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CROP WATER REQUIREMENT AND PRODUCTIVITY

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ABSTRACT

Irrigation strategies must be designed to maximize or optimize production while conserving water and minimizing polution of the environment. When irrigation is excessive, water is wasted through deep percolation and soil evaporation. In addition, deep percolation tends to carry fertilizers and pesticides and cause ground water pollution, and soil evaporation tends to give rise to salt crusting at the soil surface. On the other hand, when irrigation is insufficient, crop productivity will suffer. The challenge of good irrigation management is to minimize these problems by matching the irrigation water application to the amount of water needed by the crop for maximum production. That need is determined by a number of climatic, plant, and soil factors, as well as the desired level of production. The use of empirical water requirement tables or calculations for irrigation management is well-known, but cannot account for some important crop and management variables specific for a field.

This paper discusses the basis of crop water requirement and the physiology of crop water use and productivity. First, the central role of energy supply in determining evapotranspiration and crop water use is reviewed. Secondly, the hand-in-hand relationship between crop dry matter (biomass) production and cumulative transpiration from the crop, and the prospect of improving water use efficiency for biomass production, are discussed. This is followed by an examination of the efficiency of water use to produce yield (e.g., grain, fruit, etc.), with emphasis on how the partition of biomass, as reflected in the harvest index, may be altered by crop water status and irrigation management. The final section of this paper considers the importance of timing and severity of water stress in affecting the key components making up crop productivity. How irrigation management should take the differential sensitivity of productivity components to water stress into account is briefly described.

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Most of the water taken up by the crop (98 to 99%) is lost to the atmosphere as water vapor on the same day by transpiration. In addition, water is lost by evaporation from the soil when its surface is wet. If the leaching requirement is ignored, then the crop water requirement is merely the sum of crop transpiration and soil evaporation, termed evapotranspiration (ET). The rate of ET is dependent on climatic, crop, and soil factors. The climatic effects are discussed mostly in terms of the energy needed to evaporate water; the plant and soil factors are discussed in terms of the effective "wetness" of the crop and soil surface.

Evapotranspiration and Energy Supply

For water to be evapotranspired, it must be converted from the liquid phase to vapor phase. Water has an unusually high latent heat of vaporization – it takes 2.4kJ (580 calories) of energy to evaporate one gram of water. For a crop field, virtually all of this energy comes from the environment. By far the most important source of energy for ET is solar radiation absorbed by the field. A minor source is the direct heating of the crop and soil by air going over the field, which occurs only when the air is warmer than the crop and the soil. Because of the importance of the absorbed radiation, daily or weekly ET from a fully wet field can be estimated from the net radiation (incoming minus outgoing radiation) measured over the field for the same period. Such estimates usually fall within 10 or 20% of the true ET. Deviation is caused by the warming or cooling of the field by the overhead air mass. ET (when converted to energy units) would be greater than net radiation if the air has a net warming effect on the field, and would be less if the air is mostly cooler than the field and has a net cooling effect.

If the energy supply is suddenly reduced for an evapotranspiring field by a passing cloud blocking out the sun, ET would continue momentarily at nearly the same rate, but with part of the energy supplied by the sun for evaporation now coming from the heat stored in the crop and soil. The use of the stored heat for ET causes the temperature of the crop and soil to drop. The cooler temperature then leads to a lower water vapor concentration in the crop and at the soil surface, which in turn slows down ET. If the energy supply is suddenly increased, ET would remain momentarily at near the original rate, until the extra energy heats up the crop and soil. The higher temperature then raises the water vapor concentration in the crop and at the soil surface, hence increasing ET.

An integrated measure of the capability of the atmosphere (climatic factors) to supply the energy for ET and carry away the water vapor is potential evapotranspiration (ET_o). ET_o is now commonly calculated from pan evaporation data, or from weather data of radiation, temperature, wind, and humidity (Doorenbos and Pruitt, 1975). It takes into account the effect of weather and is indicative of the evaporative demand of the atmosphere. The influence exerted by the crop and the soil on ET, however, is not included in ET_o.

