APPLIED PLANT RESEARCH

Non-destructive root oxygen use measurement III

Cucumber propagation in rockwool in a climate chamber, July-August 2001

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Summary

Cucumbers were propagated in rockwool cubes in a climate cell for four weeks. The complete root system of each cucumber was enclosed in an airtight box. Each box was connected to an air bag, which acted as an air reservoir. A peristaltic pump ensured air circulation in the system. Treatments included maintenance of oxygen levels at 21%, 7% and 2% in specific box-bag systems.

The goal of this experiment was to measure the critical oxygen supply rate for normal production. Additional goals were to characterise plant and root growth affected by low oxygen availability.

With a spectrophotometer it proved possible to measure and monitor the oxygen level in the box-bag system at various points. A critical oxygen re-supply level between 8 and 12% was found for this system. A maximum oxygen use of 5.8 mg/h was reached by plants with a growth equal to the reference plants. The above ground growth reaction to mild prolonged sub-optimal oxygen supply rates included a 20-50% reduction in leaf area, fresh and dry mass production and, less pronounced, a reduction in plant length and root dry mass production. The root growth reaction to mild prolonged sub-optimal oxygen supply rates included a decrease in root mass production rate in proportion to the above ground dry mass production rate. The root oxygen use rate during the light period was 5-10 times higher than during the night period.

It is unlikely that the absolute oxygen level causes the growth reduction. Local oxygen depletion in the substrate is a more likely cause. Local oxygen depletion might be the result of the interaction of oxygen supply rate and substrate diffusivity. Other possible causes are the accumulation of gasses as carbon dioxide and ethylene to phytotoxic concentrations.

1. INTRODUCTION

This report describes part of a program executed by the Glasshouse Crops Research Unit of Applied Plant Research. The Ministry of Agriculture of The Netherlands finances this program. The participation of the government in this program as in other projects aimed at improving culture methods, is justified by the economic importance of the Dutch Horticulture.

This experiment on the transport and use of oxygen in substrates was a part of a larger project, which studies the transport processes of water and gasses in substrates (Wever, 1999; Wever et al, 2001; Blok, 2001). The goal of this work was:

- To measure the critical oxygen supply rate
- To characterise growth affected by low oxygen availability
- To characterise rooting affected by low oxygen availability

Gerrit Wever was the project manager. Chris Blok organised the experiment, which was realised by Sylvain Gerard, with the occasional help of A. van Winkel and A.A. van Leeuwen.

The oxygen consumption of roots of cucumber plants in propagation was measured in a former experiment (Cassamassimo and Blok, 2001). To do this, the complete root system of each cucumber had to be enclosed in an airtight box. Each box was connected to an air bag, which acted as an oxygen reservoir. A peristaltic pump ensured air circulation in the system. With a spectrophotometer it was possible to measure and monitor the oxygen concentration in the box-bag system at various points.

Blok and Cassamassimo, 2001 found an oxygen consumption rate of 3.0 mg/h/plant for their experimental layout (Figure 1). The oxygen levels aimed at where High (H) with 21 % of oxygen, Intermediary (I) with 7 % of oxygen and Low (L) with only 2 % of oxygen. These percentages represent 100% of air, a mixture of 33% air and 67% Nitrogen and a mixture of 10% air and 90% Nitrogen.

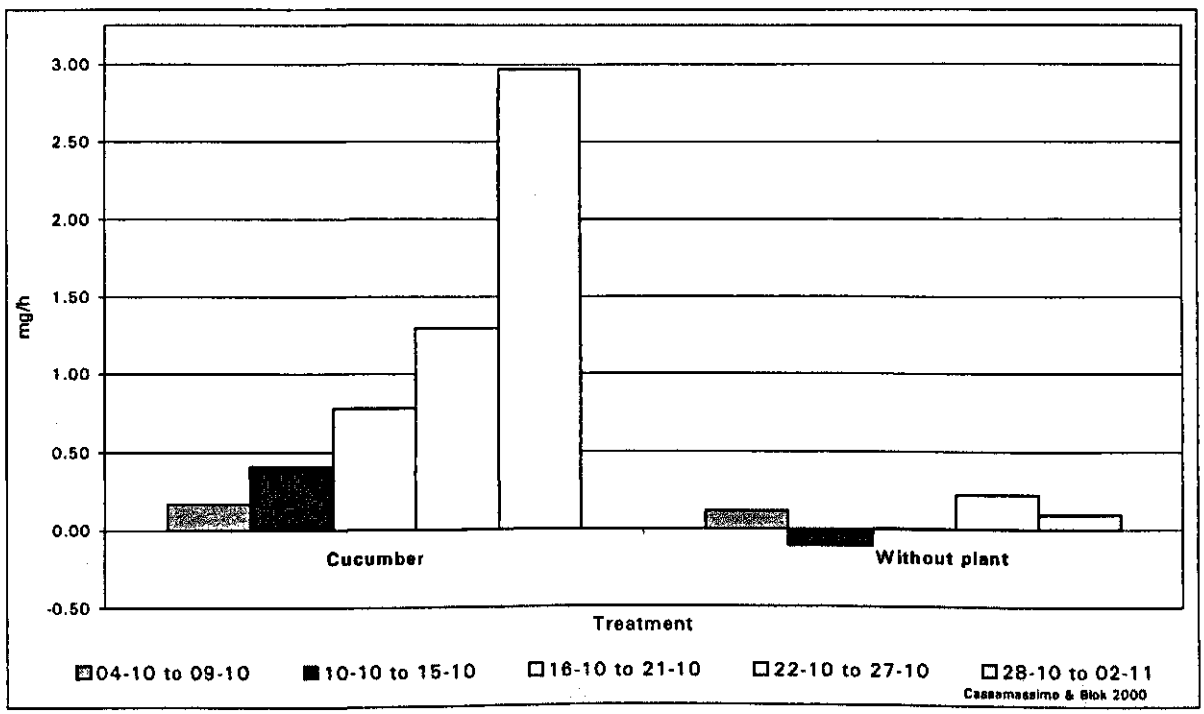

Figure 1 - Oxygen consumption during five periods (Cassamassimo and Blok, 2001)

Based on assumed starting concentrations of 21, 7 and 3% of oxygen and an increasing oxygen use by an increasing plant mass, Figure 2 was made. Figure 2 shows the anticipated hypothetical pattern of oxygen consumption reflected in the oxygen concentration in the system gasses. Note that intermediary and low treatments have periods of zero-oxygen concentration. In the low-level case, these periods represent more than a half of the time. So with these three treatments, the plants suffer respectively no, mild and severe oxygen absence.

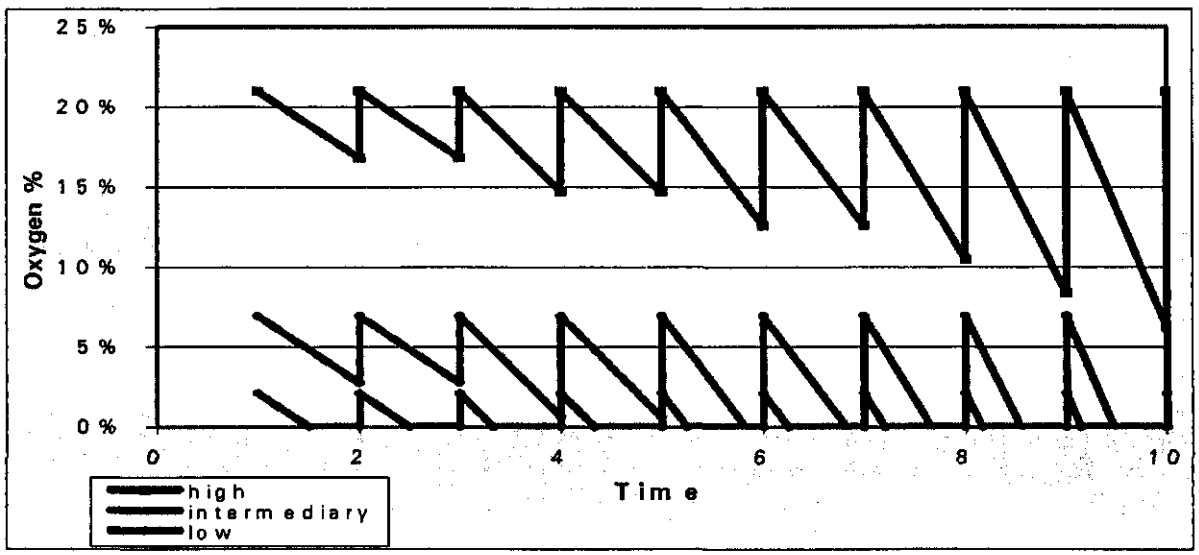

Figure 2 - Hypothetical oxygen concentration in the system gasses in time

Former experiments suffered from technical problems with the oxygen measurement, the refilling with gas mixtures and the unknown amount of water used for transpiration (Cassamassimo and Blok, 2001). In this experiment technical improvements were made to overcome these problems.

2. MATERIAL AND METHODS

To study the oxygen use of cucumber roots the substrate and the roots were enclosed in an airtight box of polyvinylchloride (PVC). This box was connected to a nutrient solution supply system and to an air circulation system (Figure 3). The treatments were applied to twelve boxes (Apppendix 1).

