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Malick S Ouattara, Anabelle Laurent, Magali Berthou, Elsa Borujerdi, Arnaud Butier, et al.. Identifying Factors Explaining Yield Variability of *Miscanthus x giganteus* and *Miscanthus sinensis* Across Contrasting Environments: Use of an Agronomic Diagnosis Approach. *BioEnergy Research*, 2022, 15, pp.672 - 685. 10.1007/s12155-021-10332-x . hal-03442398

HAL Id: hal-03442398

<https://hal.inrae.fr/hal-03442398v1>

Submitted on 10 Oct 2023

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Identifying Factors Explaining Yield Variability of *Miscanthus x giganteus* and *Miscanthus sinensis* Across Contrasting Environments: Use of an Agronomic Diagnosis Approach

Malick S. Ouattara¹ · Anabelle Laurent¹ · Magali Berthou² · Elsa Borujerdi³ · Arnaud Butier¹ · Pierre Malvoisin⁴ · Dominique Romelot⁵ · Chantal Loyce¹

Received: 2 February 2021 / Accepted: 7 September 2021 / Published online: 5 October 2021
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Abstract

Miscanthus is a perennial C4 crop whose lignocellulose can be used as an alternative to the production of biosourced material. *Miscanthus x giganteus* (*M. x giganteus*) has demonstrated high maximum yields but also high yield variability across farmers' fields. *Miscanthus sinensis* (*M. sinensis*) can be an alternative to *M. x giganteus* because it is considered to be more tolerant to water stress and to produce more stable yields. This study aimed to identify the main factors explaining the variability of yields across site-years for *M. x giganteus* and *M. sinensis*. A multi-local and multi-year trial network was set up in France (Ile de France and Center regions). Four treatments were established on seven sites, from spring 2013 to winter 2019: at each site, two treatments of *M. x giganteus* (a treatment from rhizome and a treatment from rhizome-derived plantlets) and two treatments of *M. sinensis* (a treatment from seed-derived plantlets established in single density and a treatment from seed-derived plantlets established in double density). We experienced 5 years of harvest because miscanthus was not harvested in 2014. First, we characterized yield variations across site-years for both genotypes. Second, we defined and calculated a set of indicators (*e.g.*, water stress indicator, sum of degree-days of the previous year, number of frost days) that could affect miscanthus yields. Finally, we performed a mixed model with re-sampling to identify the main indicators that explained yield variability for each genotype specifically. Results showed that water stress and crop age mainly explained yield variability for both genotypes. *M. sinensis* yields were also affected by the sum of degree-days of the previous year of growth. Hence, genotype choice must take into account environmental characteristics. *M. sinensis* could indeed achieve higher and more stable yields than those of *M. x giganteus* in shallow sandy soils or in locations with a higher risk of low rainfall.

Keywords Miscanthus · Yield variability · Indicator of limiting factor · Water stress · Mixed model

Introduction

Miscanthus x giganteus (hereafter named *M. x giganteus*) is a perennial C4 grass with a growing period of 15–20 years and yields progressively increasing every year during the first years of growth [1]. Introduced into Europe from Japan in 1930, it is now cultivated across the continent [2]; it reaches a high potential biomass production, from 10 to 25 t ha⁻¹ of dry matter, in experimental conditions [1]. *M. x giganteus* is therefore the only genotype now cultivated in European farmers' fields [2]. However, using a single clone presents some disadvantages, such as loss of genetic diversity, or risks of pest and disease development in the future. To date, no miscanthus pest or disease control is required for miscanthus production in Europe [3].

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Yield variability of *M. x giganteus* that takes sites and years into account together has reached 73%: Alexopoulos et al. [4] indeed obtained a yield variability with a cv amounting to 31% of *M. x giganteus* at a site in Italy over a period of 24 years, and Ouattara et al. [5] showed that yields of *M. x giganteus* were variable (with a coefficient of variation ranging from 64 to 73%) between 2013 and 2019 on six sites in France. Yield variability has been shown to be greater in clayey soils than in sandy and loamy soils (37% vs. 10% in 22 sites field experiments of *M. x giganteus* with growth years greater than or equal to 5 years) because *M. x giganteus* is noticeably slower to establish in clayey soils [6]. In addition to soil effect, climatic conditions have a significant effect on *M. x giganteus* [7], which is sensitive to low temperatures and water availability [1, 8].

Miscanthus sinensis (hereafter named *M. sinensis*) is more tolerant to water stress and frost [1, 7, 8], which allows it to be suited to a broader range of soil and climatic conditions. *M. sinensis* achieves lower yields than *M. x giganteus* but is less variable across different sites and years [5, 6]. It could therefore be an alternative to *M. x giganteus* on less favorable sites.

Several studies have been conducted on factors that could impact *M. x giganteus* yields [1, 9]. To our knowledge, *M. sinensis* has received little attention in the literature, while research is mostly focused on *M. x giganteus* because of its higher yield. Yet under stressed environmental conditions, *M. sinensis* could achieve higher yields [9]. Today, almost all commercial production of miscanthus is based on the *M. x giganteus* genotype alone [3, 10]. In addition, there are not many studies that have been conducted under field conditions to determine which genotype would be best suited to contrasting environmental conditions. Few studies have been carried out to identify some factors affecting the yields of *M. x giganteus* and, to a lesser extent, *M. sinensis* [11–14].

It is therefore necessary to specifically identify the factors that could explain the yield variability of each genotype across site-years. Factors explaining yield variability could differ between *M. x giganteus* and *M. sinensis* [7], as *M. sinensis* is more tolerant to water stress and to frost. Mineral nutrition could also explain this variability in yields of the two genotypes. It is known that miscanthus is a crop with low nitrogen requirements [10] but nutrients like P and K could be interesting to assess for explaining yield variability. This last aspect will not be studied in this paper.

An agronomic diagnosis [15–18] was used in this study to identify and assess the main limiting factors explaining the variability of *M. sinensis* and *M. x giganteus* yield under field conditions, and across several pedo-climatic conditions in France. This would in turn support the identification of potential actionable levers to overcome the limiting factors.

Material and Methods

A Multi-Environment Experimental Network

A multi-environment experimental network was set up on seven sites in France from 2013 to 2019: six sites in the Ile de France region and one site in the Center region. The trial network was characterized by different types of soils, with various textures, depths, and stoniness (Table 1). Trials were either located on agricultural lands, *i.e.*, lands that were cultivated with annual crops before carrying out the experiment (Bioferme and La Bondue sites), or on marginal lands, *i.e.*, lands that were previously maintained as set-aside land, mainly because they were located between several roads/highways and were therefore difficult to get to with agricultural equipment, such as the Marne et Gondoire site. The range of maximum soil water content (SWC_{max}) of these sites is wide, from 72 mm for La Bondue site to 317 mm for the Bioferme site (Table 1). Lastly, annual mean temperatures from March 25th to October 15th ranged from 14.7 to 18.4 °C across years.

