

## Fruit Trees and Climate. I.

### Temperature, Carbon Dioxide Concentration and Growth in Apple Trees

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#### Summary

The effect of carbon dioxide supply and misting upon the growth of 'Golden Delicious' in growth chambers was investigated in 1971. In 1972 the effects of carbon dioxide supply, additional light and temperature were investigated. Both years comparisons were made with trees growing under natural conditions. Trees with many as well as with few fruits were included in the experiments.

Growth values for leaves and shoots were lowest for trees growing out-of-doors, where also the temperature was lowest. Total shoot length was reduced, but the shoots thicker, when day temperatures in growth chambers were decreased from ca. 24.5 to 22° C. Shoot growth was increased by additional light and carbon dioxide supply (3–4 times normal concentration for an average of 8–10 hours daily). Misting increased shoot growth to a small degree but only in non-bearing trees. The variation in fruit yield was mainly due to different fruit set. Root growth was highest on trees out-of-doors. The total dry matter production per tree was not significantly affected by treatments in 1972, while in 1971 it (exclusive leaves) was greater outdoors and in a growth chamber with additional carbon dioxide supply than by the other treatments in the growth chambers.

It is concluded that differences in climatic factors affect the distribution and utilisation of assimilates within the tree to a greater extent than does the total production of assimilates in the leaves.

#### Resumé

Væksten hos 'Golden Delicious' blev i 1971 undersøgt i vækstkamre med og uden CO<sub>2</sub>-tilførsel samt med og uden overbrusning. I 1972 blev virkningen af CO<sub>2</sub>-koncentration, lystilskud og forskellig temperatur undersøgt. I begge år blev der sammenlignet med et hold træer på friland. Både træer med og uden frugt indgik i forsøgene.

Skud- og bladtilvæksten var ringest hos træerne på friland, hvor temperaturen også var lavest. Der var en mindre samlet skudlængde, men tykkere skud, når dagtemperaturen i dyrkningsrummene blev sænket fra ca. 24.5 til 22°C. Skudtilvæksten blev øget ved lystilskud og CO<sub>2</sub>-tilførsel (3–4 gange normal-koncentration i gennemsnitlig 8–10 timer daglig). Overbrusning gav kun hos ikke-bærende træer en lidt øget skudtilvækst. Frugtudbyttet varierede især på grund af forskel i frugtsætningen. Rodtilvæksten var størst hos træer på friland. Den samlede tørstofproduktion pr. træ var ikke signifikant forskellig mellem klimabehandlingerne i 1972. I 1971 var den (excl. blade) størst hos træerne på friland og ved CO<sub>2</sub>-tilførsel i dyrkningsrummene.

Det konkluderes, at forskelle i klimafaktorer i højere grad har virket på fordeling og omsætning af assimilater i træer end på den samlede produktion af assimilater i bladene.

## Introduction

Climatic factors play an important rôle for growth and fruit development in a fruit tree. Two groups of processes, as well as the interaction between them, are decisive. They are the processes of assimilate formation in the leaves, and the processes of transport and utilisation of assimilates by growth in different parts of the tree. In an attempt to analyze the absolute and relative importance of some climatic factors on these processes, experiments on apple trees were carried out in some simple growth chambers. It has been shown previously that the partitioning of growth within a tree affects not only the distribution of assimilates from the leaves, but also their intensity of production. F.ex. leaves near fruits have higher intensities of photosynthesis and transpiration than leaves not affected by the proximity of fruits (Hansen 1970, 1971). So the experiments were carried out on trees with many as well as on some with few fruits. However, fruit set varied, mainly due to other reasons. The greatest importance therefore is attached to the reactions by trees with few fruits, while the effects upon the fruits will be investigated further in future experiments.

The growth chambers were built in a greenhouse. It is not possible in such rooms to control and record the climatic conditions as accurately as in real climate chambers, hence only the greater differences and effects can be detected significantly. However, a certain biological variation will always exist where large individual specimens such as fruit trees are used so that only a limited number can be subjected to each treatment.

