Chapter 14

Synthesis, Actions, and Further Research to Improve Response of Crop System Models to Water Stress

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Abstract

As stated in the preface, the purpose of this book is to document "recent advances in understanding and modeling of water stress (water deficit) effects on plant growth and developmental processes," so that this information can be used to improve models of crop response to water stress for use in optimizing crop production under limited water conditions. Toward this goal, we first attempt to present here a synthesis of knowledge contained in the preceding chapters of this volume. Then on the basis of this synthesis we develop and prioritize a list of action items that will help improve the water stress response of current models and additional disciplinary and transdisciplinary research needed for further improvements of simulation models in general.

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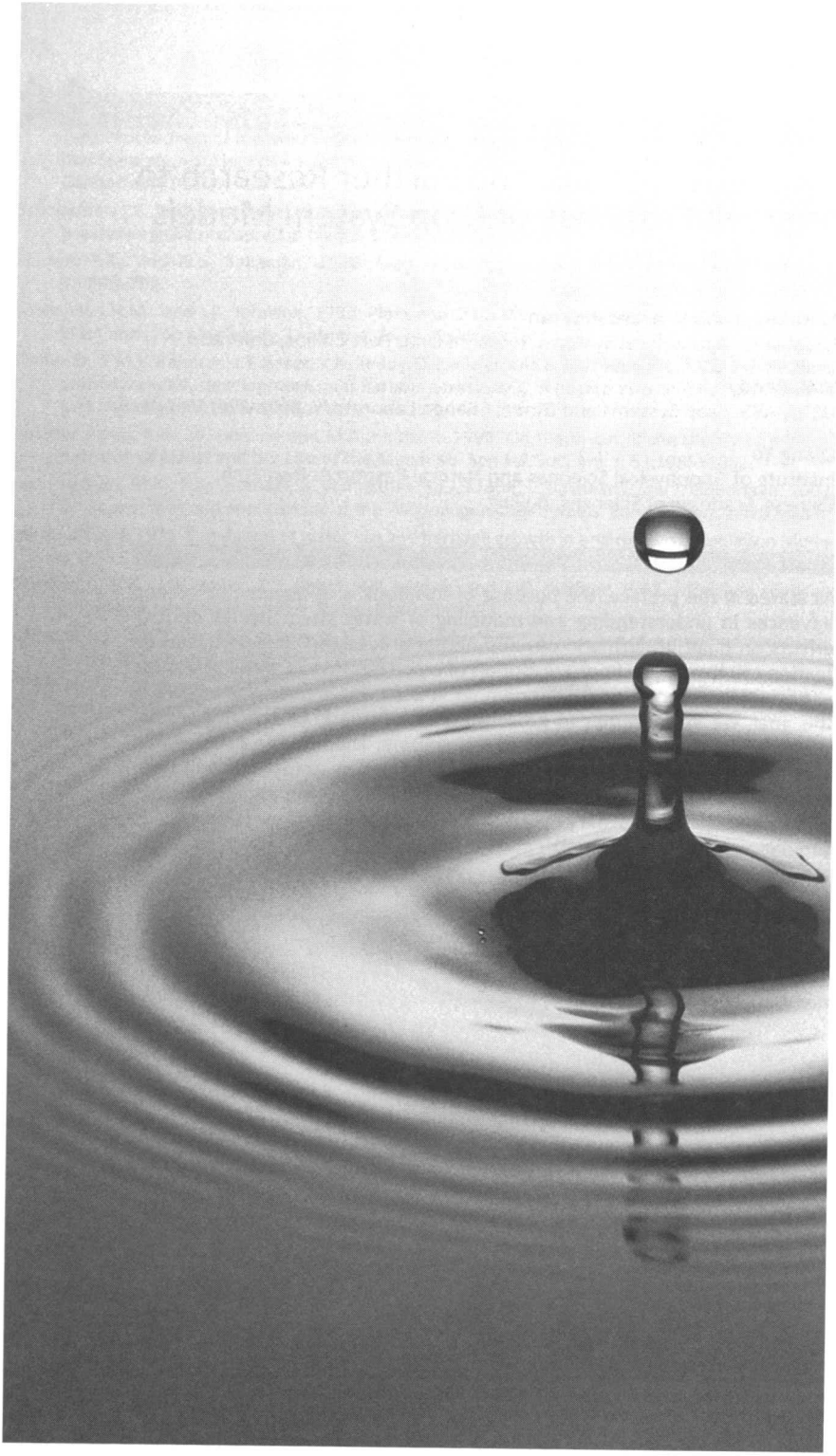

