HortTechnology October – December 1998 8(4)

# Effect of Carbon Dioxide Enrichment and Light

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**ADDITIONAL INDEX WORDS.** $C0_2$, high-pressure sodium, HPS, pretransplanting conditioning, plug, supplementary lighting

**SUMMARY.** Since they grow nearly exponentially, plants in their juvenile phase can benefit more than mature ones of optimal growing conditions. Transplant production in greenhouses offers the opportunity to optimize growing factors in order to reduce production time and improve transplant quality. Carbon dioxide and light are the two driving forces of photosynthesis. Carbon dioxide concentration can be enriched in the greenhouse atmosphere, leading to heavier transplants with thicker leaves and reduced transpiration rates. Supplementary lighting is often considered as more effective than C02 enrichment for transplant production. It can be used not only to speed up growth and produce higher quality plants, but also to help in production planning. However, residual effects on transplant field yield of $CO_2$ enrichment or supplementary lighting are absent or, at the best, inconsistent.

Carbon dioxide enrichment in greenhouse nurseries could be used as a way to reduce propagation time, improve sturdiness, and possibly favor growth in the field after planting during spring months in northern latitudes, as little ventilation is necessary, except on hot sunny days. The almost entirely juvenile tissues of seedlings are all expanding, and could be utilizing and diluting the enhanced photosynthate production in an enriched $CO_2$ atmosphere (Lindhout and Pet, 1990). Hence, the greatest advantage of $CO_2$ enrichment would be realized in the vegetative growth of young plants (Kimball, 1983). As leaf tissues formed early in seedling culture begin to mature, starch accumulation begins to slow photosynthetic rates and relative growth rate (RGR) (Thomas et al., 1975).

High energy costs have induced greenhouse growers to use energy saving techniques some of which may lead to decreased fight transmission through the structure covering (Bruggink and Heuvelink, 1987). In northern latitudes, the wide variations in growth which occur during the winter season can be explained almost completely by the wide variations in radiation (K1apwijk, 1981). A decrease of 1% in light level will lead to 1% less yield in a greenhouse, but this relationship does not necessarily hold in the case of young plants (Bruggink, 1987). Manipulating light conditions for vegetable transplant crops could result in benefits not only during the nursery period but also later in the field.

The two major driving forces of photosynthesis are $CO_2$ and light. The greenhouse industry has taken advantage of manipulating these factors to the benefit of crops grown in controlled conditions for extended periods. When plants are young, they grow nearly exponentially while older plants grow more in a linear fashion (Lindhout and Pet, 1990). For crops in their juvenile phase it may therefore be even more profitable to adjust $C0_2$ and light conditions.

This review will consider research results involving the use of $CO_2$ enrichment and varying light conditions in greenhouse for growing vegetable transplants aimed mainly at field production.

## Transplant growth

**EFFECT OF $CO_2$.** The key enzyme for $C0_2$ fixation is rubisco. Its activity depends on the ratio of the $0_2$ and $C0_2$ concentration in the atmosphere. The major effect of $C0_2$ enrichment is the shift in balance between the carboxylation and oxygenation activity of rubisco. This effect is just as important at low as at high light levels as the percentage effect on relative growth rate is about the same over a range of light levels. Kimball (1983) stated that, on average, yields of crops should increase by 33% with a doubling of $C0_2$ concentration in the earth's atmosphere. Although these estimates have been developed for plants over their complete life cycles, enhanced growth and dry matter accumulation are correlated with higher net photosynthetic rates in young vegetative tissues under $C0_2$ enrichment as well.

Optimal $C0_2$ concentrations in greenhouses lie between 700 and 900 $\mu L \cdot L^{-1}$. Brewer et al. (1986) reported taller tomato (*Lycopersicon esculentum* L.) transplants as $C0_2$ concentration changed from 330 to 660 and to 990 ppm. In a study of 96 genotypes of tomato plants, $C0_2$ enrichment (320 vs. 750 ppm) was found to increase young plant growth on average by a factor of

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2.3 (Lindhout and Pet, 1990). Differences in behavior with regard to $C0_2$ enrichment among genotypes were relatively few. Carbon dioxide enrichment increased transplant leaf area, shoot and root dry weight and decreased the leaf area ratio of celery (*Apium graveolens* L.) transplants (Tremblay et al., 1987).

