

## The Photosynthesis Response of Tomato to Air Circulation

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**Keywords:** adaptation, air movement, modelling, photosynthesis characteristics, tomato

### Abstract

The closed greenhouse is a new development in protected cultivation. As air is not ventilated to the outside environment, CO<sub>2</sub>-concentrations are higher than in conventional greenhouses, causing 15-20% increased production. The question remained as to whether increased air flow rates in a closed greenhouse cause photosynthetic adaptation. This was evaluated in a tomato crop that was planted in the summer of 2005 in The Netherlands in regular greenhouse compartments, in which air tubes were placed low and high in the canopy. Photosynthesis light-response curves were established at these two heights at 400, 700 and 1000 ppm of air CO<sub>2</sub>. Increased CO<sub>2</sub> concentration and a higher position in the canopy caused an increase of the maximum photosynthetic rate, confirming earlier knowledge. However, the pattern of air circulation did not change the photosynthesis light-response curve. This corresponded with the absence of differences in total dry matter production and cumulative fruit growth. The INTKAM tomato model adequately simulated growth and development. It is therefore concluded that the pattern of air circulation did not cause adaptation of the photosynthetic apparatus, and that yield increases are attributable to the instantaneous effects of elevated CO<sub>2</sub>-concentrations.

### INTRODUCTION

Closed greenhouses were recently introduced in protected cultivation in The Netherlands. They combine new concepts of temperature and air humidity management with year-round closure of the greenhouse cover. More elaborate descriptions are given by Opdam et al. (2005) and Heuvelink (2006). Since there are no ventilation losses, it is possible through injection to maintain greenhouse air CO<sub>2</sub>-concentrations substantially higher than in conventional greenhouses. This is especially the case in summer, when the combination of relatively high radiation and CO<sub>2</sub>-levels results in increased dry matter growth and production. On-farm trials have shown that production increases are in the range of 15-20%, which can be explained by the increased CO<sub>2</sub>-levels if the different situations are analyzed with the INTKAM crop growth model (Elings et al., 2004).

However, since the conditioning of the air requires relatively high air flow rates, one might wonder whether air speeds of up to 0.5 m s<sup>-1</sup> may cause adaptation of the photosynthetic apparatus of leaves used to air movements of 0.1 m s<sup>-1</sup> at most. Also, amongst some growers, it is believed that the air flow and related plant movement do have an effect on photosynthesis. When considering environmental effects, a clear distinction must be made between the instantaneous effects of environmental factors on the photosynthetic rate, and the long-term, possibly adaptive, effects of prolonged specific environmental conditions on the photosynthetic apparatus. An example of the first is a mid-day radiation peak causing a higher photosynthesis, and an example of the second is the continuously higher radiation in the top of the canopy in comparison with locations lower in the canopy, which causes a higher maximum photosynthesis rate at a given radiation level.

Literature reports higher photosynthesis rates in case of forced air circulation (Shibuay et al., 2006; Kitaya et al., 2003, 2005; Nguyen et al., 2001; Yue et al., 1993; Zobayed et al., 1999). All reports, however, seem to concern the instantaneous effects of forced air circulation, and on the consequences for young plants that are not older than a

few weeks. The higher photosynthesis rate for small, young crops can be attributed to the decreased leaf boundary layer resistance if the air flow rate is increased. It remains to be seen whether this is the case for an adult crop with a much greater canopy. There are indications of morphological adaptations (such as indentation and hairiness of leaves), although this is to much higher wind speeds (Grace and Wilson, 1976; Schreuder et al., 2001).

A study on the adaptive effects of long-term forced air circulation on photosynthetic characteristics was considered necessary, to fully understand the crop physiological mechanisms in a closed greenhouse.

## MATERIALS AND METHODS

The experiments included three air circulation treatments, viz., the control treatment in which no forced air circulation was applied, forced air circulation at low canopy depth (LOW; tube at 0.6 m from the soil surface), and forced air circulation at high canopy depth (HIGH; tube at 2.5 m from the soil surface). Each treatment was realized in two compartments. Air circulation was realized by horizontally placing air tubes in the canopy (five per compartment of 9.6 m by 14 m). The polyethylene tubes had a diameter of 38.2 cm, and had small perforations of 8 mm diameter at 30° and 60° left and right from the top. Ventilators, which were placed at one end of the tube, operated at global radiation levels above 15 W m<sup>-2</sup>. Air speed at the perforations was 10 m s<sup>-1</sup>, resulting in air speeds in the canopy between 0.2 and 1.0 m s<sup>-1</sup> in the region of the perforations. Elsewhere in the canopy, air flow rates were not affected. This implies that a possible adaptation occurs only close to the air tubes.

