CHAPTER 9

PHYSIOLOGICAL PROCESSES TO UNDERSTAND GENOTYPE × ENVIRONMENT INTERACTIONS IN MAIZE SILKING DYNAMICS

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Abstract. Variation in maize yield across environments often reflects genotype-specific responses in crop-flowering dynamics. The most widely observed effect is the temporal separation of male (anthesis) and female (silking) floral maturity, referred to as the anthesis–silking interval (ASI). Many studies have shown that maize yield also is a function of crop growth rate around flowering. At present, however, the relationship between growth rate and flowering dynamics is not fully understood. In this chapter, we present a conceptual basis and experimental approach for quantifying and analysing maize female flowering responses to variation in plant growth. We show how this approach can be applied to resolve contrasting genotypic behaviour under a range of environmental conditions. Because maize canopies are composed of plants exhibiting a range of growth rates, understanding plant-to-plant variability is critical for evaluating genotypic and environmental effects on female flowering dynamics. We propose a simple model, based on well-established population dynamics, to capture intrinsic plant-to-plant variability within maize canopies. Specific genotype parameters were identified that integrate biomass production and partitioning into a framework to describe the flowering response of a particular genotype in a particular environment. These results have important implications for understanding yield formation in maize. They provide an approach to evaluate genotype × environment interactions, and a framework to evaluate genes regulating flowering dynamics.

INTRODUCTION

As in most extensive crops, variation in maize (*Zea mays* L.) yield is related more to the number of harvested kernels than to individual kernel weight. As such, the period of development when kernel number is defined has been referred as the 'yield critical period'. Numerous studies have shown that maize kernel number (and yield) is a function of crop growth rate around flowering (Early et al. 1967; Andrade et al. 1999). Environmental conditions that alter plant growth during this period affect specific aspects of flowering dynamics. The most widely observed effect is the temporal separation of male (anthesis) and female (silking) floral maturity, referred

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to as the anthesis-silking interval (ASI). The relationship between final grain yield and the ASI has been described in numerous studies (Woolley et al. 1962; Moss and Stinson 1961; Edmeades and Daynard 1979; Hall et al. 1982) and has attracted considerable attention in maize-breeding programmes (Bolaños and Edmeades 1996; Bruce et al. 2002; Bänziger et al. 2004; Campos et al. 2004). The relationships between plant growth and specific aspects of the flowering process, however, have not been fully resolved. Identifying the physiological mechanisms that regulate the visually observed changes in flowering dynamics has important implications for overcoming current limitations to grain yield in maize.

Maize is a monoecious plant, with staminate (male) flowers borne on an apical inflorescence (commonly referred to as a tassel) and with pistillate (female) flowers produced on one or more lateral branches, which develop into grain-bearing rachises (commonly referred to as ears). At the individual plant level, anthesis is defined as the beginning of pollen shed from the tassel, and is visually determined when at least one anther has dehisced and is liberating pollen. Appearance of the first pollen-receptive stigmas (commonly referred to as silks) from within the surrounding husks on the primary ear defines the silking date for each plant. As such, both flowering descriptors are qualitative traits that define a change of state. At any point in time, a plant either has or has not reached these flowering stages (anthesis or silking).

When these flowering processes are considered at the population level, anthesis and silking dates are set when a pre-determined proportion of plants in the population reach the stage. In general, anthesis or silking for a population is reported when 50% of the plants attain the stage. This simplification reflects the fact that all plants in a population do not achieve anthesis or silking at the same time. Rather, flowering throughout the population is recognized as a continuous (but finite) process. Thus, for the population, floral anthesis is a quantitative process; for individual plants, it is a qualitative process.

Using a mechanistic framework to analyse a biological phenomenon involving a qualitative process at the individual level and a quantitative process at the population level has met with considerable success. An excellent example is the prediction of seed-lot performance across contrasting environments from quantitative information of germination at the population level and a qualitative assessment of individual seed germination (Ni and Bradford 1992; Bradford 2002). As shown below, a clear understanding of the flowering process at the individual plant level is critical for resolving environmental effects on maize phenology at the population level. This is particularly evident when plant-to-plant variability within the population is large, as is often the case in maize crops, especially under stressful growing conditions.