The preceding crop before setting up the trials was a set-aside field at the Subdray site. Since 1992, La Bondue and Episy sites had been maintained as set-aside lands. The Marne et Gondoire and Evry sites had also been maintained as set-aside lands since 2003 and 2005, respectively. The preceding crop was winter barley (*Hordeum vulgare*) for the Bioferme and Chanteloup sites (Table 1).

We located the growth cycle of miscanthus between March 25 (regrowth or emergence in the first year) and October 15 (beginning of senescence). Climatic parameters were assessed over the period corresponding to the cycle before its senescence.

Climatic conditions followed the same trend throughout the trial network with little variation across sites, except for the rainfall recorded at Chanteloup (between 300 and 400 mm), which was lower than for the other sites in the Ile de France region and less variable across years compared to the other sites of the trial network (Fig. 1). In 2015 and 2018, rainfall was lower over the entire network, except for the Chanteloup and Marne et Gondoire sites in 2018. The climatic water balances (rainfall minus potential evapotranspiration) of these two years, *i.e.*, 2015 and 2018, were also the lowest ones. Lastly, the Subdray sites recorded the highest climatic water deficits in 2015 (−435 mm) and 2018 (−582 mm).

Treatments

Each trial of the multi-environment network was composed of four strips, with an area of 141.4 m² (27.2 m × 5.2 m)

Table 1 Main characteristics of the site-years

Sites	Lat. and long	Soil texture (0–30 cm)	Rooting depth (cm)	PS (%)	Preceding crop	SWC _{max} (mm)	Year	PAR ¹ (MJ/m ²)	T ¹ (°C)
La Bondue	48° 19' 20" N, 3° 2' 13" E	Sandy clayey loam	78.5	48	Set-aside	72	2013	1643	14.7
							2014	1638	15.4
							2015	1737	15.7
							2016	1546	15.5
							2017	1688	15.4
							2018	1784	17.1
Episy	48° 21' 37" N, 2° 49' 36" E	Clayey sand	75	19	Set-aside	78	2013	1643	14.7
							2014	1638	15.4
							2015	1737	15.7
							2016	1546	15.5
							2017	1688	15.4
							2018	1784	17.1
Evry	48° 51' 7" N, 1° 59' 6" E	Clayey sandy loam	81.5	37	Set-aside	96	2013	1562	15.1
							2014	1662	15.7
							2015	1739	15.7
							2016	1558	15.6
							2017	1709	15.5
							2018	1792	17.4
Subdray	47° 1' 50" N, 2° 19' 52" E	Loamy sandy clay	48	18	Set-aside	105	2013	1647	16.1
							2014	1744	16.7
							2015	1778	16.7
							2016	1635	16.0
							2017	1779	17.0
							2018	1849	18.4
Marne et Gondoire	48° 51' 58" N, 2° 39' 45" E	Clayey sandy loam	77.5	15	Set-aside	131	2013	1583	15.4
							2014	1555	16.1
							2015	1466	16.2
							2016	1546	16.3
							2017	1688	16.8
							2018	1784	17.8
Chanteloup	48° 57' 46" N, 2° 2' 11" E	Sand	102	15	Winter barley	149	2013	1526	15.3
							2014	1553	15.8
							2015	1667	15.7
							2016	1478	15.8
							2017	1608	16.3
							2018	1811	17.3
Bioferme	48° 21' 17" N, 3° 1' 57" E	Clayey sandy loam	142	0	Winter barley	317	2013	1643	14.7
							2014	1638	15.4
							2015	1737	15.7
							2016	1546	15.5
							2017	1688	15.4
							2018	1784	17.1

PS proportion of stones in volume over the rooting depth, SWC_{max} maximum soil water content, PAR photosynthetically active radiation, T temperature

¹Average of daily value between March 25 and October 15

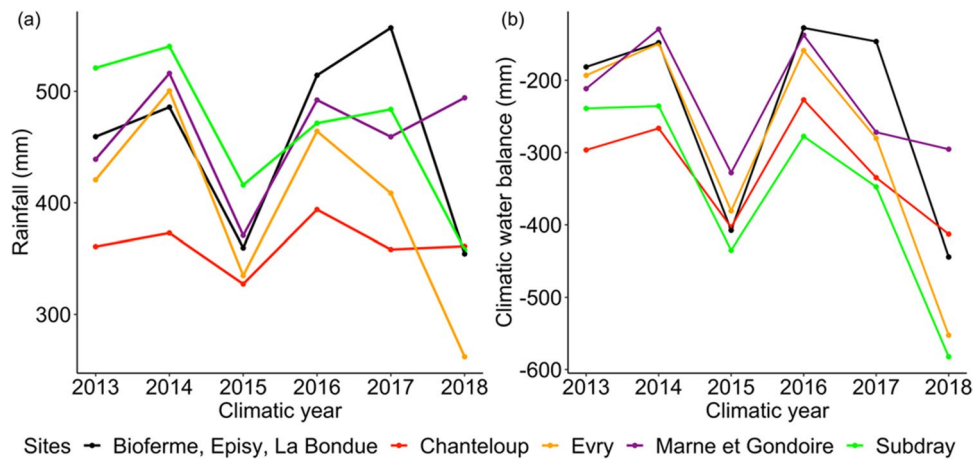


Fig. 1 Rainfall (mm) (a) and climatic water balance, *i.e.*, rainfall minus potential evapotranspiration (mm) (b), covering the growth cycle of miscanthus (*i.e.*, from March 1 to October 15) from 2013 to 2018. For the Bioferme, Episy, and La Bondue sites, we used the meteorological data of Nangis because these sites are close to one

another. The weather data used originated from meteo France and from the French National Institute for Agriculture, Food, and Environment (INRAE) on-line platform CLIMATIK (https://intranet.inra.fr/climatik_v2/ClimatikGwt.html)