Tomato cultivar 'Aromata' was planted on rockwool substrate on May 18, 2005 at a density of 3.3 plants m<sup>-2</sup> in experimental greenhouses at Naaldwijk, The Netherlands. A relatively high air temperature of 25-30°C was maintained to enhance early crop development; after June 30, the balance between vegetative and generative organs justified normal air temperatures and commencing the air circulation treatments. All side shoots were removed. One-third of the plants were topped on August 17 to reduce stem density at the onset of autumn, and the remaining plants were topped on September 18. One of the LOW compartments was confirmed to be infected by pepino mosaic virus on August 17, leading to very strict quarantine measures and its complete clearing on September 8. ELISA-tests did not show infections in the other compartments. Average actual temperature and air CO<sub>2</sub> concentration of the control compartments were set points for the compartments with air circulation treatments. In this manner, the greenhouse climate was similar for all compartments, apart from the air circulation treatment. Production (number of fruits and fresh harvest weight) of three rows per compartment was registered, and fruit dry matter content was determined twice. Fresh and dry plant organ weights, and leaf area were determined on 12 randomly selected plants at planting, and from one plant per compartment after the air circulation treatments were started. Accuracy is obtained by the high frequency of observations, rather than by a high number of plants per observation.

Photosynthesis characters are adaptively influenced by the radiation level, which decreases over canopy depth. Therefore, photosynthesis measurements were conducted at two canopy depths, viz., at the top of the canopy (TOP), defined as the first or second not-shaded leaf below the uppermost flowering truss, and halfway the canopy (HALF), defined as a leaf between the fourth and fifth truss. Also, measurements were conducted at three CO<sub>2</sub> levels, viz., 400, 700 and 1000 ppm. Each photosynthesis light-response curve was determined at 1395, 930, 698, 465, 233, 93 and 0 μmol PAR m<sup>-2</sup> s<sup>-1</sup>. Those values are 93% (transmission of the measuring chamber) of the radiation levels of the light source. With two compartments per air circulation treatment and three randomly selected plants per compartment, this resulted in 3 (air circulation treatments) x 2 (compartments) x 3 (plants) x 3 (CO<sub>2</sub>-levels) x 2 (canopy heights) = 108 photosynthesis light response curves.

Measurements were conducted between August 3 and September 13 with a portable photosynthesis measurer (LCpro+, ADC, UK), using forced air circulation to realize a constant boundary layer resistance, and at a constant air temperature of 25°C (greenhouse air temperature varied between 22 and 25°C), and a relative air humidity of 80% of the outgoing air. This ensures sufficient transpiration at realistic levels of relative air humidity. Twice a day the CO<sub>2</sub> loss due to leakage by the measurement chamber (approximately 0.5%) was determined; afterwards, data were corrected for this. Each photosynthesis light response curve was fitted to a non-rectangular hyperbole:

$$Ass = \left( \epsilon R + (A_{max} - R_d) - \sqrt{\left( (\epsilon R + A_{max} - R_d)^2 - 4\Theta \epsilon R (A_{max} - R_d) \right)} \right) / (2\Theta) - R_d,$$

in which two parameters were measured:

Ass = rate of net CO<sub>2</sub> assimilation (μmol m<sup>-2</sup> s<sup>-1</sup>)

R = Photosynthetically Active Radiation (PAR; μmol m<sup>-2</sup> s<sup>-1</sup>)

and four parameters were estimated:

A<sub>max</sub> = net assimilation at very high radiation (μmol m<sup>-2</sup> s<sup>-1</sup>)

R<sub>d</sub> = dark respiration (μmol m<sup>-2</sup> s<sup>-1</sup>)

ε = initial light use efficiency (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> / [μmol PAR m<sup>-2</sup> s<sup>-1</sup>])

Θ = curvature factor

It was evaluated whether the estimated parameters were significantly different, as two curves differ significantly if one of the four curve parameters are not equal. Because of the clearing of one LOW compartment the experimental design had become unbalanced, which required a residual maximum likelihood (REML) analysis of variance. Air circulation, CO<sub>2</sub> concentration and measuring height were the main effects.

Crop growth was simulated with the INTKAM crop growth model for tomato (Elings et al., 2004) for each compartment separately, as it is not justified to average environmental data. The INTKAM model simulates crop growth and plant-water relations. Leaf photosynthesis is computed with a biochemical model (Farquhar et al., 1980). Leaf transpiration rate is calculated with the Penman-Montheith equation, and makes use of the stomatal conductance model described by Nederhoff and de Graaf (1993). Planting date, dry organ weights at planting, dates of shoot formation and topping, and boundary layer resistances at various canopy depths were defined. The latter were derived from measured leaf sizes and local air flow rates, determined with a hot-wire anemometer and computational fluid dynamics calculations (Fluent Inc., 1998).

