex ante* evaluation revealed the most promising species to be intercropped with banana. Finally, the SIMBA-CC model was used to define the light interception traits of a virtual cover crop that satisfy the three indicators in the case of intercropping with banana. We showed that to satisfy the three criteria, cover crops with low values of optimal photosynthetically active radiation (PARopti) should have moderate maximal biomass productivity, while crops with higher PARopti values should have a higher maximal productivity. The use of functional traits and modeling appears effective to disentangle the relations between intrinsic traits of cover crops and effect traits that affect the performances of the intercropping system.

1. Introduction

There is currently a surge in reintroducing biodiversity in agricultural systems to reduce chemical inputs, suppress pests, and close biogeochemical cycles (Altieri, 1999; Tilman et al., 2002). Cover crops are an easy way to reintroduce biodiversity in fields (Teasdale, 1996) and are a frequent option for weed management (Bàrberi, 2002). Cover crops have the potential to decrease chemical use against weeds and pests by promoting natural enemies. They are part of global management of the agro-ecosystem (Lewis et al., 1997). Suitable species of cover crops should be able to grow in appropriate conditions, should not compete with the main crop for nutrients or water (Celette et al., 2008, 2009), and should compete with weeds for light and space. Such functional traits are narrow because they are somewhat opposed; there is a tight balance between invasive species traits (Ren and Zhang, 2009) and low competition traits. In natural or semi-natural ecosystems, these functional traits explain the structure of the plant communities (Navas and Violle, 2009).

Selecting a cover crop species means searching for the plant with the best trade-off between competition against weeds and competition with the cultivated crop (den Hollander et al., 2007b; Picard et al., 2010). Finding an appropriate cover crop is thus a key stage in the design of cover-cropping systems and agronomists need rapid and easy means to assess the growth of new cover crop species. This assessment is usually carried out by measuring all the characteristics of all the possible cover crops grown in intercropping conditions (den Hollander et al., 2007a). Usually, the efficiency of the cover crop is evaluated through the difference of yield of the main crop in cover cropping and bare soil systems and with the capacity to control weeds (usually measured through biomass) (Kruidhof et al., 2008; Zhang et al., 2008a). Because of time and financial constraints, and the large number of cover crop species to be tested, there are generally few measurements on each species and few studies on long-term trends. Furthermore, most of these studies are valid only for the case and conditions in which they have been carried out. Models are broadly used to predict the performances of cropping systems (Brisson et al., 2002; Jones et al.,

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2003; Keating et al., 2003; Tixier et al., 2008a) and of cover-cropping systems (Bachinger and Zander, 2007; Zhang et al., 2008b; Blazy et al., 2009). Models are widely used to predict weed population dynamics in the field (Holst et al., 2007). Models are also used to predict the interaction between weeds and different genotypes of cultivated plants (Paolini et al., 2006; Zhao et al., 2006a,b; Wang et al., 2007). Similarly, to study genotype × environment interactions, models can help disentangle the trade-offs between the traits of cover crops and the constraints of performance of cropping systems. Also, early use of models to select plants serves to explain pest dynamics, e.g. nematodes, for a given genotype (Tixier et al., 2008b).

In tropical environments, weeds and cover crops interact differently than in other environments because they are not constrained by seasons; growth is constant because the climate is relatively stable. In these conditions, variation in radiation due to canopy closure is one of the major drivers of growth (Malézieux et al., 2009). The shade of the cultivated crop is thus a key parameter to take into account to understand cover crop growth (Stilma et al., 2009). In the case of banana, cover crops are under the canopy and the shade varies with the growth of banana crops, e.g. it is maximal at flowering stage. Additionally to the stage variation of each plant, the shade of the canopy in banana plantations follows a complex pattern over cropping cycles because of increases in stage inhomogeneity of banana plants (Tixier et al., 2004). Indeed, bananas are rhizomatous herbs whose terminal bud produces the inflorescence. Each plant successively produces a series of bunches, each from a lateral shoot, and the sequence can be repeated for 1–50 generations. Banana crops represent a collection of individual plants that develop at their own rhythm and do not follow a synchronous cycle. During the first cropping cycle, plants are relatively synchronized and the canopy size reaches its maximum at flowering stage, but after four or more cropping cycles, the plant population is completely heterogeneous.

Export bananas cover nearly one million ha worldwide (FAO, 2008). Banana-cropping systems remain based on bare soil and thus use large quantities of herbicides, 3–4 kg ha^{-1} year^{-1} of herbicide active products in the French West Indies (Chabrier personal communication). Environment quality may be adversely affected by the frequent applications of these herbicides and by soil and plant management practices that may lead to severe erosion. These risks are magnified in fragile, tropical, insular conditions such as those found in Guadeloupe and Martinique, in the French West Indies (F.W.I., 14°39′48.07″N, 60°59′57.54″W), where inhabited areas, coral reefs, and rainforests are close to agro-systems (Bonan and Prime, 2001; Bocquene and Franco, 2005). This issue also concerns all areas of intensive production of banana (Matthews et al., 2003; Castillo et al., 2006; Chaves et al., 2007).