BIOMASS PARTITIONING DURING FLOWERING AND SILKING DYNAMICS

Biomass partitioning and silking

In maize, biomass partitioning to the female reproductive structures varies with plant

growth rate. Edmeades and Daynard (1979) used biomass partitioning to show that the tassels were a much higher priority sink than the ears at high population density, where individual plant growth is reduced. Figure 1, redrawn from Andrade et al. (1999), shows how ear growth varies over a wide range of individual plant growth rates during the 30 day period bracketing flowering. In this example, population densities were employed to alter radiation intercepted per plant, and consequently, individual plant growth rate around flowering. It is noteworthy that there was a positive ear growth only if aerial biomass increased at a greater rate than ca 1 g pl^{-1} d^{-1} during the 30-day period bracketing flowering. Above this threshold biomass partitioning to the growing ear was greatly enhanced (Figure 1). This example illustrates that biomass allocation to the maize ear is not a constant ratio of the total biomass produced around flowering. It is important to note that these analyses were made possible by testing plant responses across a wide range of population densities, and by examining the response of individual plants within each population rather than using population averages. Recent studies using this approach have exposed significant genotypic differences in the minimum threshold for ear growth and maximum ear growth rates at very high rates of plant growth (Echarte et al. 2004).

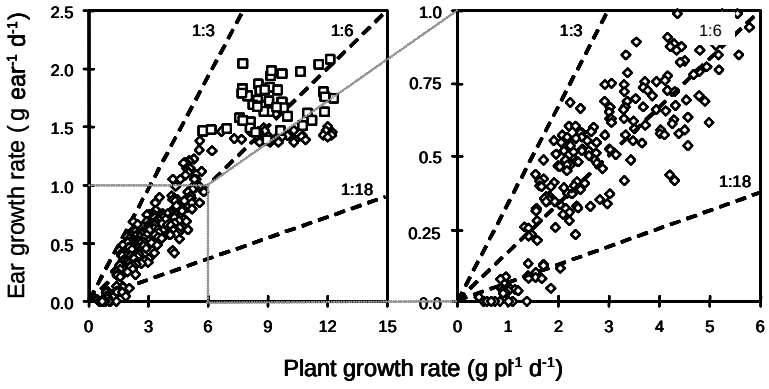

Figure 1. *Relationship between ear growth rate and plant growth rate around flowering for individual plants. The variability in plant growth rate was achieved with population densities ranging from 2.2 to 16.9 plants* m^{-2}*. Adapted from Andrade et al. (1999). Dotted lines show constant biomass partitioning to the ear during flowering (1:3, 1:6, and 1:18 ratios)*

Since the silking process is a function of ear expansion growth (Westgate and Boyer 1986; Cárcova et al. 2003), time to silking historically has been considered an indirect indicator of biomass allocation to the ear (Moss and Stinson 1961; Buren et al. 1974; Jacobs and Pearson 1991). Even though ears are growing continuously around flowering, there will be a finite ear biomass value at which silking occurs. Although it would seem intuitive that silking is a function of biomass allocation to the ear, examples illustrating this relationship are lacking. Therefore, we collected ears from a single genotype as it approached silking to determine if there was a critical ear biomass at this stage. As shown in Figure 2, ears of this genotype grown

at 10 plants m^{-2} reached silking when accumulated ear biomass was around 0.75 g ear^{-1}. Effects of the environment on this value are currently unknown. But it is clear from Figure 1 that low plant growth rates around flowering that reduce the ear growth rate would increase the time for the ears to reach the critical ear biomass to achieve silking.

