Interactions of Physiology with Multiple Environmental Stresses in Horticultural Crops

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In spite of the need to simplify the plant-environment complex experimentally, understanding plant responses to multiple stresses in the field requires a very broad perspective. The important plant processes of interest and the organizational level (i.e., molecular, cellular, tissue, organ, plant, or crop level) must be clearly defined. Varying sensitivity at different stages of plant or organ development can have a large effect on plant response to environment and must be understock Morphological or anatomical variations and/or adaptations may modify the environment actually sensed by a tissue and may play an important intermediary role between the environment and the resulting physiological responses. Physiological adaptations to multiple stresses in the environment are central to the variations seen in plant responses to stresses. There is a need to evaluate how such adaptations are manifested on the whole-crop level. Since production of fruit or seed is central to horticulture, the interactions of cropping and plant responses to stresses need to

be understood better. Integration and interpretation of the breadth of data needed in studies of the plant-environment complex requires a broad perspective, a pursuit of principles rather than limited "rules of thumb", and an increasing use of systems modeling.

The study of the effects of environmental stresses on plant performance has yielded much information in the past few decades; yet, many of these results have been inconsistent or apparently contradictory. Since initial research on any problem requires a narrowing of the possible complicating factors to develop understanding of given processes, there have been many "single stress/single process" studies (e.g., water stress effects on stomatal conductance) reported in the literature.

As the complexity of the plant–environment system has unfolded, we have realized that the results of these apparently simple studies are very difficult to interpret due to the lack of other measurements of plant status or environment. When these studies are conducted

in the field, the natural dynamics of essentially all environmental factors raises the level of complexity dramatically and makes measurement under comparable conditions difficult to achieve. An additional level of complexity is added for those working on perennial crops that carryover environmental and internal effects from year to year.

The discussion of the complexity of studying environmental physiology is not designed to discourage, but to acknowledge the complexity of the plant-environment systems we are trying to characterize. This paper will provide some examples of how the physiological status and morphological characteristics of the plant may influence its response to the complex of environmental factors encountered in the field. Because of the complexity just described, the examples in the area of water, radiation, and high-temperature stresses are meant to be illustrative and simply reflect my lack of knowledge of the complexities of cold temperature, flooding, salinity, pollutant, and nutrient stresses.

Definition of plant processes of interest

Before any discussion of plant responses to any factor can be considered, a clear definition of which plant process is of interest is needed. It has been known for some time that different plant growth stages or physiological processes exhibit different sensitivities to given stresses (Hsiao, 1973). In studies in our laboratories on effects of soil water stress on grapevines in the field in New York, we have found that varying soil water status greatly affected vegetative growth. The yields, however, were little-affected until quite severe stresses developed. The soluble solids concentrations of the berries showed almost no response to the soil water stress.

Additionally, whole-plant or whole-crop processes, such as yield, may respond quite differently to a stress compared to the individual components (leaf area development or photosynthesis, for example). A particularly good example is that of whole-crop transpiration and its component, crop conductance (primarily stomatal). If the crop is low and dense, such as a grass, a high crop boundary layer against water vapor movement can develop. This makes crop transpiration almost independent of crop conductance over a very wide range of stomatal opening (McNaughton and Jarvis, 1983; Jarvis, 1985). Thus, a stress that causes a 50% reduction in stomatal conductance may have little effect on whole-crop water use of short, dense crops, while having a major effect in forests or orchards. If winds, however, decrease the crop boundary layer, the grass or field crop will respond similarly to that of the forest or orchard. Therefore, the importance of stomatal behavior (and, thus, studies of stomatal behavior!) to crop water use would be expected to be greater in taller crops and on shorter crops in windy areas.

Research in crop physiology, especially dry matter productivity, has pointed out the lack of correlation of photosynthetic rate per leaf area to yields in most cases. This situation occurs because of the overall dependence of biological and economic yield on leaf area development, duration, and the resulting light interception, not just photosynthetic rate per leaf area (Evans, 1983; Monteith, 1977; Gifford and Jenkins, 1982; Good and Bell, 1980; Gifford et al., 1984). A particularly good example of how these principles apply is that of the effect of drought on productivity of barley in a study by Legg et al. (1979). They measured crop leaf area development, light interception, photosynthesis, quantum efficiency, and stomatal conductance throughout a season with several timings of drought. Their conclusions were that, for all treatments, the major limitation of yield induced by drought was the reduction in light interception. Limitations on photosynthesis and stomatal conductance had their maximum relative effect if the drought occurred late, after canopy closure.