## RESULTS AND DISCUSSION

Table 1 summarizes the average net photosynthesis rates at the highest applied radiation level of 1395 μmol PAR m<sup>-2</sup> s<sup>-1</sup>, and Figure 1 gives the photosynthesis light response curves for 700 ppm CO<sub>2</sub>. The measured net photosynthesis rate in the top of the canopy is 45.4 μmol m<sup>-2</sup> s<sup>-1</sup> at a relatively high CO<sub>2</sub> level of 1000 ppm. A CO<sub>2</sub> level below 700 ppm, lower radiation and a lower canopy height all led to lower photosynthesis rates. Similar differences were found at other radiation levels. Maximum rates at saturating radiation levels were only found at 400 ppm CO<sub>2</sub>. It can be assumed that photosynthesis rates increase at radiation levels higher than 1395 μmol PAR m<sup>-2</sup> s<sup>-1</sup>, at 700 and 1000 ppm CO<sub>2</sub>. This is reflected in the value of A<sub>max</sub>.

The results of the analysis of variance are summarized in Table 2. The type of air circulation did not have a significant effect on any of the four parameters describing the non-rectangular hyperboles. CO<sub>2</sub> level significantly influenced A<sub>max</sub>, R<sub>d</sub> and ε, while measuring height in the canopy significantly influenced A<sub>max</sub> and Θ. This implies that four significantly different curves were found (Fig. 2): 1) at 400 ppm CO<sub>2</sub> in the top of the canopy; 2) at 700 and 1000 ppm CO<sub>2</sub> in the top of the canopy; 3) at 400 ppm CO<sub>2</sub> half-way the canopy; and, 4) at 700 and 1000 ppm CO<sub>2</sub> half-way the canopy.

Air circulation was therefore found not to have an adaptive effect on the photosynthetic characteristics. Adaptation was neither found when sweet pepper plants were exposed to prolonged high or low CO<sub>2</sub>-levels (Dieleman et al., 2003). This suggests

a great stability of the photosynthetic apparatus. It should be stressed that this has no consequences for the instantaneous effects of for example high radiation. However, as in our experiments the various treatments were exposed to similar environmental conditions, differences in instantaneous effects were not created.

Increased photosynthetic rates at higher levels of radiation and air CO<sub>2</sub> are known physiological phenomena (Farquhar et al., 1980). An increased photosynthetic rate at higher levels in the canopy is an adaptation to higher radiation levels, as has also been shown for sweet pepper (Dueck et al, 2005). The control treatment shows from 400 to 1000 ppm CO<sub>2</sub> a 49% increase in photosynthesis rate from 30.4 to 45.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which corresponds with the 44% increase that Heuvelink (1996) measured between 340 and 900 ppm CO<sub>2</sub>. It is remarkable that the measured photosynthesis rate at 700 ppm CO<sub>2</sub> is relatively high and that consequently, no significant differences were found between photosynthetic rates at 700 and 1000 ppm CO<sub>2</sub>. There is no clear reason as to why the maximum photosynthesis rates were reached at 700 ppm CO<sub>2</sub>, while normally this is reached at higher CO<sub>2</sub>-levels. Heuvelink (1996) found for tomato between 500 and 900 ppm CO<sub>2</sub> a 17% increase in photosynthesis rate, and Dieleman and de Zwart (2004) found for sweet pepper between 600 and 1100 ppm CO<sub>2</sub> a 48% increase.

Observed differences in total crop growth were small, and did not suggest an effect of air circulation on photosynthesis and growth. Observed cumulative total above-ground weights for the control, LOW and HIGH treatments were 2.66, 2.63 and 2.61 kg m<sup>-2</sup>, respectively, and observed cumulative fruit dry weights were 1.71, 1.63 and 1.68 kg m<sup>-2</sup>, respectively. Cumulative observed organ weights show an occasional decrease (Fig. 3), which is caused by the fact that each measurement represents only one plant, and not the average of a number of plants. Cumulative weight at any moment was determined from three components: 1) the organs weights of the standing plant, 2) the weights of the harvested leaves and fruits of the destructively harvested plants in the past, and 3) the weight of the ripe fruits harvested at high frequency. The first component, the organ weights of the standing plant, could actually show a temporary decrease over time, attributable to normal between-plant variation and the fact that each time only one plant was measured, leading to a temporary decrease of the cumulative weight. The high frequency of observation provides the required accuracy, which is provided by the larger number of observed plants per moment of observation if the frequency of observation is lower. Simulation results therefore have to be compared with the trend in observations.