## Material and methods

### Growth chambers:

4 rooms, ground area  $5.5 \times 2.25$  m<sup>2</sup>, height 2.5 m, were built with walls and roof from clear plastic in a greenhouse. A shutter and a ventilator, controlled by a thermostat and a control watch, were placed near the floor in the gable of each room. When the temperature

increased beyond the desired level, the shutter was opened into the free atmosphere, the ventilator was started, and air from the outside was drawn in (declared amount 20 m<sup>3</sup>/minute). At the same time a shutter near the roof in the opposite gable was opened. When the temperature was lower than the desired one, so that the shutters were closed and the ventilators switched off, a control watch released ventilation of the rooms for a period of 8 minutes every 90 minutes from 6 a.m. to 10.30 p.m.

## Experiments

### 1971

'Control' : Growth chamber functioning as above with thermostat at 27°C.

'H<sub>2</sub>O' : As 'Control', but misting with rain water for 10 seconds every 10th–30th minute, when the relative humidity of the air was below 90 %. The intervals between misting were shortest in hot periods. Control unit: Honeywell.

'CO<sub>2</sub>' : As 'Control', but with the supply of 35 litres of CO<sub>2</sub> every time the shutters closed during the day time. Each period of supply was recorded automatically.

'H<sub>2</sub>O, C<sub>2</sub>O' : Misting and CO<sub>2</sub> supply as above in the same room.

'Open air' : Trees placed under natural weather conditions.

### 1972

The treatments 'Control', CO<sub>2</sub>' and 'Open air' were carried out as in the previous year. Further treatments were:

'CO<sub>2</sub>, light' : CO<sub>2</sub> supply like in 1971, furthermore two 400 W Hg-lamps were placed close above the roof of the room. They were switched on from sunrise to sunset. The walls of the room were screened by white plastic.

'Low temperature' : The thermostat was adjusted to 19°C (against 27° in the remaining rooms). The door of room

facing into the greenhouse was kept open.

Each treatment in 1971 was carried out on 12 trees, in 1972 on 10 trees. Half the trees of each lot kept all fruits (F), while on the remaining trees most of the fruits were removed (N). The trees were divided according to size as uniformly as possible upon the treatments.

#### Plant material:

1971: Three-year-old 'Golden Delicious' in 15 litres plastic pots were used. The treatments started June 16. The trees were sampled in October.

1972: Two-year-old 'Golden Delicious' in pots; the experiment started June 9 and was terminated September 12 due to signs of spray damage.

The trees were well supplied with water and nutrients by a daily watering with nutrient solution.

#### Measurements:

Thermometers and thermohygrographs were

used. Carbon dioxide concentration was measured in air samples in 500 ml flasks placed in the rooms the previous day. At 8 a.m. 10 ml of 0.01 N Ba(OH)<sub>2</sub> was added. The flasks were quickly closed with rubber stoppers, and after at least 6 hours titrated with 0.01 N HCl using 0.04 % cresolphthalein as indicator. The CO<sub>2</sub> concentration was calculated by comparison with samples of normal air which were pre-set at 325 ppm CO<sub>2</sub>.

Shoot length and diameters of trunks were measured several times during 1971. At the conclusion of the experiments the fruits were counted and weighed while vegetative parts were separated, dried (80°C), and weighed.

#### Results

##### Climatic conditions:

##### 1971

'Open air' temperatures were lowest (Table 1), but also air humidity and light conditions here differed from the other treatments. Average temperatures in the growth chambers were nearly identical. Due to the large volume of