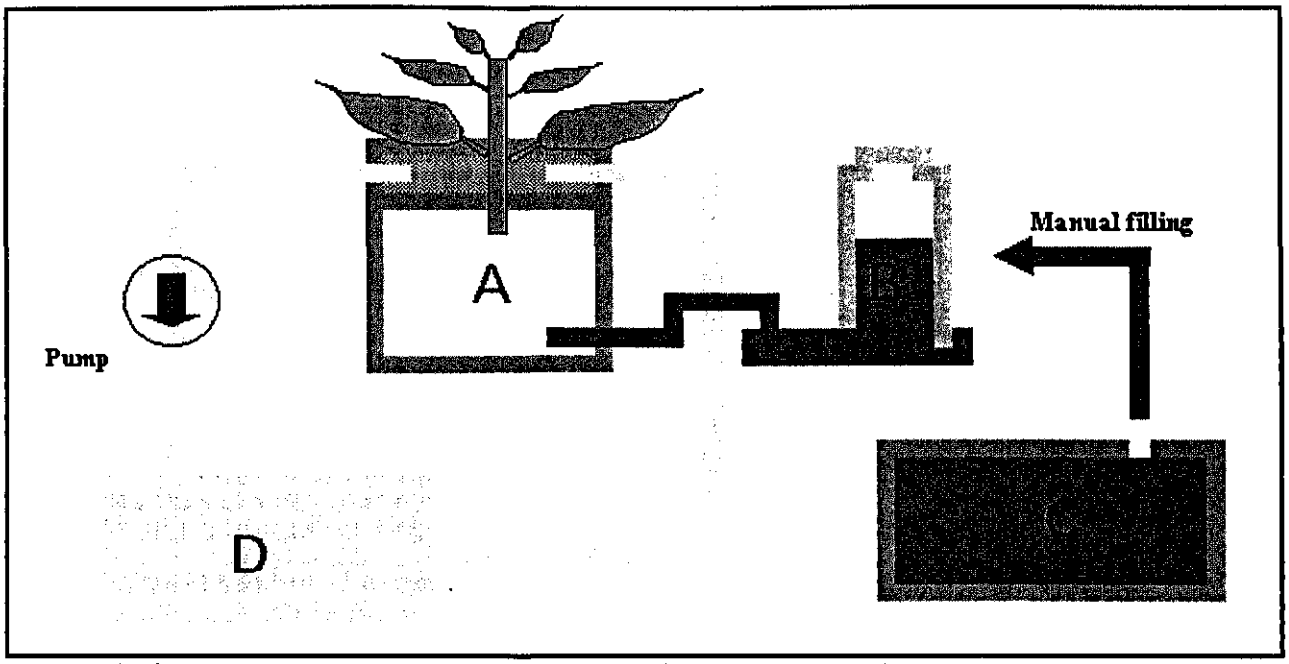

Figure 3 - System to control the water and oxygen supply, showing a box with substrate and a plant (A), the water supply (B), a nutrient solution container (C) and an air bag (D)

2.1. CLIMATE CELL

A climate chamber was used to control light level, carbon dioxide level and air humidity. If the light level changes, oxygen consumption by roots can also change (Nagel, 1998; Scheible et al 1997). The same observation can be made about carbon dioxide and air humidity. Therefore the control of these three parameters was imperative for the interpretation of the results. The cell was equipped with an automatic control of temperature, carbon dioxide level, air humidity and light (short waves and long waves). Table 1 shows the settings for main climate parameters. Daily the conditions in the cell were verified by checking the graphic representation of minute values over the past 24 hours (Appendix 2).

Table 1 - Climate parameters

Parameters	Range	Unit
Light*	200	µmole PAR (photo active radiation)
Temperature	20 (26)**	° C
CO_2	400	PPM
Humidity	75	%

* Whether the lights were on or off, was registered with thermocouples close to the lamps
** Germination

2.2. ROCKWOOL CUBES AND NUTRIENT SOLUTION

2.2.1. ROCKWOOL CUBES

The Rockwool cubes used, during this experiment, had a bulk density of 65 kg/m^3. The dimensions were 10x10x6.5 cm with a central hole of diameter 27mm and depth 35mm. Two indentations of 10x2x0.7 were made at the bottom of the rock wool cubes. Two holes were made in each cube to be able to insert two sampling pipes. The cubes were placed in boxes the 11th of July 2001. Before sowing all the cubes were saturated in nutrient solution. On the 23rd of July of 2001, the seeds were planted in 24 rockwool cubes. Twelve seeds were divided over three treatments, 4 were sown as reference with box (RB) and 8 as reference without box (RWB). Nutrient solution was added twice to all plants to reduce the yellow colour of the leaves: 120 ml on the 30th of July, 50 ml on the 7th of August, and 25 ml was added just after sowing.

2.2.2. NUTRIENT SOLUTION

For this experiment a nutrient solution for cucumbers in closed systems was used (De Kreij et al, 1999). On 02-08-2001, the nutrient solution was analysed to check on any inadequacy of elements, which would explain the yellow colour of cucumber leaves. Table 2 shows the standard values and the result of analysis.

The plants in the boxes had contact with the nutrient solution through a wick construction made of a plastic tube with a special polypropylene cord inside. The tip of the tube was immersed in a petri dish to prevent air entry into the tube (figure 4). The Petri dish was at the same level as the box bottom (which results in 80 to 95 % of water content in the rockwool cubes). The solution thus was drawn into the box by capillary action. Any water used by the plants was re-supplied through the wick. To keep the volume of water available in the petri dish constant, a closed bottle with a punctured bottom was added. The water level in the Petri dish thus remained at a level corresponding with the highest part of the punctuation hole. The plants that remained without boxes (RWB) had contact with the nutrient solution through a piece of cloth.

Table 2 – A standard cucumber nutrient solution and the analysis at 02-08-01

	Units	Standard *	Analysis of 2-08-2001 (difference with standard)
EC	dS/m	3.5	3.4 (-0.1)
NH_4	Mmol/l	1.8	1.5 (-0.3)
K	Mmol/l	11.9	12.6 (0.7)
Ca	Mmol/l	5.0	6.8 (1.8)
Mg	Mmol/l	1.8	2.2 (0.4)
NO_3	Mmol/l	21.4	25.2 (3.8)
SO_4	Mmol/l	1.8	2.3 (0.5)
H_2PO_4	Mmol/l	2.3	1.9 (-0.4)
Fe	µmol/l	15.0	25 (10.0)
Mn	µmol/l	10.0	19 (9.0)
Zn	µmol/l	5.0	12 (7.0)
B	µmol/l	25.0	41 (16.0)
Cu	µmol/l	0.7	2.7 (2.0)
Mo	µmol/l	0.5	0.4 (-0.1)

The standard values at 1.7 dS/m (De Kreij et al, 1999) were recalculated to match the sample

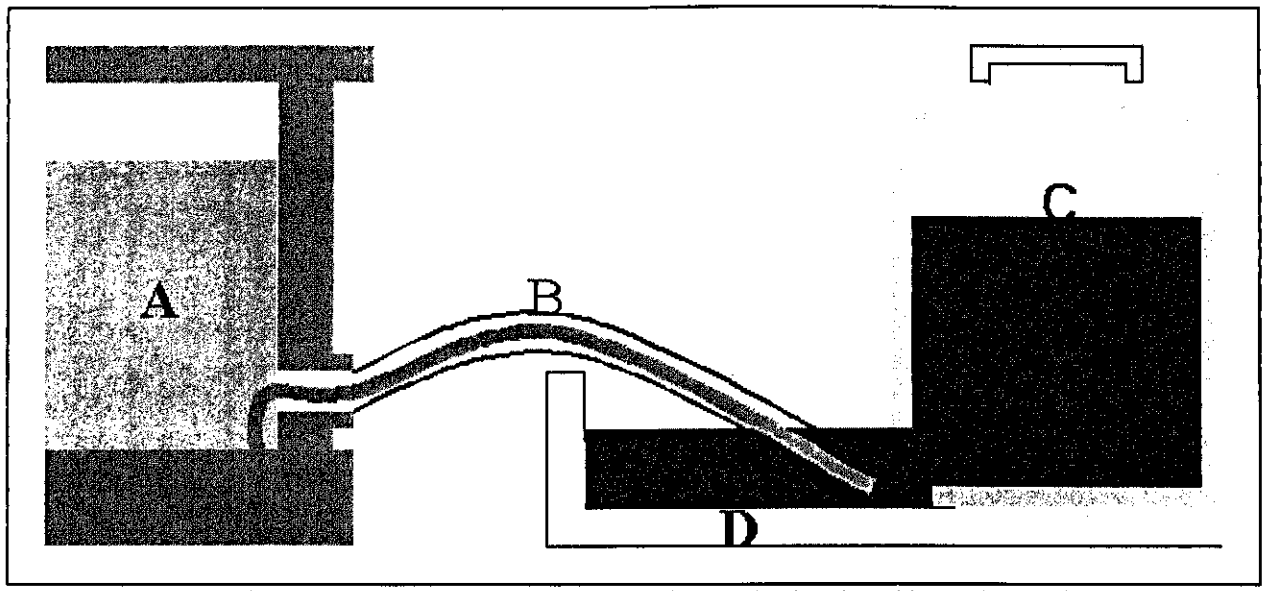

Figure 4 - Water and nutrient solution supply to the box (A) by a plastic tube with a polypropylene cord inside (B), which is fed from a petri dish (D) and a bottle with a punctuation hole (C)

2.3. AIR CONTENT REGULATION

2.3.1. BOXES

For this experiment sixteen PVC boxes, with dimensions 10x10x10 cm, were used (Figure 5). They were identical to those in a previous experiment except for the water supply system shown in Figure 4. These boxes were constructed with a brim. The lid was closed with screws and rubber. This process avoided the stress caused by closing with welding. A flexible paste was used to close the hole in the top. The boxes had to prevent gas exchange with the environment. Each box had two sampling pipes to take local gas samples from height 2 and 4 cm from the bottom and two tubes to permit air circulation between the box and an air bag. The boxes also had a plastic tube, which could serve as an emergency water supply system.

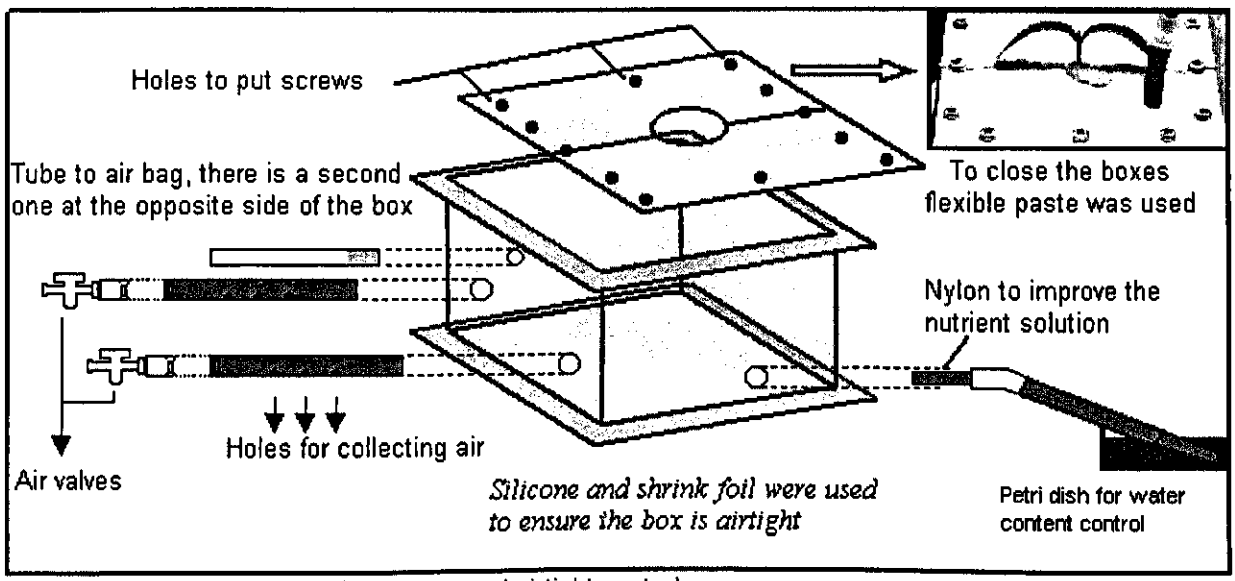

Figure 5 - Scheme of the box for oxygen and airtight control

2.3.2. AIR BAGS

Each box was connected to a plastic-bag with dimensions 31x30 cm with a capacity of 5.0 litres. The bags were made of Tedlar, which is gas impermeable. Each air bag had two access holes (Figure 6).

