

# 1 **Simulating crop phenological responses to water deficits**

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1 **ABSTRACT**

2 Accurate phenology algorithms are fundamental for accurate simulation of crop growth.  
3 Phenology frequently changes as water becomes limiting, but such responses are poorly  
4 understood and difficult to quantify. Thus, these phenological responses are often ignored when  
5 modeling phenology. This paper reviews the effects of water deficits on crop phenology and  
6 examines approaches used to simulate phenological responses to changes in water deficits. The  
7 dominant factors determining development rate are described, with particular attention given to  
8 the concept of thermal time and the correlation between thermal time and crop development rate  
9 for different phases of plant development. A survey of the literature to identify diverse  
10 phenological responses to water stress across species and genotypes is presented. Possible  
11 reasons for differences are discussed, and four mechanisms explaining phenological responses to  
12 water deficits are postulated. Different approaches for simulating phenological responses to  
13 changes in water deficits are described. Suggestions for improving the modeling of phenological  
14 development under water deficits are provided.

1           The relationship between air temperature and the timing of developmental events has  
2 been long recognized (Reaumur, 1735). This basic relationship provided the seminal idea for  
3 initial simulations of crop development. As our understanding of crop development and  
4 management increased, it became clear that knowledge of the timing of phenological events in  
5 crops is essential for effective management. Similarly, the importance of accurately simulating  
6 the timing and sequence of developmental events from seed germination to physiological  
7 maturity is well known. If developmental responses to the environment (directly or via  
8 management practices) are poorly quantified, then predictions of simulated growth, nutrient and  
9 water use, and final yield will likely have substantial errors. Such errors arise because growth  
10 processes will be simulated for different environmental conditions than occurred in the field and  
11 because the sequence of developmental events affects the activity of sources and sinks, which in  
12 turn affects the processes of resource capture, partitioning, and re-mobilization.

13           Reflecting the importance of development, simulation of phenology has received  
14 considerable attention (Ritchie and NeSmith, 1991; Jamieson et al., 2007), although arguably  
15 less than needed relative to simulations of photosynthesis, water balance, and nutrient uptake  
16 algorithms. Most simulation models consider the influence of water deficits on plant processes  
17 (e.g., photosynthesis, nutrient uptake, growth), yet few models deal explicitly with the effects of  
18 water deficits on phenology. This chapter reviews the effects of water deficits on phenology and  
19 then examines approaches used to simulate phenological responses to water deficits. Strategies  
20 for improving simulation of phenological responses to water deficits are suggested at the end of  
21 the chapter.

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## **PHENOLOGICAL RESPONSES TO WATER DEFICITS**

1           Crop development has been extensively reviewed elsewhere (e.g., Hay and Porter, 2006;  
2 Hodges 1991; Ritchie and NeSmith, 1991), so emphasis here is on modeling phenological  
3 responses to water deficits. Phenology can be viewed as the result of integrating rates of  
4 development over time up to specific end-points that correspond to developmental events or  
5 stages such as onset of flowering. Therefore, the life cycle of an annual seed crop is viewed as  
6 progressions through phases of development, demarcated by familiar stages such as seedling  
7 emergence, flower initiation, onset of flowering, onset of seed growth, and physiological  
8 maturity (Table 1). The rate of development is influenced by air temperature, and may be  
9 influenced by photoperiod, and nutrient and water availability. The direction of these influences  
10 on specific developmental events varies (e.g., McMaster, 1997; Fig. 1).

11           If the effects of air temperature are accounted for, phenology is often observed to be  
12 remarkably stable over a wide range of growing conditions, despite plants of dramatically  
13 different size and appearance within a given cultivar. The underlying explanation for the  
14 stability is that plants mark the passing of time via thermally-driven internal biological clocks  
15 (Thain et al., 2002; Millar, 2004; Hotta, 2007). One consequence of the internal clocking is that  
16 phenology is predicted surprisingly well with simple models, most based on a relationship with  
17 air temperature as an estimate of the movement of the internal clock.

18           As mentioned in the introduction, Reamur (1735) was the first to predict phenology by  
19 relating developmental events to air temperature. He proposed the concept of heat units, which  
20 has since evolved into the more general notion of thermal time. Thermal time in its basic form  
21 has two components: 1) the integral, or accumulation, of temperature over some time interval,  
22 and 2) use of this integral in a temperature response function to calculate thermal time (although  
23 sometimes the second component is not used). Thermal time typically is expressed in units of

1 degree-days ( $^{\circ}\text{C d}$ ). Many approaches have been developed for calculating thermal time. The  
2 time interval normally may range from hourly to daily time steps. The temperature response  
3 function can be a simple linear function with either an upper and/or lower threshold limitation or  
4 no limitations (McMaster and Wilhelm, 1997), or more refined such as a segmented linear  
5 function or a curvilinear response function (Jamieson et al., 2007; Streck et al., 2003; Yan and  
6 Hunt, 1999). Three cardinal temperatures are required in these more refined temperature  
7 response functions to determine the effectiveness of the integrated temperature for each time step  
8 on development rate. These cardinal temperatures are a base temperature, below which no  
9 development occurs; a maximum temperature, above which no development occurs; and an  
10 optimum temperature, where development rate is maximum. The intervals between these  
11 cardinal temperatures can be linear or nonlinear.

12 Beginning in the 1970's, a refinement to using thermal time was proposed. This  
13 refinement was to use the phyllochron, or leaf appearance rate, to represent the internal  
14 biological clock for measuring the time between developmental events (e.g., Rickman and  
15 Klepper, 1995; McMaster, 2005; Wilhelm and McMaster, 1995). In part, this approach was also  
16 driven by the realization that thermal time to maturity for wheat (*Triticum aestivum* L.) was  
17 negatively correlated with planting date (e.g., Nuttonson, 1948), and a relationship could be  
18 developed between change in photoperiod at planting date and the phyllochron (Baker et al.,  
19 1980). This approach is used in such models as SHOOTGRO (McMaster et al., 1992a,b;  
20 Wilhelm et al., 1993) and MODWht (Rickman et al., 1996), where the number of leaves that  
21 appear between developmental events is used rather than a constant thermal time estimate to  
22 predict development stages from emergence to anthesis. The Sirius model (Jamieson et al.,  
23 1998a, b) uses leaf appearance and total number of leaves produced to predict developmental

1 stages from emergence to anthesis. All models have shown some success in this approach,  
2 although Xue et al. (2004) found that a non-linear approach to simulating winter wheat leaf  
3 appearance was superior to two other phyllochron models. Streck et al. (2003) improved this  
4 non-linear approach by incorporating a chronology function into the function.