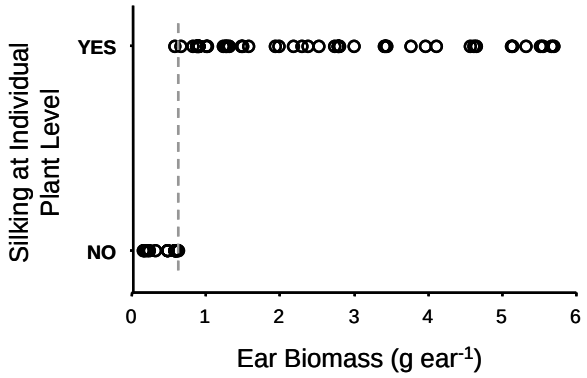

Figure 2. *Silking status of individual plants as a function of biomass accumulation by the primary ear. Data are for 63 plants sampled around silking. The dotted line was fitted by eye. The experiment was conducted in Ames, Iowa, in 2005*

Silking dynamics at the population level have been shown to be highly sensitive to reductions in plant growth rate caused by drought (Hall et al. 1982), shading (Moss and Stinson 1961) or defoliation (Yao et al. 1991) treatments around flowering. Phenology data presented in Figures 3A and 3B from Yao et al. (1991), for example, illustrate the impact of altering plant growth on the development of the female reproductive structures and resulting pattern of silking for the population. In this case, three maize populations were subjected to various levels of defoliation to decrease light interception and alter crop growth rate around flowering (confirmed from biomass measurements). The appearance of the male inflorescence was not affected by the decrease in resource capture (Figure 3A), while the silking pattern of the population was closely coupled to the source level for the crop (Figure 3B). As such, delayed silking at low plant growth rates was in accordance with a reduced biomass allocation to the ear at low plant growth rates, retarding the achievement of the needed biomass to reach silking. It is important to recognize that the defoliation treatments affected the time to silking of individual plants within the population (Figure 3). Therefore, plant-to-plant variability in ear development within each population is not a constant, and its impact on the silking dynamics of the population also must be considered.

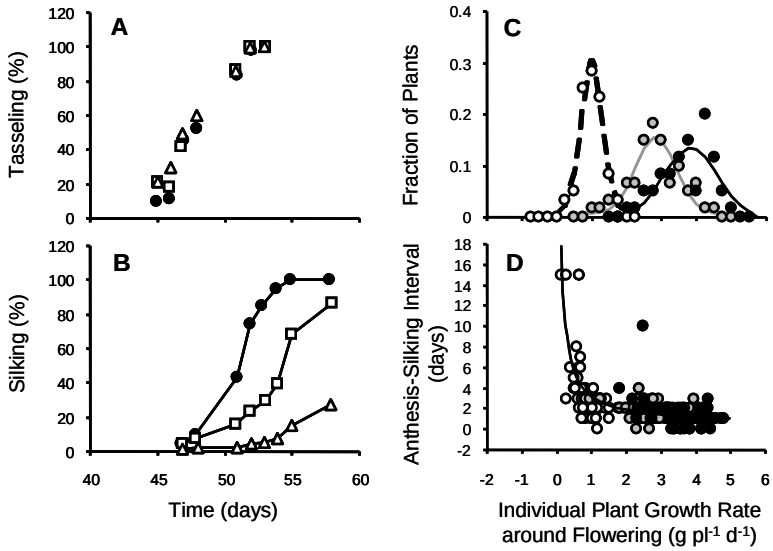

Figure 3. *Effect of reducing leaf area index of a maize canopy around the flowering period on the progress of tassel emergence* **(A)** *and silking* **(B)** *for the population. LAI = 2.3 (black circles, control), LAI= 0.6 (squares), LAI= 0.3 (triangles). Adapted from Yao et al. (1991). Description of variability in plant growth rate* **(C)** *and the anthesis–silking intervals* **(D)** *from a maize inbred line planted at 10 pl* m^{-2} *(grey circles), defoliated (ca 75% of the green leaf area removed) to reduce plant growth rate (white circles), or thinned (50% of the plants removed) to increase plant growth rate (black circles) about 15 days before anthesis. A total of 60 plants per treatment were sampled. A single power function was fitted to all 180 data points in* **D** *(*R^2 *= 0.52), as curve parameters where not different between treatments (*$P<0.05$*). The experiment was conducted in Ames, Iowa, in 2005*