Table 1. *Temperature, air humidity and CO<sub>2</sub>-measurements. 1971*

Treatment	'CO <sub>2</sub> ,H <sub>2</sub> O'	'CO <sub>2</sub> '	'H <sub>2</sub> O'	'Control'	'Open air'
<i>Av. temp., °C, 28/6-24/9</i>					
7 a.m.	17.9	18.0	17.7	17.2	
12.15 p.m.	24.2	23.7	23.4	23.7	19.0a)
4 p.m.	23.1	23.0	22.6	23.2	
Average	21.7	21.6	21.2	21.4	
<i>% relative air humidity</i>					
night and temp. < 20°C	ca. 90	80-90	80-90	80-90	
temp. > 20-22°C	70-80	40-60	70-80	40-60	
<i>Av. number of hours/day with 40-60 % rel. air hum.</i>					
in July-August	0	6-7	0	6-7	
in September	0	2-4	0	2-4	
<i>ppm CO<sub>2</sub>:</i>					
July (following supply)	970-1300	970-1300	ca. 325	ca. 325	325
Aug.-Sep. (follow. supply)	1300-2100	1300-2100	540-860	485-810	325
Aug.-Sep. (follow. ventilation)	≥ 650	≥ 650	480-590	325-540	325
<i>Av. number of hours /day with CO<sub>2</sub>-supply and light</i>					
July-August	7.5b)	7.5b)	0	0	0
Sept.-Oct.	10	10	0	0	0

a) measured at 2 p.m., 2 m height

b) CO<sub>2</sub> supplied morning and evening in particular

plant mass in the rooms the relative humidity was high also without misting, so differences between rooms were less than desired.

The CO<sub>2</sub> supply raised the CO<sub>2</sub> concentration to 3–4 times normal values during the first part of the experimental period. From ca. August 1 the concentration of CO<sub>2</sub> increased also in the rooms without artificial supply, in particular at 'H<sub>2</sub>O', which was very wet. Decomposition of soil and dead plant material may be the reason for that.

1972

Temperatures in three of the growth chambers were quite uniform (Table 2). Average day temperature was about 2.5° lower at treat-

ment 'Low temperature', while in 'Open air' it was about 6° lower. Differences in night temperature may have been even greater.

The CO<sub>2</sub> supply raised the CO<sub>2</sub> concentration to 3–4 times the normal value. On the average the CO<sub>2</sub> content was increased for about 10 hours daily. In hot periods CO<sub>2</sub> was only increased for 4–5 hours daily, in particular in the morning and in the evening. The CO<sub>2</sub> concentration in the rooms without CO<sub>2</sub> supply was essentially the same as 'Open air'.

The relative air humidity was always high during nights and during cool periods (Table 3). In hot periods from the beginning of July, and in particular during the latter half of August, the air humidity in the middle of the day was particularly low in 'Open air'; often the per-

Table 2. Temperatures and CO<sub>2</sub>-concentration. 1972

	'CO <sub>2</sub> , light'	'CO <sub>2</sub> '	'Control'	'Low temp.'	'Open air'
<i>Av. temp. °C</i>					
15/6–14/7, 8 a.m.	22.9	22.6	23.3	19.1	15.4
– 12 p.m.	25.6	25.2	26.1	23.5	19.4
– 4 p.m.	25.1	25.0	25.0	22.6	19.5
15/7–14/8, 8 a.m.	25.3	25.2	24.5	21.7	18.7
– 12 p.m.	27.4	27.8	27.6	25.5	23.7
– 4 p.m.	26.1	26.4	26.1	23.7	22.6
15/8–12/9, 8 a.m.	19.8	19.7	18.7	16.8	13.7
– 12 p.m.	24.9	24.9	24.5	22.5	18.4
– 4 p.m.	24.1	23.8	23.2	21.4	18.2
Average	24.6	24.5	24.3	21.9	18.8
<i>ppm CO<sub>2</sub> a)</i>					
14/6–30/6, 11,0 <sup>c)</sup>	1090	1120	307	307	325
1/7–31/7 <sup>b)</sup> , 9,7 <sup>c)</sup>	1020	1040	296	295	325
1/8–20/8, 10,0 <sup>c)</sup>	1020	960	330	330	325
21/8–12/9, 9,9 <sup>c)</sup>	1130	1100	362	360	325

a) av. of 10–13 measurements at 8 a.m.

b) based on analysis July 3–14 only

c) av. number of hours per day with CO<sub>2</sub>-exposure

Table 3. Size of order of relative air humidity (%) at treatments 'CO<sub>2</sub>' and 'Open air'. 1972

Period	Night		Minimum day	
	'CO <sub>2</sub> '	'Open air'	'CO <sub>2</sub> '	'Open air'
14/6– 9/7	85–90	90–95	40–70	
10/7–13/8	85–90	95	45–85	35–80
14/8–31/8	85–95	95–100	65–80	30–70
1/9–12/9	85–90	95–100	50–80	40–70

centage of relative humidity was 20–30 lower than in the growth chambers.