Woodrow et al. (1987) demonstrated that $C0_2$ affects both source metabolism and partitioning to sinks (stems, roots and leaf carbohydrate) in tomato plantlets. They found that $C0_2$ enrichment produced heavier transplants desirable for successful field establishment without elongation growth. Dry matter accumulation in shoot and root was increased as well as leaf dry weight (by 81 % over control). Transpiration rates were reduced under $C0_2$ enrichment conditions by 34%. Increased leaf dry weight accumulation and specific leaf weight (SLW) under $C0_2$ enrichment suggests that more carbohydrate may be available to the plant for future growth. Apparently, the ratio of total sugars to amino acids in the leaf is shifted in favor of sugar content. In a study with tree seedlings, Luxmoore et al. (1986) suggest that $C0_2$ enrichment may increase sucrose translocation in roots and facilitate the mobilization of N and C compounds to new root primordia.

Increased net leaf photosynthesis rate and decreased transpiration rate under $C0_2$ enrichment are well documented (Woodrow et al., 1987). One of the most important effects of $C0_2$ enrichment is the increase in water efficiency (Wong, 1979) which leads to drought tolerance. Actually, rising $C0_2$ concentration reduces the transpiration of plants by 20% to 40% (Mortensen, 1987). Radoglou et al. (1992) reported an increase in water use efficiency of bean (*Phaseolus vulgaris* L.) leaves as a result of increased assimilation rate and decreased stomatal conductance at higher ambient $C0_2$ concentrations. This higher efficiency may not be maintained for long periods of time in field conditions. In cotton (*Gossypium arborcum* L.) (Sasek et al., 1985), stomatal conductance after 40 d of $C0_2$ enrichment took 5 d to reach normal levels in nonenriched conditions.

In short, $C0_2$ enrichment of vegetable transplants shortens the nursery period and modifies photosynthate allocation to the diverse parts, leading to sturdier, higher quality plants. This, together with the fact that $C0_2$ enriched plants make a more efficient use of water may impact favorably on the plant's ability to overcome transplanting stress.

**EFFECT OF LIGHT.** The use of supplementary lighting makes sense in the case of vegetable transplant production since, the younger the plant, the more its relative growth rate will be affected by light conditions (Bruggink, 1987). Most northern growers will confirm that plants grown in glasshouses are shorter than those grown under polyethylene, which screens out more light. Increase in stem diameter during the vegetative stage of tomato has been shown to be proportional to the amount of light received by the plant (Schoch et al., 1990). For growers, this translates into sturdier, more compact and overall better quality plants, less prone to lodging once transplanted to the field. As with $C0_2$ enrichment, light integrals not only influence the rate of photosynthesis, but also morphological parameters of the plant (Bruggink, 1992). For example, supplementary lighting increased shoot and root dry weight of celery, tomato, broccoli (*Brassica oleacera* L. var. *italica* L.) and lettuce (*Lactuca sativa* L.) transplants (Masson et al., 1990, 1991a).

Differences among species as to the influence of light conditions do exist. In a comparison of tomato, cucumber (*Cucumis sativus* L.) and sweet pepper (*Capsicum annuum L.* var. *annuum*) plantlets sown at different times of the year, Bruggink and Heuvelink (1987) found that the net assimilation rate (NAR) of tomato was the most related to light integrals. Generally, NAR was maximum when the mean daily light integral was 400 $J\text{-}cm^{-2}\text{-}d^{-1}$ or more and RGR was maximum at 300 $J\text{-}cm^{-2}\text{-}d^{-1}$.

In Holland, according to Klapwijk (1981), within certain limits, for every 1 $W\text{-}m^{-2}$ of supplementary lighting provided to young tomato plants, the time period required to reach a given growth stage was reduced by 1%. Lettucc plants took 5 to 9 d less to reach the 5 to 6 leaf stage when grown under 40 $W\text{-}m^{-2}$ supplementary lighting compared to 20 $W\text{-}m^{-2}$ (Poniedzialek et al., 1988). Shorter growing periods for transplants result in a more efficient use of greenhouse space.