Evapotranspiration as Influenced by Crop and Soil Factors

ET from a field is affected by two of its characteristics, "roughness" and "wetness". Air moving over an aerodynamically rough field is more turbulent than that passing over a smooth field, and hence, is more effective in carrying energy to, and removing water vapor, from the field. This is not a major effect for crops. ET from a tall row crop, such as maize, is only about 15 or 20% greater than ET from a smooth short grass when both are well-supplied with water, fully cover the ground, and are actively growing. On the other hand, ET can be influenced markedly by the "wetness" of the field. For a field of bare soil, its "wetness" would be determined by the wetness of the soil surface. For a field fully covered by foliage canopy of the crop, its "wetness" would be determined by the extent of opening of the stomata of the leaves of the crop. Open stomata permit the ready diffusion of water vapor from the leaf interior to its exterior, making the surface of the crop canopy essentially "wet", much like the wet surface of a soil. Partly closed stomata conduct water vapor less readily, making the canopy surface less wet, and hence, restricting transpiration. If the crop canopy covers the soil only partially, as is the case when the crop is young and the canopy still developing, the "wetness" of the field would be the combined wetness of the soil and of the crop canopy, approximately in proportion to the relative areas occupied by them. The climatic factors and the roughness of the field determine the rate of ET as long as the surface of the field is effectively fully wet. When the soil surface begins to dry out, and when the stomata of the crop begin to close, the surface of the field would be less than fully wet, and ET would then slow to below its potential rate.

During the day time when there is sufficient light for photosynthesis, stomata of healthy and actively growing crops not short of water would be fully or nearly fully open, and transpiration would be at the potential rate. As soil water depletes and the crop starts to run out of water, stomata begin to close in response, as a protective mechanism, and transpiration is reduced. Stomata also tend to close when growth conditions are unfavorable, when the crop matures and the leaves senesce, and when the crop is deficient in nutrients (Hsiao, 1975)

The ratio of crop ET to ET_o is known as the crop coefficient (K_c):

$$ET = K_c ET_o$$

Since ET_o is an expression of the effect of the weather on ET, K_c then is a measure of the "wetness" of the surface of the field, and of the roughness of the field.

Pattern of Water Use by Annual Crops

An example of the pattern of ET of an annual crop over much of the season is given in Fig. 1. Although the effects of day-to-day variations in weather on ET are discernible, features attributable to the development of crop canopy cover and soil surface wetness stand out. For the first half of the graph, there is a gradual rise in base-line ET. Added to this base line are several ET peaks occurring at more or less regular intervals, after each irrigation. The peaks are due to evaporation from the soil surface after it is wetted by the irrigation water. As the soil surface begin to dry one or two days after an irrigation, evaporation declines. The basal ET is due to evaporation from the partially dry soil surface, and transpiration from the crop. In the first two or three weeks after planting, the plants have only very few leaves and the canopy covers only an insignificant portion of the ground. Therefore soil evaporation accounts for virtually all of the ET. As the canopy of the crop develops, more and more of the ground is covered by the canopy, which continues to transpire regardless of the wetness of the soil surface, as long as the crop is obtaining sufficient water from the deeper part of the soil to keep its stomata open. Hence, base line ET rises with time in Fig. 1, until the canopy fully covers the ground.

With full ground cover, the canopy intercepts nearly all the radiation energy and accounts for most of the ET. Soil evaporation is insignificant. ET is then insensitive to the wetting of the soil surface under the canopy, and hence is not affected perceptively by irrigation. In Fig. 1, the soil was mostly covered by the crop canopy about 55 days after planting. There were therefore no marked irrigation spikes in ET after that time, in spite of the irrigations. At the end of the time period depicted in Fig. 1, the older leaves of the canopy began to turn yellow. This senescence apparently accounted for the decline in ET at that time. The dip in ET on days 54, 66, 74 and 75 after planting were the result of cloudy and cool weather.