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The first chapter, by Saseendran et al., presents a brief review of water stress effects on plant growth processes and how these effects are simulated in the most common agricultural system models used currently. By definition, the plants experience stress when the soil water is low and the root water uptake fails to meet the transpiration demand imposed by the atmospheric conditions. Besides a reduction in transpiration, the water stress leads to stomatal closure that affects photosynthesis and leaf turgor; these changes, in turn, modulate initiation and expansion of leaves and other growing points of the plant, carbon partitioning and allocation between shoots and roots or among shoots, roots and grain, root growth and distribution in soil, and plant developmental rates. In most of these models, photosynthesis is modeled on the basis of the simple radiation-use efficiency (RUE) approach where the RUE parameter is a constant or a hyperbolic function of light intensity. The effect of water stress on photosynthesis and carbon partitioning in vegetative growth stages is accounted for by a stress factor between 0 and 1 in a certain water stress range. The stress factor is defined somewhat differently in different models, but it is mostly a ratio of actual water-limited daily transpiration to potential daily transpiration rates. Potential transpiration is generally calculated by variants of the Penman–Monteith equation; in some cases a simpler Priestley–Taylor equation is used assuming the wind effects are negligible. The effect of stress on leaf expansion, flowering, and grain-filling stages is accounted by a similar stress factor but starting at lower levels of stress. The change in root growth is assumed to occur in proportion to carbon partitioned to roots. The effects of water stress on phenology and developmental rates of the plants is generally neglected or considered in a simple fashion.

Although the RUE approach calibrated on the seasonal basis has been shown to give reasonable results for well-watered conditions, a number of scientists have argued that the RUE approach with a stress factor between 0 and 1 does not adequately describe the effects of stress on photosynthesis and, in turn, on growth and yield of different crops, especially the quick growing crops like corn. These scientists suggest that during periods of stress, it is better to use the so-called transpiration-use efficiency (TUE) or water-use efficiency (WUE) approach.

The TUE or WUE approach is based on the observations that biomass production in a crop is commonly linearly related to actual transpiration in different environments when adjusted for the vapor pressure deficits. In this approach, one determines the actual transpiration from water-limited root uptake and then calculates photosynthesis. The chapter by Stöckle et al. presents the fundamentals of the RUE and WUE approaches and explores the assumed constancy of their parameters over within-season weather variations at several locations, with respect to a more detailed coupled transpiration–photosynthesis energy balance model (described below) assuming that this detailed coupled model is correct. They report that the RUE parameter fluctuates dramatically with weather conditions, especially with temperature, even under no water stress conditions and when soil and crop conditions are kept the same for all locations. On the other hand, the WUE parameter was an exponential function of vapor pressure deficit without major fluctuations attributable to temperature. Under water stress condition, the WUE parameter value increased approximately linearly with ratio of actual to potential transpiration (T/T0) up to T/T0 value of 0.80 and then varied a great deal. The biomass decreased linearly with T/T0 below T/T0 value of 0.80. This shows that T/T0 is not linearly related to photosynthesis or biomass in the entire range as assumed in the use of T/T0 as a stress factor of 0 to 1 in the current simple models of plant growth. Their work suggests the use of WUE approach, with the parameter dependence on vapor pressure deficit and stress as described above. It should also be kept in mind that the WUE approach requires an accurate estimate of the value of actual transpiration (T) for both nonstress and stress conditions of soil water. Further research is needed to confirm these findings and the validity of the coupled transpiration–photosynthesis energy balance model.

