**Chapter 5:** Identifying maize ideotypes from observed or unconstrained phenotypic spaces of model parameters in contrasting environmental scenarios.

In this chapter, I use the model developed in chapters 1 and 2, the simulation framework developed in chapter 3 and parameters of phenology for best-adapted genotype in each site as identified in chapter 4, to simulate the impact of the genetic variability of leaf growth parameters on plant production and identify best ideotypes in European conditions.

**Identifying maize ideotypes from observed or unconstrained phenotypic spaces of model parameters in contrasting environmental scenarios.**

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## Abstract

The ideotyping approach uses crop models to define which combination of parameter/trait values could maximize crop production in target environmental scenario. Defining an ideotype which could be attainable by breeding is possible only if (i) crop models have adapted formalisms capturing the genetic diversity and simulating genotype by environment interactions as observed for yield in rainfed environments and (ii) if the set of possibilities considering all traits/parameters together is well-defined. We used two approaches to determine maize ideotypes of leaf expansion and sensitivity to evaporative demand, soil water deficit and light which maximise yield in 59 European sites, 36 years and 3 irrigation scenarios. The first approach considered an unconstrained phenotypic space of 216 virtual maize hybrids defined by a grid of parameter values. The second approach considered an observed phenotypic space determined by phenotyping 254 maize hybrids maximising the genetic diversity. This phenotypic space was constrained by observed relationship between parameters values, limiting the field of possibilities for breeding. Analysis of results in four clusters of environments depending on pattern of water stresses resulted in contrasted ideotypes in both approaches, with sensitive hybrids being better for southern region under rainfed conditions while less-sensitive genotypes better in northern Europe or in irrigated fields. However, the best combination of parameters determined in the unconstrained phenotypic space was not available in the observed genetic diversity. Overall, this study indicates to breeder the environmental scenarios in which such or such leaf growth strategy would be beneficial and highlight the importance of considering observed constraints between parameters in ideotype studies

## Introduction

In the context of climate change, yield improvement will largely depend on the capacity of breeding new varieties that perform better in stressing environments (Casadebaig et al., 2008). Indeed, crops will probably experience higher frequencies of abiotic stresses (Bindi and Olesen, 2011) such as warmer temperatures and limited rainfall in summer (Asseng et al., 2014; Harrison et al., 2014; Reynolds et al., 2016). Breeding of such varieties is a long process, but the use of crop models may allow identifying traits of interest for yield improvement in specific target environment (Perego et al., 2014; Martre et al., 2015; Rötter et al., 2015; Tao et al., 2017). This is possible only if crop models have the capacity of capturing and simulating genotype by environment interactions (Parent and Tardieu, 2014; Chenu et al., 2017). Recent advances in crop modelling allow adaptation of formalisms to integrate the observed diversity of parameter values (Hammer et al., 2010; Martre et al., 2015). If the model design is convenient, it can be used to analyse the sensitivity of a given trait to environment variables, thereby guiding breeders to identify traits of interest in each targeted environmental scenario (Jeuffroy et al., 2014; Marcaida et al., 2014; Gouache et al., 2017).

In this context, testing trait values for parameter linked to leaf growth appears crucial. Indeed, leaf expansion is one of the first processes affect by water stress and evaporative demand with a large genetic variability observed in crops such as maize (Welcker et al., 2011), rice (Parent et al., 2009) or wheat (Parent et al., 2015). Limiting leaf expansion allows plant to reduce transpiration and save water for late stages of crop cycle but decreases carbon acquisition. This trade-off results in contrasted yield benefit or loss depending on environmental scenarios (Tardieu, 2012) and the necessity of defining which strategy is positive in such or such environment. A possibility is to explore it via crop modelling, the ‘*ideotyping*’ approach (Casadebaig et al., 2011; Chapman et al., 2012; Asseng et al., 2014; Challinor et al., 2014; Rötter et al., 2015). This approach aims at defining the best combination of parameters to maximize crop production in each environmental scenario (Jeuffroy et al., 2014; Perego et al., 2014).

A difficulty of such an approach is the definition of the set of possibilities considering all traits/parameters together. Indeed, in the observed genetic diversity, all combinations of trait values are not available, and sometimes will never be, due to physiological or physical constraints resulting in genetic correlations between traits. This defines the phenotypic space of parameters, which is of great importance if the aim is defining an ideotype which could be attainable for breeders (Yin et al., 2003). For example, the leaf economic spectrum (Wright et al., 2004) defines physiological constraints linking leaf nitrogen, specific leaf area and net photosynthesis in plant kingdom. Development of phenotyping facilities now allows to measure several traits in hundreds of genotypes (Tardieu et al., 2017), to highlight potential trade-offs between traits, and allows the bounding of the possible parameters combinations (Townsend et al., 2017).