Here, we present a model-based method with a reduced number of parameters to help select cover crops in the context of banana cover-cropping systems. We developed the SIMBA-CC model that focuses on radiation interception. The model was calibrated for 11 cover crop species and used to predict their long-term growth under the banana crop canopy. These simulations served to assess, for these cover crop species, three criteria: (i) ability to cover soil and compete with weeds, (ii) ability to grow in biomass and compete with banana crops, and (iii) ability to grow continuously in the long term under the shade of the banana canopy. Finally, to maximize these criteria, we searched for the best functional traits associated with radiation interception and growth.

2. Materials and methods

2.1. Field data

We studied 11 species of cover crops from three families (*Fabaceae*, *Poaceae*, *Convolvulaceae*) that may be of interest for banana cover cropping (Table 1). These species have a wide range of growth characteristics, in terms of maximal biomass, leaf area index, nitrogen content, and optimal conditions of radiation for their growth. Within these species, some are legumes and can fix atmospheric nitrogen. Each species was grown in a plot in pure stand of 20 m^2 area. The soil was a nitisol derived from volcanic (andesitic basalt) ashes. This type of soil is characteristic of the lowlands in central Martinique, with a clay portion of 74% (loam 15%, sand 11%), with 2% of organic matter. We performed five replicates per species, located randomly over the field. The soil was plowed and prepared before sowing; it had been fallow for two years.

For all species of cover crops, we sowed on April 8, 2008 at optimal sowing density as recommended by the seed company (Table 1). These densities provided a uniform and fast growth to cover the soil. No fertilizer was added during the experiment. Irrigation was sometimes provided during the first two weeks to ensure optimal plant emergence. No irrigation was necessary after this stage because it was rainy season (827 mm during the 23 weeks of experiment). Growth conditions can be considered as optimal, without major limiting factors. For each tested species, to mimic shade increases on young banana plantations, we installed (week 17 after sowing) shading nets that provided 50% and 75% of shade on two of the five replicates. We measured dry biomass and leaf area index (LAI) 8, 13, and 22 weeks after sowing. The biomass of the entire shoot of the plant was measured using three samples of 0.625 m^2 (0.25 by 0.25 m) per plot. Aliquots of plant samples were dried in oven at 60 °C during 48 h and weighed. Another sample served to determine the LAI: we separated living leaves (green ones), scanned in black and white (two colors) all these leaves without overlapping, analyzed the proportion of black pixels corresponding to leaves, and then calculated the surface of leaves (proportion of black pixel × surface scanned). During the experiment, all climatic data (temperature, humidity, radiation, wind speed) were measured using a Campbell Scientific^{TM} meteorological station (Shepshed, UK) beside the plot at 1 m above the ground. We measured the nitrogen content of all species using the dry combustion analyzer (Flash2000, Thermo Scientific).

To validate the model, we established a dataset of cover crop biomass measured in association with banana. Banana and cover crops were planted and sown June 15, 2009 in a plot in the same soil and climatic conditions as before. Each of the five replicates included three treatments of 49 banana plants associated with *Neonotonia wightii* (NW), *Paspalum notatum* (PN), and *Pueraria phaseoloides* (PP), respectively. The five blocks were randomly distributed over the plot. Bananas were planted at a density of 1980 plants per ha and cover crops were sown at the seed density shown in Table 1. Irrigation was applied to satisfy the banana demand. Nitrogen fertilizer was applied monthly on banana plants (133 kg of N per ha and per banana-cropping cycle). We measured the cover crop biomass 8, 12, 18, 26, and 34 weeks after sowing. In the case of PN, the cover crop was mowed weeks 12, 17, and 30 after sowing.

2.2. Model description

We used the SIMBA-CC model to simulate the growth of aerial parts of the cover crops. The SIMBA-CC model is a growth model based on radiation interception and conversion to biomass. SIMBA-CC can be used alone to simulate the growth of cover-crops or related to the comprehensive SIMBA framework (Tixier et al., 2008a). When linked to SIMBA, it interacts with the nitrogen module SIMBA-N (Dorel et al., 2008), allowing simulation of the competition between the cover-crop and the banana. Here, it was used stand-alone. This simple model is suitable to study the interaction between radiation interception parameters and growth of the simulated crop and has a minimal number of biologically meaningful parameters. The SIMBA-CC model runs at a week step

Table 1
Tested species, code, family, names, and sowing density of the species of cover crops tested.

Name	Code	Family	Common name	Sowing density ($kg\,ha^{-1}$)
Alysicarpus ovalifolius	AO	Fabaceae	Alyceclover	25
Brachiaria decumbens	BD	Poaceae	Signal grass	15
Chamaecrista rotundifolia (coated)	CR	Fabaceae	Wynn cassia	20
Cynodon dactylon	CD	Poaceae	Couch grass	15
Dichondra repens (coated)	DR	Convolvulaceae	Kidney weed	20
Macroptilium atropurpureum (coated)	MA	Fabaceae	Siratro	30
Neonotonia wightii cv. Cooper	NW	Fabaceae	Glycine Cooper	15
Paspalum notatum cv. Pensacola	PN	Poaceae	Bahia grass	60
Pueraria phaseoloides	PP	Fabaceae	Puero/Kudzu	15
Stylosanthes guianensis cv. Oxley	SG	Fabaceae	Fine stem stylo	20
Stylosanthes hamata cv. Amiga	SH	Fabaceae	Caribbean stylo	20

Table 2
Description of parameters of the SIMBA-CC model; mean values were calculated on the basis of the 11 tested species of cover crops.