The chapter by Boote et al. documents the experiences of the authors on testing and gradual improvement of the CROPGRO model over the years with respect to water balance, evapotranspiration, and water stress effects on plant processes. It is a good synthesis and discussion of the step-by-step evaluation and improvement of different components of the model. Some of the work was published but also a lot that has not been documented earlier and lays out areas where further improvements are needed. This synthesis will be very useful to scientists for further improvement of water stress response of crop models.

In plants, the processes of carbon assimilation (photosynthesis), transpiration, stomatal behavior, canopy temperature, CO_2 concentration effects, and overall energy balance are coupled. In the RUE and WUE approaches, there are no explicit simulations of leaf temperature, leaf energy balance, and stomatal conductance and no explicit coupling of the above variables in quantifying photosynthesis and transpiration. Especially for improved simulations of crop growth

and development under water stress conditions, accurate simulation of these coupled processes is essential. The chapter by Saseendran et al. briefly reviews and presents examples of some available coupled models. Boote et al. also describe an hourly energy balance option built into the CROPGRO model that is linked to stomatal conductance and photosynthesis of sunlit and shaded classes of leaves. The chapter by Timlin et al. presents an overview of how water affects processes that are important from the perspective of modeling stomatal control and gas (CO_2 and water vapor) exchange, summarizes more recent research in this area for plant response to water stress, and shows how these advances can be used to improve modeling of plant growth and development under limited water conditions. They review several new approaches to coupled modeling of stomatal conductance, carbon assimilation, and transpiration. Models of stomatal control that use vapor pressure deficit and carbon assimilation rate as inputs, coupled with models of photosynthesis, provide realistic simulations of photosynthesis and transpiration. However, they still have a high level of empiricism. Other approaches of stomatal control that involve signaling of water deficits by plant hormones, hydraulic conductance of plants, and stomata guard cell dynamics are promising but need further work for integration into the coupled models. These models do not address the plant adaptations such as the change in leaf angle under water stress. However, the increasing number of papers in the literature support the relevance of the coupled approaches. These approaches need to be integrated with continuing plant growth development through the growth period of the crops, including partitioning of assimilates to various organs, leaf expansion, reproductive growth and development, dynamic root growth, water uptake, and interactions with nutrient demand and supply. Timlin et al. have recently developed a corn model that does this integration and gives some initial results that show the promise of their model. One perceived drawback of these new detailed approaches is the need for more measured data at biochemical and hydraulic level for parameterization; however, progress is being made to overcome this requirement. On the other hand, the authors of these approaches claim that the parameters are more robust. Perhaps, a happy compromise is to use these detailed models to improve the concepts and parameter estimation (through functional dependences) of the simpler RUE- and WUE-based models. The chapter of Stöckle et al. discussed above in connection with RUE and WUE approaches provides an example; they showed that the WUE parameter was an empirical exponential function of vapor pressure deficit. The chapter by Kremer et al. (described below) provide further evidence of this possibility.

Different versions of the coupled approach are evaluated for limited time periods in the succeeding three chapters by Tuzet and Perrier, Kremer et al.,

and Yu and Flerchinger, respectively. In a 2003 paper, Tuzet et al. used a coupled energy balance model, utilized a big-leaf approach to simulate canopy level processes, and included the effects of roots and water uptake. They were able to replicate diurnal variations in stomatal conductance, assimilation rates, and transpiration in maize in both well-watered and drying soil conditions. Tuzet and Perrier added a new plant hydraulic system submodel and the effects of water stored in the plant body (capacitance) in the coupled model. The stored water delays the onset of stomatal closure in the morning and limits the closure in the afternoon at high evaporative demand. Capacitance is shown to greatly affect plant and soil water potentials, transpiration, and assimilation rates. A test of the model with field data for a period of time showed good simulations of soil water, xylem water potential, transpiration, and energy balance components. Kremer et al. present another variant of the coupled energy balance model that includes partitioning of canopy into sunlit and shaded leaves for calculating transpiration, biochemical models of photosynthesis, dynamic stomatal conductance, and root water uptake and its effect on stomatal conductance. Model simulations of the transpiration rates for wheat and maize crops showed good agreement with field lysimeter data for well-watered conditions. Yu and Flerchinger provide a simpler version of a coupled model applied to different layers of a canopy. The model gave reasonable responses for internal CO_2 concentration, stomatal conductance, transpiration rate, and assimilation rate to changes in light intensity and CO_2 concentration. The model needs to be linked to a complete plant growth model.