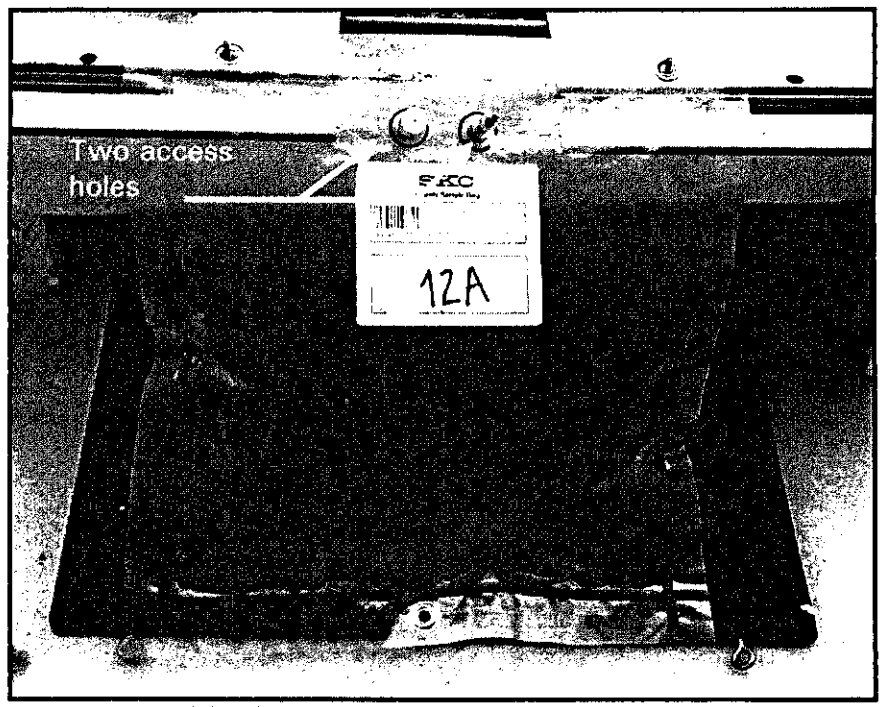

Figure 6 – An air bag and the sticker for identification of the treatment

The procedure used to fill the bags was based on the principle of communicating vessels. 3.0 l of water was used to push 3.0 l of air into the system. To speed filling, nitrogen over-pressure was used (figure 7).

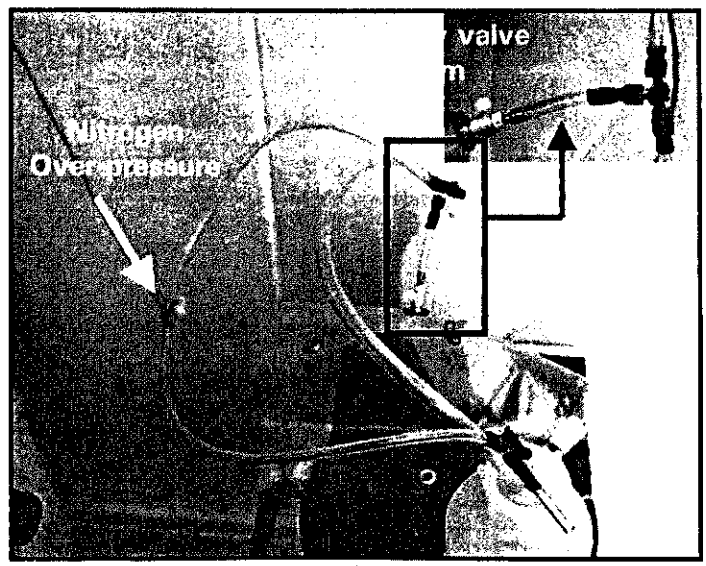

Figure 7 - Filling system with two bottles, three-way valves, a bottle with liquid nitrogen and pressure regulation

2.3.3. AIR PUMP

A small peristaltic pump was used to circulate the air of 12 box-bag systems simultaneously. A rotator pushed the air through flexible tubes with a constant flux of 3 ml of air/min, which is 4.3 l of air/day. This volume of air was thought to give ample oxygen supply to the roots in the H treatment, a prerequisite for an acceptable comparison between the RB and H measurements. Connections between air bag, box and pump were made with plastic tubes. Air was pushed from the bag to the box through the pump (Figure 8).

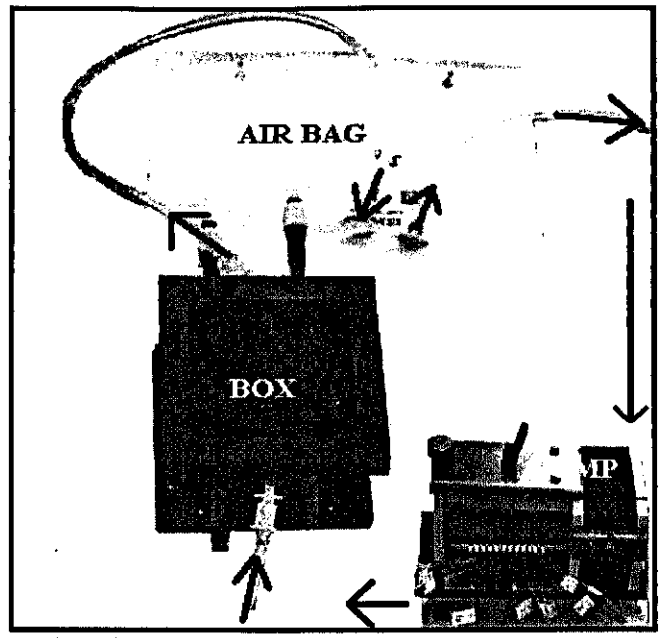

Figure 8 - Air circuit between bag, box and pump.

2.4. OXYGEN METER

The oxygen meter used was a compact, highly sensitive miniature spectrophotometer. The sensor tips were specially coated to suit the anticipated use in this experiment. The oxygen sensors were connected to the AVS-S2000 spectrophotometer and a Tungsten Halogen light source by bifurcated optical fibre cables. The spectrophotometer data were processed by a laptop computer using a DAQ-700 interface. A second sensor was added to the meter as a slave channel (Figure 9).

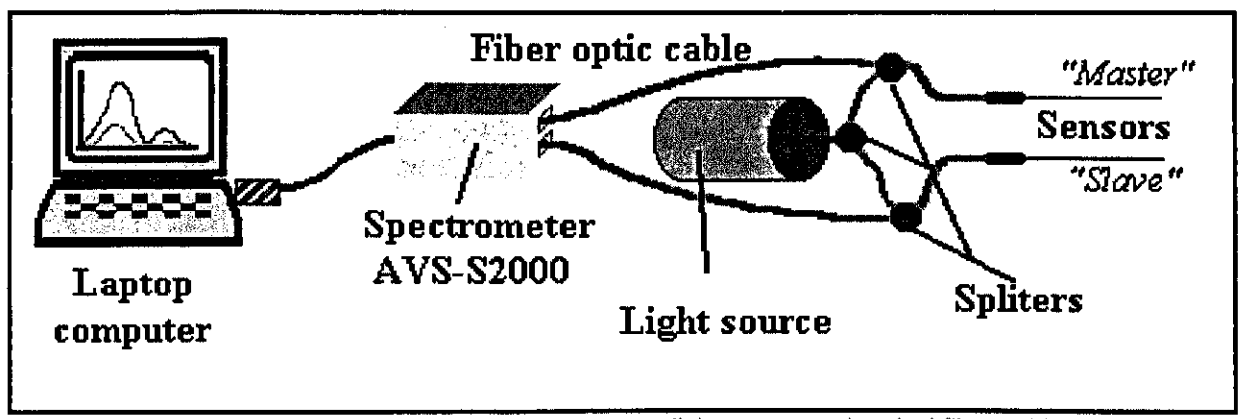

Figure 9 – Spectrophotometer, laptop computer, sensors, light source and optical fibre cables. The optical fibre cables are split to serve two sensors and two spectrophotometer entries with one source

2.5. WEIGHT AND HEIGHT

Just before cutting, on the 14th August 2001, plant heights were measured with a ruler. After cutting, total plant weight as well as leaves and stem weights were taken. Leaf area was measured with a LICOR leaf area meter. During the experiment, approximations of leaf area were made based on leaf width measurements. The model used was Area=0.7*(Width)^2. The dry weight of stems and leaves was obtained after keeping the cut plants in an oven at 80°C for 24 hours. To calculate the dry weight of organic material in the cubes, as a measure of the root mass, the initial weight and the dry weight (80°C for 48 hours) of the cubes were measured. The loss on ignition at 600°C for 4 hours was also measured. The loss on ignition was calculated as dry weight minus the ignited dry weight and corrected for the organic binder present in each cube (0.95 grams according to Cassamassimo and Blok, 2001). Each cube was cut in three equal layers after drying (80°C for 24 hours) to study the distribution of roots in the rockwool cubes.

3. RESULTS

3.1. CLIMATE DATA

The desired climate conditions were reached (Appendix 2). During the first days condensation appeared on the roof's windows. This phenomenon was the result of too cool air in the cooling-system of the tube lights. The peaks in the CO_2 graph were triggered by the daytime activity in the cell but peaks have no effect on the plant growth. During the first week the temperature was 26°C to improve the germination. The last two days, temperature was down to 16°C to restrain the growing of the plant. In conclusion, all the plants received the same normal treatment.