5         Photoperiod also can modify rates of development, as first demonstrated by Garner and  
6 Allard in the 1920's. The photoperiod response of many crops has been studied and quantified  
7 for use in simulation models (e.g., Streck et al., 2003; Ritchie and NeSmith, 1991). Cultivars  
8 often differ in photoperiod sensitivity and increasingly, genetic and molecular studies are  
9 revealing underlying mechanisms. Examples of this include positional cloning of the *Ppd-H1*  
10 locus for barley photoperiod response (Turner et al., 2005), the *VRN1*, *VRN2*, and *VRN3*  
11 vernalization loci in wheat (Yan et al., 2003; 2004; 2006), and the *Ma3* maturity locus related to  
12 phytochrome B synthesis in sorghum [*Sorghum bicolor* (L.) Moench; Childs et al., 1997].  
13 Understanding gene networks involved in controlling flowering is rapidly advancing from  
14 *Arabidopsis thaliana* to crop plants such as barley (*Hordeum vulgare* L., e.g., Laurie et al.,  
15 2004).

16         Environmental factors such as water and nutrient availability also influence development.  
17 Seeds usually require a threshold water content before germination begins, after which  
18 temperature (and the continued availability of water) influences the rate of development. In  
19 wheat and barley, early developmental stages such as jointing and flag leaf appearance showed  
20 little response to soil water availability. Later developmental stages such as anthesis and  
21 physiological maturity occurred as much as 13 and 15 days (or over 360 growing degree-days)  
22 earlier, respectively, under severe drought conditions (i.e., less than half of long-term mean  
23 growing season precipitation; McMaster and Wilhelm, 2003). In maize (*Zea mays* L.), anthesis

1 and silking occurred slightly later under water-stressed conditions and the anthesis-silking  
2 interval increased (Campos et al., 2004). Abrecht and Carberry (1993) reported that when severe  
3 water stress was imposed for 19 days following emergence, maize silk and tassel initiation were  
4 delayed, primarily by slowing the rate of leaf appearance, but subsequent developmental stages  
5 were reached earlier, somewhat contradicting other observations such as those reported by  
6 Campos et al. (2004).

7         The various responses to water deficits demonstrate the need for rigorous assessment of  
8 how changing water deficits affect phenological responses on a species-basis and for all  
9 developmental stages. Unfortunately, few summaries exist that synthesize the entire  
10 developmental sequence of shoot apices and correlate this with other developmental events under  
11 any environmental conditions. McMaster et al. (2005) published developmental sequences and  
12 phenological responses to water deficits between irrigated and severe (but not lethal) drought for  
13 wheat, barley, and maize. An example of these sequences is shown in Figure 2 for sorghum, and  
14 phenological responses of sorghum to water stress are presented in Figure 3. Similar  
15 developmental sequences have been developed (unpublished, McMaster) for sunflower  
16 (*Helianthus annuus* L.), proso millet (*Panicum milaceum* L.), and hay millet [*Setaria italica* (L.)  
17 P. Beauv.] and are used in a computer program for simulating phenology in multi-crop  
18 production systems (<http://arsagsoftware.ars.usda.gov>).

19         While such summaries provide a foundation, better quantification and verification of  
20 phenological responses to changing water deficits in these crops (and for descriptions of  
21 genotypic variation within a species) are needed. Furthermore, the approach should be expanded  
22 to other crops where simulation models are lacking. To partially address this need, a brief  
23 review of the phenological responses to water deficits for different crops is given in Table 1,

1 based on the literature and unpublished studies. Compilation of this table proved difficult for  
2 several reasons. First, most field experiments lacked treatments with severe water deficits early  
3 in the life cycle. Second, even supposedly “well-watered” treatments (i.e., those considered as  
4 fully irrigated) often showed evidence of water deficits (e.g., Gardner et al., 1981; McMaster and  
5 Wilhelm, 2003). Third, although many physiological studies have detailed measurements of  
6 plant water relations, most of these studies failed to report effects on phenology. Perhaps most  
7 importantly, these field studies rarely report plant water relations throughout the crop cycle,  
8 rather they present results for only a few points in time. These reasons limited our ability in  
9 Table 1 (and this paper) to characterize the degree of water stress of the plant that likely is  
10 critical in understanding the variable phenological responses. Therefore, our primary objective  
11 was to qualitatively determine phenological responses to extremes of water deficits (e.g., fully  
12 irrigated compared to some level of reduced available soil water) in Table 1, and then quantify  
13 the responses if possible.

14 Responses to water deficits would be expected to be a function of the timing, intensity,  
15 and history of the stress, and species and genotypes respond differently. For instance, Gardner et  
16 al. (1981) applied varying levels of irrigation at different developmental stages for two sorghum  
17 cultivars. In general, no differences in phenological responses were observed for any water  
18 deficit for the two different cultivars. However, development of one cultivar was delayed about  
19 10 days under the most severe water deficits, and the delay may have been caused by delayed  
20 emergence. Rosenow et al. (1983) found that sorghum cultivars differing for the stay-green trait  
21 responded similarly when severe water deficits developed slowly over the entire growing season,  
22 but when severe water deficits developed quickly near flowering, cultivars lacking the stay-green  
23 trait matured sooner. Donatelli et al. (1992) showed the severity of water stress from floral



1 initiation to flowering for six sorghum genotypes did not influence flowering time until water  
2 stress reached a threshold level resulting in delays of up to 20% relative thermal time in  
3 flowering for all genotypes of non-stressed plants. These studies illustrate that water deficits are  
4 part of the response, but it is unlikely the plant has a constant response to the same water deficit.  
5 At some stages, the same water deficit will have a greater effect (e.g., flowering and grain filling  
6 as noted below), and often there is a genotype by environment interaction. Some assessment of  
7 acclimatization to the water deficit is needed in addition to the degree of the water deficit to fully  
8 describe genotype sensitivity to water deficits.

9         Other than emergence, developmental stages up to about flowering of many crops seem  
10 relatively unaffected by water deficits (Table 1). Sunflower leaf number is minimally influenced  
11 by water deficits, and when water deficits have been shown to influence leaf appearance rates the  
12 stress was quite severe and leaf appearance rates decreased with increasing stress (e.g., Marc and  
13 Palmer, 1976).

14         The formation of flower primordia at the shoot apex marks the shift from a vegetative to  
15 reproductive phase. As with leaf number, generally little response of the timing of flower  
16 primordia formation to water deficits was found (Table 1). Furthermore, for many crops flower  
17 primordia formation begins at a fairly early leaf number (e.g., about 2 leaf stage for spring wheat  
18 and barley, McMaster et al., 2005; about 6 leaf stage for maize, McMaster et al., 2005; and about  
19 8 leaf stage for sorghum, Rosenow et al., 1983). As mentioned earlier, the minimal phenological  
20 response noted for early developmental phases is partly because in many environments, severe  
21 water deficits seldom occur early in the life cycle. Also, it might be indicative of examining only  
22 a few cultivars to represent a crop, hence large differences were not found due to few genotypes  
23 sampled.