Response of crops to water stress and optimizing the use of limited available water are also very much influenced by the level of N uptake and likely other nutrients. First, N concentration in the leaf tissue is a factor in the coupled photosynthesis–transpiration–stomatal control processes and thus affects carbon assimilation, transpiration, and water use efficiency. N deficit also reduces root hydraulic conductivity and water uptake in the above coupled processes, and it affects partitioning of assimilates to different tissues. Second, higher levels of rainfall or irrigation cause leaching of a part of soil N and, depending on the amount of N applied, may actually decrease crop yield. As a result, N deficiency may enhance water stress effects in many cases. These water-N interactions are very important in modeling the response of crops to limited water and optimizing both water and N-use efficiencies. Wu and Kersebaum present a thoughtful description of how process models simulate root water and N uptake and water-N interaction effects on plant processes. Just as with the water stress factors, these models use a N stress factor approach in simulating effect of N deficiency on photosynthesis, leaf growth, assimilate allocation, and harvest index, with often different stress factors for the processes. N stress factor varies with growth stage

as the N demand varies. When both water and N stresses are present, the models use either the minimum of the two stress factors, based on the Liebing's Law of minimum or a product of the two factors. The mechanism that justifies the product approach is not clear. Interaction responses are simulated through simultaneous effects on plant processes. Cropsyst and Daisy models seem to have good simulations. Cropsyst includes effect of N deficiency on stomatal conductance. Under some conditions, moderate water stress may be compensated by N and vice versa, but none of the models simulate this compensation. Further research is needed to improve simulations of water and N uptakes and the effects of their interactions on plant processes. For example, a majority of the models assume the influence of water or N stress on plant growth is constant throughout the growth period, whereas the effects may well be stage dependent. Only a couple of models consider two-dimensional root growth and uptake. Water uptake is controlled by root distribution, assuming that all roots contribute to uptake. An alternative approach suggested in the literature is the one based on the assumption that plants minimize their energy in extracting water and nutrients. In addition, the known effect of increasing CO_2 on photosynthesis, stomatal conductance, and water and N-use efficiencies need to be added to more of the models. Finally, a validation and comparison of how individual water and N effects and interaction are simulated and which approach is the best can only be realized when simulation of all other processes in a system model are kept the same. This calls for use of an advanced component-based model building system where the components are easily replaced and compared.

At this point, we might also note that a model's response to water stress and limited water may also be influenced by how soil water itself is simulated. That includes the processes of infiltration, unsaturated soil water movement or redistribution, and soil water storage. In our work, we have found that simpler methods of simulating infiltration and runoff (such as the curve number method), redistribution (such as the tipping bucket method), and the upper and lower limits of water availability seem to work reasonably well. However, their use may influence the values of the crop cultivar coefficients that are calibrated from the observed plant data on phenology, biomass, and LAI, as compared with simulating detailed soil water dynamics. The same could perhaps be said about the N balance components. Simulating detailed water balance dynamics is important for including the important effects of management practices on infiltration and soil water, such as no-till and residue cover, crusting, and canopy and residue interceptions.