As air flow rates were affected only very close to the tubes, and not elsewhere in the canopy, leaf boundary layer resistances reduced for leaves relatively close to the tubes. At most locations, computed boundary layer resistances were 190 m s<sup>-1</sup>. Exceptions were the top of the control canopy (170 m s<sup>-1</sup>), the bottom of the LOW treatment (80 m s<sup>-1</sup>) and the top of the HIGH treatment (75 m s<sup>-1</sup>). Although this has consequences for leaf photosynthesis rates, the integrated effect for crop photosynthesis is not significant. This is shown by both observations and simulations on growth.

Total above-ground dry matter production was well simulated by the INTKAM simulation model (Fig. 2). Dry fruit weight is slightly over-estimated, at the cost of a slight under-estimation of dry stem weight. The moment of first harvest is correctly simulated, and simulated dry matter concentration of the fruits and harvested fresh weights correspond well with observations. Also simulated specific leaf area (SLA) corresponds well with observed SLA, but simulated leaf area index (LAI) is under-estimated at the end of the season. This may be caused by a more frequent leaf harvesting than was realized in reality. Consequences of this under-estimation are limited: if simulations are performed with observed LAI as input, then simulated total dry matter production increases only 1.7%. This is associated with the low radiation levels at the end of the season, causing just a small increase in intercepted radiation if LAI is assumed to be larger.

## CONCLUSION

Air circulation in our experiment did not have an adaptive effect on the photosynthetic characteristics of the tomato crop, and had only local effects on leaf boundary resistance, without significant effects for photosynthesis at the crop level. The yield increases of 15-20% that are in practice observed in closed greenhouse systems in The Netherlands, can therefore be fully attributed to instantaneous effects of the elevated CO<sub>2</sub>-level.

## ACKNOWLEDGEMENTS

This research was funded by the Dutch Ministry of Agriculture, Nature and Food Quality, and the Dutch Product Board for Horticulture.

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## **Tables**

Table 1. Average net photosynthesis rates at 1395  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ , at two depths in the canopy, for three types of air circulation, and at three levels of air  $\text{CO}_2$ .

Canopy level	Air circulation	Net photosynthesis rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at various $\text{CO}_2$ levels (ppm)		
		400	700	1000
Top	Control	30.4	44.6	45.4
	High	31.9	46.1	45.1
	Low	31.2	43.9	45.2
Half-way	Control	24.4	33.1	40.5
	High	23.9	36.3	36.1
	Low	20.7	33.8	35.0

Table 2. *p*-values for the four parameters that describe the fitted photosynthesis light response curves, for the main effects, viz., air circulation,  $\text{CO}_2$  level and measuring height in the canopy.

Parameter	Air circulation	$\text{CO}_2$ level	Canopy level
$A_{\text{max}}$	0.87	<0.001*	<0.001*
$R_d$	0.61	0.04*	0.05
$E$	0.64	<0.001*	0.09
$\Theta$	0.97	0.10	0.01*

\*significant at  $P < 0.05$

Table 3. Average parameter values describing significantly different photosynthesis light response curves for two heights in the canopy and three  $\text{CO}_2$  levels.

Canopy height	Parameter	$\text{CO}_2$ level (ppm)	
		400	700 and 1000
Top	$A_{\text{max}}$	35.2	52.6
	$R_d$	0.11	0.14
	$\epsilon$	-1.2	-1.2
	$\Theta$	0.48	0.48
Half-way	$A_{\text{max}}$	24.5	39.2
	$R_d$	0.11	0.14
	$\epsilon$	-1.2	-1.2
	$\Theta$	0.61	0.61

