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Environmental Effects on Stem-Cutting Propagation: A Brief Review[®]

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INTRODUCTION

Propagules have been reproduced asexually from stem cuttings to retain desired genotypic traits using mist propagation since the 1950s (Snyder, 1965). The successful initiation and development of roots is dependent on an optimum atmospheric and edaphic (or rooting) environment. Increased success of *de novo* root formation came with the introduction of natural and synthetic auxins. Wounding, basal auxin application, and control of the atmospheric environment, the latter being the primary interest in research and practice, have increased rooting percentages and root quality. Applying mist irrigation or shade cloth, or enclosing the propagules in polyethylene achieves increased relative humidity, decreased irradiance, and lower air and leaf temperatures. These environmental control methods maintain cell turgor in the absence of functional roots, retaining cell competence to form root initials (Hartmann et al., 1997). Further advances in the rate of root emergence and the quality of developing roots came with studies of the edaphic environment, the most significant being that higher basal stem temperatures increase the rate of metabolic processes. In addition, researchers continually study rooting media to determine what mixtures provide an optimal ratio of air and water to root individual stem cutting of specific taxa. The combination of proper atmospheric and edaphic environment result in high percent of cuttings rooted with a quality root system.

ATMOSPHERIC ENVIRONMENT

The atmospheric environment encompasses irradiance; temperature; relative humidity; gas exchange; and stem, leaf, or root pathogens. These factors greatly influence leaf retention, the ability to root, and propagule physiology. In the last 50 years, static intermittent mist (5 sec of mist every 5 min) has been the predominant industry method of propagating cuttings. Mist humidifies the air surrounding the canopy and reduces leaf temperature, thereby decreasing the vapor pressure difference. Another common propagation method is a low-cost polyethylene (PE) enclosure system that increases relative humidity to minimize the vapor pressure deficit (VPD). Both systems can work successfully, depending on the greenhouse atmospheric environment and diurnal and seasonal variation separately or in combination.

Cultural and mechanical problems have existed since the development of mist propagation. Cultural problems reducing the efficiency in propagation include excess soil moisture, alga growth, increased leaf-borne diseases, and nutrient leach-

ing (Wells, 1965). These problems have been addressed through the development of new devices that reduce mist frequency, including photoelectric cell, electronic leaf (Vanstrone, 1959), and dynamic mist control techniques (Zolnier, 1999). These new sensors have been advantageous, but have not eliminated the mechanical problem with clogged mist nozzles or the labor required to monitor the water status of cuttings (Bryson 1980). Mist applications are never evenly applied, creating spatial variation in VPD and leaf temperature, inducing propagule stress that cannot be overcome throughout the nighttime hours when propagules regain maximum turgidity (Loach, 1977) as a result of higher air temperature and relative humidity. In polyethylene enclosures used for propagation, cuttings do regain turgidity overnight (Loach and Whalley, 1978), but the system is limited to low irradiance that can maintain low leaf temperatures and high relative humidity that sustain the water potential of the cutting (Hartmann et al., 1997). The polyethylene propagation system microclimate is compromised if opened because relative humidity falls dramatically, inducing hours of propagule stress after being re-closed (Newton and Jones, 1997). Polyethylene systems have also been reported to limit photosynthesis through the depletion of carbon dioxide during daytime hours (Rosenberg et al., 1992).

Temperature and light are two key environmental components that determine rooting success. Maintaining lower air temperatures reduces shoot or stem temperature. This, in turn, reduces the rate of shoot and leaf growth that could deplete carbohydrate reserves and desiccate the propagule (Kester, 1970). Reduced cutting stem and leaf temperature is achieved with mist, but may result in sub-optimal rooting medium temperatures because of evaporative cooling (Mastalerz, 1977). Air and basal temperatures also play a role in the regulation of respiration, a metabolic process that must be balanced by an $\sim 10^{\circ}\text{F}$ (5.6°C) warmer root zone than air temperature to reduce shoot growth that would become a competitive sink for photosynthates (Kester, 1970). Howard (1965) reported a two-fold dry weight and three-fold root number increase in cuttings rooted at an air temperature of 15.5°C and a basal stem temperature of 26.5°C compared to higher air temperature. Contrary to these studies, it has been reported that increased air temperature resulted in better rooting due to higher metabolic rates, primarily respiration (Preece, 1993). Water content of the rooting medium has also been found to be more favorable under high air temperature (31°C) and low light (Graves and Zhang, 1996). It also should be noted that maintaining minimal nighttime air temperatures may improve rooting percentage, root number and length of the rooting zone (Alegre et al., 1998). *Forsythia* and *Weigela* have fewer and shorter roots under high light intensities, with relative cutting growth rate at low light levels surpassing those cuttings treated with high irradiance (Loach and Gay, 1979).