This study aims at defining the best ideotypes from the genetic diversity of parameters linked to leaf growth and its sensitivity to evaporative demand, soil water deficit and radiation, in multiple environmental scenarios over European maize growing regions. We have used two strategies to deal with the constraints on phenotypic space. The first strategy considers a grid of parameter values without *a priori* information on the constraints or correlation between parameters (named “unconstrained phenotypic space” hereafter). The second strategy considers measured parameter values in a panel of 254 hybrids maximising the genetic diversity of maize (“observed phenotypic space”). However, this second strategy still involves virtual hybrids with (i) cycle duration adapted to each site as identified in Chapter 4 and (ii) all parameters other than those involved in leaf growth and in cycle duration considered as common to all tested hybrids.

Simulations were performed for three irrigation scenarios, namely rainfed, optimised irrigation and fully irrigated, in 36 years and 59 sites summarising the European maize growing region. Results were summarised by clustering environments into 4 classes depending on frequencies and types of water stresses encountered by the crop in each site defined by Harrison et al. (2014). The study on the unconstrained phenotypic spaces resulted in contrasted ideotypes, with sensitive hybrids being better for southern region under rainfed conditions and non-plastic hybrids being better for northern region or in irrigated fields. The second approach based on observed phenotypic space gave similar tendencies but showed that the best combination of parameters was not available in the observed phenotypic space. These differences between the two approaches highlight the importance of considering observed constraints between parameters in ideotype studies and gives keys to breeders for plant improvement in different target environments.

## Complements of material and method

### Model parameters

Two strategies were adopted in this study, by considering either an unconstrained space of three parameters linked to leaf growth or the observed phenotypic space of these parameters. For both strategies, parameters related to phenology as well as sowing dates were fixed for each site as those maximising yield in each site (Chapter 4). All other parameters used in the crop model are those of the reference hybrid, for which simulations were tested over a network of site (DROPS network) around Europe for end of season leaf width and length and grain number and grain yield (B73, Chapter 2).

Measured parameters of the three traits of interest for the 254 hybrids were estimated from platform and field measurements. Briefly, maximum leaf elongation rate (‘a’) and the sensitivity of leaf elongation rate to water deficit and evaporative demand (‘c0’) were estimated by analysing the dynamics of leaf expansion in platform experiments under optimal conditions and soil water deficit (Chapter 1 and 2). ‘c0’ is the x-intercept of the relationship between leaf elongation rate and soil water potential, i.e. the water potential value that stops leaf elongation. It was better adapted to this study than the slope of relationships, which are highly correlated to the maximum elongation rate a. The response of leaf widening (‘sRAD’) to intercepted radiation was estimated from leaf width measurements in field and platform experiments (Chapter 2).

The grid of parameters values used in the unconstrained phenotypic space was constructed by using the 6 sextiles of the parameter distributions, and considering all combinations between parameter values to obtain a set of 216 (63) sets of parameter values .

### Drought scenarios

We have used the four drought scenarios identified in Harrisson et al., 2014 (Fig. 5.1 A and B), calculated by clustering the time courses of supply/demand ratios over 36 years of simulations for the reference hybrid in 55 sites. This analysis was extended here with the same algorithm as Harrisson et al., 2014 on the four new sites added in Chapter 4. The algorithm used was the function ‘kmeans’ (R software) for clustering mean values of supply demand ratio in classes of 50 °Cd during the studied period.

The four drought scenarios (Fig. 5.1, B) presented different frequencies of occurrence between sites (Fig. 5.1, A). One cluster (‘no stress’: supply demand close to 1 during the whole cycle) shows relatively low to no stress during the whole crop cycle, and is mostly dominant in the northern sites. The most severe scenario (‘Early terminal’: water deficit during and after flowering) is dominant in southern sites, and intermediate scenarios (‘Late terminal’: water deficit after flowering ; ‘Recovery’ : water deficit at flowering with soil rehydration during grain filling) were dominant in intermediate latitudes.

### Simulations and analyses

Simulations were performed for all sets of years (36) x sites (59) x irrigation scenarios (3) x parameter values in both strategies (observed and unconstrained phenotypic spaces, respectively 254 and 216 genotypes), leading to 3 001 212 simulation runs.