1           The effects of water deficits on developmental stages become more pronounced from the  
2 onset of flowering and thereafter (Table 1). Under severe water deficits, cereal crops such as  
3 wheat and barley have earlier anthesis, while maize and peanut (*Arachis hypogaea* L.) show a  
4 few days delay of anthesis. Dry beans (*Phaseolus vulgaris* L.) show a range of response in  
5 flowering to water deficits from little response (White and Izquierdo, 1991) to a delay in  
6 flowering under the highest level of water deficits (Robins and Domingo, 1956). Sorghum and  
7 many perennial rangeland and forage grasses can show a considerable delay in flowering under  
8 severe water stress (Donatelli et al., 1992).

9           Part of this variation in response of flowering to water deficits may relate to the whether  
10 wild progenitors of a given crop followed strategies of escaping (avoiding) or enduring  
11 (tolerating) water deficits, a difference closely related to annual or perennial growth habit,  
12 respectively. Annuals must produce seeds, and therefore will reduce investment in non-seed  
13 plant parts and processes as much as possible. Perennial plants have the option of delaying  
14 reproduction when the environment is extremely stressful and instead, focusing resources on  
15 responses that promote plant survival. For perennials, the need to develop and support the  
16 perenniating tissues (crown, bulbs, buds, etc.) complicates the situation, especially those that  
17 produce relatively large quantities of seeds. Indeed, producing seeds in severely limiting  
18 environments may lower the probability of successful establishment of new seedlings.

19           All seed crops appear to shorten seed filling duration under water deficits (Table 1).  
20 Whether a shortened seed filling duration under water deficits will change the time of  
21 physiological maturity is partly dependent on the timing of flowering in response to water  
22 deficits. In crops such as wheat and barley with earlier flowering and shortened seed filling  
23 under water deficits, physiological maturity will be reached earlier. For crops such as maize that

1 slightly delay flowering but have accelerated seed filling under water deficits, physiological  
2 maturity date under water deficit conditions may vary slightly around non-deficit conditions  
3 (McMaster et al., 2005). The shortened duration of seed filling in crops such as sorghum often is  
4 insufficient to offset the large delay in flowering under water deficits, resulting in delayed  
5 physiological maturity.

6         Across species and genotypes, plants display numerous phenological responses to water  
7 deficits. Part of the explanation for the multiplicity of responses is associated with different  
8 strategies to survive drought (by avoidance or tolerance). A better understanding of these  
9 responses may be gained by examining the components of each developmental event. Although  
10 cell division and expansion are a part of every developmental event, events can be distinguished  
11 by their “growth” (cell expansion) or “development” (cell division) components. For instance,  
12 production of a leaf or spikelet primordium on the wheat shoot apex is primarily an event of cell  
13 division. Development of the leaf primordium into a leaf is a result of cell division of the  
14 intercalary meristem and subsequent cell expansion and differentiation producing the leaf blade  
15 and sheath (McMaster et al., 2003b). Stem (i.e., internode) elongation is primarily cell  
16 expansion of newly formed cells from cell division of the intercalary meristem near the node,  
17 with heading in grasses merely the sum of internode elongation. Similarly, seed development is  
18 characterized by early dominance of cell division for the embryo and endosperm (approximately  
19 the first third of seed development) followed by cell expansion (approximately the last two-thirds  
20 of seed development; McMaster, 1997; Herzog, 1988). The variable response of different  
21 developmental events to water deficits may have some relationship with the “relative  
22 dominance” of cell division or expansion in the developmental event. As Hsaio (1973)  
23 discusses, cell expansion is extremely sensitive to water deficits, more so than cell division

1 (which is more a function of temperature). Therefore, the phenological responses of  
2 developmental events with a large cell expansion component to water deficits (e.g., leaf  
3 appearance, internode elongation, seed growth) might be expected to be particularly responsive  
4 to water deficits. A final point to consider is that genotypes can vary greatly in their ability to  
5 avoid or tolerate water deficits, and that many studies may be of limited value if a small selection  
6 of germplasm is used to characterize the species response.

7

## 8 **MECHANISMS EXPLAINING RESPONSES TO WATER DEFICITS**

9 Our understanding of the processes underlying the variable phenological responses to  
10 water deficits outlined in Table 1 is incomplete, and substantial research on the physiology and  
11 associated genetics remains to be done. Nonetheless a series of mechanisms can be postulated to  
12 explain the observed responses, particularly for the timing of anthesis and physiological maturity  
13 (and therefore duration of seed filling). The hypotheses are not mutually exclusive, and it is  
14 doubtful that a single hypothesis fully explains all observed responses.

15

16 *Hypothesis 1: Water deficits lead to reduced stomatal conductance and transpiration, thus*  
17 *increasing daytime canopy temperatures and altering development rates through a thermal*  
18 *response.*

19 It is well established that water deficits cause stomatal closure and lead to higher canopy  
20 temperatures. Depending greatly on the environmental conditions (e.g., the level of water  
21 deficit, atmospheric humidity, solar radiation levels, nutrition level), the increase in leaf  
22 temperature associated with reduced transpiration usually is only a few degrees under most  
23 circumstances (Hsaio, 1973), but under severe water deficits canopy temperatures can be much

1 higher than air temperature. Ehrler et al. (1978) measured elevated temperatures of up to 9°C for  
2 wheat, and Gardner et al. (1981) observed temperature differences of over 6°C for sorghum. The  
3 ability to accurately (and inexpensively) measure canopy temperature is continually improving,  
4 and some crop simulation models (e.g., ECOSYS, Grant et al., 1995; Sirius, Jamieson et al.,  
5 1998a, b) calculate crop energy balances, including dynamic estimations of canopy temperature.

6 Elevated canopy temperatures may influence development, but only when the  
7 differentiating tissue is located in the canopy. This is because normally air temperature above  
8 the canopy (and occasionally soil temperature at the depth of the shoot apex) is used in  
9 calculating thermal time, and the assumption is that air/soil temperature gives an adequate  
10 relationship with plant temperature (e.g., shoot apex and intercalary meristems, cell expansion  
11 zones of leaves and internodes). Clearly these relationships between plant tissue temperature and  
12 air temperature are affected by changes in canopy temperature due to water deficits. Thermal  
13 time approaches incapable of describing changes in canopy temperatures (either above or below  
14 air temperatures) resulting from changes in transpiration will not reflect even gross effects on  
15 crop development. However, the role of temperature on plant developmental rates is  
16 complicated by the fact that phenological processes occur in many different locations within the  
17 plant and that all parts of the plant (i.e., canopy and roots) are experiencing different  
18 temperatures. These different temperatures of different tissues can offset each other. In addition,  
19 temperature responses where the phenological process is occurring can change, or be changed  
20 by, supply of assimilates, nutrients, water, and chemical signals (McMaster et al., 2003b).