Root growth is still largely a black box in modeling because of the lack of understanding, stemming from the difficulty in directly observing root growth patterns and changes in their activity with time. Almost all the current crop

system models represent the root system as a root density profile. Generally, the main change in the shape of this profile from crop to crop and cultivar to cultivar is due to a change in the maximum depth of rooting in the model. In nature, there is a large diversity of root phenotypes with different architecture or rooting patterns and different root ages and functional characteristics within and between species. Models of root architecture, structure, and function have evolved significantly over the last 20 yr and have begun to provide useful insights into traits, other than density distribution, that may influence water and nutrient uptake and their use efficiencies. Such traits include root architecture, anatomy, plasticity, age, and rhizosphere changes. This information can help to improve our current models of root growth and uptake of water and nutrients. Postma et al. present recent advances in modeling root architectures, structures, age, and functions. These models have the benefit of explicit positional information, which permits consideration of developmental processes and activity along the root axes, distinct root classes, intra- and interplant competition for resources, and root interactions with soil domains. However, these 3-D models are much more complex and parameter intensive. It is to be hoped that these models can be used to improve the active root density profiles and water and nutrient uptake routines, as functions of root factors such as age or class, in the simpler models. For example, if the roots are distributed in clusters rather than uniformly distributed in the soil profile, water stress may occur earlier. Root anatomy changes may be important since it can affect the radial resistance to water flow in to the root. Postma et al. show a theoretical example where increase in root cortex aerenchyma (air filled tissue) increased root length density in the top soil and reduced water stress. Aerenchyma is an adaptation by plants that reduces the metabolic cost of soil exploration by reducing respiration.

The life cycle of the annual plants is a progression through phenological stages of growth and development, demarcated as seedling emergence, flower initiation, onset of flowering, seed growth, and physiological maturity. The rate of growth and development varies with stage and is governed by environmental variables such as temperature, photoperiod, available soil water, and nutrients. Major phenostages, such as flower bud initiation and flowering, are governed primarily by environmental temperature and can also be influenced by photoperiod. The stages between flower bud initiation to flowering and flowering to fruit or seed maturity are mostly governed by organ temperature. The leaf addition rates as, represented by phyllochron and plastochron intervals, are governed by temperature but modulated by stress effects. Most models consider the influence of water deficits on plant processes (such as photosynthesis, transpiration, and growth), yet few models deal explicitly with effects of water stress on pheno-

logical progression. McMaster et al. review the current state of knowledge on the effects of water stress on phenology, then examine the approaches used to simulate these effects in some current models, and present strategies to improve these simulations. They note that effect of water stress on phenology varies with growth stage, intensity and history of stress, with species and, likely genotypes, responding differently. Other than emergence, early growth stages up to flower initiation of many crops seem relatively unaffected by moderate water stress, although they note that most studies do not examine the role of water stress earlier in the life cycle. The reproductive stages of anthesis and grain-filling duration are the most affected by water stress. In wheat and barley, anthesis has been reported to advance faster, whereas in maize and sorghum, it is delayed with moderate water stress, and dry beans showed a range of responses. All seed crops appear to shorten seed-filling duration under water deficits (this may be due to increased canopy temperature under water stress conditions). Severe stress may have different consequences, depending on when it occurs; it may cause delay or a total lack of development and maturity. The authors present four potential hypothetical mechanisms that, individually or in combination, might explain the observed effects of water stress on phenology, and may serve as the basis for improving their simulations. These mechanisms include (i) an increase in canopy temperature under water tress that may accelerate or delay development, (ii) a loss in turgor pressure of cells that reduces cell expansion and to lesser degree cell division, (iii) chemical signaling that may have variable effects, and (iv) reduced photosynthesis and assimilate supply that may result in smaller seeds and early maturity. The major crop system models vary greatly in simulating the effects of water stress on phenology, from no direct effects considered to using some empirical effect factors. In the CROPGRO family of models, the empirically determined factors change the rate of development as a function of an index of water stress, and these factors vary with stage of growth and species. The factor values can vary between –1 to +1, indicating a delay or advancement in growth or development, respectively. In SHOOTGRO and PhenologyMMS models, the water stress explicitly affects the number of leaves or thermal time between growth stages. Sirius model does not explicitly incorporate effects of water stress, although seed-filling duration is reduced because of the higher canopy temperatures resulting from water deficits. Further research should examine the hypotheses noted above and suggest more biophysically based methods of simulating the water stress effects.

