As we have been discussing in the last four issues of FNN, plants need six different limiting factors for good growth, four of which are found in the ambient environment (see Figure A). This issue, we will close out the ambient factors with a look at carbon dioxide (CO 2)'

Limiting Factors - Carbon Dioxide

Carbon dioxide is an anomaly - of the 16 nutrients that are essential for plant growth, it is the only one that is obtained solely from the atmosphere. CO2 is a rare atmospheric gas, but about 40% of the dry weight of a typical plant is composed of carbon. Plants obtain CO_2 from the air through the stomata in the leaves in a very complicated physiological process that also involves water vapor and oxygen.

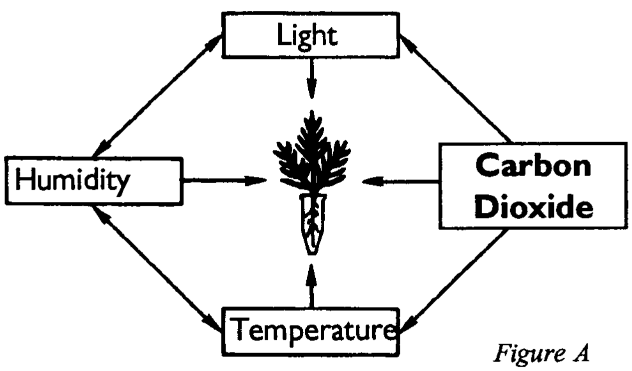

Figure A

But, although known to be a principal limiting factor of photosynthesis, $C0_2$ is rarely managed in forest and conservation nurseries. This should not be interpreted to mean that $C0_2$ is not important to tree seedling culture, however, as many research studies have shown that increased CO_2 levels can significantly accelerate photosynthetic rates. So, should nurseries managing this important limiting factor? Let's take a look.

Biophysics of carbon dioxide

Carbon dioxide is a colorless, odorless gas that exists in minute concentrations in the ambient atmosphere - currently around 0.035% (350 ppm). This was not always the case, however, as CO_2 was more common than oxygen in the primitive atmosphere. The rapid development of plant life quickly utilized this $C0_2$ and released oxygen, which made possible the evolution of larger and more advanced organisms. The CO_2 level of the earth's atmosphere appears to have stabilized at its lowest level (280 ppm) in the mid-1800's. Since that time, the industrial revolution has produced a gradual increase in ambient CO_2 concentrations. The combustion of fossil fuels, in combination with massive deforestation, have caused the atmospheric CO_2 level to increase 1 to 2 ppm per year. This trend is unlikely to change in the near future and has resulted in much-publicized concerns about "global warming".

The ambient CO_2 level around a nursery can vary from 200 to 400 ppm, depending on location; higher values can be found in industrial areas, due to combustion of fossil fuels, and in low wet areas, such as swamps and river bottoms, where plant materials are decomposing. Carbon dioxide concentration measured in weight per unit volume also decreases with elevation, decreasing about 40% from sea level to 4,500 m (14,800 feet).

In contrast to its positive effects on plants, high concentrations of CO_2 can adversely effect humans (Table 1). Dangerous levels could develop in greenhouses with faulty heating systems or poorly adjusted $C0_2$ generators.

Table 1 - Effects of carbon dioxide levels on plants and humans

Response	Carbon dioxide concentration (ppm)
Plant effects	
Negative growth	<100
CO_2 compensation	50-100
Reduced growth rate	100-350
Ambient CO_2 Level	350
Enhanced growth rate	350-1000
Marginal benefits	1,000-2,500
Possibility of adverse effects	>2,500
Human effects	
Worker exposure limit	5,000
Headaches and listlessness	> 5,000
Loss of consciousness and death	> 80,000

Measuring CO_2

Carbon dioxide levels can be described and measured in several different ways. Because it is a gas, CO_2 can be described in pressure units but these are not widely used for horticultural purposes. Plant physiologists measure photosynthesis by the amount of CO_2 consumed and commonly express it by weight in milligrams (mg) or volume in microliters (ul) per unit volume. However, for operational nursery work, concentration units—parts per million(ppm)—are the simplest and most appropriate way to measure CO_2.

Carbon dioxide measuring instruments vary considerably in cost and complexity. Small hand-pump CO_2 testers of reasonable accuracy are available for around $200; the air is pumped through a glass tube that contains a CO_2-sensitive chemical that changes color as an air sample is drawn through it. The more sophisticated and expensive infrared gas analyzer ($1,400), is much more accurate and precise. Because they can measure CO_2 continuously and can interface directly with environmental computer systems, infrared gas analyzers are often used in fully-controlled greenhouses.