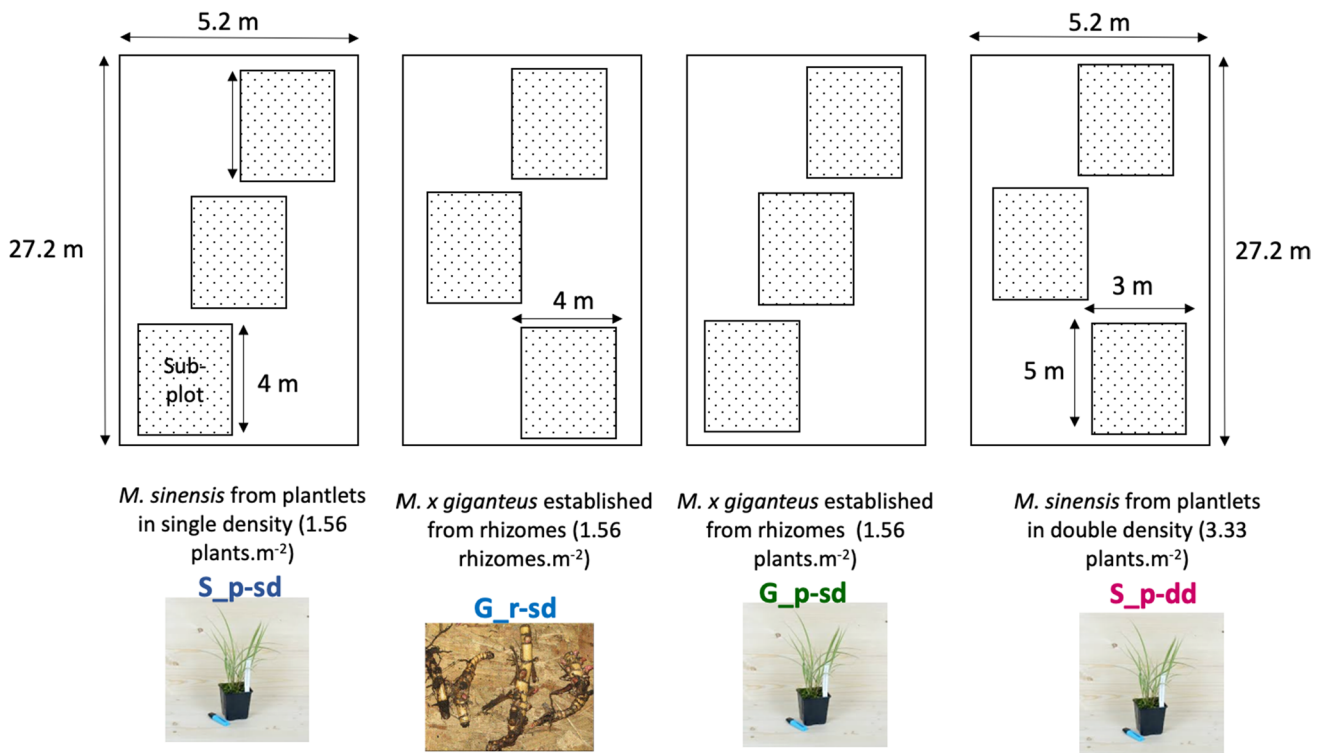


Fig. 2 Experimental design setup on each site. G_r-sd: *M. x giganteus* established from rhizomes. G_p-sd: *M. x giganteus* established from plantlets. S_p-sd: *M. sinensis* K1399 established from plantlets at sin-

gle density. S_p-dd: *M. sinensis* K1399 established from plantlets at double density

for each strip (Fig. 2). Four treatments were established (one per strip): two treatments with *M. x giganteus* established from rhizomes (G_r-sd) or from plantlets (G_p-sd) and two treatments with *M. sinensis* K1399 (population

variety whose seeds were provided by Wageningen University & Research) from plantlets in single (S_p-sd) and double (S_p-dd) density, *i.e.*, 3.33 plants per m² instead of 1.56 plants per m². Seedlings were raised in greenhouses

before transplanting [5]. To summarize, 4 treatments of *M. x giganteus* and *M. sinensis* were carried out under 7 sites \times 5 years of harvest. However, the G_p-sd treatment was not successfully established at the Chanteloup site, which led to the loss of this treatment from the start of the experiment.

Three sub-plots were positioned on each treatment after the establishment phase. For single density (G_r-sd, S_p-sd, G_p-sd), five rows and five plants per row were selected for a plot area of 16 m² (distance between plants and between rows: 0.8 m). For the double density (S_p-dd), the plot area was 15 m² with five rows and ten plants per row (distance between plants: 0.5 m; distance between rows: 0.6 m) (Fig. 2).

Yield Measurements

Yields had been measured every year in February–March for the three sub-plots of each treatment, from 2015 to 2019, before harvesting the whole trial. Miscanthus was not harvested the first year (2014); the aboveground biomass was chopped and left on the soil surface. The following years, miscanthus was harvested in late winter (*i.e.*, in February or March) either using a manual cutting tool (brushcutter) (Chanteloup, Subdray, Marne et Gondoire, and Evry sites) or with a silage harvester (Bioferme and Episy sites). To assess yields, we considered only shoots higher than 1 m. Shoots were cut 15 cm from the ground. The fresh matter of the biomass (FM) was immediately weighed using a scale. A sub-sample of 1.5 to 2 kg of fresh matter (FW) was taken and then put in the oven for 48 h at 80 °C and weighed to get its dry weight (DW). The following equation was used to calculate the yield in t of DM per ha:

$$Y = \frac{FM \times \frac{DW}{FW} \times 10}{A}$$

where Y is the yield (t.ha⁻¹ of DM), FM is the fresh matter of the sub-plot (kg), FW is the fresh weight of the sub-sample (kg), DW is the dry weight of the sub-sample (kg), and A is the sub-plot area (m²).

These measurements were fully described in [5].

Identification of Candidate Indicators Explaining Yield Variations Across Sites

Choice and Calculation Method of Candidate Indicators

Age Since miscanthus is a perennial crop with yields that increase every year during the first years of growth, variability in yields could be related to the age of the crop. This indicator is expressed in years.

Initial Aerial Biomass (IAB) The amount of aerial biomass after the first year of growth provides information on the initial conditions for crop startup, which could affect the evolution of yields in the following years. The initial aerial biomass was chopped the first year (in February–March 2014) and left on the soil as a mulch. To assess initial aerial biomass (IAB), 10 plants inside each strip (treatment) but outside the sub-plots were selected to avoid disturbing the sub-plots, cut at 15 cm from the ground, and weighed (SW_s). Shoot numbers have been counted (SN_s) for these 10 plants. A 2–3-kg sample was put in the oven at 80 °C for 48 h to determine the dry matter (DM). The number of plants on each sub-plot was counted (SN_p) and the yields measured in kg.m⁻². The sub-plot area (A_p) was 15 or 16 m². We multiplied by 10 the formula described below to express the aerial biomass in t.ha⁻¹. The aerial biomass produced during the first year was obtained as follows:

$$IAB = \frac{SW_s}{SN_s} \times \frac{SN_p}{A_p} \times \frac{DM}{100} \times 10$$

with IAB : initial aerial biomass the first year of production (t.ha⁻¹ of DM)

SN_s : shoot number per m² of the sample

SW_s : shoot weight of the sample (kg)

SN_p : shoot number of the sub-plot (kg)

A_p : area of the sub-plot (m²)

DM : dry matter (%)

Water Stress Indicator (Ks) The calculation of the water stress indicator (Ks) was carried out from March 25 to October 15. This indicator was previously assessed and used by [17]. The water stress indicator (Ks) ranged from 0 to 1. When the crop was not water-stressed, Ks was equal to 1 and when it was stressed, it was lower than 1. The maximum soil water content (SWC_{max}) was calculated by the Gras method [19] and was a function of soil texture and rooting depth of *M. x giganteus* and *M. sinensis* for each site. Water balance was initialized on March 1 of the growth year, assuming that SWC_d on that date was equal to SWC_{max} (*i.e.*, the soil was at field capacity). SWC_d is calculated as follow:

$$SWC_d = SWC_{d-1} + P_d - AET_d$$

where SWC_d is the daily soil water content (mm), SWC_{d-1} is the previous day soil water content (mm), P_d is the daily precipitation (mm/day), and AET_d is the actual daily evapotranspiration (mm/day).

$$AET_d = Ks_d \times Kc_d \times PET_d$$

where PET_d is the daily potential evapotranspiration, Kc_d is the daily crop coefficient defined as a function of degree-days [20] and using data from the French multisite experimental network REGIX and information about Kc of

sugarcane as defined by the FAO [21] and ranged from 0.4 to 1.18, and Ks_d is the daily water stress indicator.

