
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 understood. 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 (CO₂ 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