In a first step, results were analysed in each site, considering the average yield for each genotype (set of parameters) in each site and irrigation scenario. In this case, the ‘best ideotype’ is the genotype with highest mean yield in that environment (site x irrigation). In a second step, we used the clusters of environments to analyse simulations. Results of any set of year x site x irrigation were grouped in one of the four cluster. In this case, an ideotype was therefore the set of parameter maximising yield for the considered scenario, regardless of the year, site or scenario of irrigation.

## Results

***Ideotypes for leaf growth largely depended on scenarios of water deficit within an unconstrained phenotypic space.***

The observed genetic variability was high for the three studied parameters, which all displayed normal distributions in spite of a tendency to a skewed distribution for c0 (Fig.5.2). From these observed value, an unconstrained phenotypic space of three dimensions was built, based on the sextiles values of the distribution of each parameter (Fig.5.3, red points). This leads to 216 sets of parameter values covering this theoretical phenotypic space. For each combination of site x year and irrigation, the set of parameter values maximising final yield was identified every year (Fig.5.4). A set of parameter values maximising mean yield over the 36 year was then identified. A large G x E interaction was observed at European scale with the best set of parameter largely differing between sites and irrigation strategies (Fig.5.5).

In fully irrigated conditions, the best sets of parameter values were similar in all sites (Fig. 5.4: A, D,G), with highest maximum elongation rates (a = 4.73 mm°Cd-1), low sensitivities to water deficit and evaporative demand (c0 = -1.4 MPa) and high sensitivities of leaf width to intercepted light (sr = 0.94 cmMJ-1). A strategy with high use of resources was therefore always beneficiary in the absence of water constraints. Conversely, in southern sites with rainfed conditions, the best ideotypes were those with lowest maximum elongation rate and highest sensitivity to water deficit and evaporative demand (Fig. 5.4, B,E,H). Although maximum sensitivity of leaf width to intercepted light was most often beneficial, the opposite result was observed in some southern sites. An intermediate pattern between full irrigation and rainfed conditions was observed in optimised irrigation regimes.

When sites, year and irrigation regimes were analysed jointly, a clear relationship was observed between best parameter values and the supply / demand ratio (Fig.5.6). For the three parameters, those resulting in highest leaf area resulted in best yields in the absence of water deficit (S/D from 0.8 to 1). This involved highest values of maximum leaf elongation rate, minimum sensitivity (elongation continuing till -1.5 MPa) and maximum leaf width in high intercepted light. Conversely, low elongation rates, highest sensitivities to water deficit and lowest leaf width resulted in the highest yields under severe water deficit (S/D from 0.5 to 0.65).

We have then analysed these results per drought scenario, for each of the four patterns of water deficit determined by clustering, namely (i) no water deficit, observed in all sites for the well-watered treatment, but also in northern sites in rainfed conditions (Fig.5.1); (ii) early terminal stress, with water deficit occurring before flowering and continuing during grain filling, mostly observed in southern sites in rainfed conditions (Fig.5.1), (iii) late water deficit occurring after flowering time and (iv) water deficit with recovery during grain filling. The last two scenarios were mainly observed in rainfed conditions at intermediate latitudes. Simulated yields were the highest in the “no stress” scenario (Fig. 5.7**:** from 7.8 to 12.3 tha-1) and the lowest in the early stress scenario, ranging from 5.4 to 5.8 tha-1. Intermediate values were simulated in the other two scenarios, with yield ranging from 6.8 to 7.4 tha-1 for the ‘recovery’ scenario and from 6.9 to 7.7 tha-1 for the ‘late stress’ scenario.

Four classes of maximum leaf elongation rate are presented in rows of Fig. 5.7, and scenarios are presented in columns. In each panel, all combinations of Srad and c0 are presented, with highest yields in green. In the ‘no stress’ scenario, the best ideotype was the one with the highest maximum leaf elongation rate (a = 4.73 mm °Cd-1) and the lowest value of sensitivity to soil water deficit. Results were opposite in the other three scenarios with the best ideotypes showing the lowest values of parameter a (3.19 mm °Cd-1) and c0 being within the two highest sensitivities. A high sensitivity of leaf width to plant intercepted radiation was positive in nearly all cases when considering the best set of parameters for the two other parameters. However, in the “late terminal” and “recovery” scenarios, a low sensitivity to intercepted radiation was positive when combined with highest values of maximum leaf elongation rate.

Overall, these results show a clear pattern, with the ideotype in well-watered conditions maximising light interception via highest values of elongation rate, the highest sensitivity of leaf width to intercepted light and the lowest sensitivity to water deficit. In all scenarios of water deficit, ‘conservative’ ideotypes resulted in highest yields, with lowest maximum elongation rate and maximum sensitivity to water deficit. Noteworthy, a small interaction was observed between the sensitivity of leaf width to intercepted light and the other two parameters.

