Ten Years of the Maize Nested Association Mapping Population

For example, flowering time in maize is controlled by many common, small effect QTL, none of which affect flowering time by more than 1.5 d (Buckler et al., 2009). However, in self-pollinated species like rice (Oryza sativa), sorghum (Sorghum bicolor), and Arabidopsis (Arabidopsis thaliana), much of the variation for flowering is controlled by a few QTL with large effects (Huang et al., 2012; Salomé et al., 2011; Li et al., 2011). Similar contrasting architectures were observed for leaf structure in maize compared to the self-pollinated species rice, Arabidopsis, and barley (Hordeum vulgare) (Turner et al., 2005; Takahashi et al., 2009; Koornneef et al., 2004). The distinct patterns of genetic architecture of maize complex traits relative to inbreeding species may be related to differences in the evolutionary strategies of selfing and outcrossing species. Selection may favor

small effect sizes in outcrossing species, in which the sum of small effects keeps the individual

phenotypes closer to the population mean (Wallace et al., 2014; Buckler et al., 2009). In

outcrossing species, the two parental genomes are shuffled and recombined at every generation,

and large effect loci may not be passed on to progeny. Polygenic trait architectures may also have

helped maize adapt to diverse environments, where the effects of selection are spread across

numerous segregating loci (Flood and Hancock, 2017). Selection might have also favored

independence of traits over pleiotropy, as certain combinations of phenotypes may be favorable in

some environments but not others (Wallace et al., 2014).

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The timing of reproductive development is a critical component of individual plant fitness and is shaped by a combination of environmental signaling pathways that converge at the growing tip (shoot apical meristem; SAM).

Internal signals tell the plant about its health, energy resources 40 (e.g. stored carbohydrates), and ability to secure further resources (e.g. leaf area and height); 41 whereas external factors (e.g. temperature, daylength, and water availability) signal existing or 42 upcoming growing conditions for both the plant and its interacting community (e.g. pollinators 43 and pathogens). In both cases, these cues determine whether, when, and how quickly the plant 44 allocates resources to flower production, so the plant survives long enough to produce abundant 45 viable lifetime seed. From a human perspective, flowering time has major consequences for crop 46 production, both in terms of vegetative biomass in the case of vegetables, and inflorescence biomass primarily in the case of grains, fruits, and seeds.

A potential caveat to this is the fact 60 that, concomitant with population growth, the global climate is becoming warmer with the 61 expectation of longer and more severe weather events, such as droughts, monsoons, heatwaves, 62 and frigid temperatures (Ummenhofer and Meehl, 2017). Since extreme weather events will affect plant growth and development both directly, based on innate stress tolerance, and indirectly, through variation in the reliability of cues for phenological shifts such as flowering, it is of increasing importance that we understand the extent to which plants are pre-adapted to these novel climates and/or how quickly they can adapt.

highlight new discoveries of genetic pathways that can 77 be manipulated to affect better and more reliable yields in diverse and changing climates,

Parrish & Fike 2005

II. E. Phenology & Temperature Relations

Switchgrass displays distinct developmental patterns in response to accumulated temperature and to day length, but these relationships are greatly affected by genotype x environment interactions.

The rate of growth of switchgrass is thought to be dependent on temperature, with minimal growth occurring below a putative base temperature (BT). A BT of 10 C for vegetative and reproductive development is commonly used for growth models (Mitchell et al 1997; Sanderson and Wolf, 1995a). [Li has used a BT of 12 C: Kiniry 2005, 2008a; Behrman et al 2013]. BT vary by cultivar and are as low as 2.8 C for northern cultivars and 6.5 C for southern cultivars (Madakadze et al 2003).

However, BT requirements for greenup may be higher, or there may be a photoperiod or vernalization mechanism rather than a temperature threshold *per se* for triggering spring growth (Parrish and Fike 2005).

A relationship between vegetative morphology and GDD has been shown in environments from Texas USA to Quebec Canada; but the nature of the relationship changes quantitatively and qualitatively with cultivar and location (Madakadze et al 1998c; Sanderson and Wolf, 1995a, 1995b).

While the rate and extent of vegetative development is closely related to GDD, reproductive development is more tied to day-of-the-year, or photoperiod. Switchgrass is a short-day plant; it flowers when exposed to shortening days of a specific length (Benedict, 1940).

[so what is daylength of flowering for each plant\_id \* site – and is it the same across sites for individual plant\_ids? Or different? If the same, this is the driver; if different, something else is the driver.]

A strong relationship between timing of reproductive development and day-of-the-year has been reported in several studies (Cornelius and Johnston, 1941; Eberhart and Newell, 1959; Hopkins et al., 1995a; Sanderson and Wolf, 1995a). However, time of flowering has some degree of genetic variation within a population; selection for early and delayed floral initiation within Alamo germplasm resulted in plants that flowered from 10 days earlier to 12 days later than their parents (Van Esbroeck et al., 1998). The photoperiod response displayed within a given strain naturally differs with its latitude of origin and can be a point of exploitation in forage and biomass production systems. Flowering is delayed for southern populations that are moved northward. Because day lengths short enough to trigger reproductive development do not occur until later in the season at more northern latitudes, southern populations remain vegetative later into the growing season, increasing leaf number and yields. Conversely, moving northern populations to southern latitudes with shorter photoperiods hastens the transition to reproductive development (Sanderson et al., 1996), reducing vegetative growth and biomass yield. We will discuss practical applications of these relationships in the section on agronomy of switchgrass-for-biomass. Reproductive development, although linked to day-of-the-year, is not independent of other environmental factors. For example, flowering requires temperatures greater than those needed for growth. Balasko and Smith (1971) grew switchgrass across a range of temperature regimes and reported that anthesis was delayed when switchgrass was grown under a 21/15◦C regime, and was completely inhibited at 15/10 C.

The nature of photoperiodicity in switchgrass has been examined recently by Van Esbroeck et al. (2003), who tested the response of a northern/upland (Cave-in-Rock) and a southern/lowland (Alamo) cultivar under 12- or 16-hour photoperiods. Both cultivars produced panicles in both environments— not to be expected if the tillers rely upon shortening days as the cue to initiate the reproductive phase. Under the extended day length, initial panicle emergence was delayed for Cave-in-Rock, but not for Alamo. The duration of reproductive development wasextended for both cultivars, however, as the time required for the full exsertion was increased.

Despite the close relationship between GDD or day-of-the-year and the developmental phases of switchgrass, prediction equations with broad application remain elusive. A day-of-the-year prediction model for morphological development based on the staging scheme ofMoore et al. (1991) has proved suitable for use only in its region of development (the Great Plains) and with upland cultivars (Mitchell et al., 1997). In the study that produced that model, day-of-theyear proved a better predictor than GDD. However, the model has not proved useful with other cultivars in other regions of the United States (Sanderson and Moore, 1999). Sanderson and Wolf (1995a) found close association ofGDD and development of both upland and lowland cultivars, but they noted that, to be truly useful, such models must be made location-specific.

For genome paper

As noted previously, switchgrass exhibits tremendous diversity in form – so much so that some populations would appear to be well on the way to evolutionary divergence from one another (Parrish and Fike 2005).

Parrish DJ, Fike JH. 2005. The Biology and Agronomy of Switchgrass for Biofuels. Critical Reviews in Plant Sciences 24:423-459.