Supplementary lighting may not only shorten crop cycles but may be instrumental for crop scheduling and planning. Krug and Liebig (1989) proposed an equation considering temperature, radiation and transplant period to calculate ideal sowing dates for uniform lettuce production time intervals. As natural light conditions improve during spring, the benefit of supplementary lighting becomes marginal. In the Netherlands, intensities of artificial light over 10 $W\text{-}m^{-2}$ had little promoting effect on RGR of young tomato, sweet pepper and cucumber plants and this effect was found only from the middle of November to the middle of February.

Koontz and Prince (1986) cited studies where the weight of young tomato plants were more influenced by photoperiod than by irradiance. Riobe and Baubault (1983) also found that long photoperiods tended to reduce losses of photosynthates through respiration. Light in the red and far-red portion of the spectra influenced growth of tomato transplants (Decoteau and Friend, 1991) most probably through an influence on phytochrome. End of day red light treatment or the use of fluorescent light was found to reduce tomato (Decoteau and Friend, 1991) and pepper (Graham and Decoteau, 1995) seedling height. However, there was not much effect on subsequent plant growth in the field or fruit production. End of day light manipulation was suggested to be a low-cost and environmentally safe method of transplant height regulation.

Thus, supplementary lighting can be seen as a way to shorten transplant production cycles in greenhouses and make the production planning more predictable and less dependent on natural light conditions. As with $C0_2$ enrichment, supplementary lighting results in better quality transplants with a potential positive influence on growth performance in the field.

**INTERACTION BETWEEN $C0_2$ AND LIGHT.** There is obviously a potential for synergism between $C0_2$ and light (Hurd and Thornley, 1974).

Madsen (1974) showed that young tomato plants grown under high light intensities were able to utilize an increase in $C0_2$ concentration up to 2200 ppm. In strongly limiting lighting conditions, Canham (1974) rated supplementary lighting as more important than either $C0_2$ enrichment or temperature management in the production of greenhouse tomato transplants. Hurd (1968) found that effects of 1000 ppm $C0_2$ enrichment on young greenhouse tomato plants corresponded to a 30% increase in light intensity. Krug and Liebig (1994 and 1995) produced models integrating, among other aspects, the use of $C0_2$ enrichment and supplementary lighting for the planning of lettuce transplant production. However, the relationship between $C0_2$ and light conditions may be relatively loose. The relative increase in net assimilation rate due to an increase in $C0_2$ concentration from 200 to 1000 ppm was almost as great at the lower as at the higher light level studied. The light compensation point is lowered by increased $C0_2$ concentration (Mortensen, 1987). Fierro et al.(1993) demonstrated interactive effects of $C0_2$ and light enrichment on tomato and pepper transplants. If either were applied 3 weeks before transplanting tomatoes and peppers, they increased accumulation of dry matter in shoots by ≅50%. Fierro et al. (1993) results suggested that it is more important to achieve optimal light conditions first, and then make use of $C0_2$ enrichment.

## Effects on yield

**EFFECT OF $C0_2$.** Woodrow et al. (1987) cite inconsistent reports indicating that acclimation to high $C0_2$ presents either an advantage, a disadvantage or no effect when plant tissues are transferred to low $C0_2$ levels around 300 ppm. According to these authors, the inconsistencies may be due to the age of the leaf tissue under study. They found no effect of $C0_2$ enrichment on height, total leaf area or number of nodes to harvest of young tomato plants. Bélem (1990) reported field studies with early yield increases for tomato and pepper transplants grown under $C0_2$ enrichment but only on one site out of two. Thomas et al. (1975) reported that vegetative growth of tobacco (*Nicotiana tabacum* L.) plants under $C0_2$ enrichment was accelerated temporarily, but declined to a magnitude close to that of plants raised under ambient $C0_2$ when transferred to normal $C0_2$ conditions. Carbon dioxide enrichment of celery produced larger transplants but did not affect the total and marketable shoot weight of celery at harvest (Tremblay et al., 1988). In the same study, on the contrary, N fertilization of transplants showed significant effects at harvest.