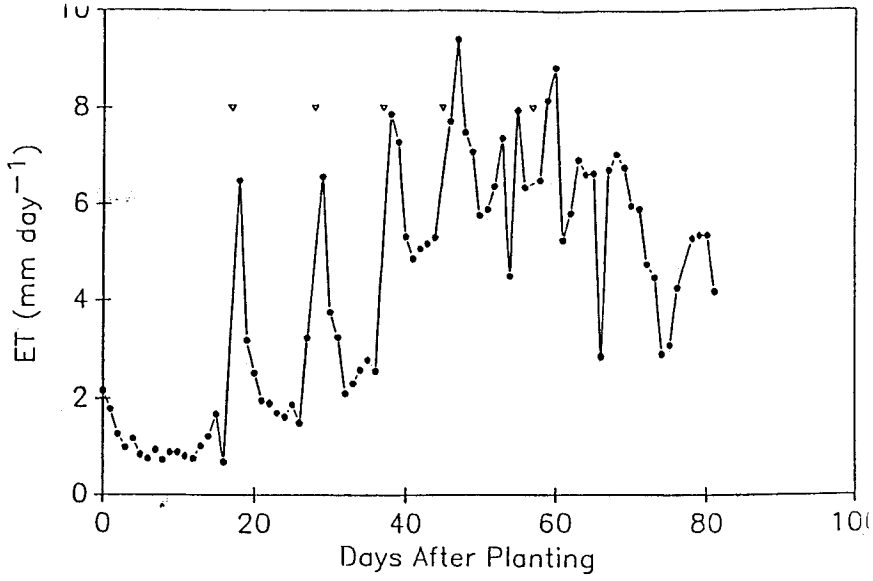

Fig. 1. Evapotranspiration of a bean field over growth stages and as influenced by irrigation at Davis, California. Summer, 1982
Arrows indicate the days of sprinkler irrigation. Beans were planted on a large (6.1 m diameter) weighing lysimeter and in the surrounding field at a spacing of 76 cm between rows.

PRODUCTIVITY IN RELATION TO WATER USE

Productivity of a crop is inextricably linked to its transpirational use of water (De Wit,1956). For the production of biomass, this linkage appears to be fundamental, and lies in the closely coupled relationship between transpiration and carbon dioxide assimilation.

Transpiration in Relation to CO_2 Assimilation

Biomass production is the cumulative result of net photosynthetic assimilation of CO_2 from the atmosphere. Photosynthesis and transpiration have much in common. Both processes depend on the capture of radiation, and both involve the transport of gas (CO_2 and water vapor, respectively) through the stomatal pores of the leaf and the calm boundary layer of the air surrounding the leaf. These interrelations are depicted in Fig. 2. The amount of radiation absorbed by the crop is shown to be dependent on the intensity of solar radiation. In addition, radiation capture is shown to be dependent on the effective crop-absorbing area per unit land area, which in turn is affected by leaf area per unit of land area (leaf area index, LAI), the

geometry of leaf display, and spatial distribution of the plants (planting pattern). The development of leaf area is most important for the capture of radiation for photosynthesis and maintenance of high productivity. How water stress reduces productivity by restricting leaf area is discussed in a later section of this paper. Changes in either the radiation level or effective or radiation absorbing area will affect transpiration and CO_2 assimilation similarly. The fact that photosynthesis uses only radiation in the wavelength range of 350 to 700 m, (photo-synthetically active radiation, PAR) in