Parameter	Unit	Description	Mean value
PARopti	$J\,m^{-2}\,w^{-1}$	Optimal PAR radiation	67.7
P_{max}	$kg\,m^{-2}\,w^{-1}$	Biomass produced at PARopti	0.41
LTL	w	Length of tissue life	8.73
SLA	$m^2\,kg^{-1}$	Massic surface	2.89
K	–	Radiation interception parameter	0.65
PN	%	Percentage of nitrogen in tissues	2.29
LAI_{max}	$m^2\,m^{-2}$	Maximal Leaf Area Index	5.16

using radiation inputs. A week step integrates possible fluctuations within one week; it can lead to results slightly different from a day step. Here, we consider that this level of precision is sufficient for our objectives and match the time step of the SIMBA framework, making linkage easier between modules. Tables 2 and 3 describe the parameters and variables of this model. All equations are presented in Table 4. Eq. (1) presents the interception of photosynthetically active radiation of the crop at step t (PARi(t)) as a function of the radiation at step t (Rg(t)), the leaf area index of the crop at step t, and the interception parameter K. The calculation of the biomass newly formed follows a parabolic function with parameters a and b (Eqs. (2) and (3)). Eq. (4) accounts for plants with different maximal productivities (P_{max}) and with different values of optimal PAR intercepted (PARopti) (Fig. 1). The LAI follows a logistic growth, up to LAI_{max} (Eq. (5)). The growth of LAI at step t accounts for the massic surface of leaves (SLA) and the proportion of newly formed biomass allocated to shoots (Eq. (6)). Newly formed LAI is added to the LAI of the previous time step (Eq. (7)). Biomass at step t is the sum of biomass at step $t-1$ and newly formed biomass minus the tissue decay TS(t) (Eqs. (8) and (9)). The nitrogen content in the newly formed biomass is the newly formed biomass at step t multiplied by the percentage of nitrogen (Eq. (10)).

Table 3
Model variables.

Variable	Unit	Description
Rg(t)	$J\,m^{-2}\,w^{-1}$	Total radiation at step 't'
PARi(t)	$J\,m^{-2}\,w^{-1}$	Photosynthetically active radiation intercepted at step 't'
Dbiom(t)	$kg\,w^{-1}$	Biomass newly formed at step 't'
LF(t)	–	Leaf area index logistic factor
Dlai(t)	$m^2\,m^{-2}\,w^{-1}$	Leaf area index newly formed at step 't'
LAI(t)	$m^2\,m^{-2}$	Leaf area index at step 't'
BIOM(t)	$kg\,m^{-2}$	Biomass at step 't'
N(t)	$kg\,m^{-2}$	Nitrogen content in biomass at step 't'
TS(t)	$kg\,m^{-2}$	Tissue senescence at step 't'
p	–	Proportion of PAR
a; b	–	Parameters of the biomass production as a function of PARi(t)

With t the time step of the model in weeks.

Table 4
SIMBA-CC model equations; all variables and parameters are described in Tables 2 and 3.

$$\mathrm{PARi}(t) = p\,\mathrm{Rg}(t)(1-\exp(-K\,\mathrm{LAI}(t))) \quad (1)$$

$$a = \frac{P_{max} - b\,\mathrm{PARopti}}{\mathrm{PARopti}^2} \quad (2)$$

$$b = \frac{2\mathrm{PARopti}}{P_{max}} \quad (3)$$

$$\mathrm{Dbiom}(t) = a\,\mathrm{PARi}(t)^2 + b\,\mathrm{PARi}(t) \quad (4)$$

$$\mathrm{LF}(t) = \frac{\mathrm{LAI}_{max} - \mathrm{LAI}(t)}{\mathrm{LAI}_{max}} \quad (5)$$

$$\mathrm{Dlai}(t) = \mathrm{Dbiom}(t)\,\mathrm{SLA}\,\mathrm{LF}(t) \quad (6)$$

$$\mathrm{LAI}(t) = \mathrm{LAI}(t-1) + \mathrm{Dlai}(t) \quad (7)$$

$$\mathrm{BIOM}(t) = \mathrm{BIOM}(t-1) + \mathrm{Dbiom}(t) - \mathrm{TS}(t) \quad (8)$$

$$\mathrm{TS}(t) = \mathrm{Dbiom}(t-\mathrm{LTL}) \quad (9)$$

$$\mathrm{DN}(t) = \mathrm{Dbiom}(t)\,\mathrm{PN} \quad (10)$$

With t the time step of the model in weeks.

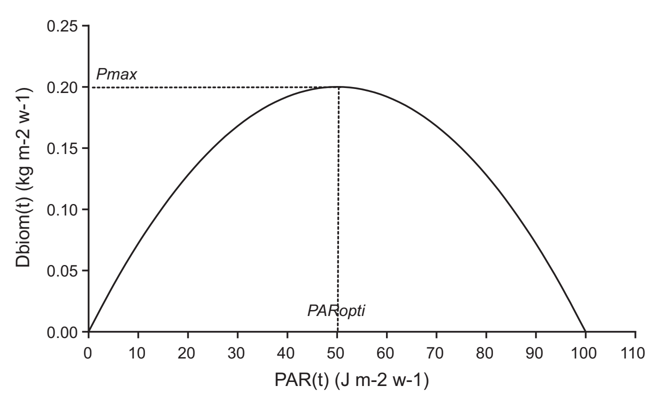

Fig. 1. Parabolic relation between biomass production at step t for a PAR intercepted at step t.