Effects of CO_2 on seedling growth

Plants consume CO_2 during photosynthesis and give it off through respiration; during daylight hours these processes occur simultaneously. In plant leaves, when the CO_2 level reaches the **compensation point**, the point at which photo-synthesis and respiration are equal (Table 1), the seedling will not grow but only maintain itself. If CO_2 concentrations are enhanced above ambient levels, the photosynthetic rate increases because high CO_2 concentrations increase the diffusion gradient from the ambient air, through the stomata, to the mesophyll cells where the chloroplasts use CO_2 in photosynthesis. Seedling growth rate increases when the net photosynthate is exported from the leaves, where photosynthesis takes place, to the meristems, where growth occurs. There are numerous studies on the beneficial effects of enhanced CO2 on tree seedling growth.

There is an upper limit to how much more CO_2 can use, however, as high concentrations of CO_2 can cause stomatal closure. Although the limits

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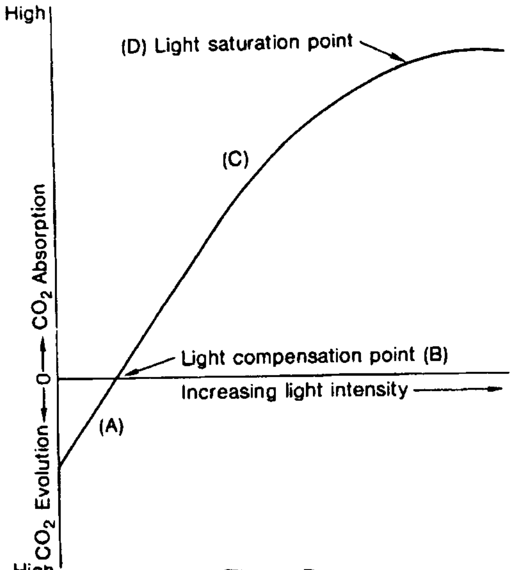

Figure B

vary considerably with light intensity and between different plant species, CO_2 levels over 1,000 ppm generally show diminishing benefits. Carbon dioxide concentrations over 2,500 ppm are rarely beneficial and may actually result in reduced growth (Table 1).

The effects of CO_2 cannot be considered alone, however, for they are highly interrelated to the effects of other factors limiting to plant growth, especially light, temperature, water, and mineral nutrients. As the CO_2 concentration changes and the photosynthetic rate varies, the optimum levels of the other environmental factors also change.

Light - Photosynthesis***,*** as measured by CO_2 utilization, increases linearly with light until the light saturation point is reached (FIGURE B). As long as the other factors are not limiting, the light saturation point becomes progressively greater as light intensities and CO_2 concentration increase. In fact, high CO_2 levels can, to a degree, compensate for low light intensity, which often occurs on cloudy winter days. When supplemental photosynthetic lighting is used in greenhouse culture, CO_2 enrichment is essential in obtaining the full benefits from the additional light.

Temperature - Nursery seedlings are primarily cooled by transpiration under normal growing conditions. Because stomatal aperture controls both CO_2 and water loss, ambient CO_2 levels affect transpiration rates. Artificially high CO_2 levels, resulting from improperly adjusted CO_2 generators, could cause stomatal closure and subsequent heat injury to succulent nursery seedlings.

Water and mineral nutrients - The rapid growth rates of plants grown under CO_2 enrichment result in an increase in water and mineral nutrient uptake. Seedling water use will increase because the increased foliage has a larger transpirational surface. The increased growth resulting from the higher photosynthetic rate will also create a demand for more mineral nutrients. Often, the increased growth rate of the many seedlings under CO_2 enrichment does not persist, because mineral nutrient deficiencies are caused by the rapid growth.

Growers who supply extra CO_2 to their crops will have to be aware of these potential problems and make appropriate adjustments to their cultural regimes.

Modifying CO_2 in Nurseries

So, the potential of stimulating seedling growth by increasing CO_2 levels is high but is that really practical in an operational nursery? Actually, there are only two options: increasing air exchange, and CO_2 generators. The first is feasible in all types of nurseries, whereas the latter is only practical in enclosed growing environments like greenhouses.

Increasing air exchange - Good circulation of air is necessary to make CO_2 available at the leaf surface. Therefore, growers can stimulate seedling growth by merely encouraging good ventilation. During the day when the air is stagnant, the CO_2 concentration in the boundary air layer around a seedling can be considerably lower than the ambient conditions, so increasing the air flow over the leaves makes the gas more available for photosynthesis. In studies with field crops, researchers have shown that merely increasing the wind velocity over the leaf surface can significantly increase photosynthesis. Under calm

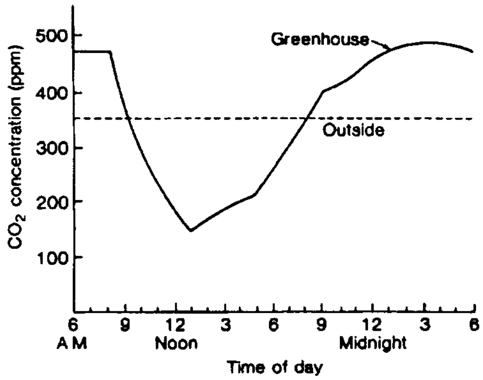

Figure C

conditions, CO_2 levels have been shown to be limiting in dense crops grown in open fields, resulting in a 10 to 20% decrease in photosynthetic rate. So, while it would be impossible to control the wind, bareroot nurseries can insure that all seedlings have access to adequate supplies of CO_2 by lowering seedbed growing densities.