If $SWC_d > 2/3 \times SWC_{max}$, then $Ks_d = 1$, else $Ks_d = SWC_d / SWC_{max}$

$$Ks = \frac{1}{n} \sum_{d=1}^n Ks_d$$

where n is the number of days and Ks is the average water stress indicator.

The Number of Frost Days (FD) This indicator aims to identify the effect of frost on crop regrowth and therefore on yields. Miscanthus is sensitive to frost during crop regrowth. Miscanthus base temperature for regrowth is 6 °C for *M. x giganteus* [22] and 5 °C for *M. sinensis* [23]. The number of frost days (FD) corresponds to the number of days spent by the crop under minimum temperatures below 0 °C. The choice of 0 °C is based on the work of [24]. FD is calculated from April 1 to May 30 for *M. x giganteus* and from March 15 to May 30 for *M. sinensis*.

The Sum of Degree-Days (DD) of the Previous Year Miscanthus has a “memory effect” between two successive years of growth: when this crop reaches the end of its development cycle for a given year of growth, it transfers nitrogen from the aerial parts to its rhizomes. It then reuses the nitrogen stored in the rhizomes to start its regrowth the following year [25, 26]. Hence, a sufficient sum of degree-days must be accumulated by the crop to complete its cycle. The following year, the vegetation regrowth could then benefit from a satisfactory N remobilization from the aerial biomass to the rhizome [26]. The sum of the degree-days was calculated as the difference between the average daily temperature and the base temperature of the crop. The calculation of the sum of degree-days was obtained as follows:

$$DD = \sum_{d=1}^n (T_d - T_0)$$

where n is the number of days, DD is the sum of degree-days (°C), T_d is the daily mean temperature (°C), and T_0 is the base temperature of the crop (°C).

The base temperature (T_0) of *M. x giganteus* is 6 °C [22]. A base temperature of 5 °C was used for *M. sinensis* [23].

Statistical Analysis

First, we performed a principal component analysis (PCA) using the software R version 4.0.2 [27] between the different candidate indicators to detect possible correlations

that could lead to confounding effects between candidate indicators.

Second, we used the mixed-model approach [28] to identify indicators that explain variability in yields across sites. This method assesses all possible linear combinations between the yield and candidate indicators. It allowed us to rank the importance of each indicator on yield variability through the Akaike weight. For each genotype (*M. x giganteus* and *M. sinensis*), all the possible linear combinations were performed as follows:

$$Y_i = \mu + \alpha_1 x_{1,i} + \dots + \alpha_p x_{p,i} + e_i$$

where the explained variable Y_i is the yield of the miscanthus (t.ha⁻¹ of DM) for the i^{th} site, $x_{1,i}, \dots, x_{p,i}$ are the explanatory variables (*i.e.*, Age, IAB, Ks, FD, DD) for the i^{th} site, μ is the global average of the explained variables, and $\alpha_1, \dots, \alpha_p$ are the parameters associated with the explanatory variables. Y_i is assumed to follow independent Gaussian distribution with mean and constant variance σ^2 . $e_i \sim N(0, \sigma^2)$. The mixed-model method [28] was used to select the explanatory variables $\times 1, \dots, xp$ and to estimate the model parameters $\alpha_1, \dots, \alpha_p$. We used the package MMIX [29] to implement this method.

The calculation of the Akaike weight (w_i) was based on the models which have a high predictive value, *i.e.*, with the lowest AIC (Akaike Information Criteria) [30]. It was calculated as follows:

$$w_i = \frac{e^{-0.5(AIC_i - AIC_{min})}}{\sum_{i=1}^n e^{-0.5(AIC_i - AIC_{min})}}$$

where w_i is the Akaike weight obtained for the i^{th} combination explanatory variables, AIC_i is the AIC value for the corresponding model, AIC_{min} is the smallest AIC obtained for all possible model combinations, and n is the number of possible models.

The Akaike weight w_i is the probability that, given a set of models, model i is the best AIC model. The relative importance of each explanatory variable is estimated, *i.e.*, the sum of the Akaike weights of all models where this explanatory variable is present. The higher the sum of the Akaike weight was, the more important the considered explanatory variable was [28]. All the explanatory variables can be ranked according to their importance following the sum of the Akaike weight. The Akaike weight ranged from 0 to 1.

The next step was to assess the stability of the mixed-model results using the bootstrapping method, as described by [17]. The bootstrap allows us to see if a change in our initial data set leads to a change in our results. If the results obtained after the bootstrap are the same or vary very little from the initial results, our results will be robust. Throughout the bootstrap, we generated new data sets based on the initial data set, *i.e.*, the database with all indicators for each

treatment, each species, and for all sites. A total of 10,000 bootstrap samples were generated by random sampling with replacement. We then recalculated the Akaike weight to assess the uncertainty of the selection method. For each explanatory variable, the frequency of selection, the mean of the estimated parameter values, and the standard deviation of the estimated parameter values were calculated. For a given variable, a high selection frequency combined with a low standard deviation indicates that results are stable. A selection frequency close to 0 or 1 means that the results are stable, while a frequency close to 0.5 indicates an instability in the selection of variables.