2.3. Parameter calibration and fitting

Table 2 presents the calibrated value of parameters. This calibration was performed with literature values for RSR and K; these parameters are related to plant architecture. We considered the value of similar plants in the plant database of the STICS model (Brisson et al., 2002). LAI_{max} and SLA (Table 2) were measured directly. PARopti, P_{max}, and LTL (Table 2) calibration was performed by fitting the model to field measurements. The fitting procedure consisted in searching, with an iterative procedure, for the values of the three fitted parameters in order to minimize the root mean square error (RMSE) between measured and simulated data.

2.4. Simulations

We performed calibration simulations with the radiation corresponding to the experiment, including the different levels of shading. For exploration simulations, we used the radiation profile corresponding to the radiations below the canopy of a banana field, in an area representative of the banana production area in Martinique. This radiation profile follows the development of the banana population, with the progressive un-synchronization of the banana plant stages (Tixier et al., 2004). We established this radiation profile with direct measurements of radiation under the canopy of banana plants and then extrapolated values using the LAI of banana plants, which was simulated with the SIMBA model (Tixier et al., 2008a). We performed simulations for the parameters of the 11 species of cover crops tested.

2.5. Parameter exploration

Finally, we exhaustively explored combinations of PARopti and $Prod_{max}$ parameters. In these simulations, we fixed all other parameters to mean values corresponding to a mean crop; mean values of K, LAI_{max}, LTL, PN, RSR, and SLA are presented in Table 2. We used the same radiation profile as before to be representative of under-banana-canopy conditions.

2.6. Evaluation criteria

We defined three criteria of evaluation issued from the long-term simulations. They can be considered as effect traits that represent the functions assessed. These criteria are based on the mean value of state variables in order to assess plants during critical periods. We defined:

- BIOM0-15, the mean biomass between 0 and 15 weeks after sowing. We considered this value as an indicator of the capacity of the cover crop to compete with weeds because biomass is an integrated variable that encompasses the competition for space in different strata of the canopy, for radiation, and for mineral resources.
- BIOM50-150, the mean biomass between 50 and 150 weeks after sowing. We considered this value as an indicator of the capacity of the cover crop to persist over time;
- N50-150, the sum of nitrogen necessary for newly formed biomass DN(t) between 50 and 150 weeks after sowing. We considered this value as an indicator of the demand in nitrogen of the cover crop close to steady state.

We defined thresholds for these indicators, above which their values are considered acceptable. We selected:

- 0.25 kg m^{-2} for BIOM0-15, which according to our observations is the minimal biomass to ensure fair control of weeds; in other conditions, similar biomasses necessary for weed control were observed, e.g. 0.5 to 0.7 kg m^{-2} for cover crops associated with tomato (Campiglia et al., 2010).
- 1 kg m^{-2} for BIOM50-150 because below this biomass the cover crop is negligible and can thus be considered durable under the simulated canopy.
- 0.3 kg m^{-2} for N50-150 because it is about half of the mineralization of soil organic matter during one cropping cycle, for the soil type we studied (Dorel et al., 2008). We considered this value as the maximal competition sustainable in banana fields.

Table 5
Parameter values of the tested cover crops and the RMSE (in kg of biomass per m^2) of the parameter fitting. Descriptions and units of parameters are presented in Table 2.

sp.	K	LAI_{max}	SLA	P_{max}	PARopti	LTL	PN	RMSE
AO	0.85	4.82	3.85	0.20	100	10	2.00	0.17
BD	0.50	9.69	1.77	0.50	100	8	1.65	0.26
CR	0.85	6.00	3.27	0.20	100	18	1.63	0.82
CD	0.50	5.25	1.77	0.18	44	8	1.06	0.08
DR	0.70	3.44	4.25	0.11	75	2	1.94	0.10
MA	0.50	3.84	2.20	0.16	40	4	4.12	0.05
NW	0.50	6.18	3.13	0.17	50	4	2.49	0.06
PN	0.50	6.76	4.14	0.13	43	12	0.89	0.11
PP	0.50	4.70	3.02	0.11	38	8	3.54	0.08
SG	0.85	1.97	2.26	0.90	30	14	2.71	0.11
SH	0.85	4.13	2.09	0.31	125	8	3.20	0.24

3. Results

3.1. Model calibration

We calibrated the parameters of the 11 tested species of cover crop (Table 5). The RMSE varied between 0.05 and 0.82 kg m^{-2}. Fig. 2 presents examples of simulations performed for calibration for *Brachiaria decumbens* (BD), *Cynodon dactylon* (CD), *Neonotonia wightii cv. Cooper* (NW), and *Dichondra repens* (DR, Table 1), representative of the variability of the cover crops studied in terms of functional groups: gramineous with high biomass, gramineous with low biomass, legume, and low biomass, respectively. Shading in week 17 after sowing had a strong depressive effect on BD biomass: more than 50% of the biomass with full sunlight. This effect was lower for CD and NW. There was a confusing effect of shading for DR; indeed, there was less growth for 50% shade than for 75%. CD and NW had relatively low values of PARopti (44 and 50 J m^{-2} w^{-1}, respectively), showing this plant has optimal growth under shade.