3.2. TREATMENTS

Figure 10 shows the results of the daily measurements of oxygen in the bag. The oxygen level of the three treatments was reached as planned. During the experiment, the oxygen level of bag 10 rose inexplicably due to a leak somewhere in the system, so all data of plant 10 were omitted from this study. Plant 1 had a very low water use so it was omitted too. The bags were filled with fresh air-nitrogen mixtures four times: the 31st of July, the 6th, the 10th and the 13th of August. The amount of air-nitrogen added depended on the level to achieve (Appendix 3). The 1st of August, a correction was done on the 31st July filling.

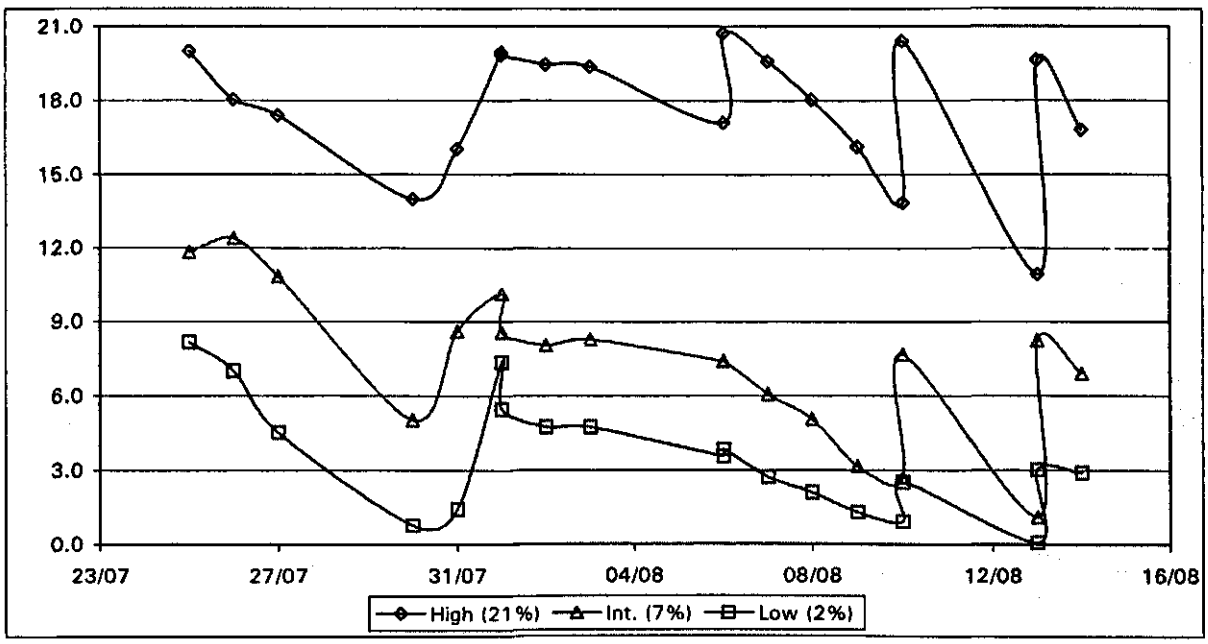

Figure 10 – Oxygen content in time for each treatment

3.3. OXYGEN MEASUREMENTS

The spectrophotometer somehow created a pattern of sudden too high/ too low values. To eliminate this instability in the data, a filter was successfully used. It compared each value with the average of the five previous values and the five next values. If the value was within ± 20 % of the average, the value was kept. Routinely, the master sensor had to be re-calibrated each day before oxygen bag content measurement. The spectrophotometer was calibrated with a supposed maximum of 21% oxygen in the air but the air might have had a lower oxygen level.

3.3.1. MONITORING

Using two sensors, monitoring was realised on a low treatment box during the whole of the experiment. (Figure 11). The oxygen level decreased during this period from 14% to 0.8 %. During the lights on period the decrease was more important than during the lights off period (Table 3). The adaptation of the oxygen use to the light level changes took place well within 30 minutes. The tip of the sensor was inserted through a tube in the top of the box and the tip was close to the top of the rockwool, in a space full of growing adventitious roots.

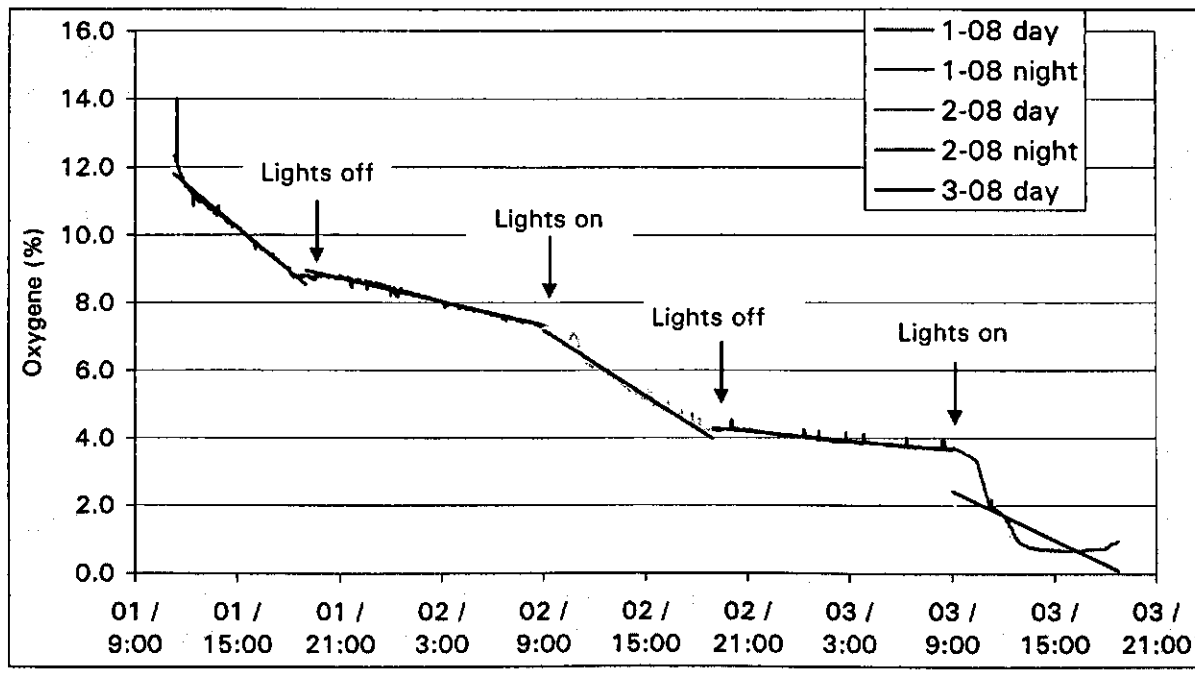

Figure 11 - Evolution of the oxygen level in L treatment box nr. 5 between 1-08 and 3-08

Table 3 – Oxygen use in mg/h per plant and r^2 of linear regression equations of Figure 11

Period	Hours	mg/h*	r^2
1-08 day	7.7	29.6	0.95
1-08 night	13.9	6.8	0.98
2-08 day	9.9	19.6	0.98
2-08 night	13.9	2.6	0.93
3-08 day	9.7	18.1	0.58

* Assuming a system volume of 4.5 litres (3.0 l in the bag and 1.5 l in the rest of the system)

3.3.2. OXYGEN MEASUREMENT

The absolute quantities of oxygen put into the system and taken from the system by changing the Tedlar bags were registered (Appendix 3). The absolute quantity of oxygen used in or lost from the system could thus be calculated (Table 4).

Table 4 – Maximum oxygen consumption* per treatment in ml, ml/h, mg/h and ml/h/grams of fresh root

Treatment	Total consumption (ml)	Hourly consumption (ml/h and mg/h)**		Consumption in mg/h/gr of Fresh Root
H	85	4.05	5.79	0.20
I	40	1.90	2.72	0.08
L	5	0.21	0.31	0.01

* Average of 3 plants for treatment H and I and 4 plants for treatment L.
** Time between the measurements of the 13-08 and 14-08 was 21 hours

The bags were refilled with nitrogen or air to obtain the desired percentage of oxygen in the bags. The H treatment always received fresh air. The I and L treatments received nitrogen on 31-07-2001 and on 6-08-2001 and fresh air on 10-08-2001 and 13-08-01.

3.4. WATER USE

The water consumption from the bottles was measured and the cumulative water use per box and per treatment was calculated (Figure 12 and Appendix 4). The water consumption of treatment L was lower than all other treatments from July 31 on. Between August the 6th and August the 12th, the RB and RWB treatments started to use more water than the I and H treatments. At harvest time, the H and I treatments had used 80% of the amount used by the RB/RWB treatments. The L treatment used only 35 % of this amount. Box number 1 that represented an H treatment didn't use enough water (three times less than the other H boxes). Therefore all data of plant 1 were omitted from this study.

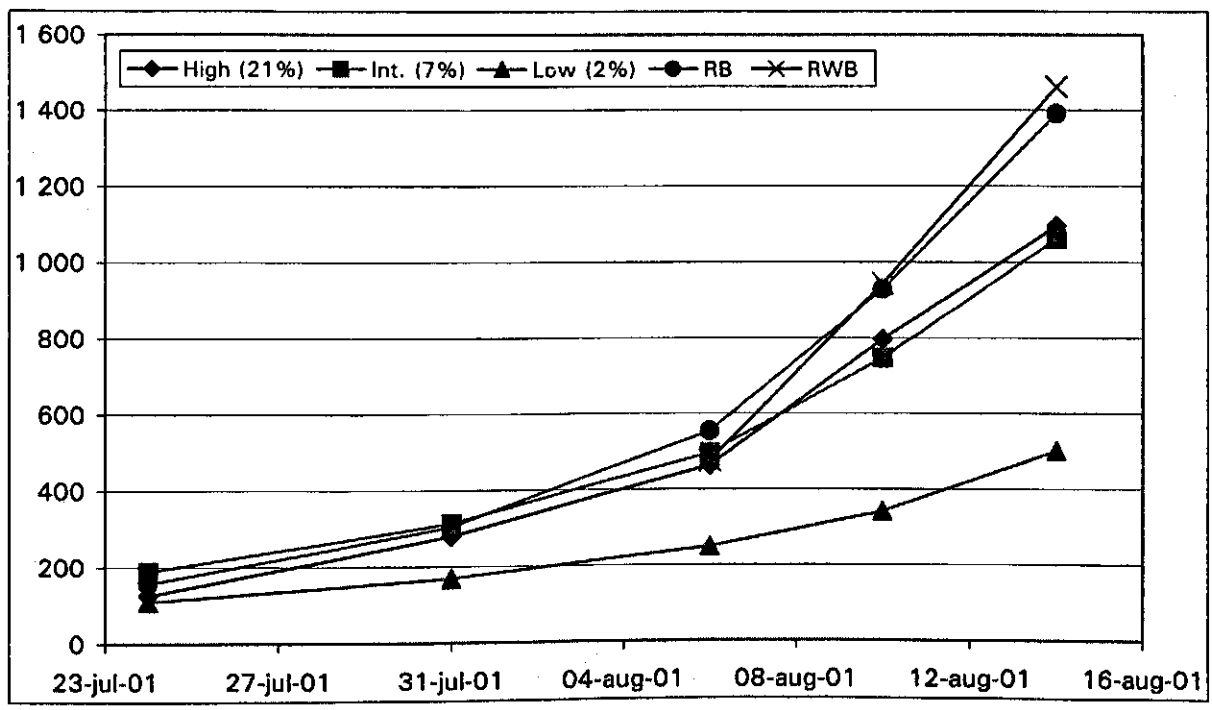

Figure 12 – Total water consumption (ml) per treatment between 24-07 and 14-08

3.5. LEAF AREA IN TIME

Leaf area differences between the H/RB/RWB treatments, and I and L treatments became apparent from 6-08-2001 on (Figure 13 and Appendix 5). At the harvest date the H/RB/RWB treatments were within 8% of each other. The I and L treatments produced 71% and 62% of this area respectively.