Finally, we performed a simple linear regression between yields and the candidate indicators that had been identified by the mixed model as indicators explaining the variability of yields for *M. sinensis* and *M. x giganteus*. This regression was performed according to the following formula:

$$Y_i = \mu + \alpha_1 X_{i,1} + \dots + \alpha_n X_{i,n} + e_{i,ei} \sim N(0, \sigma^2)$$

where Y_i is the yield in $\text{t}\cdot\text{ha}^{-1}$, for the i^{th} site, X_i is the indicators (*Age*, *Ks*, *FD*, *IAB*, and/or *DD* depending on

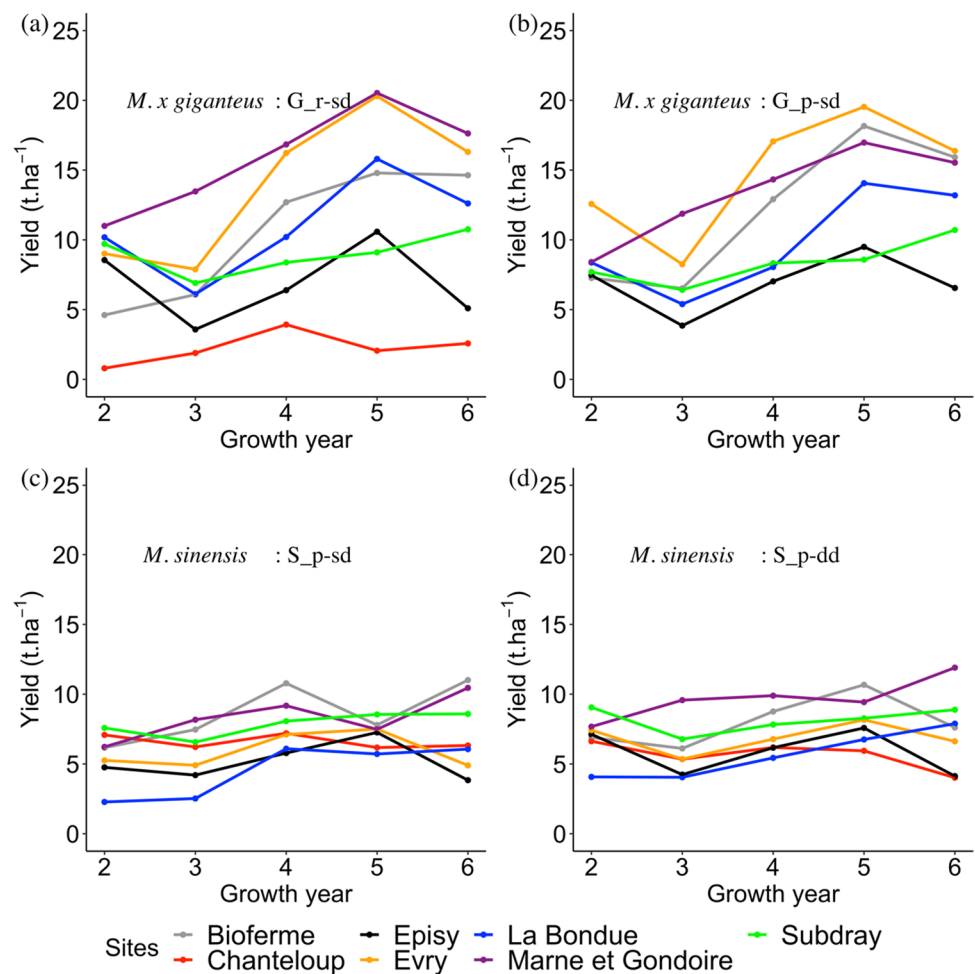
mixed-model results) for the i^{th} site, n is the number of explanatory variables considered and is between 1 to 5, μ is the global average of the explained variable, and α is the parameter associated with the explanatory variables. Y_i is assumed to follow independent Gaussian distribution with mean and constant variance. This regression allowed us to estimate which part of the total yield variability the selected indicators explained (through the R^2 value).

Results

Yield Variability Across Site-Years

Yields of *M. x giganteus* and *M. sinensis* varied across site-years (Fig. 3). Site-year variability was greater for *M. x giganteus* (coefficient of variation amounted to 54% and 40% respectively for G_r-sd and G_p-sd) than for *M. sinensis* (coefficient of variation amounted to 30% and 27% respectively for S_p-sd and S_p-dd). Yields tended to increase with the age of the crop, especially for *M. x giganteus* (Fig. 3a, b). Yield trends of G_p-sd treatment in Chanteloup site are

Fig. 3 Yields trends across site-years for *M. x giganteus* (a, b) and *M. sinensis* (c, d). G_r-sd: *M. x giganteus* established from rhizomes. G_p-sd: *M. x giganteus* established from plantlets. S_p-sd: *M. sinensis* K1399 established from plantlets at single density. S_p-dd: *M. sinensis* K1399 established from plantlets at double density



missing because the establishment of this treatment did not succeed, as mentioned above (Fig. 3b).

For *M. x giganteus*, G_r-sd treatment yields ranged from 0.8 to 20.5 t.ha⁻¹ with an average of 9.9 t.ha⁻¹ and yields of G_p-sd treatment ranged from 3.8 to 19.5 t.ha⁻¹ with an average of 10.9 t.ha⁻¹ (Fig. 3a, b). Average yields of *M. sinensis* treatments were respectively of 6.7 t.ha⁻¹ and 7.1 t.ha⁻¹ for S_p-sd and S_p-dd. S_p-sd yields ranged from 2.27 to 11.01 t.ha⁻¹ and that of S_p-dd from 4 to 11.9 t.ha⁻¹ (Fig. 3c, d).

Yields and yields of the preceding year of both genotypes were correlated, except for the growth year 2 of *M. x giganteus* (Fig. 4). For a perennial crop such as Miscanthus, an interpretation of that correlation could be that yields could be significantly affected by yields of the previous year. Another interpretation could be that miscanthus experienced the same limiting factors on the same site (due to soil characteristics for instance) from a year to another. This correlation was found to be stronger for growth year 2 ($R^2=0.51$), growth year 3 ($R^2=0.40$), and growth year 4 ($R^2=0.72$) (Fig. 4b) for *M. sinensis* and growth year 4 ($R^2=0.82$), growth year 5 ($R^2=0.84$), and growth year 6 ($R^2=0.66$) for *M. x giganteus* (Fig. 4a).

Relationships Between All Candidate Indicators

The principal component analysis showed that the candidate indicators were not correlated with each other: the risk of confounding effects between indicators is therefore low (Fig. 5).