EDAPHIC ENVIRONMENT

The edaphic environment comprises water content, aeration, temperature, gas exchange, pH, mineral nutrition, and soil-borne pathogens. This environment is dynamic and properties are directly related to the rooting medium and its components. The rooting medium provides four functions: supplies water, supports cutting, supplies oxygen for the metabolic process of root initiation and elongation, and provides a dark environment for root initiation to occur (Loach, 1985; Hartmann et al., 1997). Edaphic factors are closely linked to the components of the propagation

medium and the propagation tray dimensions. Propagation media components include bark, sphagnum peat, coir, and volcanic rock such as pumice or perlite. These components affect water holding capacity, air space and infiltration, water availability, water uptake, and pH.

Grange and Loach (1983) found that cutting water content was directly proportional to soil moisture content, with an optimum number 50% (0.50 m³ water/m³ substrate). Rein and coworkers (1991) reported similar findings that regardless of species, xylem water potential increased moisture content of the medium. Stem cuttings stuck in perlite were observed to have greater water uptake when compared to peat mediums and their mixtures, which has a greater water volumetric content, because water is more tightly bound. The results of Grange and Loach (1983) led to the conclusion that free water present in a perlite rooting medium was more readily available and in greater contact with the cutting stem base, allowing greater cutting water uptake when compared to other media substrates. Perlite is an inert siliceous rock that is expanded by 4% to 20% its original size by heating. In the firing process micropores are created, filling the particle with approximately 50% air that allows it to absorb 200%–600% water by weight. Stem length, root length, and root and total dry weight of *Chrysanthemum* sp. increased with an increasing proportion of perlite (Oh, et al., 1998). These increases may have been due to lowered porosity and higher air-filled porosity when compared to peat alone.

Volumetric air soil content of the rooting medium is also affected by temperature and irrigation methods. The amount of dissolved oxygen decreases as soil water temperature increases, affecting medium aeration. Gislerd (1983a) reported inadequate rooting in poinsettia stem cuttings due to high soil moisture content. Air content of the medium, a function of oxygen diffusion through the medium, is reduced as soil moisture content increases. Gislerd suggested that lower root number and root length could be related to available oxygen, ethylene accumulation, and altered endogenous hormone levels. In a separate study, root number, root length, and rooting percentage of *Ficus benjamina* increased proportionally to dissolved oxygen concentration, the maximum being 8 mg·L⁻¹ O₂ (Soffer and Burger, 1988). Aminah and coworkers (1995) also reported that the greatest rooting percent and root number occurred in gravel, which had the lowest water content and highest air content of all the media evaluated in the study. However, cuttings stuck in gravel underwent the greatest water stress, having the highest leaf temperature (25.8 °C), six-fold increase in VPD, and the greatest stomatal conductance.

Basal stem temperature is a function of air temperature, cutting tissue temperature, and medium temperature. Temperature affects both the rate of metabolic processes within the cutting and the rooting medium. Increasing basal stem temperature increases leaf temperature, VPD, and disease potential while drying the medium that results in a reduction in soil moisture content (Loach, 1992). The generic optimum constant basal stem temperature for rooting was reported as ranging from 18 to 25 °C while maintaining a day air temperature of 21 °C and a night air temperature of 25 °C (Hartmann et al., 1997). *Poinsettia* stem cuttings roots evaluated at 20, 24, 28, and 32 °C were found to have optimum root length at 24 °C, and root formation was inhibited at temperatures greater than 30 °C, yet these effects disappeared when light intensity was reduced (Gislerd, 1983b). Dykeman (1976) found that a larger number of *Chrysanthemum* roots initiated more quickly when exposed to 30 °C, and that root elongation and root mass were maxi-