Figures 3C and 3D illustrate individual plant growth and ASI for a maize inbred grown at three growth conditions. One group of plants was partially defoliated 14 days before anthesis (ca 75% of the green leaf area removed) to reduce plant growth rate. A second group was thinned to 5 pl m^{-2} at the same time, to increase individual plant growth. A third set left at 10 pl m^{-2} served as controls. Measured plant growth rates around flowering on average were 0.87, 2.63 and 3.70 g pl^{-1} d^{-1} for the defoliated, control and thinned treatments, respectively (Figure 3). The plant-to-plant coefficients of variations (CV) were 0.36, 0.26 and 0.20% for the defoliation, control and thinning treatments, respectively, which were in general agreement to previous observations (Edmeades and Daynard 1979; Vega and Sadras 2003). Time to silking and anthesis was monitored for each individual plant in each population. Plants with reduced plant growth were delayed in silking, resulting in an increase in ASI for these plants, which was most dramatic at very low plant growth rates (Figure 3D).

Developing a model to describe silking dynamics

Having described the basic relationships between plant growth rate around flowering, ear growth rate and time to silking (Figures 1, 2 and 3), we developed a model to predict the silking pattern of maize populations based on their plant growth. This model was based upon the understanding that:

- Biomass allocation to the ear is not constant, and varies with total plant growth around flowering. At low plant growth rates, the ear growth is reduced not only because of reductions in total plant growth, but also because partitioning of plant biomass growth around flowering changes. The proportion of biomass allocated to the ear decreases at low plant growth rates.
- Maize populations are composed of plants that grow at differential rates around flowering, impacting the time to silking for the various growing fractions of the population. At commercial stand densities, variability in plant growth rate around flowering is ca 30% (CV), and increases in stressful environments (Vega and Sadras 2003).
- Silking is a change of state at the individual plant level; this change in state can be related to accumulated ear biomass.
- At the population level, silking for each fraction of the population can be defined by their ear growth rates. Ear growth rate for each fraction of the population can be calculated from the mean plant growth rate for the population and the variability around this value.

The silking model parameters include: (i) the parameters that relate ear growth rate with plant growth rate using an hyperbolic function (Vega et al. 2001): the minimum plant growth rate that gives a positive ear growth rate (PGRb), the initial slope, and an attenuation coefficient; (ii) the minimum ear biomass at which individual ears reach silking; and (iii) two parameters describing an exponential growth pattern to calculate accumulated ear biomass. When all these parameters are considered on a unified framework, it is possible to simulate silking dynamics for a population or populations of plants. Figure 4 shows silking dynamics for individual plant growth rates within a population of plants (Figures 4A and B), and silking dynamics for three populations of plants differing in the mean plant growth around flowering (Figures 4C and D).

When predicting the silking dynamics of a maize population, the mean plant growth rate and the distribution of growth rates within the population have to be measured or estimated. These variables are specific to the genotype and its response to the environment (Glenn and Daynard 1974; Vega and Sadras 2003).

The mechanistic framework for predicting silking patterns was used for testing changes in specific parameters. Genotypic differences in silking patterns and yield performance under source-limited conditions around flowering have been well documented (Moss and Stinson 1961; Buren et al. 1974; Soriano and Ginzo 1975; Bruce et al. 2002). The physiological mechanism(s) underlying these differences in stress tolerance, however, remain obscure. At present, genotypic differences in rapid silking seem to be related more closely to differences in biomass partitioning than in plant biomass production around flowering (Edmeades et al. 1993; Chapman and Edmeades 1999; Monneveux et al. 2005). As such, we modelled the silking

dynamics of two genotypes differing in the base plant growth rate at which higher plant growth rates give positive ear growth rates (1 vs. 2 g pl^{-1} day^{-1}) in two environments with contrasting mean plant growth rates (2 vs. 6 g pl^{-1} day^{-1}).