**Growth:**

Growth of shoots and leaves was lowest in 'Open air', where temperature was lowest. On the other hand, growth in roots was greater here than under other treatments (Figure 1 and 2). The differences were greatest in 1971, in particular for trees with few fruits, as the fruit load in the remaining trees suppress the growth in other parts of the tree. Also at 'Low temperature' the shoot length is less than in the other rooms, opposite the shoots are thicker (Table 5). The root growth is not greater here than in the other growth rooms.

The CO<sub>2</sub> supply also raises the shoot growth values, in 1971 in the first part of the season in particular (Table 4). In 1972 shoot growth is greater when CO<sub>2</sub>, as well as additional light, is given (Table 5). Misting increases shoot growth a little only for trees with few fruits (Figure 1).

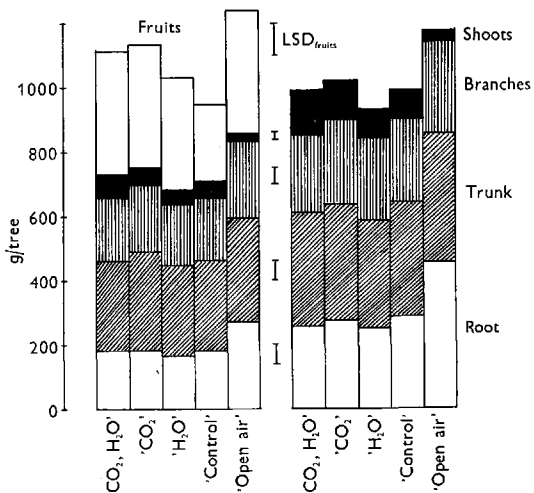


Fig. 1. Dry matter of different organs. Left hand group shows fully cropping trees. Av. of 6 trees. LSD = least significant difference (95 % level). October 1971.

Total fruit crop per tree in 1971 is lowest at the 'Control' (Figure 1) because of a low fruit

Table 4. Growth of extension shoots (cm/shoot) during different periods. 1971  
Av. of 5 shoots per trees, 12 trees per treatment.  
Av. shoot length at June 16: 20.0 cm

Treatment	'CO <sub>2</sub> ,H <sub>2</sub> O'	'CO <sub>2</sub> '	'H <sub>2</sub> O'	'Control'	'Open air'	LSD
16/6–16/7	19.1	19.2	15.5	10.0	5.6	2.6
16/7–18/8	22.8	24.8	16.0	25.8	3.7	4.1
18/8–29/10	8.6	6.0	7.1	5.6	0.2	2.9
16/6–29/10	50.5	50.1	38.6	41.5	9.5	6.0

Table 5. Growth of extension shoots and number of fruits. 1972  
Av. of 10 trees (for fruit number 5 trees)

	'CO <sub>2</sub> , light'	'CO <sub>2</sub> '	'Control'	'Low temp.'	'Open air'	LSD
g extension shoots (dry matter)/tree	74.3	62.2	50.0	46.0	35.5	23.1
cm extension shoots/tree	960	764	630	496	392	181
number of extension shoots/tree	24.8	20.9	16.7	15.6	15.8	5.1
cm/shoot	39.2	38.6	41.1	34.3	25.1	6.5
mg dry matter/cm	75.4	81.0	76.0	91.9	84.2	10.8
number of fruits/tree	25.2	18.8	24.2	24.0	43.0	13.9