**Best ideotypes identified within the unconstrained phenotypic space were not available within the observed genetic variability, although tendencies remained similar in observed and unconstrained phenotypic spaces.**

We have then analysed the behaviour of virtual hybrids presenting existing combinations of parameter values in the panel of 254 maize hybrids. Some combinations of parameter values did not exist within this panel. For example the correlation between maximum leaf elongation rate (a) and sensitivity to evaporative demand and water deficit (c0, Fig.5.3A, R² = 0.38) results in the fact that there is no hybrid presenting both a high maximum leaf elongation rate and a low sensitivity to water deficit. The same appears for hybrids with low maximum leaf elongation rate and high sensitivity. Conversely, there was no correlation of these two parameters with the sensitivity to intercepted radiation so all combinations were possible (Fig. 5.3 BC).

Best ideotypes (Fig. 5.8, A to I) showed a pattern with latitude and water deficit that was consistent with the analysis of unconstrained phenotypic space. In fully irrigated conditions (Fig. 5.8, ADG), the best genotype was the same in all sites, with the highest measured maximum leaf elongation rates (5.1 mmdd-1), a moderate value of sensitivity of elongation rate to water deficit (-0.91 MPa) and a high sensitivity of width to intercepted radiation (0.64 cm.MJ-1). With lower irrigation regimes, ideotypes with lowest maximum elongation rate performed the best, as above (Fig. 5.9 A), but the optimum sensitivity to water deficit was essentially similar at all levels of water deficit (Fig. 5.9 B).

Hence, we have observed appreciable differences in results between un-constrained and constrained strategies for identification of best ideotypes. Broadly, the trends were similar in both approaches with water-saving strategies and maximisation of leaf area growth resulting in highest yield in water deficit and well-watered scenarios, respectively. This difference in result can be observed in Fig. 5.10 that presents heat maps similar to those of Fig. 5.7, but in the observed phenotypic space. In well-watered conditions**,** the best ideotype within the observed phenotypic space had a lower response of width to intercepted light compared to that in the unconstrained space (Table 5.1 : 0.36 compared to 0.94 cmMJ-1) and a higher sensitivity to water deficit (Table 5.1 : -1.02 compared to -1.4 MPa). The yield of the best ideotype was also lower than with an unconstrained phenotypic space (-2.8%). In intermediate scenarios (late terminal and recovery) the best ideotype in the observed and unconstrained phenotypic space had the lowest maximum leaf elongation rate (Table 5.1: respectively 3.23 and 3.19 mm°Cd-1) and highest response to intercepted radiation (Table 5.1: respectively 0.86 and 0.94 mm°Cd-1) but the best ideotype did not reach the low values of sensitivity to water deficit as those determined within the unconstrained phenotypic space (Table 5.1: respectively -0.74 and -1.44 MPa). This led to an average yield loss of -3.2% and -4.2% compared to the ideotype with unconstrained phenotypic space. Finally, in the highest level of water deficit (early terminal), maximum leaf elongation rate and sensitivity to water deficit had similar values with the two approaches (Table 5.1: respectively 3.23 and 3.19 mm°Cd-1 and -0.74 and -1.44 MPa), but the main difference was on the sensitivity to intercepted radiation, lower for the ideotype of the observed phenotypic space (Table 5.1: 0.24 and 0.94), with an average difference in yield reaching 3.9%.

Overall, while similar trends were identified for the two approaches, the best ideotypes found within the unconstrained phenotypic space were not available within the observed genetic diversity in any of the four environment types, resulting in yield losses from 2.8 to 4.2 % in average.

## Discussion

*Predicting G x E interaction via crop models including genetic diversity.*

Predicting when and where a trait value would lead to yield benefit is of particular importance in rainfed environments because drought scenarios can highly vary between years and cause large G x E interaction on yield. Indeed, depending on the pattern of the drought scenarios, any trait value can have positive or negative effects on crop production (Tardieu, 2012). This is particularly true for traits linked to leaf expansion and transpiration because of the trade-off between water saving and carbon acquisition. However, to our knowledge, there is no available study testing where and when it should be positive to select genotypes with combinations of high elongation rate, high width and low sensitivity to water deficit. The model used for simulation in this study (Lacube et al., 2017, Chapter 1 and 2) uses formalisms that describe leaf growth with several environmental effects (radiation, evaporative demand and soil water deficit), and integrates genotypic variability on these parameters. It therefore gives the possibility to predict genotypic effects in new environments for which the model was not directly developed, and overall in a virtual network which would never be available with conventional field trials.