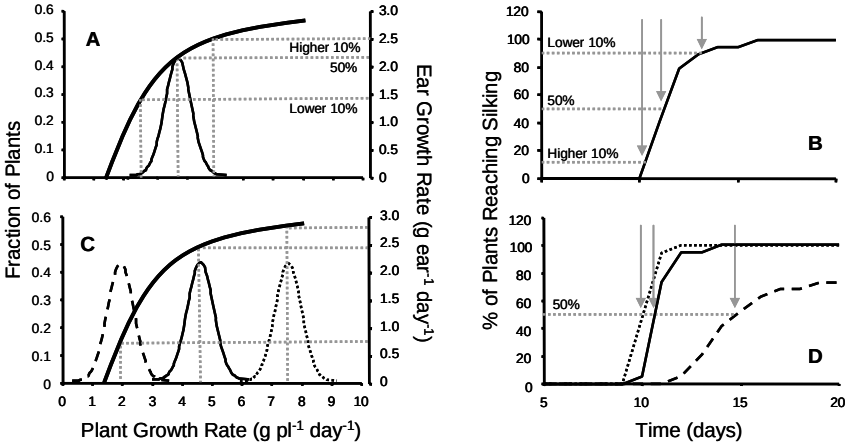

Figure 4. *Schematic diagram relating silking dynamics to individual plant growth rates within a single population of plants* **(A** and **B)**, *and silking dynamics for three populations of plants differing in the mean plant growth around flowering* **(C** and **D)**. *Note that differences in plant growth rate among population fractions* **(A)** *or among population means* **(C)** *are not linearly related to differences in ear growth rate (bold line), and this has an impact on the silking pattern. In* **(B)** *arrows indicate time to silking for different fractions of plants within the same population (10, 50 and 90 %). In* **(D)** *arrows indicate time to silking for 50% of the plants from three plant populations*

Under favourable growing conditions, silking dynamics for the two genotypes were nearly identical (Figure 5). This would be expected because all plants of both genotypes had plant growth rates well above the minimum to support ear growth. Under less favourable growing conditions, however, silking dynamics were very different for these two genotypes. The one with a higher minimum plant growth rate to support ear growth showed a greater delay in silking and some plants failed to silk. This difference in genotype response reflected a higher proportion of plants with slow or zero ear growth. As such, this genotype was much more sensitive to reductions in plant growth around flowering than the other. The differential response of these two hybrids to a similar reduction in plant growth rate arose directly from the natural variation in plant growth within the population and the inherent genetic variation in partitioning to the ears.

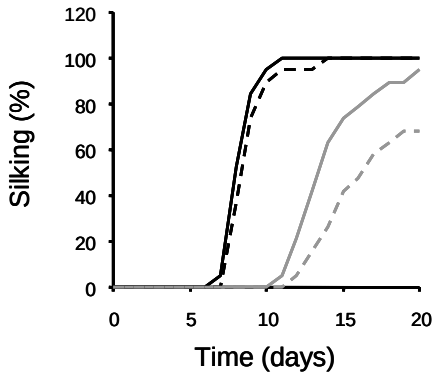

Figure 5. *Silking dynamics for two genotypes differing in the minimum plant growth rate to support ear growth (PGRb) and at two mean plant growth rates. Solid lines: PGRb =1 g pl^{-1} day^{-1}, dashed lines: PGRb = 2 g pl^{-1} day^{-1}. Black lines: mean plant growth rate = 6 g pl^{-1} day^{-1}, grey lines: mean plant growth rate = 2 g pl^{-1} day^{-1}. The CV of the populations was set at 30% for both genotypes and environments*

CONCLUSIONS

Considering maize-flowering dynamics as a quantitative trait at the population level and as a qualitative trait at the plant level enabled us to identify and integrate key genotypic coefficients needed to quantify silking behaviour. These factors are: (i) the relationship of plant growth rate and ear growth rate; (ii) the pattern of ear biomass accumulation during early growing stages; and (iii) the amount of accumulated biomass an ear needs to accumulate to reach the silking stage. We showed the value of using a population-based approach by taking into account the plant-to-plant variability to understand time to silking in maize crops. Methodologies, such as allometric models (Vega et al. 2000), are currently available to describe these plant-to-plant differences. For the first time, a framework to predict the silking dynamics of a maize population is presented that can explain environmental and genotypic differences affecting plant growth.

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