Good air exchange can be more challenging in container nurseries, especially those with enclosed growing environments. Carbon dioxide levels follow a typical diurnal pattern in a closed greenhouse environment (Figure C). At night, green plants release CO_2 through respiration and so concentration in a closed greenhouse rises to over 400 ppm; however, at dawn, photosynthesis begins and the concentration drops rapidly. The CO_2 concentration can become critically low in a greenhouse on a cool, cloudy day when ventilation is not required; in a greenhouse with only two air exchanges per hour or less, the CO_2 concentration often drops below 200 ppm and so can limit photosynthesis (Table 1).

Research has shown that increasing the air flow rate to 50 cm/sec (99 feet per minute) is equivalent to a 50% increase in CO_2 levels. The potential for increasing ventilation is limited, however, as the wind velocity at maximum ventilation is around 42 cm/sec (83 feet per minute) in a fully-enclosed greenhouse. Because new energy-efficient greenhouses are much more air-tight than older ones, growers can no longer depend on normal air exchange to keep CO½2 levels adequate. Growers with shelterhouses should stimulate photosynthesis by raising the sides whenever air temperatures permit, and those with fully enclosed structures should use fan-jet ventilation systems that encourage good air mixing within the greenhouse. Even on days when outside temperatures are low, it may prove beneficial to bring in outside air and heat it, especially early in the morning when photosynthetic rates are highest.

Carbon dioxide enrichment **-** The potential of CO_2 enrichment has been demonstrated in growth chamber experiments where growth of tree seedlings has been increased 50 to 100%, so CO_2 generators are often used in high-tech greenhouses. The feasibility of CO_2 enrichment depends on the type and the condition of growing structure and the proportion of the time the vents remain closed.

There are several potential ways of supplying CO_2 to greenhouse crops. Decomposing organic matter will eventually release 1.4 times its weight of CO_2 and, although the potential has been demonstrated for forest seedlings, this technique is not considered practical because of problems with sanitation and disposal. In modern container nurseries, there are two realistic options for supplying CO_2: injection of pure CO_2 and combustion of carbon fuels.

Injecting pure CO_2 from pressurized liquid tanks is the safest technique but it is expensive. Complete combustion of any carbon compound will produce CO_2. Kerosene was the first fuel to be used in greenhouses but its cost and concerns about sulfur dioxide phytotoxicity have made it unpopular. In modern container nurseries, natural gas and propane are more commonly used, and the difference is primarily one of cost and availability. Commercial CO_2 generators that burn propane or natural gas and the CO_2 production rate is controlled by modulation of the burner. The principal disadvantage of these CO_2 generators is that exhaust leaks or incomplete combustion can release phytotoxic gases into the greenhouse. Approximately 15 burners per hectare (6 per acre) should generate 1,000 ppm CO_2 in a well-sealed greenhouse. Microcomputer control systems use infra-red gas analyzers and a system of solenoid valves to regulate the CO_2 concentrations in the greenhouse to within 100 ppm. In spite of the proven potential for increasing seedling growth, CO_2 enrichment is not widely practiced in container tree nurseries. Only 17% of the nurseries in the United States and Canada reported CO_2 management programs in a survey for the Container Tree Nursery Manual.

Well, that rounds up our discussion of the atmospheric factors that can limit seedling growth: light, temperature, humidity and carbon dioxide. In the July, 1993 issue of FNN we'll take a look at mineral nutrients and various options for fertilization in forest and conservation nurseries.

References:

Hicklenton, P.R. 1988. ***CO_2 enrichment in the greenhouse: principles and practices.*** Portland, OR: Timber Press. 58 p.

Kramer, P.J.; Kozlowski, T.T. 1979. ***Physiology of woody plants***. Berlin: Academic Press. 811 p.

Landis, T.D.; Tinus, R.W.; McDonald, S.E.; Barnett, J.P. 1992. ***Atmospheric environment, Vol, 3, the Container Tree Nursery Manual*** Agric. Handbk. 674. Washington, DC: U.S. Department of Agriculture, Forest Service. 145 p.