In relation to the above discussion, the choice of plant material and growing conditions must be considered. There is a strong tendency to simplify experimental designs and reduce required resources (space, time, etc.) by using seedlings, or small plants grown in a greenhouse or growth chamber. Although most conditions are better controlled (CO_2 is a notable exception), the researcher must ask if a small plant in a growth chamber is a valid model of a mature plant in the field with respect to environmental responses. I do not believe it is safe to assume that they necessarily are valid models. We have found that potted apple trees, even growing outside, showed little osmotic adjustment, while nearby field trees showed >2.0 MPa of adjustment. In many cases, a brief comparison of water and osmotic potentials plus leaf conductance or photosynthesis between the model plants and field plants can provide useful information in this regard.

These examples are provided to encourage a) a clear definition of the goals of research in environmental physiology of horticultural crops and b) an evaluation of which processes are in fact limiting the productive process of interest.

Stage of plant development

The most obvious way in which the physiology of the plant will affect responses to environmental stresses is the stage of development. Dormant seeds or plants are notoriously resistant to many stresses, but the emphasis here will be on the active growing season. In addition to the chronological stage of development of the plant, the relative sensitivities of different plant processes or organs to stresses at different times is important.

In the study of the drought effects on barley productivity discussed earlier (Legg et al., 1979), it was found that the timing of drought was important to yield; early drought had greater effect than later drought. In this case, though, the investigators found little effect of drought timing on partitioning to the grain. This is not true for many crops. Typically, in fruit crops, stresses that occur before or during the flowering and post-bloom cell division periods have disproportionate effects on yields via decreased numbers of fruits and likely reductions in cell numbers of the remaining fruits (Powell, 1974, 1976). Later stresses will typically reduce final fruit size or quality (and, thus, economic yield) more than total yield. These factors have led to grower recommendations that irrigation is most critical in the early season (Goldhamer, 1988).

In some crops, especially fruits with double-sigmoid growth patterns, periods occur when the stress resistance of fruit development is quite high. The growth of the grape berry is a good example. During the first period of development through cell division, berry growth is quite sensitive to soil water deficits. However, during the lag phase and in the early part of the final growth phase, berry growth has been found to be surprisingly insensitive to water deficits (Hardie and Considine, 1976; Freeman and Kliewer, 1983). In peach, the resistance to water deficits during the lag phase also occurs, but the third stage of rapid growth becomes sensitive again (Chalmers et al., 1981). Pear fruit growth exhibits a different pattern in that fruit growth appears to be relatively resistant to water deficits for about the first third of the season, while fruit is growing slowly (Mitchell et al., 1984).

These periods of stress resistance provide management opportunities to reduce water use and/or use imposed stress to manage excessive vegetative growth. In many crops, especially fruit crops, there are important localized light exposure requirements for best yield and quality (Jackson, 1980; Smart, 1985). The limitation of leaf area development to the level that is sufficient for good light interception, but does not cause excessive within-canopy shading, can lead to optimal yields and quality. Ironically, one stress (water deficit) can be used to alleviate another stress (within-canopy shade) to optimize productivity.

The role of leaf and plant morphology

There are a multitude of morphological differences among crop plants, all of which probably influence plant response to imposed stresses to some degree. Although extreme cases, such as cacti, are rather obvious adaptations for survival in stressful environments, most crop species are somewhat more mesophytic in morphology and have been selected for high productivity, not only survival. It is worthwhile to examine some examples of how the morphology of our crops may affect stress responses or even induce additional stresses.

As mentioned earlier, the mass and energy exchange as influenced by the stature and continuity of the crop canopy and the environment may be important to whole-crop response to a stress

such as water deficits. Jarvis (1985) has suggested that this aspect should be considered when extrapolating stress response data from studies done on plants grown in different conditions (e.g., results from isolated plant studies being applied to closed-canopy crops). Changing canopy densities or closing spacings of fruit trees from discrete rows to closed beds may change the characteristics of the crop in such a way that old stress response results may not apply.