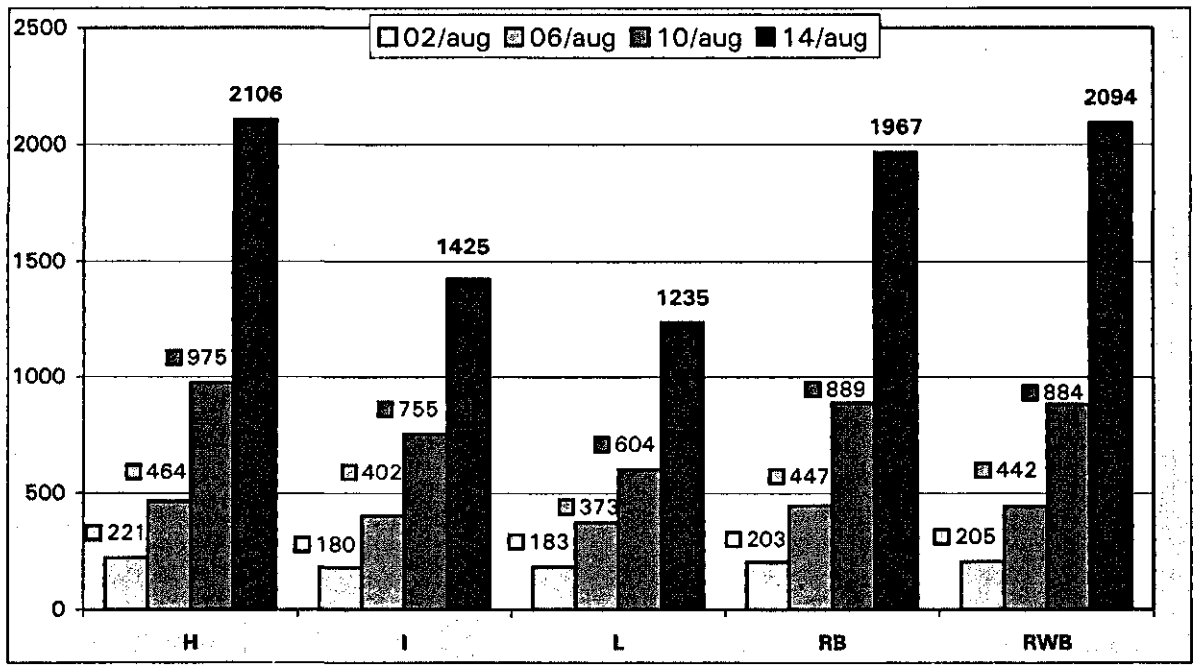

Figure 13 – Leaf area in cm^2 in time per treatment

3.6. HARVEST MEASUREMENTS

3.6.1. HEIGHT, LEAF AREA, PLANT WEIGHT

Table 5 shows the averages of the height, leaf area and fresh and dry weight of plant, leaves and stem (all data are grouped in Appendix 6). Appendix 8 shows photos of the plants at different dates.

Table 5 - Plant data (height, weight and area) per treatment

Treatment	Height (cm)	Leaf area (cm^2)	Fresh weight (g)			Dry weight (g)		
			Leaves	Stem	Plant	Leaves	Stem	Plant
LSD	10.2	545	10.0	10.1	19.9	1.27	0.51	1.76
H	34.7a	2106bc	37.7c	34.8c	69.5c	4.6ab	1.7b	6.7b
I	27.7a	1425ab	25.8ab	19.4ab	45.2ab	3.9ab	1.3ab	5.1ab
L	27.9a	1235a	20.8a	16.3a	37.1a	3.6a	1.2a	4.8a
RB	39.2b	1967b	34.0bc	28.2bc	62.2bc	4.7b	1.6ab	6.3ab
RWB	38.9b	2093bc	37.6c	32.5c	70.1c	4.9b	1.8b	6.7b

* LSD, least significant difference at p=<0.05 as calculated with ANOVA for all plants (including 1 and 11)

As already stated the final leaf area of the H/RB/RWB treatments were within 8% of each other. The I and L treatments produced 71% and 62% of this area respectively. The RWB and H treatments had the largest fresh weight. The RB treatment produced 90% of the fresh mass produced by the RWB/L treatments. The I and L treatment produced 68% and 55% of that mass. The dry weight produced by the RWB and H treatments was equal. The RB, I and L treatments produced 94%, 76% and 72% respectively. The length of RB and RWB plants was equal. The H, I and L plants had lengths of 89% and 71% and 72% respectively.

The statistical data have to be regarded with care. Because the number of repetitions is very low, any extra deviation by method or mistake will drastically increase the LSD. The fact that no significant difference is found therefor does not prove that there is no such difference. Only in large populations, with n>12-20, it is possible to make such statements. It is therefor highly likely, though not certain, that all the differences in weights and leaf areas between the H, I and L treatments can be statistically discerned with a larger number of repetitions.

3.6.2. ROOT SYSTEM AND ORGANIC MATERIAL

Fresh and dry root weights were registered (Table 6 and Appendix 7). It proved difficult to get a fresh root weight without some adherent water in the rockwool mass. Fresh root weights may therefore be overestimated and are not discussed. The RWB root fresh weight included the large root mass in the capillary cloth. The extra root mass formed is therefore to be regarded as an effect of the growing system used. The lower root dry mass produced by the RB system is also partly caused by a difference in the growing system. As ambient air circulates over the top of the rockwool and light was present, very few adventitious roots could be formed in the RB system. The H, I and L treatments on the other hand showed considerable amounts of adventitious rooting.

Table 6 - Fresh and dry weight (averages) per treatment

Treatment	Root Weight (grams)	
	Fresh	Dry
H	67.3	4.0
I	62.1	3.5
L	39.9	3.1
RB	60.6	2.7
RWB	184.3	4.3*

Only the roots in cubes were measured. Roots in the tissue were not included in the measurements.

The H, I and L treatments produced 148%, 130% and 115% of the root dry mass produced by the RB treatment.

4. DISCUSSION AND CONCLUSIONS

4.1. DISCUSSION

The absolute oxygen use over a day at the end of the experiments was 85, 40 and 5 ml for the treatments H, I, and L respectively (Table 4). This may be recalculated into 5.8, 2.7 and 0.3 mg/h, which is in accordance with values found in the previous experiments (Cassamassimo and Blok, 2001). When expressed per gram of root fresh weight (Table 4), the corresponding values are 0.2, 0.08 and 0.01 mg/h/gr of Fresh Roots. The maximum values are in the same order of magnitude than the 0.1-0.3 mg/h/gr FR found by others (Jackson, 1980; Veen, 1988a/b; Morard, 2000; Baas et al. 2000).

The oxygen use in the treatments decreases with the oxygen level after August the 10th (Appendix 3). At that time the oxygen level in the above ground gasses of the system was still 1-3% (Figure 10). Other authors found the oxygen use by individual detached roots is unhampered by oxygen concentrations above 1-2 % (Greenwood, 1969; Yoshida et al, 1997; Rong et al, 1999). If this holds true for the non-detached roots in this experiment, it indicates that parts of the cubes reached oxygen levels below 1%, i.e. oxygen diffusion rates in the substrate were limiting growth (Jackson, 1980; Soffer and Burger, 1988; Allaire et al, 1996; Caron and Nkongolo, 1999). It also indicates that the topmost roots could not increase their oxygen use enough to compensate for the supposed lower oxygen use further down in the cubes. Compensation of partly hindered root systems is well documented (Glenn, 2000).

Daytime oxygen use surpasses the night time use 5-10 times (Table 3). Others – under different experimental circumstances – did not report or look for such a day-night difference (Veen, 1988; Laan, 1990; Kitano et al, 1999; Baas et al, 2000; Wever et al, 2001). A possible explanation is that sugar transport to the roots is limiting the night time oxygen consumption. However, the change in oxygen consumption level is fast, probably faster than changes in phloem sugar levels. Another possibility is that the nutrient flux towards the roots is low enough to limit the uptake during the night, regardless of carbohydrate supply. The lower night time nutrient flux could be a result of the lower night time transpiration.

The leaf area development over time shows a 30% slower development for the I treatments and a 40% slower development for the L treatment (Figure 13). The leaf area in experiments under similar circumstances was highly correlated with fresh and dry weight development (R^2 >0.95; Bakker et al, 1987; Blok and Van Oosten, 2000; Kage et al, 2000). Thus the limited oxygen supply in the treatments I and L hampered production almost from the beginning of the experiment. The difference is already showing at the 30th of July, long before the oxygen levels dropped under 5%.

The water use over time shows a 20% lower level for the H and I treatments and a 65% lower use for the L treatment compared to the RWB/RB treatments (Figure 12). With ample supply, transpiration is a well-defined physical process (Lorenzo et al, 1998; Jones and Tardieu, 1998; Kage et al, 2000; Raviv and Blom, 2001). In the controlled environment of this experiment leaf area is the main parameter to explain the differences in transpiration. However, the water use of the L treatment is much lower than is to be expected based on leaf area only. One might speculate about an increased root resistance to water movement. An increase in root resistance to water movement in reaction to a poor oxygen supply has been reported (Yoshida et al, 1997).