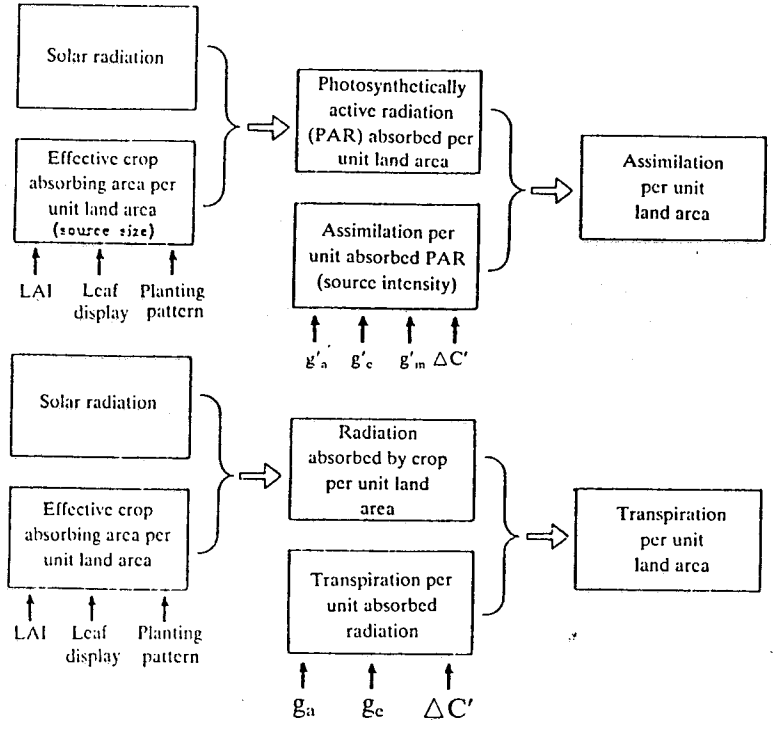

Fig. 2. Factors affecting CO_2 assimilation and transpiration per unit land area

LAI is leaf area index: g_a' and g_a is boundary layer conductance to CO_2 and water vapor, respectively; g_c' and g_e is epidermal (mostly stomatal) conductance to CO_2 and water vapor, respectively; g_m' is mesophyll or metabolic conductance to CO_2; $\Delta C'$ is the gradient of CO_2 from the bulk air to the cellular carboxylation site; ΔC is the gradient of water vapor from the intercellular space to the bulk air. Note the many common features shared between assimilation and transpiration. (Modified from Hsiao and Bradford, 1983).

contrast to the use of radiation of all wavelengths for transpiration, does not significantly weaken the similarity between transpiration and assimilation because outdoors the ratio of PAR to total radiation is quite constant.

In addition to the absorbed radiation of appropriate wavelength, CO_2 assimilation and transpiration are also dependent on the transport of CO_2 and water vapor, into the leaf and out of the leaf, respectively. Each of these transports is determined by two parameters, the ability of the pathway to conduct the gas, termed conductance (inverse of resistance) and symbolized by g, and the driving force for the transport, symbolized by ΔC. ΔC stands for the difference in concentration of the gas between its upstream source and downstream sink. In Fig. 2, the parameters of g and ΔC are primed for CO_2 (g′ and $\Delta C'$) and left unprimed for water vapor. The conductance for CO_2 differs from the conductance for water vapor by only a constant. In fact, g= 1.6 g′. When stomata close partly, the passage way for CO_2 and water vapor becomes more restrictive, and the consequent decrease in epidermal (mostly stomatal) conductances ge′ and ge will reduce assimilation and transpiration simultaneously. When the wind dies down, the calm boundary layer of air surrounding the leaf becomes thicker and there is less turbulence to transport the gas to or from the leaf. This is expressed as reductions in ga′ and ga, leading to the partial suppression of both asimilation and transpiration.

The many common features shared between CO_2 assimilation and transpiration (Fig.2) presumably account for the frequently observed linear relationship between biomass production (De Wit, 1958) or yield (Hanks, 1983) and cumulative ET, when productions were altered by variations in water supply.

Photosynthetic Water Use Efficiency

Photosynthetic water use effiency (WUE) of a crop may be defined as the ratio of net CO_2 assimilation to transpiration. The linear relationship between biomass production and cumulative ET, mentioned above, suggests that in those cases, photosynthetic WUE is essentially constant in spite of the variations in water supply. Again, this is apparently the result of the many common features shared between assimilation and transpiration. However, Fig.2 also depicts some features not shared between the two processes, and these distinguishing features may offer the opportunity for manipulation to improve crop WUE. It has already been pointed out that photosynthesis uses only a part of the radiation spectrum, instead of the whole as transpiration. Unfortunately, the evidence so far indicates that it would be extremely difficult to reduce the absorption of radiation in the

non-photosynthetic wavelength range without reducing PAR in a similar way. An outstanding example is the spectral characteristics of leaves with thick leaf hair (pubescence), evolved in some plant species as a means of adapting to hot deserts. Ehleringer and Bjorkman (1978) showed that these leaves reflect as much the PAR as the radiation of longer wavelengths (infrared range).

Another distinction between assimilation and transpiration is the driving force for the transport of the respective gases. The driving force for CO_2 transport and assimilation, $\Delta C'$, is the difference in concentration of CO_2 between the atmosphere and the biochemical site of CO_2 fixation in the leaf. The driving force for water vapor transport and transpiration, ΔC, is the difference in concentration of water vapor between the leaf interior and the atmosphere. If assimilation is increased by increasing $\Delta C'$ while transpiration and ΔC are little affected, then photosynthetic WUE will increase. Plant species possessing the four-carbon pathway of photosynthesis (C_4 species) have generally lower CO_2 concentrations in the leaf interior and hence larger $\Delta C'$ than C_3 species. WUE is therefore higher in C_4 species as a rule. It is also well-established that WUE can be increased by CO_2 enrichment of the air (e.g., Carlson and Bazzaz, 1980), which increases $\Delta C'$. Although elevated CO_2 has long been used to enhance production in greenhouses, it is not a practical means to increase WUE in the open field. On the other hand, the unrelenting rise in global atmospheric CO_2 will improve WUE worldwide in time.