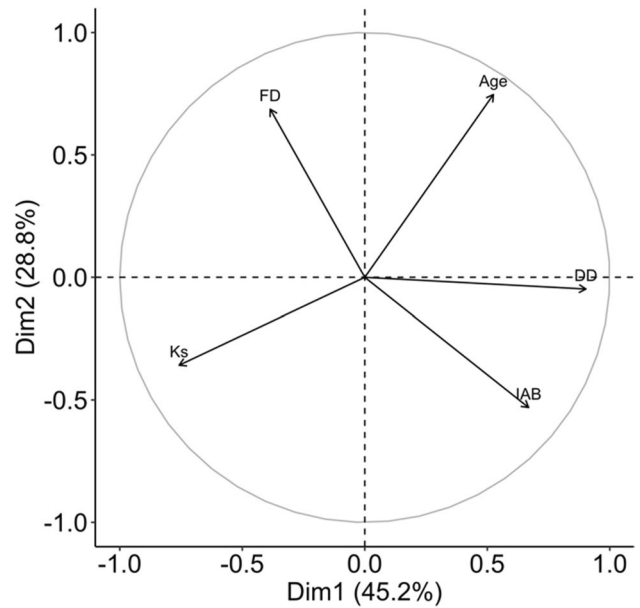


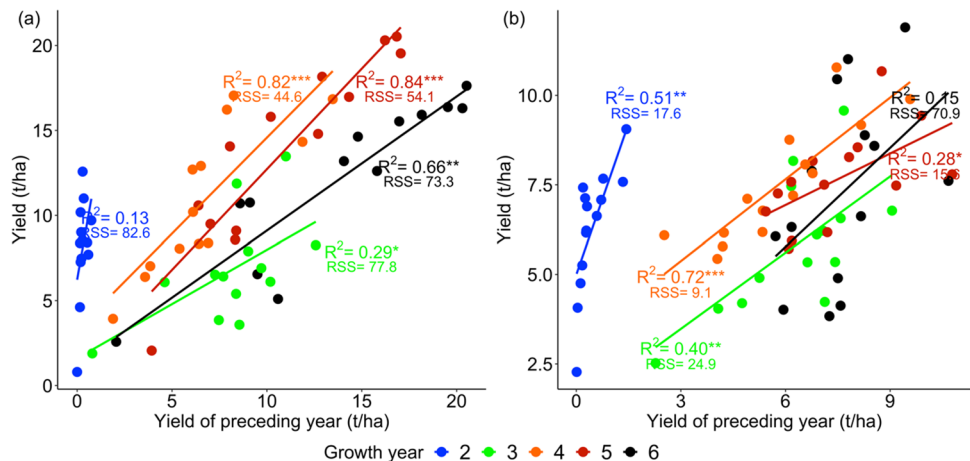
Fig. 5 Principal components analysis between the candidate indicators. FD: frost days, Age: age of cultivation, DD: sum of degree-days of previous year, IAB: initial aerial biomass, Ks: water stress indicator

Identification of Indicators Explaining Yield Variability for Each Genotype

Indicators Explaining *M. x giganteus* Yield Variability

The sum of Akaike weight (w_i) before the bootstrap showed that age (0.99) and water stress indicator K_s (0.99) mostly explained the variability in yields across site-years. This result was robust after implementing the bootstrap procedure, *i.e.*, when the data set was modified. The sum of Akaike weight did not change or changed slightly (it was equal to 0.99 and 0.93 for age and K_s respectively, and the

Fig. 4 Relationship between the yields of the preceding growth year and the yields of the current growth year for *M. x giganteus* (a) and *M. sinensis* (b) from the second growth year to the fifth growth year. RSS: residual sum of squares. *** p -value < 0.001, ** p -value < 0.01, * p -value = 0.05



other candidate indicators still had a lower sum of Akaike weights).

Parameter values (Table 2) showed that yields increased with K_s . Years 3 and 6 experienced the highest water stress, with K_s values lower than 0.7 (Fig. 6). Once we take into account this effect of K_s , we also observed in Fig. 6 that yield of miscanthus increased with the age of the crop, as shown in the parameter values in Table 2. When we performed a simple linear model with the crop age and the water stress indicator, we explained 31.9% yield variation across site-years ($R^2=0.32$).

Indicators Explaining *M. sinensis* Yield Variability

The age of the crop (*Age*), the sum of degree-days in the previous growth year (*DD*), and the water stress indicator (K_s) best explained the inter-site and interannual variability of *M. sinensis* yields (Table 3). The sum of Akaike weight values was similar (for *Age* and K_s) or only slightly changed after the bootstrap (for *DD*), which indicated that the results were robust when the data set was modified.

Our results showed that *M. sinensis* was sensitive to water stress. The lowest yields of *M. sinensis* are obtained for low K_s values (Fig. 7a). The years that experienced lower average yield were year 3 (5.82 t.ha⁻¹) and year 6 (7.3 t.ha⁻¹), which were also the years with the highest water stress (Fig. 7a).

The sum of the degree-days of the previous growth year also explained yield variations of *M. sinensis*: yields of *M. sinensis* increased when the sum of degree-days of the previous year was high (Fig. 7b). The lowest yields were obtained for *DD* values ranging from 2100 and 2300 °C.

A yield can be high while being considered in a stressed condition for an indicator. At this point, it is necessary to relate it to other indicators to explain its position. For example, when we look at the red dots at the top for *DD* (Fig. 7b),

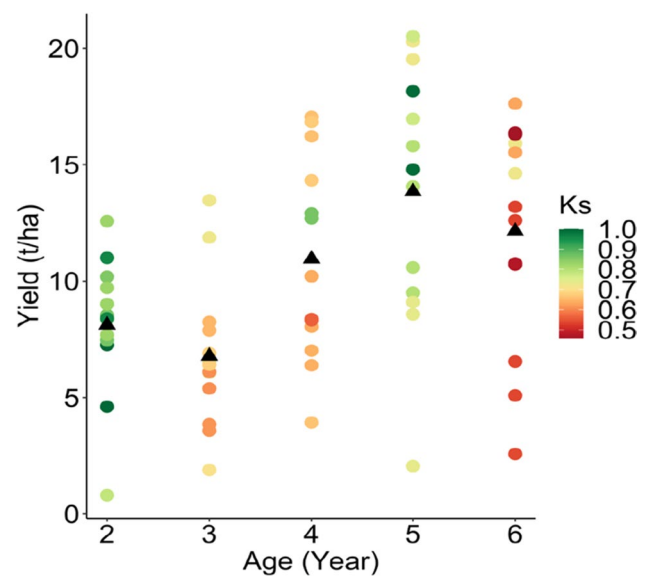


Fig. 6 *M. x giganteus* yields as a function of crop age for different values of water stress indicators (K_s). The black triangle is the average yield

the same dots are green on the K_s figure (Fig. 7a). Therefore, these yields were negatively impacted by *DD* but these dots were under good water conditions which explains their presence at the top of the *DD* figure.

When we implemented a simple linear model with the crop age, the water stress indicator, and the sum of degree-days, we explained 49.9% of yield variations across site-years ($R^2=49.9$).