The harvest data length, fresh weight and dry weight of stem and leaves all show the order predicted by the non destructive leaf area measurements. The length of the H, I and L treatments was 90%, 70%, and 70% of the RB treatment length. The H, I and L treatments produced, respectively, 110%, 75%, and 60% of the fresh weight produced by RB and, respectively, 100%, 85%, and 80% of the dry weight produced by RB. The implications have already been discussed with the leaf area development. The root organic material measurements show an order of 148%, 130% and 115% for respectively the H, I and L treatments as compared to the RB treatment. It means the relative amount of roots as expressed in the dry root/shoot ratio remains constant (respectively 0.61, 0.68, 0.65 for the H, I and L treatment). The root/shoot ratio

was expected to increase, as this is a typical reaction of plants to stresses. An increase in root/shoot ratio was reported in reaction to a lack of nutrients (Ericson, 1995; Marschner et al, 1996) as well as in reaction to a lack of carbohydrate supply to the roots (Nagel, 1998). An increase in root/shoot ratio is not a typical reaction to a lack of oxygen (Rob Baas, discussing this section).

The most decisive effect of the treatments is the decrease in leaf area development. From that point on differences in water use and mass accumulation are consequences of a lower leaf area. Leaf area may decrease as a consequence of low levels of the hormone IAA in combination with low levels of the hormones GA and cytokinin (Van Iersel, 1977). Leave area may also decrease as the result of a mild water stress induced by oxygen stress. In that case, the water available for cell elongation might be limiting.

4.2. CONCLUSIONS

1. The critical oxygen re-supply level for this system is between 8 and 12%.
2. The above ground growth reaction to mild prolonged sub-optimal oxygen supply rates includes a 20-40% reduction in leaf area, fresh and dry mass production and, less pronounced, a reduction in length growth and root dry mass production.
3. The root growth reaction to mild prolonged sub-optimal oxygen supply rates includes a decrease in root mass production rate in proportion to the above ground dry mass production rate.
4. The root oxygen use rate during the light period is 5-10 times higher than during the night period.

Ad 1 The growth is clearly influenced by the treatments. Additional experiments will have to decide on the more precise nature of the treatments. Possible explanations now include oxygen level, the oxygen supply rate, ethylene level and CO_2 level. Oxygen levels of 2% or higher supposedly do not hinder root function (Kitano et al, 1998). The most likely explanation without doubting the 2% threshold, is a too low oxygen supply rate, which in relation with substrate diffusivity induces spots with a too low oxygen level. These spots induce a growth decrease, which cannot be counteracted by roots in spots with sufficient supply.

Ad 2 The above ground growth reaction is very pronounced. It is not accompanied by discoloration indicating nutrient uptake problems. There is no sign of wilting of the lowest leaves in reaction to high ethylene levels as reported typical for acute oxygen stress (Laan, 1990; Visser et al, 2000).

Ad 3 There was no substantial change in the root/shoot ratio or the root distribution over height other than the large increase in adventitious rooting in the above substrate part of the closed boxes. The plants did not show any typical stress symptoms but just were smaller. If this reaction to the treatments exist in horticultural practise, it will be hard to detect.

Ad 4 The day/night pattern can be measured with such accuracy and stability that it seems possible to measure the reaction in oxygen use to the addition or depletion of specific substances. Some interesting experiments may be designed to study effects of CO_2, ethylene, toxides and changes in NO_3/NH_4 ratio. The oxygen costs of calcium uptake may also be monitored in this way.

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APPENDIX 1: LAYOUT

The treatments were installed conform to the following figure.

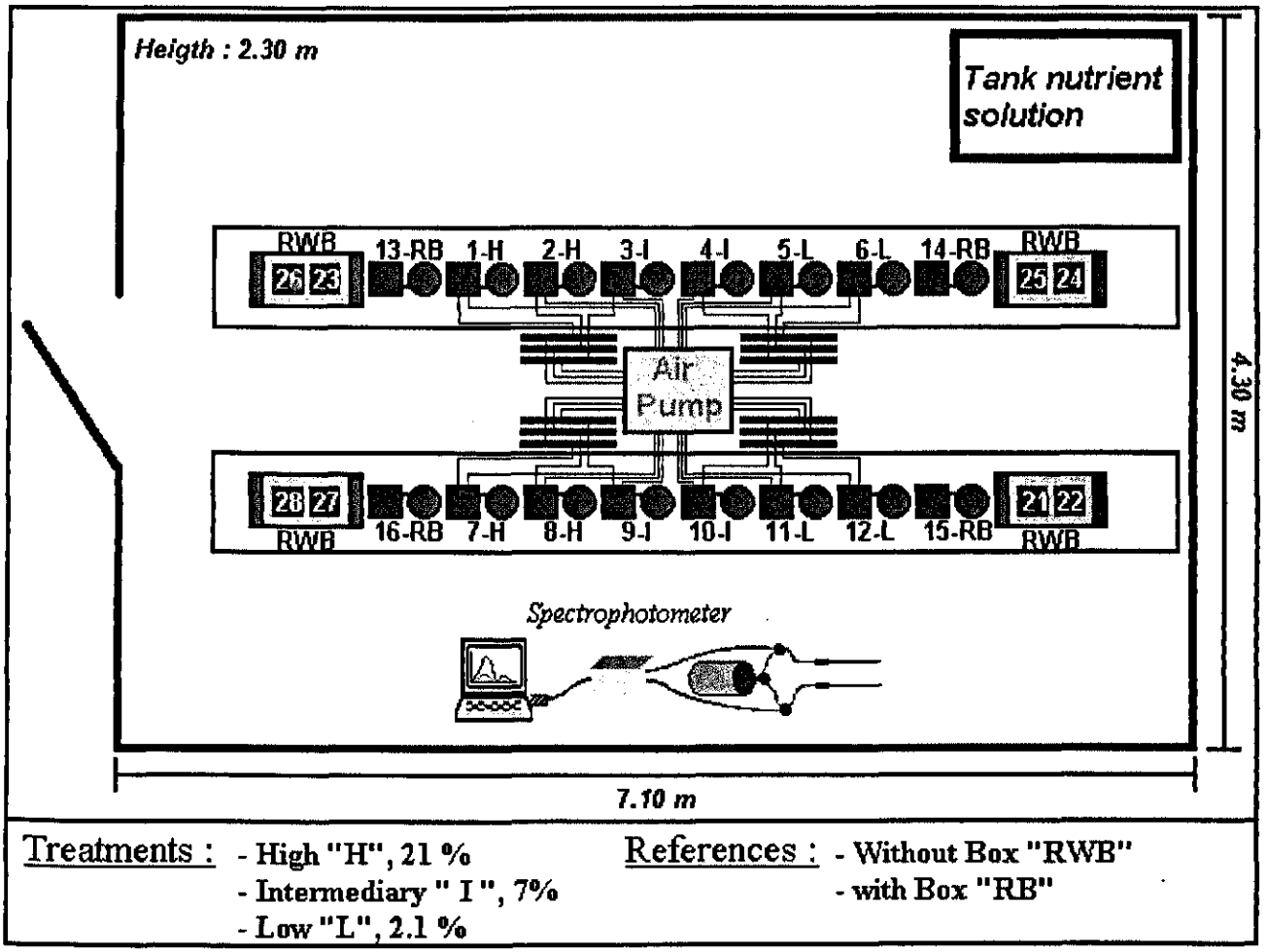
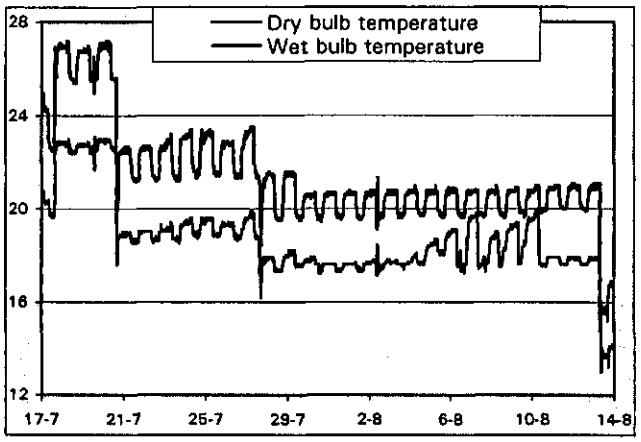


Figure 14 - Cell 128: Air bags link to the boxes by an air pump; tank of nutrient solution; boxes of the three treatments and the references; Spectrophotometer measuring oxygen percentage.

APPENDIX 2: CLIMATE PARAMETERS



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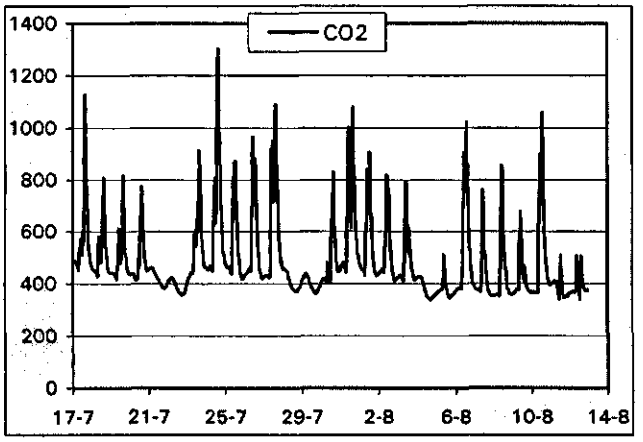

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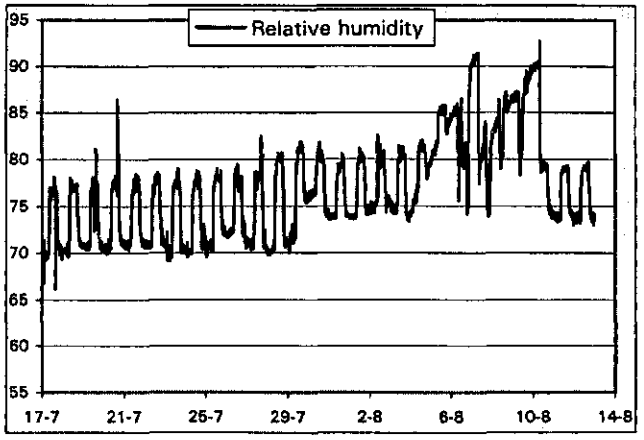