The difference in water vapor concentration being the driving force for water vapor transport, transpiration would be much reduced while assimilation is little affected if ΔC is reduced substantially by raising the humidity of the atmosphere. Thus, it may be tempting to conclude that WUE would be considerably higher in more humid climates. This, however, overlooks the fact that energy supply is the dominant factor in determining ΔC and transpiration. For a crop in a moderate to high radiation environment, higher air humidity will result in a warmer leaf temperature, as dictated by the principle of energy balance. Water vapor concentration in the leaf interior will rise because of the higher leaf temperature, partially offsetting the reduction in ΔC achieved by the increase in air humidity. This apparently is the reason for the rather modest improvements in WUE observed under conditions of low ΔC (Bierhuizen, 1976).

The other distinction between assimilation and transpiration depicted in Fig. 2 is mesophyll or metabolic conductance, g_m'. This term, present only in the CO_2 transport path, is a lumped parameter representing the coefficients for the dissolution of CO_2 at the cell wall, diffusion of the dissolved CO_2 to the carboxylation site, and the biochemical aspects of photosynthesis. In many ways, g_m' represents the photosynthetic capacity of the leaf. Changes in physiology that enhance photosynthesis, such as improved nitrogen nutrition, tend to raise g_m'. With a higher g_m', WUE would be higher. C_4 plant species have generally a higher g_m' than C_3 species. This difference contributes also to the higher WUE of C_4 species.

With the exception of the situations where $\Delta C'$, ΔC, or g_m' are altered, the commonality shared between assimilation and transpiration (Fig.2) makes it difficult to uncouple the primary or biomass productivity of a given crop from its transpiration. When transpiration is reduced by water deficits, biomass production inevitably slows in approximate proportion and photosynthetic WUE remains fairly constant.

Harvest Index and Yield Water Use Efficiency

With many crops, the valued product is not the total biomass, but only a portion of it, such as the grain or fruits. The yield of grain or fruits is dependent on the total biomass produced, as well as on the partition of the biomass to the desired harvestable product. The commonly used indication of this partition is **harvest index (HI)**, the ratio of biomass of the harvested yield to the total biomass or above-ground biomass. Because root biomass is difficult to measure in the field and constitutes only a small portion of the total for crops, most of the studies report only the above-ground biomass. Instead of biomass, it is theoretically better to measure productivity and partition in units of energy or glucose equivalent, to account for differences in energy contents of diverse compounds (e.g., starch vs. oil vs.protein) making up the harvested products. Unfortunately, information is often insufficient to allow the calculation of glucose equivalents and biomass remains as the common measure.

While biomass WUE is difficult to alter and tends to be insensitive to water deficits, yield WUE can be markedly affected by water deficits through changes in HI. An extreme example would be the case of rice, which has a very shallow root system and therefore can develop severe water stress quickly under drought when grown under upland conditions. Severe water deficits at the time of anthesis inhibited pollination and reduced HI and yield drastically (Hsiao, 1982), while the effect on biomass production was slight since the stress period was only for a few days. The literature on irrigation emphasizes the importance of maintaining high soil water status at the time of anthesis, to avoid such reductions in yields. The need, however, may be overstated because pollination is inhibited only when water stress is very severe, as is discussed below.

On the other hand, HI, and hence yield WUE, can be raised by mild water deficits in some cases. An outstanding example is the case of cotton. Under mild water stress, the plant restricts its foliage growth and sets and retains the early fruits (Hearn, 1980). In contrast, a plant well-supplied with water sheds the early reproductive structures, produces much foliage, and sets fruits only later. In locations where the growing season is short, cotton well-supplied with water would at harvesting time still be partly vegetative and with many of its bolls still green. Its HI would be low, as would be its yield WUE. In contrast, cotton subjected to mild water stress from mid-season over the reproductive phase would have fewer but more mature bolls, a higher HI, and a higher yield WUE.