Finally, under stress conditions (*i.e.*, for years 3 and 6 that were impacted by K_s and *DD*) yield losses of *M. x giganteus* (17% and 37% respectively for years 6 and 3) were higher than for *M. sinensis* (5% and 15% respectively for yields 6 and 3). The parameter estimations (and the associated

Table 2 Effect of candidate indicators on yields of *M. x giganteus*. Results from the mixed model (before and after bootstrapping)

Candidate indicators	Estimate	SD	Sum of w_i	
			Before bootstrap	After bootstrap
<i>IAB</i>	4.47	4.50	0.68	0.65
<i>Age</i>	2.38	0.46	0.99	0.99
K_s	15.25	4.79	0.99	0.93
<i>FD</i>	-0.09	0.25	0.36	0.47
<i>DD</i>	-0.00	0.01	0.33	0.48

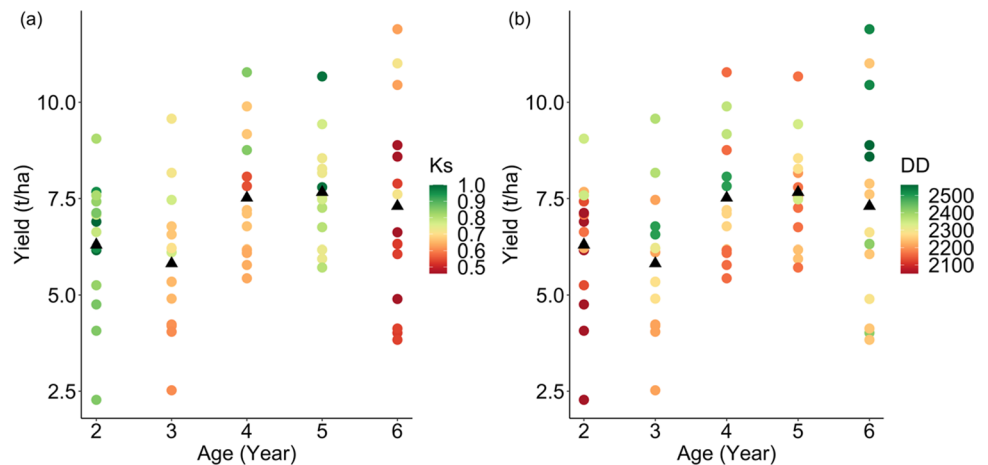
w_i Akaike weight, *SD* standard deviation, *IAB* initial aerial biomass of the first growth year, *Age* age of the crop, K_s water stress indicator, *FD* number of frost days, *DD* sum of degree-days of the previous year of growth. The estimates of the different indicators represent the coefficients of the linear relationship between them and the yield

Table 3 Effect of candidate indicators on yields of *M. sinensis*. Results from the mixed model (before and after bootstrapping)

Candidate indicators	Estimate	SD	Sum of w_i	
			Before bootstrap	After bootstrap
<i>IAB</i>	0.27	0.41	0.32	0.41
<i>Age</i>	0.65	0.16	0.99	0.99
K_s	11.67	1.85	0.99	0.99
<i>FD</i>	-0.03	0.05	0.31	0.39
<i>DD</i>	-0.01	0.00	0.99	0.96

w_i Akaike weight, *SD* standard deviation, *IAB* initial aerial biomass of first growth year, *Age* age of the crop, K_s water stress indicator, *FD* number of frost days, *DD* sum of degree-days of the previous year. The estimates of the different indicators represent the coefficients of the linear relationship between them and the yield

Fig. 7 *M. sinensis* yield trends as a function of age for different values of water stress indicator (a) and of sum of degree-days of the previous year (b). The black triangle is the average yield



standard deviations allowing us to estimate a confidence interval) described in Tables 2 and 3 showed that *M. sinensis* (with an estimate of the parameter associated with *Ks* equal to 11.67) was less sensitive to water stress than *M. x giganteus* (with an estimate of the parameter associated with *Ks* equal to 15.25) (Tables 2 and 3). The parameter estimation associated with the age effect was also higher for *M. x giganteus* (2.38) compared to *M. sinensis* (0.65) (see Tables 2 and 3).

Discussion

The Origin of the Variability in Yields Across Site-Years Is Partially Common for *M. x giganteus* and *M. sinensis*

Age is a common indicator explaining yield variability of *M. x giganteus* and *M. sinensis*. During the juvenile phase of miscanthus cultivation, yields increase before reaching a plateau [5, 10, 31, 32]. The effect of crop age on yield is more pronounced for *M. x giganteus* than *M. sinensis* because of its longer juvenile period [5]. Moreover, the higher the previous year’s yields, the higher the current year’s yields, at least for the juvenile phase. Similar results were obtained by Clifton-Brown et al. [33] who showed that there was a significant R^2 of 0.81 between the third and second year and 0.56 between the third year and the first year for several genotypes, including *M. x giganteus* and *M. sinensis* during the first 3 years.

M. x giganteus and *M. sinensis* also shared another common indicator explaining yield variability across site-years: the water stress indicator (*Ks*). Both *M. x giganteus* and *M. sinensis* yields were negatively affected by water stress. These results are consistent with those of da Costa et al. [11] who found that *M. sinensis* and *M. x giganteus* were sensitive to water stress after 15 days from the onset of the

stress in controlled conditions in the UK. Ings et al. [34] also showed that yields of *M. x giganteus* were negatively impacted by water stress with a significant reduction of the stem elongation rate after the 20th day of drought as the most sensitive response to water stress, followed by a reduction of chlorophyll content by 42% after the 32nd day of drought, resulting in lower yields. van der Weijde et al. [35] showed that for 50 genotypes of miscanthus (including 39 genotypes of *M. sinensis* and 7 genotypes of *M. x giganteus*) in drought conditions; the average loss in plant weight was 45%. However, our results differ from those of Stavridou et al. [12] who did not find a significant decrease in yields of *M. x giganteus* and *M. sinensis* under water stress conditions. This result could be explained by the small magnitude of water stress and the low duration of the experiment (8 weeks), which did not allow taking into account the whole growth cycle of miscanthus.

Water deficit affected stem weight and stem height of miscanthus [34, 35]. According to Ouattara et al. and Christian and Haase [5, 36], stems (number, weight, height, and elongation rate) are strongly correlated to miscanthus yields. Hence, these relationships could explain the yield loss in drought conditions, in addition to the effect of water stress on crop physiology as the decrease of chlorophyll content for photosynthesis and stomatal conductance [34, 36].

Our results showed that *M. x giganteus* was less tolerant to water stress than *M. sinensis*. Clifton-Brown et al. [1, 8] also showed that *M. x giganteus* was less tolerant to water stress than *M. sinensis*, particularly with *M. x giganteus* senescing more rapidly than *M. sinensis* in water stress conditions. Yield losses due to water stress of *M. sinensis* ranged from 9.2 to 12.9 t.ha⁻¹, which is lower than yield losses of *M. x giganteus*, which ranged from 12.1 to 26.4 t.ha⁻¹ [8]. Similar results were obtained by da Costa et al. [11], who showed that *M. sinensis* was more tolerant to water stress than *M. x giganteus*. In water stress conditions, the water use efficiency of *M. sinensis* was increased by 2% while that of

M. x giganteus was reduced by 7% [37]. The morphology of the plant could explain these results. *M. sinensis* is not as tall as *M. x giganteus*, and small plants need less water and are less likely to lose water through evapotranspiration due to a proportionally smaller leaf area [38]. According to van der Weijde et al. [35], the miscanthus plants that had the highest biomass production under drought conditions were genotypes with relatively small morphologies (*i.e.*, small height and/or small leaves) and low stem weight under both normal and drought conditions.