**EFFECT OF LIGHT.** The transfer of young plants from greenhouse to field conditions involves an important change in the quantity of radiation received by the plants. Plants adapted to low light conditions are unable to efficiently use the relatively higher light intensity prevailing in the field (Bjorkman, 1981). The aftereffects on yield of supplementary light level prior to planting are, however, relatively short lived.

Boivin et al. (1987) and McCall (1992) demonstrated a strong benefit of supplementary lighting applied under limiting light conditions for greenhouse tomato transplant production. Numbers of leaves formed below the first inflorescence were reduced as well as flower abortion on the first inflorescence, resulting in twice as much early marketable yield for a December sowing (Boivin et al. (1987)). The January sowing showed benefits from lighting treatments but the March sowing was not affected. As natural light conditions improved in spring, the influence of supplementary lighting was reduced.

For lettuce, early plant growth has been shown to influence head weight at maturity and positive effects from both temperature and solar radiation were reported (Wurr and Fellows, 1991). Supplemental lighting of lettuce transplants for 4 h at 13 $\mu mol\text{-}m^{-2}\text{-}s^{-1}$ photosynthetic photon flux density (PPF) after dusk increased transplants shoot dry weight but had no effect on head weight at maturity, coefficient of variation of head weight or the timing of maturity (Wurr et al., 1986). According to de Visser and van de Vooren (1975), supplementary lighting of transplants on lettuce yield could not be traced to causes other than higher weight at planting.

In a study on four species, Masson et al. (1991b) concluded that celery, lettuce, and broccoli yields remained unaffected by supplementary lighting applied during the transplant growth period. Only tomato early yields were favorably influenced by enhanced light.

Fierro et al. (1993) compared control tomato seedlings to ones that had received $C0_2$ and supplementary lighting; early yield increases of marketable fruits were 15% or 12% higher, for the early and late sowing, respectively. These yield increases were a result of a greater number of fruits.

## Need for future research

There may be two reasons for explaining the effect of $C0_2$ or light treatments on yield. The treatments may condition the young plants, determining a better growth balance between root and shoot, a higher water use efficiency or a higher content of reserves which could be used during establishment in the field. Or, the plants may be simply bigger, ahead in their dry matter accumulation; and so there would be no inherent effect of treatments. Determining the causes would help in understanding the mechanism of treatment effects.

Carbon dioxide enrichment of the root zone of seedlings (Yurgalevitch and Janes, 1988; Bialczyk et al., 1994) was not discussed in this review. However, since transplants are often irrigated by mists, their rooting could take advantage of $C0_2$ injection in the nutrient solution as suggested by results of Mortensen (1987) working with cuttings.

In a fully productive greenhouse without ventilation and without $C0_2$ enrichment of the atmosphere, $C0_2$ concentration may fall below 200 $\mu l\text{-}L^{-1}$. Carbon dioxide enrichment, even in periods where ventilation is necessary, has been found economical and is sometimes used commercially for greenhouse crops (Mortensen, 1987). Whether t e same benefit could apply to transplant canopies, which are necessarily much less active in capturing $C0_2$ in a greenhouse, remains to be seen.

New photoselective greenhouse films have been recently developed which reflect some of the green light and the near infrared resulting in higher red/far red and blue/red ratio with effects on plant growth (Verlodt et al., 1997). Effects of such coatings on growth of vegetable transplants are so far unknown.

## Conclusion

Carbon dioxide enrichment and light treatments have been shown to influence transplant growth in greenhouses. They can be used as tools to achieve high quality transplants, mostly when conditions are otherwise limiting and therefore offer an alternative to other approaches such as mechanically induced stress, temperature management or the use of growth regulators. Whether $C0_2$ and supplementary lighting have any inherent effect on final yield, other than through the production of heavier, more developed plants at the moment of planting, remains to be determined. Commercially, $C0_2$ enrichment for vegetable transplants probably has an economical potential only in northern areas where greenhouses can be kept close for a significant part of the day. As to supplementary lighting, profitability lies in the following factors: 1) cheap electricity rates; 2) growers who can take advantage of lighting installations for other crops than transplants only; 3) recuperation of the heating power of lamp fixtures to decrease heating costs.

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