Chapter 9

Plant Physiological Disorders

Robert C. Morrow and R.M. Wheeler

CONTENTS

INTRODUCTION

Physiological disorders of plants are those problems resulting from the influence of environmental and cultural factors on plant development. A number of physiological disorders arise in controlled environment facilities because environmental and cultural conditions in these facilities often are significantly different from those encountered by plants in the natural environment. Factors implicated in the occurrence of physiological disorders include irradiance (intensity, photoperiod, and spectral quality), humidity, CO_2 concentration, air temperature, air movement, growing medium temperature and moisture level, and mechanical effects. This chapter does not discuss disorders related to the mineral nutrition of plants (Robinson, 1984), disorders related to postharvest physiology (Snowden, 1990), disorders related to contaminants in the air or growing medium, or disorders arising from extreme conditions outside the tolerable limits of a particular species (see Chapter 5).

Effects of physiological disorders range from subtle symptoms not visibly apparent to severely stunted and malformed growth. In some cases, the effects can be severe enough to limit the effective use of controlled environment facilities for research and commercial production of some species. Unfortunately, physiological disorders usually are difficult to indentify and correct, and concise information concerning them often is not available. The purpose of this chapter is to describe some physiological disorders observed in controlled environment facilities and to provide information about their causes and control.

OEDEMA

Oedema, also referred to as intumescence injury, neoplasms, or genetic tumors, is a disorder that occurs almost exclusively in controlled environment facilities. This disorder has been observed in many plant species representing a number of families, including tomato (Atkinson, 1893; Lang et al., 1983), hibiscus (Dale, 1901), potato (Douglas, 1907; Petitte and Ormrod, 1986), tobacco (Kehr and Smith, 1954), geranium (Balge et al., 1969), eucalyptus (Warrington, 1980), sweetpotato (Wetzstein and Frett, 1984), and cuphea (Jaworski et al., 1988).

Oedema usually appears as 1-3 mm diameter gall-like protrusions on leaves and callus-like growth on stems, petioles, and midveins. This abnormal growth is the result of excessive cell enlargement and/or cell division. Plants developing oedema often become epinastic, and leaves can become deformed from gall formation and even abscise in severe cases. The occurrence of oedema has long been attributed to water congestion under situations of reduced transpiration. It seems, however, that water congestion only aggravates oedema development and that light spectral quality is the overriding factor in its induction. Oedema is promoted by red radiation and inhibited by far-red radiation, indicating phytochrome involvement (Morrow and Tibbitts, 1988). It also is inhibited by ultraviolet (UV) radiation (Lang and Tibbitts, 1983). Oedema has been one of the more troublesome disorders encountered in controlled environment facilities and is often mistaken for disorders caused by pathogenic organisms. The prevalence of oedema in growth chambers results because most glass or plastic lamp barriers absorb the UV wavelengths (which prevent development) from lamp radiation. Oedema also occurs frequently on sterile plantlets cultured in plastic or glass containers, i.e., in vitro (Wetzstein and Frett, 1984). Interestingly, oedema on geraniums could not be controlled by the presence of UV or far-red wavelengths and evidently has different causal factors (Rangarajan and Tibbitts, 1994).

The best recommendation for controlling oedema is to provide an adequate source of UV radiation in the growth chamber (most fluorescent and metal halide lamps provide sufficient UV, but high-pressure sodium lamps may not) and to remove UV-absorbing barriers or replace them with UV-transmitting materials. Ultraviolet-transmitting Plexiglas is effective and readily available. Most lamps, including incandescent, do not have a sufficient proportion of far-red radiation to effectively control oedema. If oedema cannot be controlled by chamber modification, it may possible to select varieties that are less susceptible to oedema development (Potter and Anderson, 1982). Several cultural procedures have been recommended to minimize oedema in geraniums (O'Donovan, 1982) and might be applicable to other species. These include using a light, well-drained, peat-vermiculite growing medium, with a pH of 5.0 - 5.5, maintaining high nitrogen and iron levels, maintaining cooler temperatures (<27°C) with good ventilation, and watering only when necessary.

ABNORMAL PHOTOPERIOD EFFECTS

The ability to control photoperiod in growth chambers offers the opportunity to create lighting cycles uncommon in nature, including continuous light or rapid cycling photoperiods.

Provided other environmental factors are maintained at reasonable levels, continuous lighting causes no obvious effects on the growth of many plant species. Some species, however, including coleus, geranium, potato, and tomato, show an intolerance to continuous light and can become severely chlorotic and stunted (Arthur, 1936; Hillman, 1956; Wheeler and Tibbitts, 1986).