Although this discussion focuses on significant changes in HI effected by changes in plant water status, it should be pointed out that for some crops (e.g., maize), HI is relatively constant with or without water stress, as long as the stress is not severe, and when factors other than water are not limiting.

Water Stress at Different Growth Stages and Productivity

The discussion of the previous section points to the need to consider the timing and severity of water stress in more detail when dealing with productivity. Depending on its timing relative to the growth stage of a crop and its severity, water stress can reduce the net CO_2 assimilation and yield of the crop in different ways and to different extents. The acquisition of assimilates and their partition to the harvestable organ are often considered in terms of sources of assimilates and sinks for assimilates. Source refers to the photosynthetic organs, mainly leaves, and is considered in terms of its size (effective area per unit of land area), and its intensity (rates of photosynthesis per unit of effective leaf area). Sinks for assimilates include vegetative growing points, as well as fruits and storage organs. From the point of view of production and yields, the important sinks are harvestable organs, such as fruits and tubers. In that case, sink size refers to the number of reproductive or storage organs per unit of land area with the potential of growing to harvestable yield. Sink strength refers to their ability to draw assimilates from the sources. For simplicity, sink strength is not considered further in this discussion.

The effects of water stress at different times of crop development on assimilation and assimilate partition are conceptually depicted in Fig. 3 for an annual grain or fruit crop. The depiction is within the context of source-sink relationships and emphasizes the relative sensitivity of the various productivity components to water stress. Overall assimilation is the product of source intensity times source size integrated over the time span in question. Adequate sink size is important for the partition of the maximal permissible amount of assimilate to fruits for high yield.

The arrows in Fig. 3 point to the effects of water stress, with the width of the arrows indicating the relative sensitivity of each process to water stress. The growth stage when the effect occurs and is important is indicated by the location on the time scale. Much attention has been directed at effects of

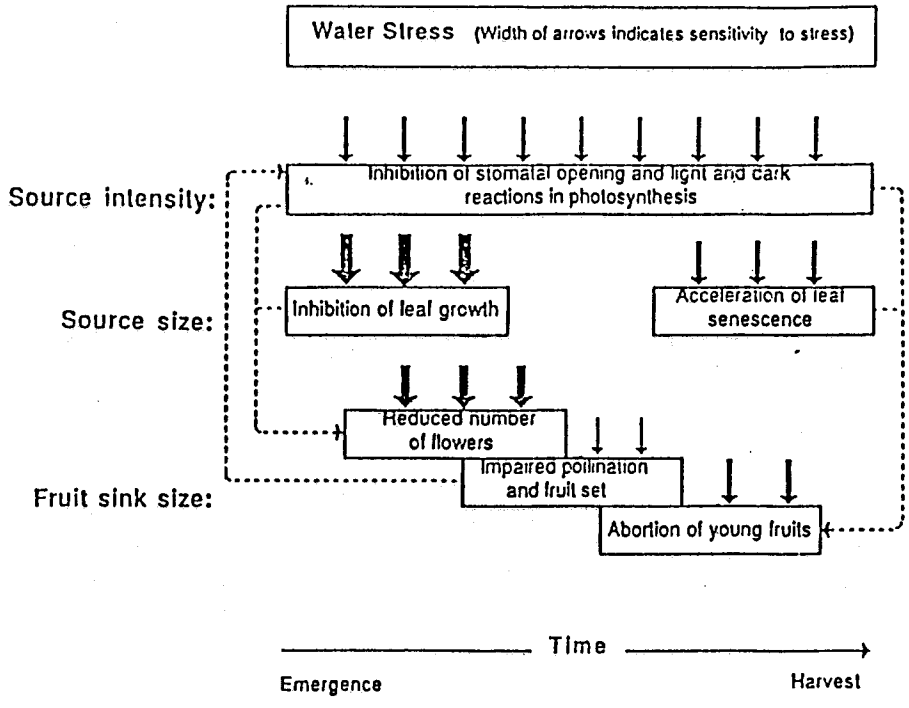

Fig. 3. Effects of water stress on parameters underlying source intensity, source size and sink size for assimilation at various times of ontogeny, generalized for annual crops grown for grain or fruit