21 In evaluating this hypothesis, the variable phenological responses to water deficits for  
22 different crops, genotypes, and environments would be explained by the degree of canopy  
23 temperature increase relative to the optimal temperatures for development. Elevated canopy

1 temperatures would accelerate development if temperatures were below the optimum or slow  
2 development if temperatures were above the optimum.

3 Minimal responses of leaf number and flower initiation would partially be explained by  
4 the location of the grass shoot apex being belowground (at least for the leaves formed up to  
5 flower primordia initiation) or in the lower part of the canopy. In these instances, the role of  
6 canopy temperature will be negligible, if in fact canopy temperature is even elevated under these  
7 conditions. Conceivably, soil temperatures near the surface (down to 5 cm), and therefore shoot  
8 apex temperatures during phases before jointing in small grains, may be warmer than air  
9 temperatures. Certainly, when the soil is moist, soil temperatures at shoot apex depths (2-4 cm  
10 below the surface) are subject to less diurnal fluctuation than air temperature. The reverse may  
11 be true when the soil is dry.

12 Data from a field experiment conducted in eastern Colorado can be used to test this  
13 hypothesis (McMaster et al., 2003). For each of two years, the three winter wheat cultivars  
14 showing the greatest difference between dryland and irrigated treatments for the intervals of flag  
15 leaf complete to anthesis and anthesis to maturity are shown in Table 2. Using the simplest  
16 thermal time approach where temperatures above the optimum do not slow development (and  
17 would invalidate this hypothesis), the increase in canopy temperature above the air temperature  
18 needed to explain the earlier occurrence of anthesis and physiological maturity observed in the  
19 dryland treatments are shown (Table 2). The necessary increase in canopy temperature in all  
20 instances except one was much above observed or reasonably expected canopy temperatures  
21 (e.g., 9°C or more). However, for cultivars showing smaller phenological responses to water  
22 deficits (not shown in Table 2) this hypothesis accounted for much of the observed response.  
23

1 *Hypothesis 2: Under water deficits, lower water potentials are reflected in loss of turgor*  
2 *pressure and hence, tissue expansion or cell division is reduced, slowing development.*

3         The critical role of turgor pressure in cell expansion has been long established and “in  
4 many species cell expansion is one of the plant processes most sensitive to water stress, if not the  
5 most sensitive of all” (Hsaio, 1973). This scenario suggests a seemingly logical relation whereby  
6 water deficits reduce tissue expansion through reduced turgor pressure. However, many lines of  
7 evidence subsequently suggest that plants actively maintain turgor by varying the osmotic  
8 potential (e.g., Krammer and Boyer, 1995; Morgan, 1977; Westgate and Peterson, 1993). The  
9 role of water deficits on cell division is also known to occur, but generally is less responsive to  
10 deficits than expansion (Hsaio, 1973). Some caution is needed in this perspective as it is difficult  
11 to observe, document, and study cell division compared to expansion. Therefore, the lack of  
12 published reports on cell division response of crops to water deficits is not surprising. As will be  
13 discussed under Hypothesis 3, a consensus is emerging that plants use specific chemical stress  
14 signals to regulate responses to water deficits rather than working directly through the physics  
15 associated with tissue dehydration as manifested through changes in water potential or turgor  
16 pressure.

17

18 *Hypothesis 3: In response to water deficits, chemical signaling triggers specific stress responses*  
19 *that can increase or slow development.*

20         Root:shoot signaling involves multiple chemical messengers (Beveridge, 2000), but for  
21 water deficits, ABA produced in roots and transmitted via xylem to specific locations in the  
22 shoot is especially important (Zhang et al., 2006). Research on *Arabidopsis thaliana* and rice  
23 (*Oryza sativa* L.) further suggest that ABA and ethylene interact to regulate rates of development

1 (Yang et al., 2004; Barth et al., 2006). Indirect support for this hypothesis includes triggering of  
2 flowering in citrus trees by water deficits (e.g., Kozłowski and Pallardy, 2002). However, at this  
3 time it is unknown how to predict which developmental rates will be affected and the direction of  
4 the response, so this hypothesis is quite speculative and as stated is not very testable.

5

6 *Hypothesis 4 (Relates to grain filling duration primarily): Water deficits lead to reduced*  
7 *photosynthesis and assimilate supply (mainly via reduced leaf area through accelerated*  
8 *senescence, but also reduced light interception through leaf rolling or leaf movement, lower CO<sub>2</sub>*  
9 *uptake due to stomatal closure, etc.) causing the canopy to die and ending grain filling.*

10 With reduced assimilate availability due to water deficits, the seed filling period may be  
11 shortened simply because assimilate to fill seed is not available or drops below a minimal  
12 threshold (e.g., NeSmith and Ritchie, 1992a). The underlying assumption is that grain maturation  
13 occurs when seed fill ceases, regardless of whether the seed is completely filled. This hypothesis  
14 is distinct from Hypothesis 3 in that it does not assume a role of a stress signal transmitted from  
15 the root system. However, it would not preclude signaling from leaves or sites of assimilate  
16 storage (e.g., stems) to the growing seed.

17 While much research supports the correlation between assimilate supply and seed filling  
18 duration, tests that separate this hypothesis from 1 and 3 are difficult to construct. Further, this  
19 hypothesis does not address phenological responses of other stages to water deficits, such as  
20 anthesis, and explain why the stages may be delayed. However, as with Hypothesis 1, it may  
21 partially explain observed shortening of the seed filling period under water deficits.

22

23 **SIMULATING PHENOLOGICAL RESPONSES TO WATER DEFICITS**



1 Ecophysiological models vary greatly in their levels of physiological, morphological and  
2 developmental detail, and in many cases do not directly simulate effects of water deficits on  
3 development. In many instances, not incorporating phenological responses to varying water  
4 deficits does not seem to be a great deficiency, both because of the over-riding dominance of  
5 temperature in controlling phasic development and water deficits must reach a threshold of  
6 severity before changes in phenology are observed. However, the robustness and accuracy of  
7 models that do not simulate phenological responses to water deficits will be reduced because of  
8 instances where phenological responses to water stress have been observed. In this section, we  
9 examine how a number of models simulate phenological responses to water deficits as a basis for  
10 suggesting how the models might be improved in the next section.