Plant form management, such as training systems of fruit crops or different genotypes of vegetables, can modify stress effects by influencing total and/or diurnal patterns of light interception. Broad, horizontal canopies such as V or T forms may intercept high amounts of radiation, which leads to large amounts of transpirative water use. Additionally, the stress levels in these plants may be greater in mid-day due to the high light interception at that time. On the other hand, thin vertical canopies will generally intercept less total light, especially if east-west-oriented, and tend to have somewhat less mid-day stress due to the lower light interception at that time (Jones et al., 1985).

Leaf size is another morphological characteristic of importance to the interactions of stresses. An important consequence of leaf size is that heat transfer by convection from leaves is strongly dependent on leaf size. Large, round leaves, such as of kiwi or 'Concord' grape, do not exchange heat effectively with the bulk air unless there is significant wind. Narrow leaves, such as olive or conifer needles, are very effective at heat exchange with the air. This difference is significant because the regulation of leaf temperature is much more dependent. on high stomatal conductance and transpiration rates in large than in small leaves. This dependence is apparent in the relation of kiwi leaf temperatures to stomatal conductance on a hot sunny day (maximum 40C), in which healthy, transpiring leaves (leaf conductance of 200 $\mu mol \cdot s^{-1} \cdot m^{-2}$) were 34C, while leaves with half the conductance were 40C. So, if another stress reduces leaf transpiration, large-leaved species may have the added stress of excessive leaf heating.

This situation has been found to be true in 'Concord' grape leaves under two situations. Soil moisture stresses that reduced transpiration led to leaf heating and, ultimately, leaf burn. Similarly, the stress of long periods in the shade of heavy canopy reduces both photosynthesis and transpiration of leaves. When re-exposed to full sunlight in mid-season after shoot positioning practices, these leaves could not transpire rapidly, and they heated 6 to 10C above normally exposed leaves. This type of re-exposure occurs when summer pruning or shoot positioning is done in mid-season in several fruit crops.

Of course, this phenomenon also occurs at low temperatures. In this case, a large-leaved species such as kiwi will have warmer tissue temperatures that may lead to greater rates of growth in the low temperatures of spring. On a calm day with the air at 18C, we have found the temperature of a 'Concord' grape canopy to be about 24C as measured with infrared thermometry. Under cold conditions, this leaf heating may help to ameliorate the effects of low temperatures. Such considerations may be helpful as new crops are being evaluated for development in new growing areas.

Plant adaptations

By definition, an adaptation to a stress is essentially a change in the response of a plant to that stress. There are a multitude of adaptations that occur in crop plants that must be understood to be able to explain and, ultimately, predict plant responses to stresses.

The acclimation of perennial crops to cold temperatures in the autumn through the onset of dormancy and cold hardiness is one of the most outstanding examples of the plant changing its response to the environment. However, because many crops are not perennial and adaptations during the growing season are not so clear, another example will be used.

Among the many responses of plants to water deficits, osmotic adjustment is one that has attracted much attention in the past 15 years (Turner and Jones, 1980; Morgan, 1984). Osmotic adjustment, in which the osmotic potential changes in the same direction as total potential, will ameliorate the effects of changing total water potential on turgor. If processes, such as cell expansion or stomatal opening, are at least partially dependent on turgor, osmotic adjust-

ment may be important to maintenance of these processes under stress conditions. This adjustment may occur actively by the regulation of osmotic solutes or passively by the dehydrative effects of lowered cell water contents with decreasing total potentials.

Although some fruit crops show limited osmotic adjustment, mature leaves of apple can osmotically adjust markedly during a season (Goode and Higgs, 1973; Lakso et al., 1984), even when measured at full turgor in the early morning (Fig. 1). This adjustment correlates well with a change in the leaf water potential required to close stomata (Lakso, 1979; Lakso et al., 1984). Thus, the response of stomatal opening to water deficits may vary greatly over the season in mature apple leaves.

The young, expanding leaves and shoot tips, however, respond quite differently to water deficits. These organs have much less negative osmotic potentials than mature leaves and do not demonstrate significant osmotic adjustment over time. This difference likely is due to the transient nature of immature leaves and the synthetic growth activities that use solutes rather than accumulate them. The consequence of the differences between these parts of the shoot is that leaf area development rates and shoot growth tend to respond almost directly to increasing water deficits while mature leaf gas exchange is maintained. This appears to be an effective set of responses that restrict the production of new transpiring surfaces while maintaining the carbon productivity of the remaining leaves.