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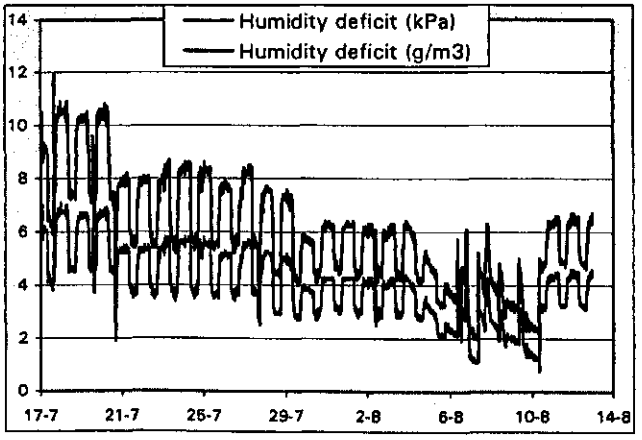

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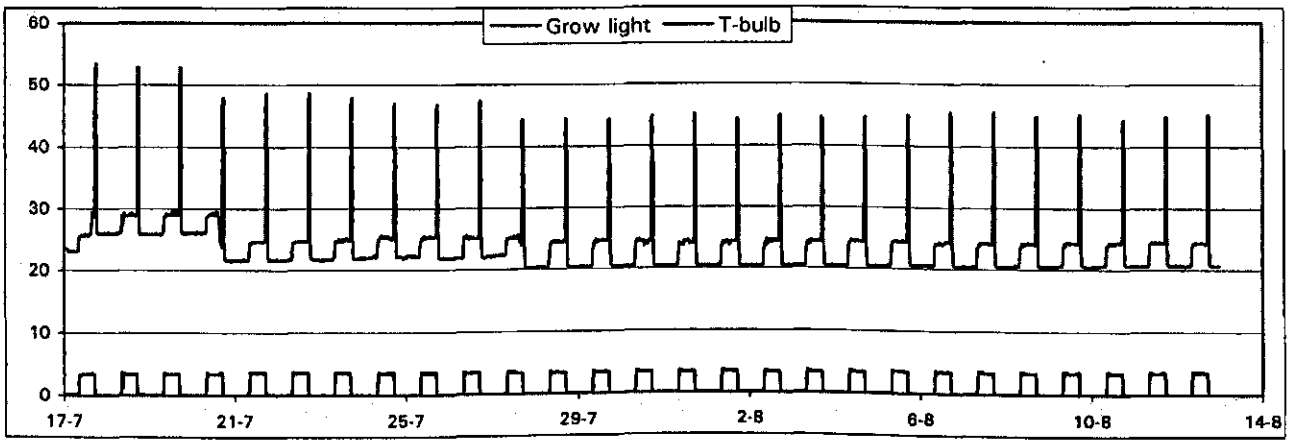


E

Figure 15 - Climate data with Temperatures (A, degrees Celsius), CO_2 level (B, in ppm), Relative humidity (C, in %) and humidity deficit (D, in kPa and gr/m^3), Light starting and stopping registration in time (E, in degrees Celsius by thermocouple) for grow light and far red light (bulbs)

APPENDIX 3: OXYGEN CONSUMPTION

Table 1: Oxygen content in the bags before and after filling per plant

A	25/jul	31/jul		06/aug		10/aug		13/aug		14/aug
Treatment	Start	Before filling	After filling	Before filling	After filling	Before filling	After filling	Before filling	After filling	Final
1 – H	19.9%	16.7%	19.9%	17.3%	20.3%	12.8%	20.6%	11.4%	19.5%	16.7%
2 – H	19.9%	17.6%	20.0%	17.8%	20.8%	15.0%	20.7%	12.0%	19.7%	17.1%
7 – H	19.6%	18.0%	20.0%	17.2%	20.8%	13.6%	20.3%	11.2%	20.1%	17.1%
8 – H	19.2%	12.5%	19.5%	16.0%	20.6%	13.0%	20.2%	9.6%	19.1%	16.2%
3 – I	10.8%	5.9%	7.8%	5.9%	7.5%	2.6%	8.1%	1.0%	8.4%	7.1%
4 – I	9.1%	8.8%	9.1%	10.3%	7.3%	4.0%	8.4%	2.2%	8.7%	7.5%
9 – I	15.5%	11.1%	8.8%	6.0%	7.5%	1.5%	6.5%	0.1%	7.6%	6.1%
10 – I	13.2%	3.8%	8.5%	11.4%	11.5%	9.2%	6.5%	3.2%	9.7%	8.5%
5 – L	6.5%	0.0%	3.9%	1.6%	2.7%	0.4%	2.7%	0.3%	3.5%	3.2%
6 – L	5.4%	0.0%	4.4%	3.5%	3.1%	0.8%	2.7%	0.0%	3.0%	2.9%
11 – L	11.6%	1.2%	6.1%	3.7%	5.1%	1.4%	2.3%	0.0%	2.7%	2.6%
12 – L	9.1%	4.5%	7.5%	5.5%	4.5%	1.1%	2.4%	0.0%	3.0%	2.9%

Table 2: Oxygen content in the bags before and after filling per treatment

B	25/jul	31/jul		06/aug		10/aug		13/aug		14/aug
Treatment	Start	Before filling	After filling	Before filling	After filling	Before filling	After filling	Before filling	After filling	Final
H	19.6%	16.0%	19.8%	17.0%	20.7%	13.9%	20.4%	10.9%	19.6%	16.8%
I	11.8%	8.6%	8.6%	7.4%	7.4%	2.7%	7.7%	1.1%	8.2%	6.9%
L	8.2%	1.4%	5.5%	3.6%	3.9%	0.9%	2.5%	0.1%	3.1%	2.9%

Table 3: Oxygen consumption between two fillings and the cumulative consumption per treatment in ml of oxygen per plant

A	O_2 consumption (ml) between two dates						Total O_2 consumption (ml)					
Treatment	25/jul	31/jul	06/aug	10/aug	13/aug	14/aug	25/jul	31/jul	06/aug	10/aug	13/aug	14/aug
1 – H	0	96	78	225	276	84	0	96	174	399	675	759
2 – H	0	69	66	174	261	78	0	69	135	309	570	648
7 – H	0	48	84	216	273	90	0	48	132	348	621	711
8 – H	0	201	105	228	318	87	0	201	306	534	852	939
3 – I	0	147	57	147	213	39	0	147	204	351	564	603
4 – I	0	9	-36	99	186	36	0	9	-27	72	258	294
9 – I	0	132	84	180	192	45	0	132	216	396	588	633
10 – I	0	282	-87	69	99	36	0	282	195	264	363	399
5 – L	0	195	69	69	72	9	0	195	264	333	405	414
6 – L	0	162	27	69	81	3	0	162	189	258	339	342
11 – L	0	312	72	111	69	3	0	312	384	495	564	567
12 – L	0	138	60	102	72	3	0	138	198	300	372	375

Table 4: Oxygen consumption between two fillings and the cumulative consumption per treatment in ml of oxygen per treatment

B	O_2 consumption (ml) between two dates						Total O_2 consumption (ml)					
Treatment	25/jul	31/jul	06/aug	10/aug	13/aug	14/aug	25/jul	31/jul	06/aug	10/aug	13/aug	14/aug
H	0.0	106.0	85.0	206.0	284.0	85.0	0.0	106.0	191.0	397.0	681.0	766.0
I	0.0	96.0	35.0	142.0	197.0	40.0	0.0	96.0	131.0	273.0	470.0	510.0
L	0.0	201.8	57.0	87.8	73.5	4.5	0.0	201.8	258.8	346.5	420.0	424.5

Table 5: Volume (ml) of nitrogen or fresh air added filling the bags to reach treatment oxygen level

Treatment		31/jul			06/aug			10/aug			13/aug		
	O_2 expected	N_2 added	Fresh air added	O_2 obtained	N_2 added	Fresh air added	O_2 obtained	N_2 added	Fresh air added	O_2 obtained	N_2 added	Fresh air added	O_2 obtained
1 – H	21.0%	0	3000	19.9%	0	3000	20.3%	0	3000	20.6%	0	3000	19.5%
2 – H	21.0%	0	3000	20.0%	0	3000	20.8%	0	3000	20.7%	0	3000	19.7%
7 – H	21.0%	0	3000	20.0%	0	3000	20.8%	0	3000	20.3%	0	300	20.1%
8 – H	21.0%	0	3000	19.5%	0	3000	20.6%	0	3000	20.2%	0	3000	19.1%
3 – I	7.0%	470	220	7.8%	0	220	7.5%	0	720	8.1%	0	900	8.4%
4 – I	7.0%	1400 +620	0	9.1%	960	0	7.3%	0	530	8.4%	0	770	8.7%
9 – I	7.0%	1100 +530	0	8.8%	0	200	7.5%	800	846	6.5%	0	990	7.6%
10 – I	7.0%	1250	560	8.5%	1160	0	11.5%	720	0	6.5%	0	640	9.7%
5 – L	2.1%	2300	300	3.9%	0	80	2.7%	0	250	2.7%	0	260	3.5%
6 – L	2.1%	2150	300	4.4%	1200	0	3.1%	0	200	2.7%	0	300	3.0%
11 – L	2.1%	2200	136	6.1%	0	1300	5.1%	0	110	2.3%	0	300	2.7%
12 – L	2.1%	1600 +1800	0	7.5%	1850	0	4.5%	0	150	2.4%	0	300	3.0%

APPENDIX 4: WATER USE

Table 1 – Water use per plant in ml in five different periods

Treatment	24/07/2001	31/07/2001	06/08/2001	10-08-2001	14-08-2001
1 – H	125	63	40	50	40
2 - H	125	63	100	200	250
7 - H	125	250	200	350	350
8 - H	125	150	250	450	300
3 - I	125	63	100	300	350
4 - I	250	63	200	250	300
9 - I	188	250	250	200	300
10 - I	125	63	40	20	10
5 - L	125	63	30	30	20
6 - L	125	63	30	40	20
11 - L	63	63	10	150	300
12 - L	125	50	250	150	300
13 - RB	125	125	300	250	150
14 - RB	250	250	350	450	600
15 - RB	125	150	250	500	700
16 - RB	125	63	100	300	400
RWB 1 (26-23)	---	---	800	1 500	1 100
RWB 2 (25-24)	---	---	1 000	750	1 000
RWB 3 (28-27)	---	---	1 000	750	1 000
RWB 4 (21-22)	---	---	1 000	750	1 050

Table 2 – Water use averages in ml per treatment in five periods (A) and cumulative use (B)