11 In simple models, phenological development is specified directly as an input giving the  
12 calendar day for a developmental stage (e.g., Andales et al., 2005). This lessens or removes the  
13 need to simulate phenology, but requires observational data on the dates and lacks robustness for  
14 use under a wide range of environmental conditions and levels of water deficits. More  
15 developmental detail is provided in models such as the EPIC-based plant growth models (e.g.,  
16 EPIC, Williams et al., 1989; GPFARM, McMaster et al., 2003a; WEPP, Flanagan and Nearing,  
17 1995; WEPS, Wagner, 1996; SWAT, Arnold et al., 1995; and ALMANAC, Kiniry et al., 1992  
18 models). Thermal time in the EPIC-based models is calculated as:

$$19 \quad \text{Thermal time} = ((T_{\max} + T_{\min})/2) - T_{\text{base}} \quad (\text{Thermal time} \geq 0)$$

20 where  $T_{\max}$  is the daily maximum air temperature,  $T_{\min}$  is the daily minimum air temperature, and  
21  $T_{\text{base}}$  is the base temperature. Input parameters for the thermal time required between sowing and  
22 emergence, sowing and maturity, and percent of life cycle (sowing to maturity, 0-1 scale) to  
23 several other stages such as start of grain filling and start of senescence for each crop must be

1 supplied. This improvement marginally addresses limitations for the simple model approach in  
2 that generalized inputs are required compared to the date-specific inputs needed in the simple  
3 models. Models in this second category do not explicitly incorporate factors (e.g., photoperiod,  
4 vernalization) influencing phenology besides temperature, although in GPFARM different  
5 thermal time parameter estimates were provided for each crop based on whether irrigated or  
6 dryland conditions were being simulated. This addition improved model robustness (McMaster  
7 et al., 2003a). Parameterization with such an approach is complicated because phenological  
8 responses to limited soil water (i.e., severe but not lethal) have not been quantified for many  
9 crops, as noted above, and the parameters are species-specific and not genotype-specific so the  
10 genotype by environment interactions commonly observed are not addressed.

11 Other crop simulation models have incorporated considerable phenological detail and  
12 more mechanisms influencing phenology. To illustrate diverse approaches to simulating  
13 phenological responses to water deficits, our discussion will be limited to four models that  
14 demonstrate different conceptual approaches (CSM-CROPGRO, SHOOTGRO, Sirius, and  
15 PhenologyMMS).

#### 16 *CSM-CROPGRO*

17 This model was originally developed from three grain legume models (soybean, peanut,  
18 and dry bean), but is now available with templates for over 15 species (Jones et al., 2003;  
19 Hoogenboom et al., 2004). Development is simulated through integration of phase-specific rates  
20 based on hourly temperature data re-constructed from daily maximum and minimum air  
21 temperatures. Development rate varies with temperature, photoperiod, and water deficits, as well  
22 as cultivar. The effect of water deficit is based on empirically determined factors that change  
23 development rate as a function of an index of water stress. These factors vary considerably with

1 phases and species (Table 3). For each developmental phase, the potential development rate is  
2 multiplied by a stress factor (FSW) calculated as:

$$3 \quad \text{FSW} = 1 + ((1 - \text{SWFAC}) * \text{WSENP})$$

4 where SWFAC is a soil water stress parameter estimated based on the ratio between potential  
5 transpiration and readily extractable soil water, and WSENP is the phase-specific parameter,  
6 which can vary from -1 to 1 depending on crop species and developmental phase.

### 7 *SHOOTGRO model*

8 The SHOOTGRO model (McMaster et al., 1992b; Zalud et al., 2003) simulates the  
9 phenology of each morphologically identified shoot (main stem and tillers) of several small grain  
10 species for the median plant of up to six age classes, or cohorts, based on time of seedling  
11 emergence. Soil water content determines the thermal time required for germination and  
12 seedling emergence rates. After germination, sequential developmental events are simulated  
13 using the number of leaves produced (e.g., phyllochron) between events up to anthesis, and  
14 thermal time after anthesis. SHOOTGRO explicitly includes the effect of water and N on  
15 phenology by adjusting the number of leaves or thermal time between developmental events  
16 from emergence through maturity. A linear reduction in the number of leaves or thermal time is  
17 based on the resource availability index factor (which combines 0-1 water and N stress index  
18 factors) between upper and lower threshold values.

### 19 *Sirius model*

20 The continuous development model of Jamieson et al. (1998a) is implemented in the  
21 Sirius wheat model (Jamieson et al., 1998b). Sirius does not follow the strictly sequential  
22 prediction of phasic development characteristic of many models. As with SHOOTGRO, Sirius  
23 assumes that the developmental “clock” from emergence to anthesis is best represented by the

1 rate of appearance and final number of main stem leaves. The effects of vernalization and  
2 photoperiod are simulated through their effect on main stem final leaf number (Brooking, 1996;  
3 Brooking et al., 1995; Robertson et al., 1996). The rate of leaf appearance is driven by  
4 temperature but modified by ontogeny (Jamieson et al., 1995). Initially the controlling  
5 temperature is assumed to be that of the near soil surface, and then of the canopy. Sirius  
6 calculates near-surface soil temperature and canopy temperature based on the surface energy  
7 balance. Water deficit influences on phenology are not explicitly simulated, however canopy  
8 senescence is accelerated in water limiting conditions resulting in shorter grain filling duration  
9 due to loss of assimilate availability and thus maturity.

#### 10 *PHENOLOGYMMS*

11         The PhenologyMMS model V1.2 (<http://arsagsoftware.ars.usda.gov>, McMaster et al.,  
12 2005) simulates the sequential phasic development of wheat, barley, maize, sorghum, sunflower,  
13 proso millet, and hay millet according to pre-determined thermal time (or number of leaves) for  
14 the extremes of either no water deficit or significant (but not lethal) water deficits. For each  
15 crop, the developmental sequence of the shoot apex is correlated with developmental stages (e.g.,  
16 Figs. 2 and 3 show sorghum). Default parameter values are provided for each crop, but can be  
17 changed by the user if desired. The standalone version of this program has no water balance  
18 submodel, so it assumes the two extremes of available water mentioned previously. The user  
19 could adjust the parameter values to an intermediate value if water deficits are considered  
20 between the extremes. The approach used is similar to SHOOTGRO in that water deficit alters  
21 the thermal time (as phyllochron or number of leaves) required between a phase according to the  
22 empirical responses observed for a crop. Some cultivar options are available for certain crops.