Simulation showed the large variability of trait values maximising yields depending on year, site, and watering scenario. In particular, traits related to a rapid growth (both high maximum elongation rate and low sensitivity to water deficit) had a positive effect on yield in non-water limiting environments whereas they both affect yield negatively in drought related environments. Those mechanisms appearing as emergent properties of the model (Wang et al., 2002) are well-known avoidance mechanisms, limiting transpiration early in the season and allowing higher water availability during the critical phases of grain filling (Schoppach and Sadok, 2012). A non-expected result was that this strategy was positive in the three tested drought pattern tested here. The corollary effect was that limiting growth in optimal conditions through a low potential growth and a high sensitivity to water deficit limits intercepted light and biomass accumulation, leading to lower yields. By contrast, responses of leaf growth to intercepted light showed less genotype x environment interaction. Knowing that the stress indices in the crop model APSIM are based on a ratio between supply (uptake of the roots from the soil) and demand (transpiration from conversion of intercepted light into biomass) for water, the limiting factor in the studied set of environments was always water availability in the soil compared to incident radiation.

Overall, these G x E interactions as emergent properties of the simulations confirmed that a favourable trait in one environment can have deleterious effects in another. It highlights the importance of future crop model improvements to be focused on the integration of measurable genotypic parameters (Hoogenboom et al., 2004), and show that traits related to leaf growth mechanisms can affect final grain yield in optimal and drought conditions and have a relevant place in crop improvement programs.

*Simulating the effect of available phenotypic space rather than sensitivity analysis on crop parameter to test future genetic gain.*

Ideotyping with crop models is probably one of the paths to study potential crop improvements to maintain crop yields in a changing environment (Hammer et al., 2002; Casadebaig et al., 2011; Tardieu and Hammer, 2012). Recent studies pointed out that in some cases, the optimisation of target traits could even increase yield in the future for several crops including maize (Rötter et al., 2015), with relative yield gain as much as 7%. In this study, we show how new ideotypes of leaf expansion could lead to yield gains in both optimal and stressed conditions, from 3 to 5%. Moreover, as climate change does not change the patterns of stress but rather the frequencies of occurrence of each stress in a specific site (Harrison et al., 2014), the study can be translated to future climatic conditions under climate change.

However, an approach based on the existing genetic variability of parameter values presents marked differences with that in an unconstrained phenotypic space. Indeed, in the process of ideotyping, studying more than one trait imposes that these traits have to be taken into account together in the model (Denison, 2015; Sadras and Denison, 2016). We show in this study that two different approaches with a constrained (observed) and non-constrained phenotypic space could give different results due to the correlations between parameters or traits. Correlations between traits that limit the phenotypic space were handled with two different strategies in the model.

– Strong correlations between measured traits were directly taken into account by the model and therefore cannot be considered independently in sensitivity analyses. For example, the sensitivity of leaf expansion to evaporative demand is common for several leaves and a unique parameter summarises behaviours for all leaves (Lacube et al., 2017). In the same way, the sensitivity of leaf growth to soil water deficit and evaporative demand are closely related in several crops such as rice and maize (REF) and as such, they were link together in the model leading to a unique parameter.

-Other correlations were analysed here but parameters could still be considered individually. For example, the correlation between maximum leaf elongation rate and sensitivity to water deficit for crops has been previously observed in various mapping populations of maize (Welcker et al., 2011) and was also observed here in the panel of maize hybrids. Without being directly inserted into formalisms, this correlation was taken into account by considering observed sets of parameters in a large panel maximising the genetic diversity of maize hybrids.

By considering both types of correlation, we assume that parameters are not independent and are either constrained by evolution and/ or physiological processes. Particularly, we showed that no set of measured traits (in the studied panel) could meet the requirements of a high potential leaf growth while having a low sensitivity of growth to water stress and a high response to intercepted radiation. If the aim was to analyse the model by itself (sensitivity analysis) or test hypothetical gain in a virtual genetic diversity, the first approach would have been sufficient, but with the aim of offering keys to breeders for future crop improvement, it was important to test whether ideotypes exist within the known genetic variability. From a practical point of view, building of elite material from virtual ideotypes requires that the corresponding genetic variability exists and is exploitable for breeding. It is possible that the ‘missing ideotypes’ exist within a larger genetic variability (e.g. flint or tropical lines), but this remains to be demonstrated. Actually, the correlation between maximum leaf elongation rate and sensitivity to water deficit was also observed in flint and tropical genetic material (Welcker et al 2011).

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