mized at 22–25 °C. He concluded that temperature should be altered for the two stages, root initiation and root elongation, of adventitious root formation for an optimal response. Burholt and Van't Hof (1971) reported that the number of cells dividing was greatest at 35 °C, but that maximum rate of cell division and cell length, which led to root growth, occurred at 30 °C. Roots exposed to supra-optimal temperatures appeared “weak and filamentous” and “browning” occurred, and worsened as the duration of exposure increased (Carpenter et al., 1973, Carpenter 1989). Duration and optimal temperatures for both developmental stages are taxa dependent. Zhang and coworkers (1997) showed that *Acer rubrum* ‘Autumn Flame’ fresh mass increased at 30 and 33 °C, but fresh mass and rooting percentage decreased by 20% at 30 and 34 °C in stem cuttings of *A. xfreemanii* ‘Morgan’ (syn. *A. rubrum* ‘Indian Summer’).

PROPAGULE PHYSIOLOGY

The physiology of the stem cutting during the rooting process for a particular taxon is not well understood, since rooting success is both taxa and environment dependent. Upon removal from the stock plant, cuttings may continue to photosynthesize (Howard, 1965) but when stuck, cuttings reduce transpiration and net photosynthesis while increasing stomatal resistance (Svenson et al., 1995). Each of these physiological processes are significantly correlated with leaf water potential (Smalley et al., 1991), which decreases upon cutting removal from the stock plant and continues to decrease until root primordia initiation (Svenson et al., 1995). Cutting water uptake from the rooting medium increased when a greater surface area of the stem cutting was exposed by slice wounding the base of the propagule, reducing “contact resistance” (Grange and Loach, 1983). Loach and Whalley (1978) reported that leaf water potential must be maintained at less than -10 bars (~-1 MPa) to maintain cell turgor, cell competence, and to support the necessary metabolic activities for root initiation.

Initial water uptake is affected by oxygen and carbon dioxide concentrations in the rooting medium (Glinka and Reinhold, 1962) and can be impaired, over time, by the blockage of vessel lumens with tyloses (Rein et al., 1991). Oxygen, diffused through the medium or the cutting (Loach, 1985), must be present at an adequate concentration to support ongoing metabolic processes that occur during root formation (Soffer and Burger, 1988). If oxygen is not abundant, mitosis will stop or be unable to begin again (Ammore, 1961a).

Root initiation can be a temperature-driven phenomenon that requires large numbers of cells to divide and differentiate. Root elongation (cell division and elongation) may be limited by carbohydrate availability. Enzymatic reactions such as respiration and the dark reactions of photosynthesis, with a $Q_{10} \sim 2$, increase with rising temperatures. Physical reactions (CO_2 diffusion, photochemical reactions) become limiting at high temperatures due to a $Q_{10} \sim 1$, but increases at a slower rate (Kester, 1970). Therefore, the influence of temperature on respiration and photosynthesis could result in adverse changes in carbohydrate utilization and translocation affecting root growth and development (Hartman et al., 1997). Erstad and Gislend (1994) reported that an elevated carbon dioxide concentration surrounding the stem base as a result of increased respiration could decrease the available energy for metabolic processes (Ammore, 1961b). Rising basal stem temperature increases the rate of respiration in the lower portion of unrooted stem cuttings, which

is higher than respiration rates observed at the time of root primordial formation (Oishi et al., 1978).

Larger cuttings may root better because of increased carbohydrate reserves, photosynthate, and endogenous root promoters resulting from larger leaf area (Grange and Loach, 1984). These larger mature tissues that have increased cell permeability (e.g., are more leaky) can make them more readily leached of nutrients from the vascular system of the leaves when misting occurs (Good and Tukey, 1966). Okoro and Grace (1976) found carbohydrate reserves (starch) were depleted by bud development and that leaf expansion in hardwood cuttings act as carbohydrate sinks, but in softwood cuttings that did not incur leaf growth during rooting accumulated carbohydrates, primarily starch that was possibly translocated from the leaves. In addition, Loach and Gay (1979) offered two hypotheses. First, that root initiation was reduced by high carbohydrate accumulation or second, that low rooting resulted in high cutting carbohydrate content. These conflicting thoughts can be explained by Haisig's (1974) statement, that seasonal variation of endogenous root promoters, most likely endogenous auxin, would replace any starch to rooting relationship that had previously or would exist.

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