Only *M. sinensis* yields were affected by the sum of degree-days of the previous year. Our results could be explained by the fact that there is a linear relationship between the sum of degree-days of the previous year and the aboveground biomass produced by miscanthus [24]. When the crop has been able to accumulate enough degree-days, it is able to complete its cycle by transferring nitrogen from the aerial parts of the crop (leaves and stems) to the rhizomes. When this transfer has been carried out, the yield of the following year could be higher [22]. The maximum yield achieved by *M. sinensis* in a growth year is earlier than that of *M. x giganteus*; however, its senescence period is longer [39], as several stem cohorts appearing as *M. sinensis* growth cycle progresses (Zapater, pers. comm.). As a result, *M. sinensis* remains functional somewhat later than *M. x giganteus* [39], which may explain the fact that *M. sinensis* is more sensitive to the sum of degree-days in the previous year.

What Could be the Origin of the Unexplained Yield Variability?

The indicators we identified explained 31.9% and 49.9% of the variability in yields for *M. x giganteus* and *M. sinensis* respectively. Other factors which were not taken into account in our study could also explain yield variability.

We did not observe an effect of frost on yield variability. However, many authors have shown that frost during regrowth could lead to stem senescence that reduces the number of stems at maturity, thus impacting yields [40–42]. Temperatures below 0 °C would kill young miscanthus shoots in winter during plant regrowth [24]. We did not observe this effect, probably because six of our sites were located in the same region and did not experience very low temperatures during the regrowth period of miscanthus (frost days ranged from 0 to 11 days for *M. x giganteus* and from 1 to 13 days for *M. sinensis* across the years 2014 to 2018).

Besides, a previous paper on the same experiment showed that the establishment mode of *M. x giganteus* (from rhizome vs. from rhizome-derived plantlets) and that doubling the density of *M. sinensis* did not have any effect on yield [5].

Solar radiation was an indispensable factor in photosynthesis. The intercepted photosynthetically active radiation

had an effect on the interannual variation in yields. All the more so as the two genotypes did not have the same light utilization efficiency, as *M. x giganteus* had a light utilization efficiency of 2.4 g.MJ⁻¹ of MS compared to 1.66 g.MJ⁻¹ for *M. sinensis* [43]. An indicator which takes into account this effect would capture some of the variability specific to each genotype [43].

Miscanthus is a crop with low nitrogen requirements because it stores its nitrogen in the rhizomes at the end of each cycle and re-mobilizes it at the beginning of each cycle [10]. However, P and K inputs are necessary because these elements are not re-mobilized. Therefore, part of the variability could be associated with mineral nutrition [31, 44, 45]. In our study, we estimated the nitrogen nutrition index (NNI) using the critical nitrogen curve of miscanthus [46] in order to use it as a candidate indicator explaining yield variability. Unfortunately, we could not use the NNI because of errors in its measurement. As a perspective, it would be interesting to deepen the analysis of the factors explaining yield variability by identifying indicators related to PK nutrition. K is taken up more by miscanthus than N, and could therefore be a good nutrition indicator [45, 47]. In our analysis, root depth could have been used as an additional indicator to assess the capacity of the crop to uptake soil nutrients (NPK). However, root depth needs to be combined with soil measurements on N, P, or K. Besides, we have already used root depth in the calculation of our indicator of water stress (K_s), which could have increased the risk of confounding effects.

What Perspectives for Genotype Choice for a Given Environment, Crop Management, and Plant Breeding?

As *M. sinensis* is more tolerant to water stress than *M. x giganteus*, it could be grown over a wider range of environmental conditions than *M. x giganteus*, including soil with low water capacity, climatic conditions with low rainfall, and high potential evapotranspiration [48]. This tolerance would allow *M. sinensis* to achieve yields that vary little across sites and years compared to *M. x giganteus* [5]. This is consistent with another study suggesting that *M. sinensis* could thrive in stressful environments, and would likely explain its wide distribution across Asia [49]. To establish miscanthus it would then be necessary to assess the maximum soil water capacity (using information on granulometry and soil depth), and in case of low maximum soil water capacity (especially associated with a low climatic water balance) *M. sinensis* could be better suited to this environment compared to *M. x giganteus*.

M. x giganteus achieved lower yields than *M. sinensis* in some pedo-climatic conditions [5]. On sandy soils, yields of *M. x giganteus* were lower than 5 t.ha⁻¹ [47], Scharwz

and J. Greef, pers. comm reported by Vermerris [50]. This was the finding at the Chanteloup site (shallow sandy soil with a maximum soil water capacity of 149 mm and rainfall lower than 400 mm) where *M. sinensis* obtained higher yields than *M. x giganteus*. Scordia et al. [37] found similar results and showed a low yielding of *M. x giganteus* compared to *M. sinensis* established in sandy soil in Italy. In a context of climate change, characterized in several regions by a higher rainfall variability, the choice of genotypes for a perennial crop should be for the most stable yields across years [37] and even better if they are high and stable. For this purpose, on sites with low water availability and sandy soils, *M. sinensis* would be a better choice than *M. x giganteus*. In 2016, Lewandowski et al. [51] recommended the use of some genotypes of *M. sinensis* instead of *M. x giganteus* in Southern Europe because of their resistance to drought, hot summers, and the advantage of having a homogeneous crop in the fields. But so far, *M. sinensis* seeds are not sterile. To enable their commercial establishment, research on the breeding of sterile *M. sinensis* seeds is needed to avoid the risk of invasiveness [52].

Hence, miscanthus breeding programs could be developed to provide a range of miscanthus genotypes able to produce high (and/or regular) amounts of biomass per hectare under contrasting pedo-climatic conditions. Studies of 15 miscanthus genotypes at several sites in Europe from 2013 to 2015 identified important genotypes of *M. sinensis* and *M. x giganteus*. These studies based on the variability of yields and phenology of the genotypes have issued recommendations of genotypes according to the major climatic zones of Europe [39, 51]. Other species of miscanthus could also be sought for breeding, as the genus miscanthus contains more than 20 species that originate from a large geographical area [53].

Acknowledgements We would like to thank all the partners who contributed to the implementation of the study for their participation and for all the additional information provided for the analysis of the results, especially in the framework of Work Package 2 of the Biomass For the Future project. The authors also thank the technical staff of UMR Agronomie for their support in the management and data collection since 2013, and Wageningen University & Research and Genech for providing plant material. Finally, we thank Liz Carey Libbrecht for language editing this paper. This paper is dedicated to the memory of Mathieu Bazot (deceased in 2017).

Funding The research from which we obtained these results received funding from the French Government, managed by the *Agence Nationale de la Recherche* (ANR) under the Investment for the Future program (BIOMASS FOR THE FUTURE ANR11-BTBR-0006 project).

Data Availability The data and material that support the findings of this study are available from the corresponding author upon reasonable request.

Code Availability The data analysis script is available from the corresponding author upon reasonable request. The script was written on the R software.

Declarations

Conflict of Interest The authors declare no competing interests.

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