1 Work is on-going to add more crops, cultivars, and verify estimated phenological responses to  
2 water deficits.

3

4 Models can be used to test hypotheses when appropriately structured. Four hypotheses  
5 that might explain the phenological responses to water deficits were presented. However as  
6 previously noted, it is both difficult to experimentally test and distinguish among the individual  
7 hypotheses. Existing models do not describe physiological processes in sufficient detail, nor do  
8 they have the structure to adequately test Hypotheses 2, 3, and 4. Models such as Sirius and  
9 ECOSYS (Grant et al., 1995) that simulate canopy energy balance could be used to test  
10 Hypothesis 1 (i.e., that water deficits lead to higher canopy temperatures that alter developmental  
11 rates through a thermal response). Unpublished work by Jamieson and Porter using the Sirius  
12 model for the U.K. examined hypothesis 1 in studying anthesis dates. They found that higher  
13 canopy temperatures under water deficits could account for about two days, but this was  
14 insufficient to explain fully the observed earliness of anthesis under water deficit conditions.  
15 These results match the experimental data presented in Table 2 and suggest that increased  
16 canopy temperatures can only on partly explain phenological responses to water deficits.

17 A further complication of using these models to test Hypothesis 1 is the difficulty in  
18 accurately simulating the genotype responses observed in Table 2. Genotypic differences in  
19 canopy temperature can be simulated only through factors that affect the energy balance (e.g.,  
20 canopy size, canopy architecture through the extinction coefficient, and rooting depth that may  
21 affect the ability to take up water). There cannot be specific ‘genotypic’ canopy temperature  
22 effects, as the physics does not allow it. Therefore, the better question than whether models can

1 be used to test hypotheses might be whether models can accurately do so in a manner that aids in  
2 understanding the biology. In this regard, models do not seem to be able to do so.

3

#### 4 **IMPROVING PHENOLOGY SIMULATION FOR WATER DEFICITS**

5 To understand better how water deficits influence phenology, the foremost need is better  
6 quantification of differences among crops and cultivars to water stress. Ultimately, the goal is a  
7 phenology algorithm that accounts for plant developmental differences as a function of  
8 temperature, photoperiod, water stress, etc. that describes the genotype by environment  
9 interaction for phenology. This algorithm may require modification of existing algorithms or the  
10 development of new algorithms. Building upon the meta analysis provided in Table 1,  
11 researchers can create shoot apex developmental sequences and phenology diagrams (e.g., Figs.  
12 2 and 3) that can be used as the basis for simulating phenological responses to varying water  
13 stresses.

14 Once the empirical responses are known for a crop, algorithms for phenology submodels  
15 must be created to reflect these responses. Models such as SHOOTGRO and PhenologyMMS  
16 already explicitly reflect these responses by modifying thermal time estimates based on varying  
17 water levels, but improvements on their thermal time approach now exist and should be  
18 incorporated. Work remains to construct still more elegant depictions of development in all  
19 crops. For instance, the temperature response curve is assumed to be linear between two  
20 threshold levels of water deficits. Additionally, insufficient knowledge exists to incorporate  
21 specific adjustments to portray genotype response. If models do not explicitly incorporate  
22 phenological responses to varying water deficits, then this enhancement would be in order. In  
23 sequential phase models like CSM-Cropsim-CERES Wheat (Hoogenboom et al., 2004; Hunt and

1 Pararajasingham, 1995; Jones et al., 2003; Ritchie, 1991) and AFRCWHEAT2 (Weir et al.,  
2 1984; Porter, 1984, 1993), two approaches for simulating the responses could be implemented  
3 based on their modified thermal time approach used. One possible modification would be to  
4 alter the pre-determined thermal development units based on soil water availability; an  
5 alternative would be to add a water stress dependent factor to the modified thermal time  
6 approach as implemented in CSM-CROPGRO.

7

8

## CONCLUSION

9 Many models can predict phenology accurately based on the primary driver of  
10 temperature, and when appropriate photoperiod. However, few models have directly addressed  
11 phenological responses to water deficits, partly because our knowledge of phenological  
12 responses to water deficits is limited. Complicating the simulation of phenological responses to  
13 water deficits is the lack of a clear understanding of the mechanisms controlling the  
14 developmental responses among crop species and cultivars to varying water deficits that occur at  
15 different times in the plant life cycle. As a result, existing algorithms have little mechanistic  
16 basis. The goal is to integrate functional genomics with whole plant physiology to understand  
17 better plant development as affected by its environment. In turn, this knowledge will foster  
18 construction of more robust and accurate crop models.

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1 Table 1. Qualitative influence of water deficits on developmental stage progression. + symbol indicates earlier occurrence of the  
 2 event under water deficits, - symbol indicates later occurrence of the event under water deficits, 0 symbol indicates no  
 3 response under water deficits. Question marks indicate conflicting or uncertain responses. Blank cells indicate no literature  
 4 reports were found for the developmental event. Developmental stages are defined as 1) flower initiation is the appearance of  
 5 the inflorescence/flower primordium, 2) flowering is the appearance of flowers (and often the start of pollen shed, or anthesis),  
 6 3) duration of seed filling is from pollination (assumed to coincide with flowering and anthesis) to physiological maturity, and  
 7 4) physiological maturity is when maximum seed dry weight occurs.

Crop	Flower initiation	Flowering	Duration of seed filling	Physiological Maturity	Sources
Barley ( <i>Hordeum vulgare</i> L.)	0?	+	+	+	McMaster et al. (2003, 2005).
Chickpea ( <i>Cicer arietinum</i> L.)		+	+	+	Johansen et al. (1994).
Cotton ( <i>Gossypium hirsutum</i> L.)		0/+	+	-/0/+	El-Zik et al., 1977; Grimes et al., 1978; Guinn et al. 1981.
Dry Beans ( <i>Phaseolus vulgaris</i> L.)	0	0/+	+	+	Robins & Domingo, 1956; White & Izquierdo, 1991.
Maize ( <i>Zea mays</i> L.)		-†	+	+	Campos et al. (2004) ; Farre & Faci (2006); Jama & Ottman (1993) ; McMaster et al. (2005); NeSmith & Ritchie (1992abc); Rosales-Serna et al. (2004).

Peanut ( <i>Arachis hypogaea</i> L.)		-	+	+	Ketring and Wheless (1989).
Sorghum [ <i>Sorghum bicolor</i> (L.) Moench]		-	+	+/-?	Donatelli et al. (1992); Farre & Faci (2006); Gardner et al. (1981); Rosenow et al. (1983).
Soybean [ <i>Glycine max</i> (L.) Merr.]			+	+	Constable & Hearn, 1978; Sionit & Kramer, 1977; Wolf (2002).
Sunflower ( <i>Helianthus annuus</i> L.)	0		+	+	Anderson et al., 1978; Marc & Palmer, 1976.
Wheat ( <i>Triticum aestivum</i> L.)	0?	+	+	+	McMaster et al. (2003, 2005).