In addition to the long-term soil water deficits that can occur, the apple tree undergoes diurnal evaporative stresses. The relatively low conductivity for water transport within the tree leads to large soil-leaf water potential gradients that are needed to supply the high transpirative fluxes. The differences in evaporative demand in relation to exposure to radiation causes an additional gradient of leaf water potential across the canopy, with the best-exposed leaves having the lowest potentials. Shaded leaves in the interior of the canopy transpire less and are typically closer to the root system; thus, less negative leaf water potentials develop. These diurnal differences in leaf water potentials caused by different exposures are compensated for by diurnal osmotic adjustment, resulting in essentially no difference in mean turgors across the canopy. This ad-
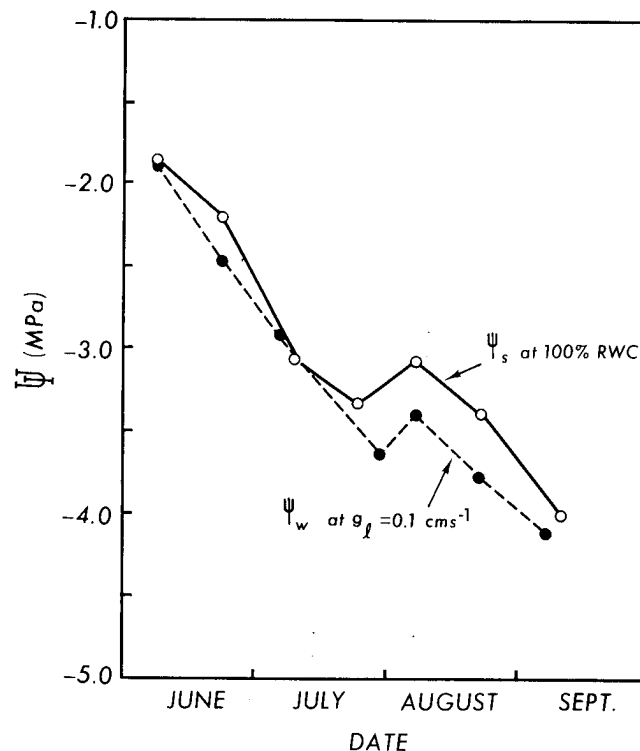

Fig. 1. Seasonal changes in apple leaf osmotic potentials at full turgor (100% RWC) compared to the leaf total water potential of excised leaves required to close stomata to a conductance of 0.1 cm·s⁻¹ (from Lakso et al., 1984).

justment results from greater levels of dehydration as well as more mid-day solute accumulation in the exposed leaves.

These examples demonstrate how a given adaptive process, such as osmotic adjustment, may play both short- and long-term roles in modifying stress responses of some organs (mature-leaves) while having little role in the response of other organs (shoot tips). The challenge of future research will be not only to identify such adaptations, but also to determine which adaptations play a major role in the whole-crop responses to the field environment. This knowledge is needed to maximize the efficiency of efforts to improve plant resistances to stress in the field, whether by cultural practice, conventional breeding, or genetic engineering.

Influence of cropping

The production of a fruit (in the broad sense) or seed is fundamental to most horticultural crops. Yet that production may be viewed as a stress on the rest of the plant. This view is especially important to perennial crops, which must maintain an adequate vegetative structure and associated reserves from season to season. Unfortunately, little research has been conducted on the interactions of cropping and other stresses. The research on the effects of cropping on the growth and physiology of the rest of the plant, however, suggests some possible interactions that we can examine.