3.2. Model evaluation

Fig. 3 presents the comparison of cover crop biomass measured in cover-cropping conditions and simulated with SIMBA-CC using parameters determined above with a pure stand dataset. The model was initialized with the measured data at week 8 after sowing; the RMSE was calculated using data corresponding to 12, 18, 26, and 34 weeks after sowing. For NW, the model reproduced very well the observed pattern of biomass (RMSE = 0.022). For PP, the model overestimated the biomass, although the pattern seems to be reproduced; the RMSE is 0.145, which is sufficient precision for early screening. For PN, the model also reproduced the biomass pattern (RMSE = 0.039); it particularly took into account the relatively slow growth between week 20 and 30 after sowing. We conclude that the model is able to reproduce the pattern observed in real cover-cropping systems for three species of cover crops (one gramineous and two legume species).

3.3. Assessment of tested species

Fig. 4 presents the growth, contextualized under a banana canopy, for the 11 species of cover crops tested. The species varied widely in speed of growth and in maximal biomass reached after many months. The maximal biomass varied between 0.2 and 3.0 kg m^{-2}. Simulations showed that species with higher biomass and faster growth were more sensitive to the variation of radiation over the cropping cycle; radiation under the banana canopy decreases after harvest and then increases until the next harvest.

Fig. 5 shows the assessment of the cover crop species on the basis of competitiveness against weeds (BIOM0-15), competition with the cultivated plant (N50-150), and capacity to persist in the

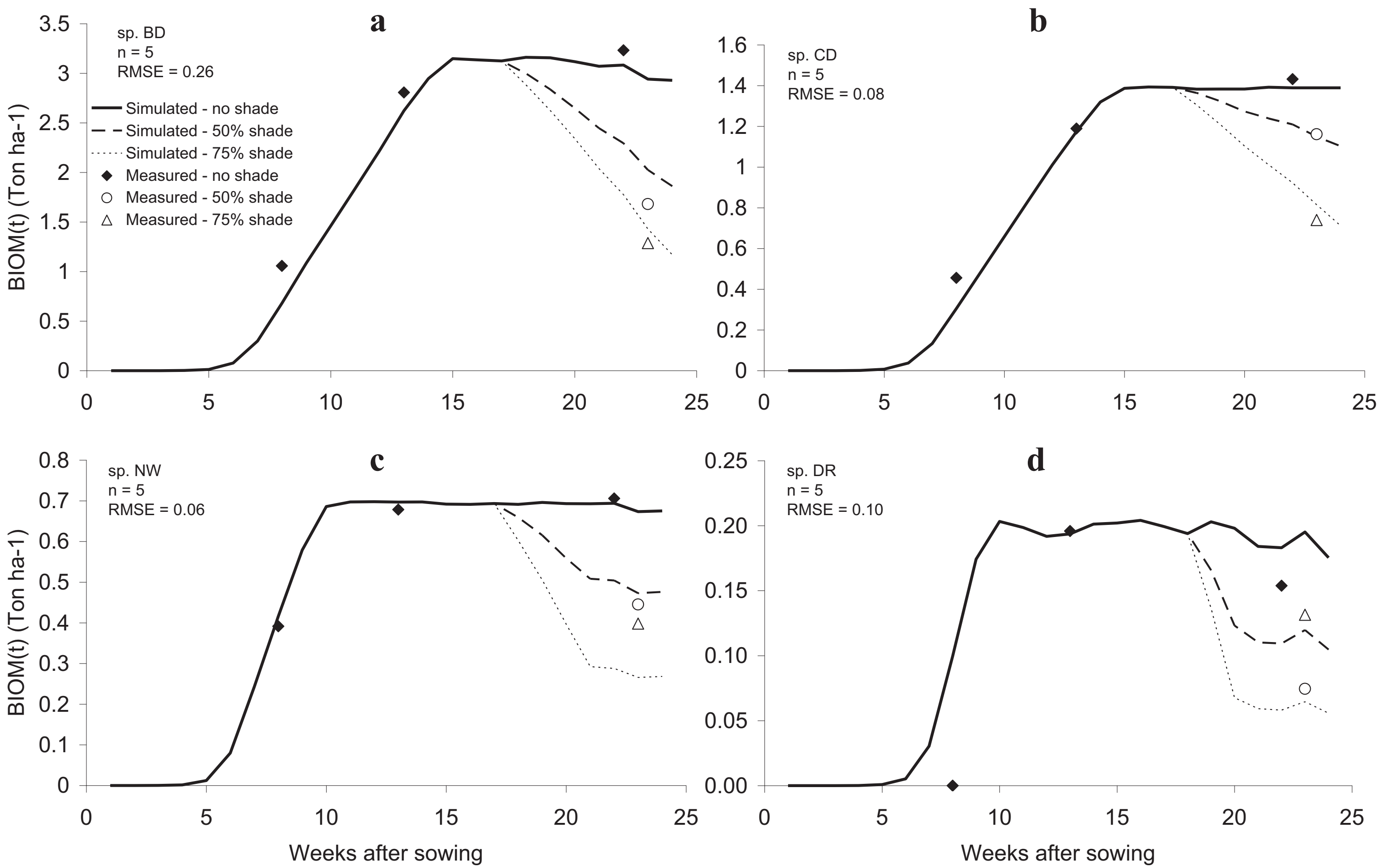

Fig. 2. Simulation of calibration for the biomass of four species of cover crops, Brachiaria decumbens BD (a) Cynodon dactylon CD (b), Neonotonia wightii NW (c), and Dichondra repens DR (d).