Tomato is among the most sensitive plants to continuous light injury, with symptoms including intervenal or total leaf chlorosis and brown, necrotic flecks on the leaves (Arthur, 1936; Hillman, 1956; Kristoffersen, 1963). Ultimately, this damage can kill the plants (Arthur et al., 1930). Potato leaves also can exhibit a mottled chlorosis and rusty flecking under continuous light, but sensitivity varies greatly depending on the cultivar (Arthur et al., 1930; Wheeler and Tibbitts, 1986). Geranium and coleus tend to show less severe reactions, typified by diminished, spindly shoot growth with small leaves (Arthur et al., 1930).

Continuous light injury to potato is not photoperiodic in nature because daylength extension with dim lighting is not injurious (Wheeler and Tibbitts, 1986). High irradiance and high CO_2 concentration aggravate continuous light injury (Wheeler et al., 1991), whereas cool temperatures can prevent it (Hillman, 1956; Kristoffersen, 1963; Tibbitts et al., 1990). A temperature change of 4-6° C each 12 hours is effective for controlling this injury in potatoes (Tibbitts et al., 1990). High humidity also has been reported to protect tomatoes (Kristoffersen, 1963), but it was not effective in protecting potatoes (Wheeler et al., 1989). The fact that high PPF and high CO_2 aggravate the injury, while cool temperatures can prevent it, suggests that the injury may be related to persistently high levels of starch in the chloroplasts (Hillman, 1956; Tibbitts et al., 1990). Yet conclusive proof for end-product inhibition is lacking, and the mechanism of injury is not well understood (Globig and Janes, 1986).

The best ways to avoid injury are to provide a dark period each day, at least 4 to 6 hours for tomato (Hillman, 1956), or to alternate temperatures each day. If continuous light and constant temperatures are used, species or cultivars tolerant to continuous light might be substituted for intolerant types.

Unusually rapid photoperiods, i.e., with light:dark (L:D) cycles shorter than 24 hours, can have detrimental effects on plant growth, including reduced dry matter accumulation, reduced leaf enlargement, and decreased stem elongation (Garner and Allard, 1931; Bonde, 1955, 1956; Berry et al., 1986; Morrow et al., 1987; Takano et al., 1987; Sager and Giger, 1980). The most severe effects are often observed under L:D cycles of shorter than 1 to 2 hours, although responses differ between species and cultivars. Often, adverse effects can diminish as the photoperiod cycle becomes even more rapid, e.g., a few minutes or less (Garner and Allard, 1931; Sager and Giger, 1980). Potatoes grown under 60 min L:30 min D (to simulate a low-earth ortibal photoperiod) produced less tuber and total plant bio– mass than plants given 16 hrs L:8 hrs D, with the amount of reduced growth varying by cultivar (Morrow et al., 1987). In addition, potatoes given the rapid L:D cycles had numerous small tubers in comparison to the fewer, larger tubers of controls, and flowers failed to open fully and reflex. Because rapid photoperiods can essentially act as a long day (Garner and Allard, 1931), the 60 min L:30 min D cycles may have directly suppressed tuber development, which is generally promoted by short days. Detrimental effects observed for other plants may also be related to the long-day effects of the rapid L:D cycles. Reductions in chlorophyll content, stomatal conductance, and photosynthesis also were observed with potatoes grown under shortened L:D cycles (Morrow et al., 1987), and similar effects have been reported with other species (Takano et al., 1987). Wheat grown in rapid L:D cycles showed increased stem length (in some cvs.), reduced tillering, and increased grain weight (Morrow et al., 1987; Bubenheim et al., 1987)

Other species reported to be adversely affected by rapid L:D cycles include mung bean

(Takano et al., 1987), sugar beet (Berry et al., 1986), tomato (Bonde, 1956), soybean, sweetpotato, cosmos, delphinium, and rudbeckia (Garner and Allard, 1931).