A study of the effects of cropping on apple tree growth and water use by Lenz (1986) confirmed earlier work (Maggs, 1963; Hansen, 1971) that cropping inhibits growth of all vegetative organs, but growth of roots typically is reduced the most by cropping (Fig. 2). When cropping was delayed until a larger vegetative structure was developed (2 years without crop), the cropping increased total dry matter production over the noncropped trees. When cropping was allowed to occur sooner (in the second year), the vegetative development was inhibited to the point of reducing the total dry matter production, although it still was higher than for the noncropped trees. Total water use by the trees paralleled the dry matter production patterns even though the leaf area fell to 70% and 50% of the noncropped trees for single-year- and double-year-cropped trees, respectively.
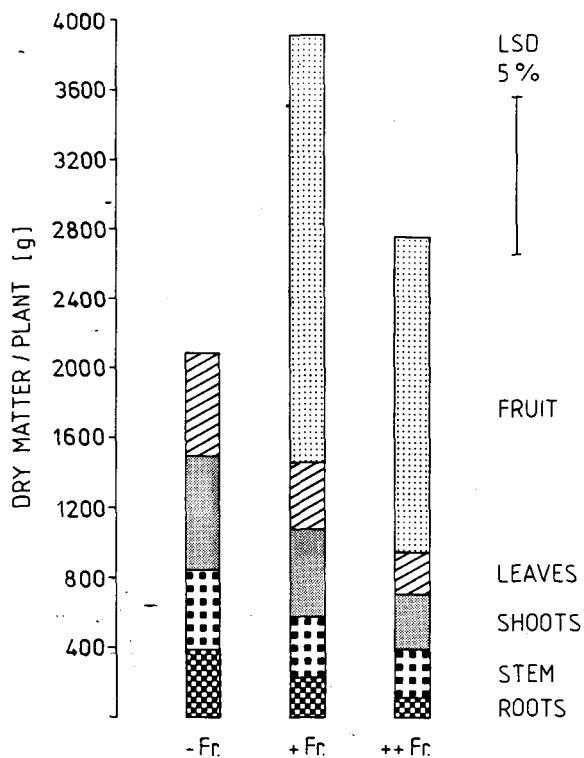
The negative effects of cropping on root development, combined with increased water use (per plant or leaf area), would be expected to increase the susceptibility of the tree to environmental stresses, especially water and heat stress. Practical recommendations on irrigation typically suggest that more water be applied to cropping trees than noncropping trees, but it is not clear whether this advice is based on different sensitivities of the trees to stress as well as on the need to maintain high water status for maximum fruit size. Such interactions are not easy to determine, and ultimately may be overriden by the economic need to produce large fruits. In the future, if more droughts occur and irrigation water is limited or not available, there will be a greater need to understand how cropping affects tree performance in both the short- and long-term to optimize the use of resources by the grower.

Interpretation of results

The examples given in this paper and the others in this colloquium have indicated. the complexity of studying multiple environmental stresses in horticultural crop systems. Proper interpretation of how such stresses affect our crops requires the collection of a broad range of data within a given experiment. This aspect is critical, since plant responses to an environmental stress may be modified by a wide range of other environmental factors, prior conditioning, and internal factors that must be considered. Once the data are gathered, a broad knowledge of the major physiological processes (on the biochemical, organ, plant, and crop level) is needed. Narrow perspectives lead to narrow interpretations that have limited generality.

To improve the efficiency of our research, whether in environmental physiology or any discipline in horticulture, it is imperative that much greater emphasis be placed on determining the general principles of crop behavior, not just determining single localized responses or convenient "rules of thumb" that only apply in some circumstances. By elucidating the underlying principles of plant response and adaptation to the environment, we will be better able to clarify apparent conflicts of results and to extend our results to other conditions. There is much that can be gained by examining the principles that have evolved from a broad range of other disciplines, such as agronomy, ecophysiology, and forestry.

Finally, the complexity of environmental stress research will increase the need for greater use of systems modeling to be able to deal with multiple interacting factors simultaneously. This approach should be helpful because modeling forces the researcher to unambiguously describe the system of interest and quantify the important relationships. This exercise is particularly useful to help the researcher evaluate the relative importance of each factor to system behavior and to help define specific testable hypotheses for further research. Recently, simulation modeling programs (such as "Stella" and "Extend") that essentially program automatically have become available. These programs will open many more opportunities for modeling in horticultural research because extensive programming expertise is much less critical. I foresee an exciting period for the research on effects of multiple stresses on horticultural crops.

Fig. 2. Dry matter gain of different organs of apple trees at the end of 3 years with no fruiting allowed (−Fr), fruiting in the 3rd year only (+Fr), or fruiting in the 2nd and 3rd years (++Fr) (from Lenz, 1986).

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