Global climate change is causing increase in temperatures and changes in rainfall patterns. Semiarid areas of the USA and other regions of the world are experiencing more frequent droughts. In these areas, higher temperatures will increase water demand of crops through increasing potential evapotranspiration

and further increase water stress under drought and limited irrigation water conditions. In addition, higher temperatures also directly affect the plant growth processes. Prasad and Ristic provide current fundamental knowledge of the effects of high temperatures or heat stress, in conjunction with and without drought, on various plant growth processes. They describe the effects at biochemical and molecular level within a cell as well as at the whole plant level. Within the optimal range, the higher temperatures accelerate the rates of growth and development. Outside the optimal range, heat or cold stresses adversely affect the processes in a linear to nonlinear fashion. Early seedling stage and reproductive stages of development are most sensitive to these stresses. Heat stress during flowering results in pollen sterility and loss of seed set. It also enhances maturity and shortens the grain-filling duration, resulting in smaller shriveled grains. Root growth has a narrow optimal range and is very sensitive to heat and cold stresses. Effects on leaf growth are not fully understood. Nonetheless, supra-optimal high temperatures enhance water stress effects under droughts and water limited conditions. The conjunctive interaction effects can be more than additive. Some of the current crop system models include heat stress effects in a simple way. Further research is needed to improve quantification of especially the interaction effects.

The chapter by Green et al. demonstrates the value of the combined use of measured sap flow and mechanistic models for better understanding, quantifying, and managing limited available water for grapevines, and they have applied this approach in New Zealand. Finally, the chapter by Reddy et al. introduces the concept of an Environmental Productivity Index (EPI) to quantify and model the effect of each limiting environmental factor (e.g., water, temperature, ultraviolet-b radiation, nutrients) on crop productivity. The EPI ranges between the values of 1 (factor not limiting) to 0 (totally limiting), relative to a common optimal level and effects of more than one stresses are assumed multiplicative (rather than taking the most limiting stress factor).

Actions and Further Research to Improve Response of Crop System Models to Water Stress

1. Test and further develop the coupled photosynthesis–transpiration–root water uptake–energy balance models as reference research models. Include the effects of increased CO_2 in this coupling. Use these reference models to improve concepts and parameterization of the simpler models.
2. Further evaluate the WUE approach of simulating photosynthesis under water stress as a replacement for the RUE approach, including the accuracy of the root water uptake to determine transpiration.

3. Improve simulation of water balance dynamics for more accurate and robust representation of water stress and uptake calculations and for including the effects of tillage, residues, and other management effects on soil water.
4. Make the calculations of different water stress factors and signals more process based and robust.
5. Compare the calculations of ET_0 and actual ET by different approaches, including the effects of canopy temperature and energy saved from evaporation.
6. Further research and testing to improve simulations of water and N uptake and water-N stress interactions and their effects on plant processes by growth stages.
7. Improve the current root growth and distribution models by simulation of root architecture, structures, age, and functional activity, as functions of soil properties in 1-D models, through learning from the detailed 3-D models.
8. Improve the simulation of water stress effects on phenology based on current qualitative knowledge, and conduct research to test the conceptual hypotheses presented here to further improve these simulations.
9. Improve quantification of heat stress effects on plant processes and its interactions with water stress in combined experimental-modeling studies.
10. Integrate the use of system models with cutting-edge field research in collaboration with field research scientists at different geographic locations to evaluate and further improve wider applicability of the models for optimizing the use of available water under water limited conditions.
11. Modelers need to collaborate and use component-based modeling approaches to facilitate their comparison for simulating individual processes, their further improvement or enhancement, their peer review and documentation, and to advance the science and technology. Modelers should start developing new or revised components in a standalone form to achieve this goal.
12. Modelers need to share experimental datasets for testing and to facilitate improving models.