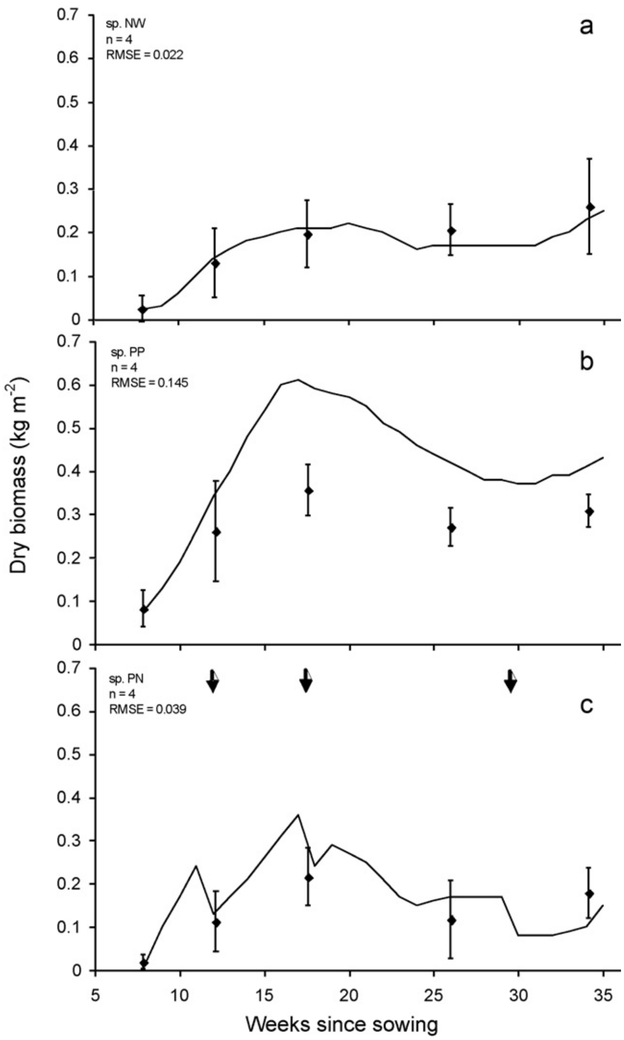

Fig. 3. Simulations and measures of the biomass of three species in cover cropping conditions, Neonotonia wightii NW (a), Pueraria phaseoloides PP (b), and Paspalum notatum PN (c). For PN, arrows show the time were the cover crop was mowed.

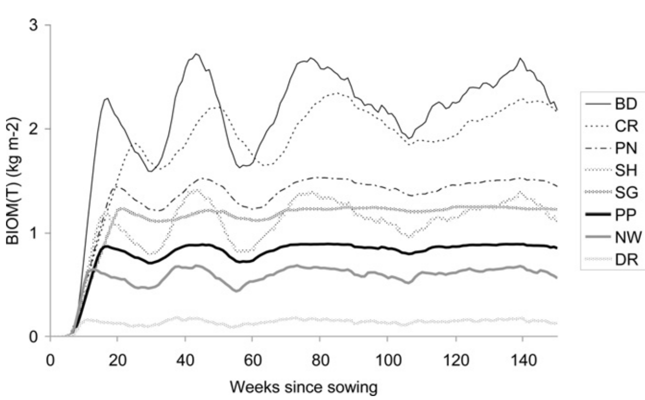

Fig. 4. Simulation of biomass dynamics of eight species of cover crops in the context of shading with banana.

simulated conditions (BIOM50-150). Fig. 5a shows that BIOM0-15 and BIOM50-150 were correlated (r^2 = 0.66, p-value = 0.0023). This correlation shows that these two indicators are not independent. Inversely, there was no relation between BIOM0-15 and N50-150 for the 11 species (Fig. 5b). Gray areas in Fig. 5a and b show the favorable ranges of BIOM0-15, BIOM50-150, and N50-150. Because of the correlation between BIOM015 and BIOM50-150, Fig. 5b is