1 †Both anthesis and silking are delayed, but silking is delayed more resulting in a longer anthesis-silking interval.

1 Table 2. Increase in daily canopy temperature required to explain thermal time differences  
 2 between dryland and irrigated dates of anthesis and physiological maturity for wheat. The  
 3 temperatures noted in the table were added to the daily maximum air temperature in calculating  
 4 the thermal time for the dryland treatments where for the interval from flag leaf growth  
 5 completed to anthesis or anthesis to maturity so that the thermal time in the dryland treatment  
 6 equaled the thermal time in the irrigated treatment. The three cultivars in descending order with  
 7 the greatest response for a phase to water deficits are presented. (Twelve cultivars were  
 8 observed, with Halt, Heyne, and Yumar never ranking in the top three responses to water  
 9 deficits.) Data from McMaster and Wilhelm (2003) for the Fort Collins, Colorado site.  
 10

Cultivar	Flag Leaf – Anthesis (+ °C)	Cultivar	Anthesis – Maturity (+ °C)
1999-2000			
1. TAM 107	24	1. 2137	19
2. Arlin	18	2. Siouxland	12
3. Akron	10	3. Prowers99	11
2000-2001			
1. Prowers99	12	1. Norstar	34
2. Alliance	9	2. TAM 107	22
3. Akron	3	3. Arlin	19

11 Thermal time =  $((T_{\max} + T_{\min})/2) - T_{\text{base}}$  (Thermal time  $\geq 0$ )  
 12 where  $T_{\max}$  is the daily maximum temperature,  $T_{\min}$  is the daily minimum temperature, and  $T_{\text{base}}$   
 13 is the base temperature.

1 Table 3. Examples of phase-specific modifiers used to adjust developmental rates as a function of water deficit levels in the CSM-CROPGRO  
 2 model (Jones et al., 2003; Hoogenboom et al., 2004). The modifiers are unitless and have a multiplicative effect whereby negative values slow  
 3 development and positive values accelerate it.

4

Developmental phase	Crop			
	Dry bean ( <i>Phaseolus vulgaris</i> L.)	Peanut ( <i>Arachis hypogaea</i> L.)	Soybean [ <i>Glycine max</i> (L.) Merr.]	Cotton ( <i>Gossypium hirsutum</i> L.)
Planting to seedling emergence	-0.30	0.00	-0.20	-0.20
Emergence to first leaf	-0.30	0.00	-0.20	-0.20
Emergence to end of juvenile phase	-0.30	0.00	-0.40	-0.05
End of juvenile phase to floral induction	-0.40	0.00	-0.40	-0.05
Floral induction to first flower	-0.40	0.00	-0.40	-0.05
First flower to first peg (peanut only)	-0.40	0.00	-0.40	0.00
First flower to first pod or fruit	-0.40	0.00	-0.40	0.00
First flower to first seed beginning to grow	-0.40	0.00	-0.40	0.00
First seed to last seed	0.70	0.00	0.70	0.20
First seed to physiological maturity	0.70	0.00	0.70	0.20
Physiological maturity to harvest maturity	0.00	0.00	0.00	0.00
First flower to last mains stem leaf	-0.60	0.00	-0.60	-0.60
First flower to end of leaf growth	-0.90	0.00	-0.90	-0.90