**Figures**

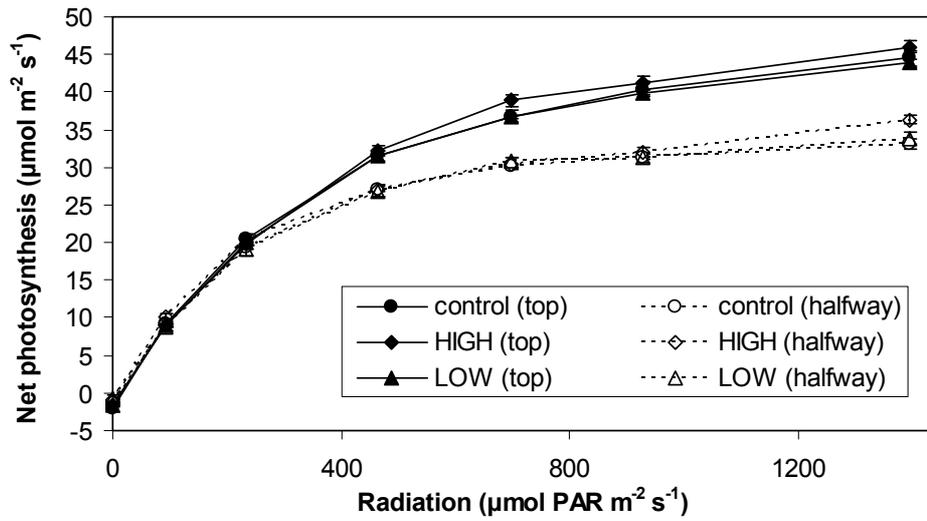


Fig. 1. Measured photosynthesis light response curves at 700 ppm  $\text{CO}_2$ ; in the top of and halfway the canopy; and for the control treatment, placement of the air tube high in the canopy, and low in the canopy.

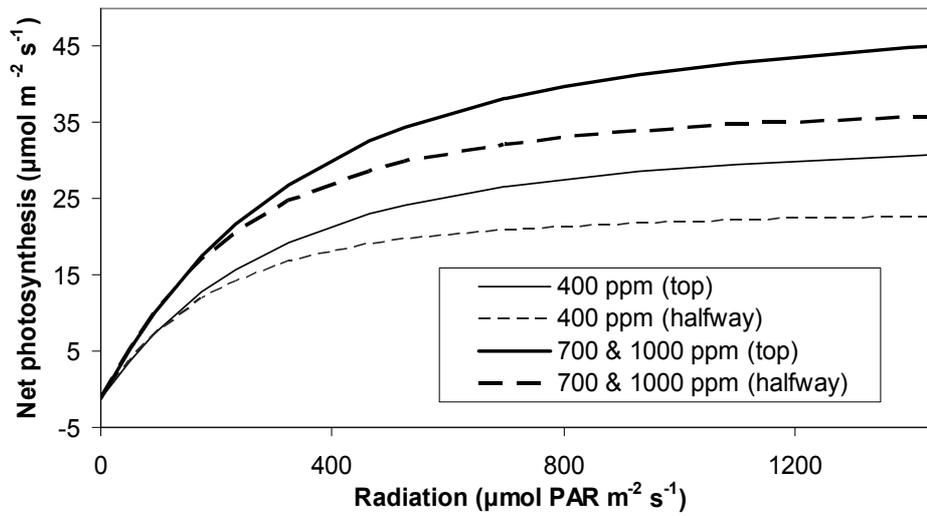


Fig. 2. The four photosynthesis light response curves which are significantly different for  $\text{CO}_2$  concentration and canopy height.

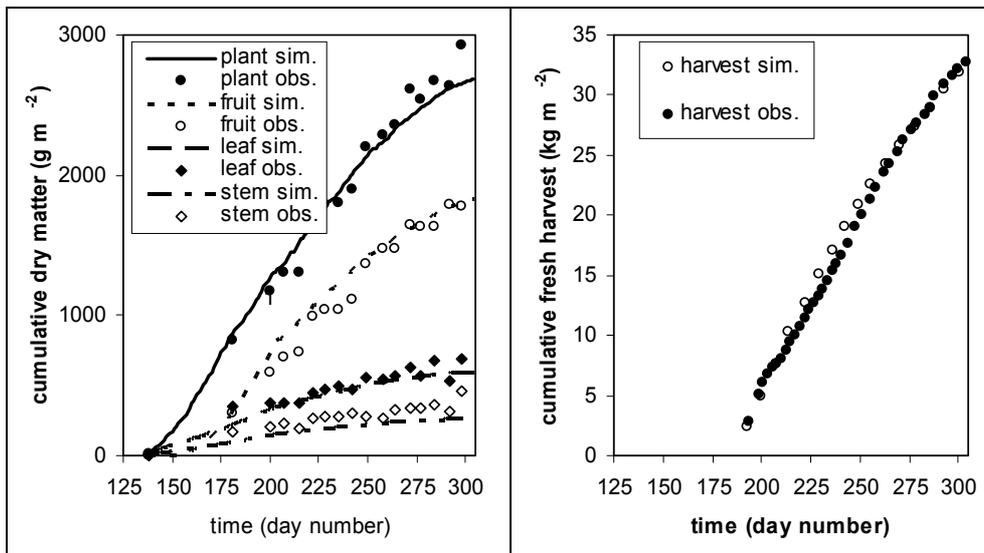


Fig. 3. Observed and simulated values of plant organ dry and fresh weight (left) and fresh fruit harvest (right), for one of the control compartments.