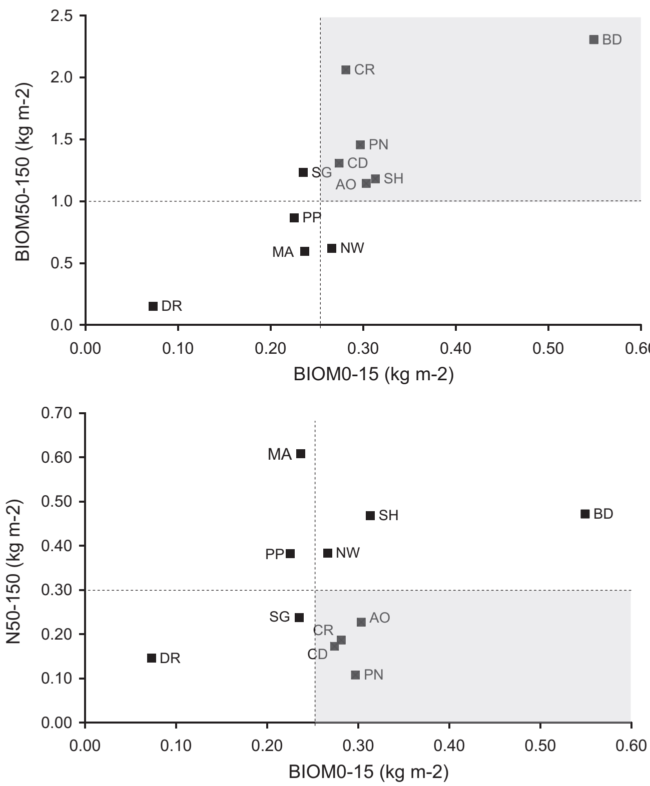

Fig. 5. Cover crop competitiveness against weeds (a) and Nitrogen demand (b) as a function of durability over time, for the 11 tested species. Dotted lines show the thresholds defined for each variable and gray area is the favorable combination of variable values.

Table 6
p-Value of the ANOVA on the three effect traits and intrinsic traits. Values in bold are significant; these correlations are presented in Appendix 1.

	LAI_{max}	SLA	P_{max}	PARopti	LTL	PN
BIOM015	**0.004**	0.122	0.369	0.238	0.443	0.496
BIOM50150	**0.031**	0.311	0.296	0.245	**0.014**	0.144
N50150	0.777	0.056	0.832	0.757	0.209	**0.006**

more informative for selecting the most suitable species of cover crops. AO, CD, CR, and PN fit the three criteria and are thus the most promising species as cover crop in banana fields in the conditions of Martinique. DR did not produce enough biomass to compete with weeds, while BD produced too much biomass, which could compete with banana crops. MA had a high N50-150, showing MA competes with banana crops. NW, PP, and SG were not very far from the thresholds we defined for the three criteria; in other radiation profiles, they could fit the criteria.

Then, we searched for correlations between intrinsic traits of the cover crops (model parameters) and effect traits in the conditions of association with banana (Table 6). Intrinsic traits are traits related to the characteristics of the crops. Effect traits are state variables of the crops, resulting from the interaction between the crop and its environment. We observed a positive correlation between LAI_{max} and both BIOM0-15 and BIOM50-150, showing that LAI_{max} plays a major role in the growth of the crop and thus its capacity to compete with weeds. Unsurprisingly, LTL (Table 2) was significantly correlated to BIOM50-150, showing that the persistence of the tissues allows better maintenance of the crop in the long term, and PN (Table 2) was strongly correlated to N50-150. More interestingly, we found no significant relation between biomass formation parameters (P_{max} and PARopti, Table 2) and evaluation traits. We did not observe any significant correlation between

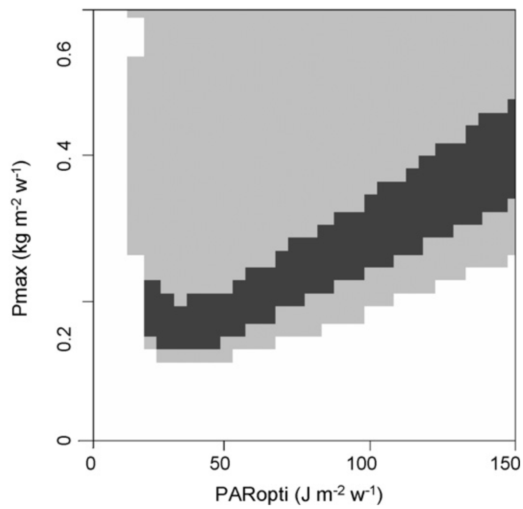

Fig. 6. Number of criteria satisfied in the biplot of maximal productivity (P_{max}) – Optimal PAR radiation (PARopti); white, gray and dark gray colors correspond to one, two, and three criteria satisfied, respectively.

intrinsic traits, showing that there was no trade-off between intrinsic traits.

3.4. Screening cover crop traits

We explored all the virtual cover crops with PARopti and P_{max} (Table 2) values ranging from 0 to 150 J m^{-2} w^{-1} and 0 to 0.6 kg m^{-2} w^{-1}, respectively. A virtual crop can be defined as a set of parameters that represents the functioning of a crop; it can correspond to existing or hypothetical species. Fig. 6 shows the number of criteria satisfied for all the combinations of PARopti and P_{max}; the dark gray area satisfies the three criteria. This gray area covers a wide range of PARopti values (from 20 to 150 J m^{-2} w^{-2}) while the P_{max} parameter is in a relatively narrow range of values (from 0.10 to 0.20 for PARopti of 20 and from 0.30 to 0.45 for PARopti of 150). This trend shows that, to satisfy the three criteria, cover crops with low PARopti values should have a moderate maximal productivity, while crops with higher values should have a higher maximal productivity.