The time intervals within the crop ontogeny when water stress can cause physiological and morphological changes are indicated by the locations of the outlining rectangles. Solid short arrows point to the changes. Arrow shaft widths indicate the sensitivity of the parameter to water stress. For example, leaf growth is the most sensitive to stress; flower number is the next most sensitive. Dashed arrows and lines (--->) indicate causal relations among the parameters. For example, inhibition of leaf growth, of stomatal opening, and of photosynthesis results in fewer flowers being differentiated. (After Hsiao, 1982).

water stress on the rate of photosynthesis per unit leaf area (source intensity). However, the effects on source size are more critical (Bradford and Hsiao, 1981). Because expansive growth of leaves is very sensitive to even mild water stress, source size is suppressed much more by water stress than is source intensity. When water stress occurs during the canopy development phase (Fig.3), canopy size can be reduced to a small fraction of that of the well-watered control. The impact on assimilation and productivity would be dramatic, since only a small fraction of the sunlight would be captured by the canopy for photosynthesis. Also, reductions in source size can be reversed only slowly, if at all, when water becomes available again. This is in contrast to source intensity, which usually recovers fully in a matter of one to a few days after rewatering. Another effect of stress on source size is the accelerated senescence of older leaves (Fig.3), leading to a smaller source size. Under field conditions, senescence appears to be slightly more sensitive to water stress than is source intensity. Because senescence is induced by water stress mostly at the maturation stage, the impact on yield can be marked. Total assimilation would be substantially reduced by the reduction in source size, as well as by the likely reduction in source intensity. As the consequence, biomass production declines prematurely. Since this occurs just at a time when nearly all of the assimilates are directly partitioned to the fruits, a lower HI is often the result, adding to the deleterious impact on yield.

The number of flowers per unit of land area is the second most sensitive to water stress, as indicated by the width of the solid arrows in Fig. 3. This is most likely the result of the extreme sensitivity of leaf and canopy growth to water stress. Geometrically, the number of sites for the formation of reproductive structures on a plant is clearly related to the size of its canopy. Physiologically, the number of fruiting sites must be dictated to some degree by the assimilates potentially available and hence by source size. This apparent causal relationship is indicated by the dashed line and arrow going from leaf growth to the number of flowers in Fig. 3.

Obviously, the number of flowers has an impact on sink size. In addition, sink size is affected by the success of pollination, and by the abortion of young fruits (Fig.3). As mentioned earlier, pollination and fruit setting are not as sensitive to water stress (Westgate and Boyer, 1986) as previously believed. In fact, among the processes depicted in Fig. 3, pollination and fruit setting appear to be the least sensitive of all. Only when water stress was very severe was pollination directly inhibited, as mentioned in the previous section for the case of upland rice. The early erroneous belief was partly based on reduced grain number per head when water was withheld at flowering time. It turned out that much of this reduction is due to the abortion of young fruits, and not to the failure of pollination (Hsiao, unpublished). When irrigation is withheld at flowering time, the crop first depletes the water stored in the soil. Only later does it suffer water stress, during the time of grain filling and maturation. This late-stage water stress then induces leaf senescence and the consequent decline in source size, probably also accompanied by a reduction in source intensity. The diminished assimilate supply then leads to the abortion of young fruits, as indicated by the dashed line and arrow in Fig. 3.

In terms of irrigation strategies for annual crops, plant water status should be managed to:
(i) speed up the development of canopy or source size early in the season;
(ii) enhance source intensity;
(iii)maintain the source size late in the season; and
(iv)enhance sink size.

Irrigation scheduling should be in accordance with the differential sensitivity to water stress of the different processes at the various growth stages, as depicted in Fig. 3. To encourage the rapid development of canopy, plant water status should be kept high early in the season. Once the canopy is complete and the crop is capturing most of the sunlight for photosynthesis, plant water status may be allowed to drop somewhat, but still kept high enough so that stomatal opening and photosynthesis per unit of canopy cover are not inhibited. Because pollination is more resistant to water stress, there is no need to apply additional irrigation water at the time of flowering, as long as photosynthesis is maintained. During the maturation stage, irrigation should not be cut off too early, to ensure that there is no premature senescence induced by water stress. When irrigation is well-managed, the amount of water applied would closely match the water requirement of the crop, photosynthetic assimilation of CO_2 would be maximized over the course of the season, and the harvestable organ of the crop would be maintained as large and strong sinks to ensure high production.

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