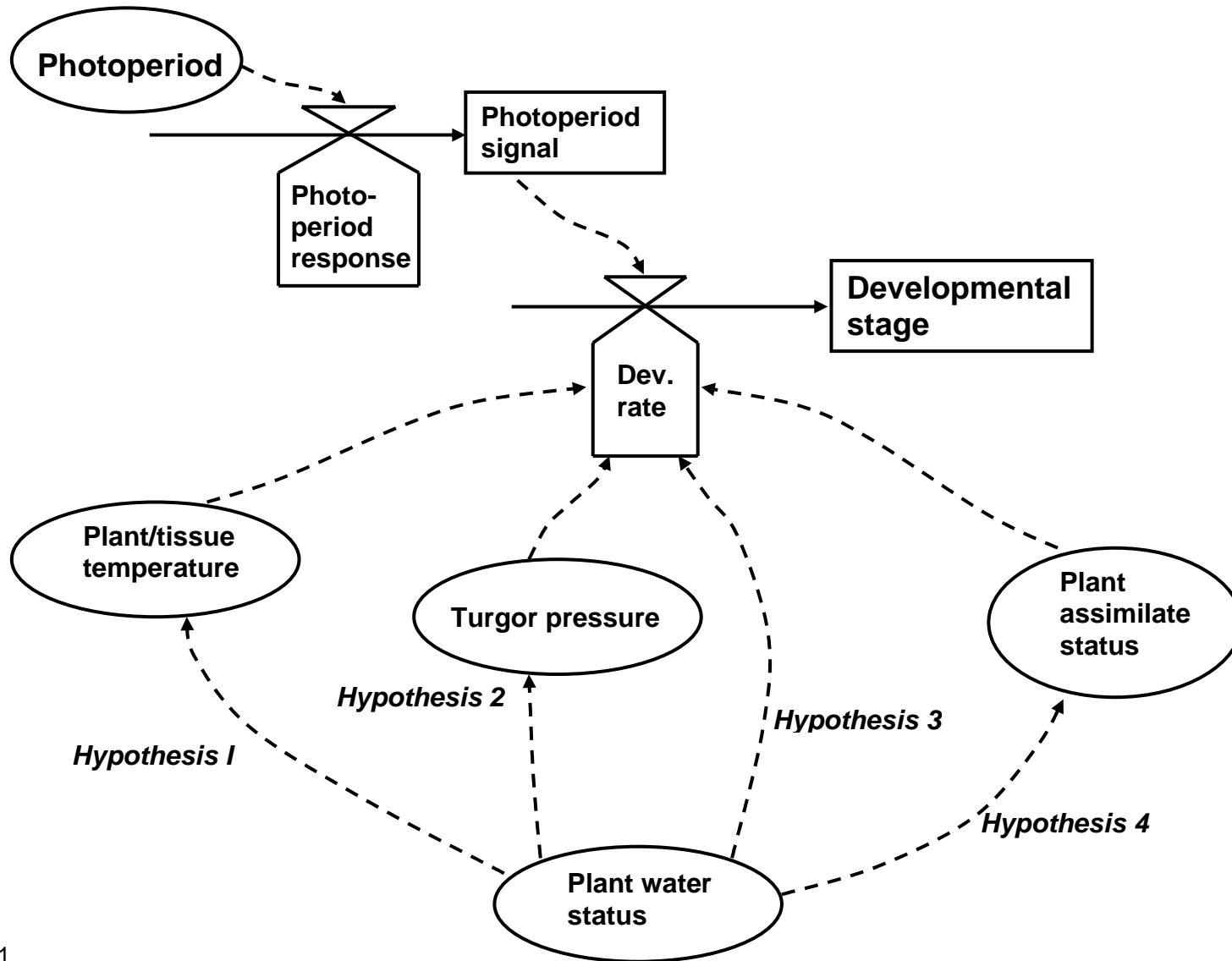
5

1 **FIGURE CAPTIONS**

2 Figure 1. Simplified Forrester diagram of possible mechanisms for water deficits to influence  
3 crop phenology.

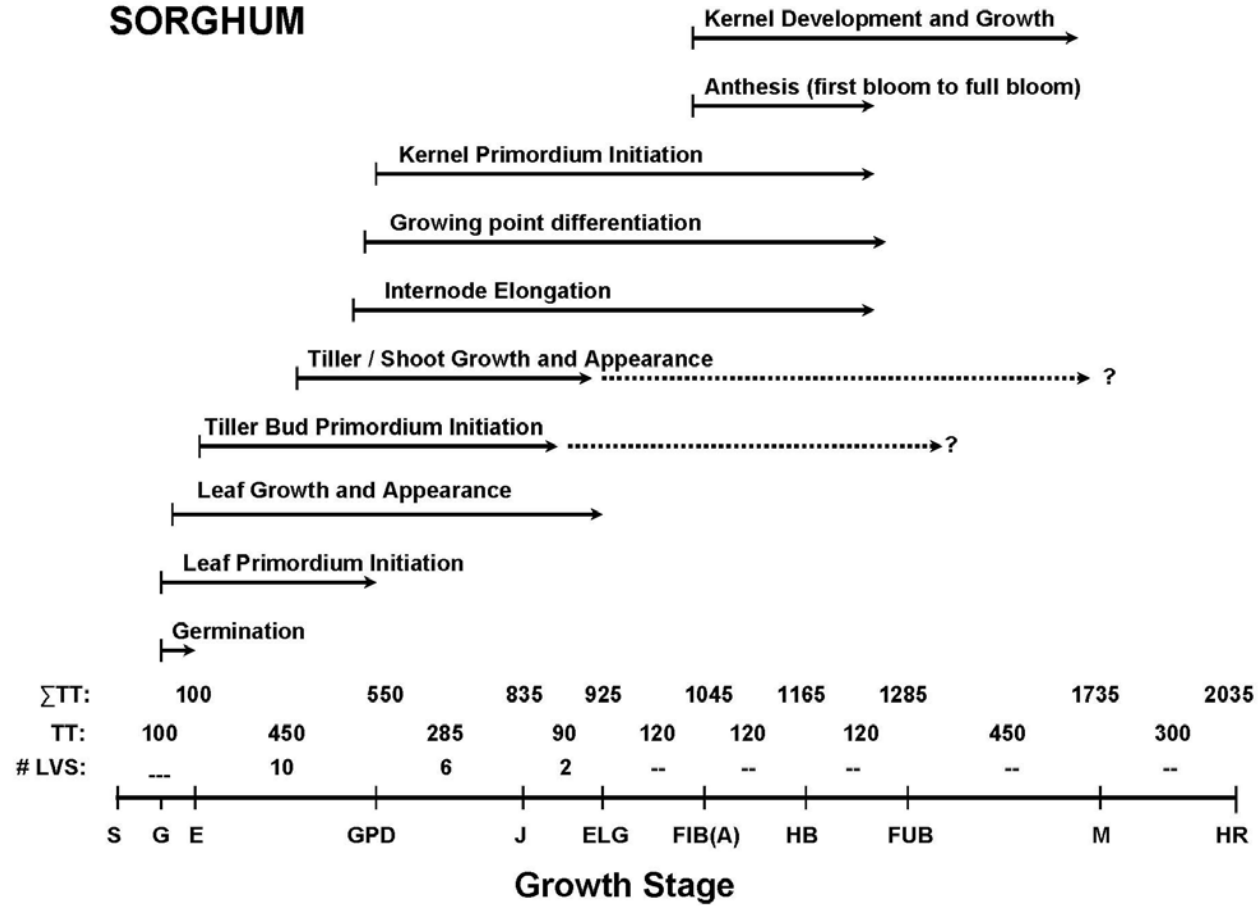
4 Figure 2. Developmental sequence for “generic” temperate sorghum. Work is based on  
5 unpublished data and literature compiled by McMaster, and modeled after the  
6 developmental sequences of McMaster et al. (2005). Thermal time (TT) is calculated by  
7  $(T_{\max} + T_{\min})/2 - T_{\text{base}}$  and  $0^{\circ}\text{C} \leq \text{TT} \leq 30^{\circ}\text{C}$ , where  $T_{\max}$  is the daily maximum  
8 temperature,  $T_{\min}$  is the daily minimum temperature, and  $T_{\text{base}}$  is the base temperature  
9 ( $10^{\circ}\text{C}$ ). The equivalent number of leaves (# LVS) is noted below the thermal time. See  
10 Figure 3 for developmental event abbreviations.

11 Figure 3. Phenological responses for minimal and maximal (non-lethal) water deficits of a  
12 “generic” temperate sorghum. Work is based on unpublished data and literature  
13 compiled by McMaster, and modeled after the developmental sequences of McMaster et  
14 al. (2005). Thermal time (TT) is calculated as given in Figure 2. The equivalent number  
15 of leaves (# LVS) is noted below the thermal time.



2 Figure 1

# SORGHUM





# SORGHUM

## Water non-limiting

	S	E	GPD	J	ELG	FIB (A)	HB	FUB	M	HR
TT:	100	450	285	90	120	120	120	450	300	
# LVS:	---	10	6	2	---	---	---	---	---	
TT:	100+?	450	285	90	145	145	145	350	225	
# LVS:	---	10	6	2	---	---	---	---	---	
	S	E	GPD	J	ELG	FIB (A)	HB	FUB	M	HR

## Water limiting

**S** = Sowing

**E** = Emergence

**GPD** = Growing Point  
Differentiation

**J** = Jointing

**ELG** = End of Leaf  
Growth

**FIB** = First Bloom  
(Anthesis Starts)

**HB** = Half Bloom

**FUB** = Full Bloom

**M** = Maturity

**HR** = Harvest Ready

1

2 Figure 3.