CALCIUM-RELATED INJURIES

Calcium-related injuries are prevalent in numerous species when grown under conditions favoring rapid growth. These disorders can be particularly troublesome in growth chambers, where near-optimal conditions can be provided for growth. Calcium-related injuries to leaves, generally called "tipburn," have been observed in lettuce, cabbage, strawberry, celery, and carrot and result in a burning or necrosis of leaf tips or margins (Shear, 1975; Collier and Tibbitts, 1982; Palzkill and Tibbitts, 1977; Guttridge et al., 1981; Tibbitts et al., 1983). Calcium-related injuries to fruit and storage organs include blossom-end rot in fruits, internal brown spot of potato tubers, bitter pit of apple fruits, and pillowing of cucumbers (Shear, 1975; Bradfield and Guttridge, 1984; Banuelos et al., 1985; Staub et al., 1988; Barten et al., 1992; Staub and Navazio, 1993). In all cases, the primary cause of injury seems to be lack of sufficient calcium reaching young, expanding tissues (Collier and Tibbitts, 1982). On a cellular level, the injury is most likely associated with the loss of membrane integrity and possible cell-wall weakening due to insufficient levels of calcium (Shear, 1975; Collier and Tibbitts, 1982). The weakened cells and adjacent tissue are then susceptible to collapse and/or rupture, leading to eventual senescence (Collier and Tibbitts, 1982).

Events or conditions that limit the amount of calcium reaching growing tissues in turn tend to promote calcium-related injuries such as tipburn. Interestingly, soil calcium deficiency rarely is associated with tipburn problems (Shear, 1975). Rather, factors that affect calcium movement within the plant are the most significant. Because calcium movement in plants is passive and closely coupled to water movement in the xylem, rapidly expanding leaves and other organs that do not transpire freely outstrip their supply of calcium (Collier and Tibbitts, 1982). High humidity environments, such as those within developing "heads" or below an enclosed canopy, can reduce transpiration and lead to injury. This observation is supported by studies demonstrating greater tipburn incidence when plants were grown under high humidity during the light period or when leaves were enclosed in plastic caps to prevent transpiration (Collier and Tibbitts, 1982; Barta and Tibbitts, 1986). In contrast, high humidity during the dark period may be somewhat protective if sufficient root pressure develops to force water and calcium into developing leaves (Palzkill and Tibbitts, 1977; Guttridge et al., 1981).

Tipburn injury of lettuce leaves typically develops as darkened or water-soaked zones along the margin or tips of young, protected leaves (Collier and Tibbitts, 1982). Water soaking is followed by tissue senescence along the leaf margin, which subsequently impairs normal leaf expansion and causes constricted, necrotic zones. The injury becomes evident as inner leaves emerge from the encircling larger leaves. Tipburn is not likely to kill the plant but can severely affect leaf development and appearance.

Control of tipburn and other calcium-related disorders can be difficult and frustrating. Lowering humidity during the light cycle or raising humidity to near saturation during dark cycles to increase root pressure may be helpful. Topical application of calcium salt solutions to susceptible tissues will provide protection if it reaches the developing terminal leaflets (Maynard et al., 1962). Providing good air circulation to decrease humidity around leaves and encourage transpiration has also been successful for reducing tipburn in lettuce (Goto and

Takakura, 1992). Use of tolerant cultivars and/or environmental conditions that reduce growth rates (e.g., lowering light or CO_2 levels) seems to be the best options for avoiding calcium-related injuries.

HIGH CARBON DIOXIDE CONCENTRATIONS

The relatively closed environment of growth chambers facilitates carbon dioxide (CO_2) enrichment studies with plants, and several commercial growth chamber manufacturers will provide CO_2 control capabilities upon request. Provided the CO_2 is clean of contaminants such as ethylene (Morison and Gifford, 1984), enrichment is generally beneficial for growth and provides maximum benefit between 0.1 and 0.2 kPa (1000-2000 ppm). Yet with certain species, enrichment above 0.1 kPa can be injurious. The injury symptoms include leaf rolling or deformation (e.g., tomato) (van Berkel, 1984; Tripp et al., 1991) and chlorosis or chlorotic mottling of leaves (e.g., bean, chrysanthemum, gerbera, and cucumber) (Ehret and Jolliffe, 1985; van Berkel, 1984; Hicklenton, 1988). With gerbera and cucumber, the chlorosis can be accompanied by abscission of older leaves (van Berkel, 1984). With other plants, symptoms are less obvious, but overall growth can be depressed if CO_2 concentrations exceed optimal levels for growth (Wheeler et al., 1993).

Injury from high CO_2 can be aggravated by high light (van Berkel, 1984; Ehret and Jolliffe, 1985; Wheeler et al., 1991), and photosynthetic rates decreased when CO_2 exceeded optimal levels (Hicklenton and Jolliffe, 1980; Peet et al., 1986). This may be related to feedback inhibition effects on photosynthesis from high carbohydrate levels in the chloroplasts (van Berkel, 1984). Recent studies have also shown that high CO_2 can increase endogenous ethylene production in some plants, which may contribute to the injurious effects from high CO_2 levels (Woodrow and Grodzinski, 1993).