4. Discussion

4.1. Calibration simulations. Analysis of results in terms of selection

Despite its reduced number of parameters, the SIMBA-CC model was able to simulate realistic values of biomass for a wide range of cover-crop species under very changing radiation conditions. Based on the three criteria we fixed to reduce competition with the banana crop and to maximize competition with weeds, AO, CD, CR, and PN are the most suitable species. Nevertheless, NW, SG, and PP might be suitable in other growing conditions if they achieved symbiotic fixation of nitrogen, thus reducing their N50-150 criterion; this would be possible for NW and SG, which are legumes (Lesturgez et al., 2004).

Although the SIMBA-CC model requires a very limited number of measurements to be calibrated and provides a long-term prospective evaluation, the quality of the evaluation relies on the quality of data used for calibration. For example, we observed two very distinct growths for SG and SH, which are both from the genus *Stylosanthes*. SG had a PARopti of 30 J m^{-2} w^{-1} and SH of 125 J m^{-2} w^{-1}, meaning SH grows better under high levels of radiations; this parameterization is consistent with the field observations (SH grew better under the 50% shade). Such different characteristics for two crops from the same genus are possible, but additional measurements should be carried out to verify these findings. Furthermore, in future studies some parameters such LTL could be directly measured, reducing the number of parameters to fit and thus increasing the accuracy of the model.

The validation of the model (for three species) shows that although it is a simple model, it is able to reproduce the observed patterns of biomass. A more complex model would increase the demand for parameters, which would introduce model errors and might not improve the model.

The output of the evaluation performed with SIMBA-CC should be completed by other criteria of evaluation. Here we focused on aerial growth, radiation interception, and competition for nitrogen, but other important criteria should be determined. For example, the allelopathic effect of the cover crop should not depress the cultivated crop. After the model-based selection, additional measurements should be carried out in real intercropping systems to verify these aspects.

4.2. Limit of the method

Here, we developed and used a simple model that requires only few parameters. This is consistent with our approach of early evaluation of cover crops on the basis of few field measurements. Here, we illustrated the functional trait approach, which may be extended to many other criteria of evaluation and other key processes. Future development of the model could integrate other relevant mechanisms such as phenology processes, which will require additional measurements. This is the case for the AlomySys model (Colbach et al., 2006), a heat unit-based approach for determining germination and emergence. The simple models proposed by Stilma et al. (2009) could be a suitable way to account for the additional biologically meaningful parameters (which could be directly measured in field experiments) without making the model too complex.

4.3. Relation between species' traits and prospects

The functional trait approach allows searching for an ideal combination of parameters that satisfy a set of criteria. A plant can be described with a reduced number of traits mostly linked to their dispersal, establishment, and persistence (Weiher et al., 1999). In the specific case of cover crops, these traits should be related to interactions with the cultivated crop. In this study, we proposed an approach that allows a multicriteria selection but should be completed by other criteria in future studies. There is a tight trade-off between the capacity of cover crops to compete with weeds for light and not compete with the main crop for water and nutrients.

The relation between SLA (intrinsic trait) and N50-150 (effect trait in the conditions of association with banana) (p-value = 0.056; slope = −0.104) could be linked to the amount of light absorbed by a leaf and the diffusion pathways of CO_2 through its tissues, which is generally negatively correlated to leaf thickness (Syvertsen et al., 1995; Vile et al., 2005). This trend is consistent with the observations of increased nitrogen content for higher SLA (Garnier et al., 1997). Here, the relation between SLA and N50-150 means that thick leaves are probably related to competition for nitrogen. Other correlations between intrinsic traits and effect traits in the conditions of association with banana show that cover crops with traits corresponding to more growth (LAI_{max}), more nitrogen demand (PN), and more persistence (LTL) will be better competitors for resources.

Our approach highlights the importance of choosing cover crop species to intercept radiation and to photosynthesize new biomass.

From a modeling point of view, it would be of interest to account for the architecture of the cover crop more precisely. Actually, it underlies the '*K*' parameter. In the future, mixing simulation outputs and indicators based on measurement of the architecture might improve the evaluation.

The first prospect will be to extend the validation of our method to other soil and climate areas. Prospects also include generalizing the distinction between 'response' and 'effect' traits as defined by Lavorel and Garnier (2002). These two types of traits allow separating traits that govern how the plant responds to the environmental factors and the ones that determine how the plant affects ecosystem function. For example, these two types of traits were used to link cover crop traits to ecosystem functions in scenarios including Hairy vetch as winter cover crop (Wilke and Snapp, 2008). In future modeling approaches to select cover crop species, models should account for 'effect' traits such as competition for water, which is more crucial in drier environments (Celette et al., 2005). Another prospect would be to perform *ex ante* evaluation not only of single species of cover crop but of a complex community. For this, models that are more complex should be developed, especially for inter-plant competition for resources (light, nitrogen, water). Models proposed by Duru et al. (2009) could be adapted to account for traits measured in early evaluation trials. The model selection of cover crops conducted here revealed that simple models can capture the essence of the criteria necessary to evaluate a cover crop, but further work is needed before a modeling framework can be applied in routine for the selection of cover crops intended for intercropping systems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.eja.2010.10.004.

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