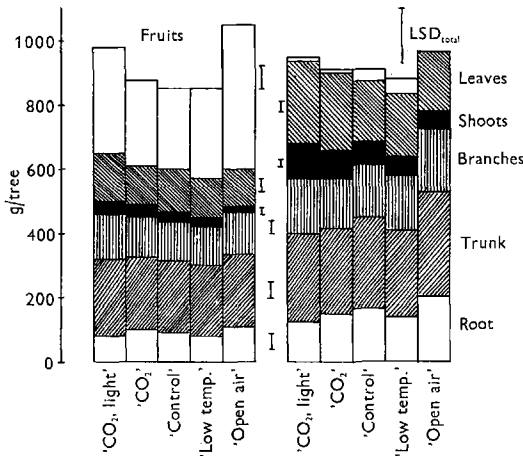


Fig. 2. Dry matter of different organs per 12th September 1972. Av. of 5 trees. Otherwise as Figure 1.

number per tree (13 against 23–26 in other treatments). But this difference in fruit set is hardly due to the treatments. In 1972 the fruit set and thus the yield per tree was particularly high at the trees in 'Open air' (Table 5).

In 1971 total leaf amount was not measured. The remaining dry matter production per tree is greatest in 'Open air' (Figure 1). Also total production is higher with, than without, CO<sub>2</sub> supply. In 1972 differences in total dry matter per tree are not significant (Figure 2).

### Discussion

The most distinct effect of changing the above climatic parameters is upon leaf and shoot growth, in particular on trees with few fruits. Leaf and shoot growth are increased by CO<sub>2</sub> supply and by additional light. Shoot growth, in particular length of internodes, is increased by additional CO<sub>2</sub> supply (Zimmermann et al., 1970; Krizek et al., 1971). A further increase in CO<sub>2</sub> concentration above the level of ca. 1200 ppm in the present experiment cannot be expected to increase growth further according to estimates based on the relationship between CO<sub>2</sub> concentration and rate of photosynthesis (Zelitch, 1971). However, exposure to addi-

tional CO<sub>2</sub> for more than 7.5–11 hours per day (Tables 1 and 2) might have augmented the effect.

The additional light was of rather low intensity for photosynthesis, and the plant material in the rooms became rather congested during the season. It is not certain, however, whether a higher light intensity would have further promoted shoot growth. Root growth, to a greater extent than leaf and shoot growth, is increased when trees at natural light intensities are compared to shaded trees (Maggs, 1960; Priestley, 1969; Cripps, 1972). Dependence of shoot growth upon light intensity varies with plant species. In some cases it is no higher, and may even be lower, at full daylight than by shadowing to 50 % or less of this light intensity (Kozłowski, 1971). Within a tree, the leaves in full light are thicker than those in shadow (Jackson and Beakbane, 1970). Fruit size is not reduced by decreasing light intensity to 72 % of natural, as it is by a decrease to 45 % (Jackson, 1968).

Shoot and leaf growth values are increased also by higher temperature. This is supported especially by comparing 'Low temperature' to the other growth rooms (Table 5), where other conditions have been similar. Extending this relationship, it seems probable that the yet smaller shoot growth in 'Open air' is caused by the even lower temperature here (Table 1 and 2). Differences in night temperature might have been even greater. Increase of a day temperature of 19°C by 5° accelerated shoot growth strongly, irrespective of whether exposure to the higher temperature took place in the early or the later part of the growing season (Tromp, 1973). Total growth in a greenhouse was a little less than outdoors (Maggs, 1961). Leaf area was greater in the greenhouse while root formation in particular was greater outdoors.

Also in the present experiments the smaller shoot growth in 'Open air' compared to other treatments is followed by an increase particularly in growth of roots (Figures 1 and 2). It might be questioned whether this is a tem-

perature effect alone. The lower air humidity may have caused a quicker drying out of the soil which may have stimulated root growth. Also growth is no higher at 'Low temperature' in the growth chamber compared to other treatments here.