HIGH IRRIDIANCE

Sudden or large increases in irradiance can often damage leaf tissues. Such a situation can occur when plants are transferred from low light levels in greenhouses during the winter to a growth chamber with high light levels (Levitt, 1980). Typically, these changes cause a bleaching or bronzing of the exposed leaves, but the damage is generally transient, and new, developing leaves seem to adapt to the higher light levels (I.J. Warrington, personal communication).

MECHANICAL STRESSES

Differences in air movement and/or vibration within growth chambers may cause various degrees of mechanical stress to plants. Studies have shown that mechanically shaking or flexing a plant for only a few minutes each day can significantly reduce stem elongation and plant fresh and dry weight (Jaffe, 1973; Mitchell et al., 1975; Wheeler and Salisbury, 1979; Pappas and Mitchell, 1985). Species reported to show reduced growth as a result of mechanical perturbation include tomato, pea, chrysanthemum, sunflower, soybean, bean, cucumber, and castor bean (Jaffe, 1973; Mitchell et al., 1975; Beyl and Mitchell, 1983; Pappus and Mitchell, 1985). The effects are most pronounced when stem elongation has been encouraged as a result of low daily PPF levels during growth (Heuchert and Mitchell, 1983; Pappus and Mitchell, 1985). The physiological mechanisms involved in mechanical stress responses are not totally understood, but seem to involve the hormones IAA, ethylene, and GA, and may act through differential cell wall growth and transient stomatal closure (Beyl and Mitchell, 1983; Pappas and Mitchell, 1985). Thus, unequal mechanical agitation of plants (e.g., from handling, vibration, air movement, or water spray) within a chamber can affect shoot and root growth differently and should be avoided or taken into consideration when designing experiments that involve persistent movement or contact with plants.

FRUIT CRACKING

Fruit cracking or splitting is a problem that may be associated with a number of environmental, cultural, genetic, and anatomical factors (Peet, 1992). Cracking occurs when there is a rapid influx of water and solutes into the fruit at the same time that other factors interact to reduce the strength and elasticity of the fruit skin. Factors thought to promote this problem include irregular watering, high temperatures and high irradiance, excessive growth rates, high differentials between day and night temperature, high humidity, and poor calcium nutrition (Peet, 1992). Problems with fruit cracking are typically associated with greenhouse environments, but the causal factors suggest that injury of susceptible plants might readily occur in growth chambers. Methods proposed to prevent cracking include selection of nonsusceptible cultivars, consistency in watering, good calcium nutrition, and possibly the use of calcium or gibberellic acid sprays (Peet, 1992).

VITRIFICATION

Vitrification, also called glassiness or water soaking, is a physiological disorder that almost exclusively affects plants maintained in sterile culture. Vitrification has been observed in a number of species (Debergh et al., 1981) and most commonly is characterized by a translucent or water-soaked appearance of leaves and stems. In addition, leaves can become enlarged and malformed, exhibiting wrinkling or curling. Because of their extreme turgidity, the translucent leaves become very brittle and can break easily. On a cellular level, vitrified leaves lack palisade tissues (having only a spongy mesophyll) and generally exhibit defective lignification of vessels and tracheids (Kevers et al., 1984). Though the mechanism responsible for the disorder is not known, one hypothesis is that vitrification results from a burst of ethylene triggered by the peroxidase-IAA-oxidase system (Kevers et al., 1984). Methods for preventing vitrification have been proposed for specific crops (Kevers et al., 1984), but in general, decreasing the water potential of the tissue culture medium seems to be an effective procedure for consistent control (Debergh et al., 1981; Pasqualette et al., 1986).

ABNORMAL NEEDLE MORPHOLOGY

Needle tip curling has been observed for loblolly pine in growth chambers (Seiler and Johnson, 1984). This injury was observed on new growth when plants were maintained under low-humidity levels (e.g., 30%). Increasing humidity levels (to approximately 70%) effectively prevented tip curling. This disorder may be related to the disorder called "leaf pleating."

LEAF PLEATING

Leaf pleating is characterized by a crinkled or accordion-like malformation on the leaves of monocots. This disorder has been observed on several sympodial orchid species (Hoyt, 1977; Riopelle and Riopelle, 1982) and a variety of small grains and ornamental grasses. The disorder seems to occur when leaf tips fail to emerge freely from the leaf sheath and become compressed within the sheath. When the leaf finally breaks out of the sheath, the pleated pattern characteristic of this disorder can be observed. Although the cause of this disorder is not known, it has been attributed to water stress of new, developing growth. Leaf pleating may stunt development of affected leaves, but overall plant growth does not seem to be seriously impaired.

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