Changing the climatic parameters affects the partitioning of growth to a higher degree than the total dry matter production per tree. The latter is not increased by increasing temperature, only a little by CO<sub>2</sub> supply, and perhaps by additional light, even though the rate of photosynthesis by a whole apple tree at light saturation depends upon CO<sub>2</sub> concentration and is decreased by lower light intensity (Sirois and Cooper, 1964). Reduction of full daylight to one third reduces the total dry matter production to half or less (Priestley, 1969). But apparently a greater total production by changing climatic conditions compared to the natural ones is obtained only when the turnover of assimilates in growth (sink-effect) can be increased accordingly. In the present experiments this has been the case only to a smaller degree. The smaller total leaf area for trees in 'Open air' has produced at least the same dry matter amount per tree as trees with larger leaf areas in the growth chambers (Figure 2).

Fruits are strong sinks and the effects of climatic parameters on fruit growth, and thus total dry matter production per tree, is of particular interest. However, due to uniform and often rather poor fruit set this has not been fully elucidated and will be investigated further. Higher crop levels of apples in southern than in northern Europe (Folley, 1973) are explained according to Landsberg (1972), mainly by differences in temperature, particularly in the early and the late part of the growing season, and the resulting effects upon translocation and growth within the tree. Differences in light intensity and potential photosynthesis seem to play a smaller rôle.

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#### References

- Cripps, J. E. L.*, 1972: The effect of shading and Alar application on apple root: shoot ratios in Western Australia. – *J. hort. Sci.* 47: 291–299.
- Folley, R. R. W.*, 1973: An estimate of the net difference in yield of apple orchards in northern and southern Europe attributable to climate differences; with notes upon the economic significance of superiority in yield. – *Scient. Hort.* 1: 43–55.
- Hansen, P.*, 1970: <sup>14</sup>C-studies on apple trees. VI. The influence of the fruit on the photosynthesis of the leaves, and the relative photosynthetic yields of fruits and leaves. – *Physiol. Plant.* 23: 805–810.
- 1971: The effect of fruiting upon transpiration rate and stomatal opening in apple leaves. – *Physiol. Plant.* 25: 181–183.
- Jackson, J. E.*, 1968: Effect of shading on apple trees. – *Rep. East Malling Res. Stn. for 1967*: 69–73.
- & *Beakbane, A. B.*, 1970: Structure of leaves growing at different light intensities within mature trees. – *Rep. E. Malling Res. Stn. for 1969*: 87–89.
- Kozłowski, T. T.*, 1971: Growth and development of trees. Vol. I. New York & London, 443 p.
- Krizek, D. T., Zimmermann, R. H., Kleuter, H. H., Bailey, W. R.*, 1971: Growth of crabapple seedling in controlled environments: Effect of CO<sub>2</sub> level, and time and duration of CO<sub>2</sub> treatment. – *J. Amer. Soc. Hort. Sci.* 96: 285–288.
- Landsberg, J. J.*, 1972: The real reason why we grow smaller apple crops than southern Europe. – *Grower* 78: 657–658.
- Maggs, D. H.*, 1960: The stability of the growth pattern of young apple-trees under four levels of illumination. – *Ann. Botany* 24: 434–450.
- 1961: Changes in the amount and distribution of increment induced by contrasting watering, nitrogen and environmental regimes. – *Ann. Botany* 25: 353–361.
- Priestley, C. A.*, 1969: Some aspects of the physiology of apple rootstock varieties under reduced illumination. – *Ann. Botany* 33: 967–980.
- Sirois, D. L. & Cooper, G. R.*, 1964: The influence of light intensity, temperature and atmospheric carbon concentration on the rate of apparent

- photosynthesis of a mature apple tree. – Maine Agric. Exp. Stat. Bul. 626.
- Tromp, J.*, 1973: Enkele fysiologische aspecten met betrekking tot de vruchtkwaliteit bij appel en peer. – *Bedrijfsontwikkeling* 4: 187–189.
- Zelitch, I.*, 1971: Photosynthesis, photorespiration, and plant productivity. – New York & London, 347 p.
- Zimmerman, R. H., Krizek, D. T. Bailey, W. A. & Klueter, H. H.*, 1970: Growth of crabapple seedling in controlled environments: Influence of seedling age and CO<sub>2</sub> content of the atmosphere. *J. Amer. Soc. Hort. Sci.* 95: 323–325.

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