A	High (21%)	Int. (7%)	Low (2%)	RB	RWB
24-jul-01	125	188	109	156	---
31-jul-01	154	125	59	147	---
06-aug-01	183	183	80	250	475
10-aug-01	333	250	93	375	469
14-aug-01	300	317	160	463	519

B	High (21%)	Int. (7%)	Low (2%)	RB	RWB
24-jul-01	125	188	109	156	---
31-jul-01	279	313	169	303	---
06-aug-01	463	496	249	553	475
10-aug-01	796	746	341	928	944
14-aug-01	1 096	1 063	501	1 391	1 463

APPENDIX 5: LEAF AREA IN TIME

Table 1: Leaf area of plants at height different dates in cm^2

Number	1	2	7	8	3	4	9	10	5	6	11	12	13	14	15	16	21	22	23	24	25	26	27	28
Treatment	H	H	H	H	I	I	I	I	L	L	L	L	RB	RB	RB	RB	RWB	RWB	RWB	RWB	RWB	RWB	RWB	RWB
25/jul *	47	44	39	49	39	33	39	45	45	42	44	34	45	39	46	42	41	39	39	39	39	39	39	39
30/jul*I	145	139	119	137	113	105	113	137	133	117	115	95	109	127	109	116	128	129	125	124	124	124	124	124
02/aug*	211	188	217	258	161	182	180	196	206	161	171	192	195	227	199	192	204	210	208	205	205	205	205	205
06/aug*	393	375	462	556	337	505	386	382	389	283	373	447	448	514	417	409	421	427	447	450	450	451	451	451
08/aug*	582	533	691	787	481	566	530	571	483	372	522	595	630	704	592	581	592	598	611	616	620	620	620	620
10/aug*	823	856	953	1117	679	739	724	878	583	513	514	804	924	901	899	834	845	851	883	906	894	910	915	917
13/aug*	1081	1310	1532	1754	1039	1255	1017	1034	781	731	1040	1173	1387	1650	1442	1376	1388	1394	1434	1465	1449	1465	1471	1488
14/aug	1390	1802	2208	2308	1411	1675	1389	1226	1035	1051	1382	1473	1855	2276	1841	1896	1986	714	2122	1938	2096	2044	2171	2291

Calculate from the width of each leaves and the model area = 0.7 ($width^2$)

Table 2: Averages of Leaf area in cm^2

Treatment	H	I	L	RB	RWB
25/jul	44	37	41	43	39
30/jul	132	121	115	115	125
02/aug	221	180	183	203	205
06/aug	464	402	373	447	442
08/aug	670	537	493	627	611
10/aug	975	755	604	889	884
13/aug	1532	1086	931	1464	1436
14/aug	2106	1425	1235	1967	2094

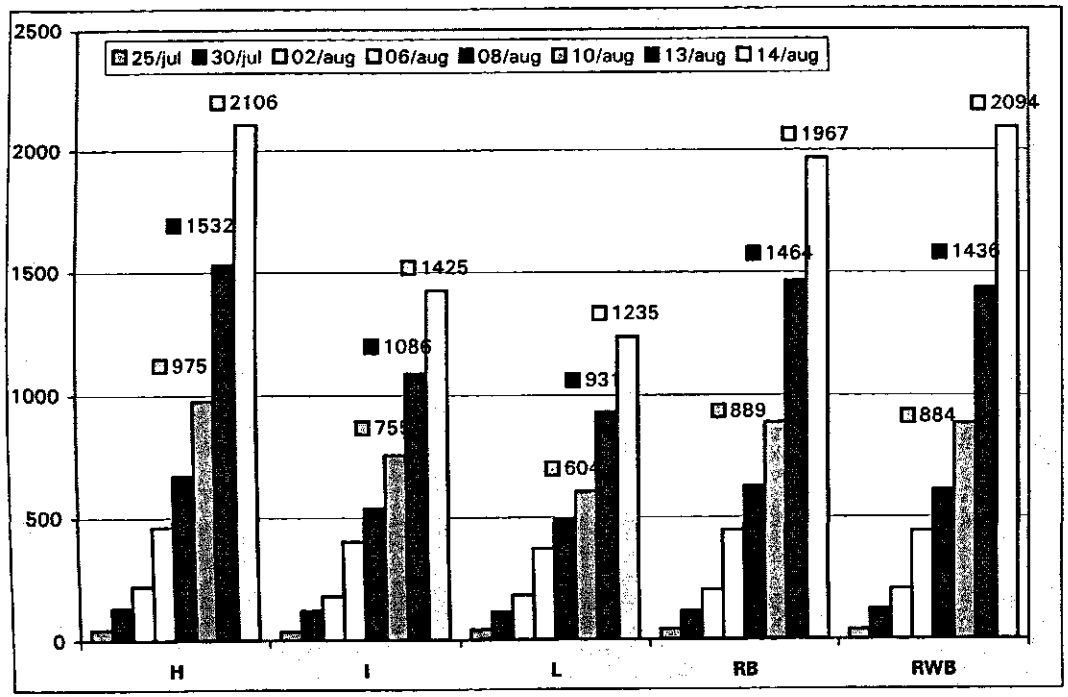


Figure 1 - Leaf area in cm^2 per treatment at eight different dates

APPENDIX 6: HARVEST MEASUREMENTS

Table 1: Height, Fresh and Dry weight of the plant, its stem and its leaves

Treatment	Height (cm)	Fresh weight (g)			Dry weight (g)		
		Leaves	Stem	Plant	Leaves	Stem	Plant
1 – H	25.0	25.36	18.37	43.73	3.88	1.33	5.21
2 – H	27.2	32.05	23.97	56.02	4.28	1.42	5.70
7 – H	36.7	40.10	34.43	74.53	5.05	1.84	6.89
8 – H	40.2	40.93	37.13	78.06	5.30	2.08	7.38
3 – I	23.3	24.97	16.75	41.72	3.68	1.08	4.76
4 – I	27.5	28.89	21.85	50.74	4.18	1.37	5.55
9 – I	31.8	23.48	19.59	43.07	3.75	1.35	5.10
10 – I	24.9	20.75	16.45	37.20	3.37	1.30	4.67
5 – L	22.6	18.04	12.39	30.43	3.51	1.01	4.52
6 – L	19.8	18.19	11.93	30.12	2.94	0.88	3.82
11 – L	31.7	23.21	19.53	42.74	3.90	1.35	5.25
12 – L	37.6	23.83	21.22	45.05	4.17	1.46	5.63
13 – RB	40.0	30.61	25.76	56.37	4.66	1.68	6.34
14 – RB	44.5	40.03	34.99	75.02	5.22	1.89	7.11
15 – RB	34.4	32.78	26.29	59.07	4.60	1.53	6.13
16 – RB	37.8	32.41	25.78	58.19	4.15	1.39	5.54
21 – RWB	39.1	35.59	31.58	67.17	4.57	1.70	6.27
22 – exRWB	20.0	11.66	10.13	21.79	1.38	0.53	1.91
23 – RWB	40.1	38.11	34.76	72.87	4.88	1.89	6.77
24 – exRWB	37.0	34.88	29.60	64.48	4.55	1.66	6.21
25 – RWB	36.3	38.01	29.83	67.84	5.13	1.72	6.85
26 – exRWB	40.5	37.33	31.88	69.21	4.95	1.75	6.70
27 – RWB	40.0	38.67	33.94	72.61	5.00	1.86	6.86
28 – exRWB	46.0	41.03	38.07	79.10	5.32	2.05	7.37
Averages* per treatment							
H	34.7	37.7	34.8	69.5	4.6	1.7	6.7
I	27.7	25.8	19.4	45.2	3.9	1.3	5.1
L	27.9	20.8	16.3	37.1	3.6	1.2	4.8
RB	39.2	34.0	28.2	62.2	4.7	1.6	6.3
RWB**	38.9	37.6	32.5	70.1	4.9	1.8	6.7

* 3 plants for H and I treatments and 4 plants for L treatment

** exRWB were omitted.

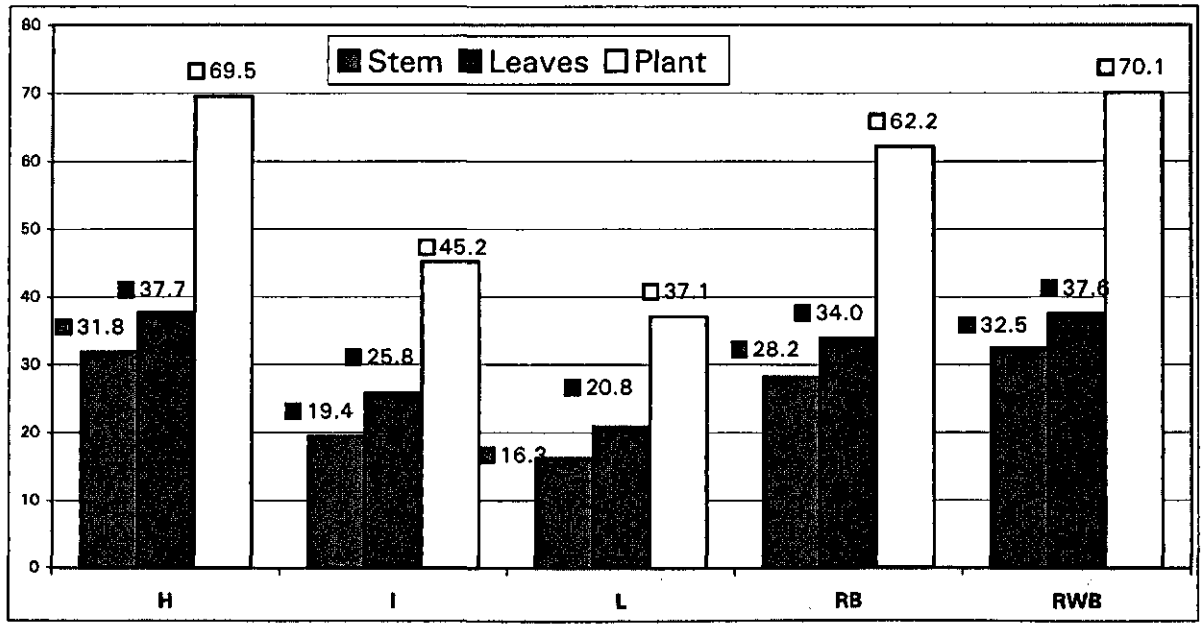


Figure 1- Fresh weights in g (averages) of plant, stem and leaf per treatment

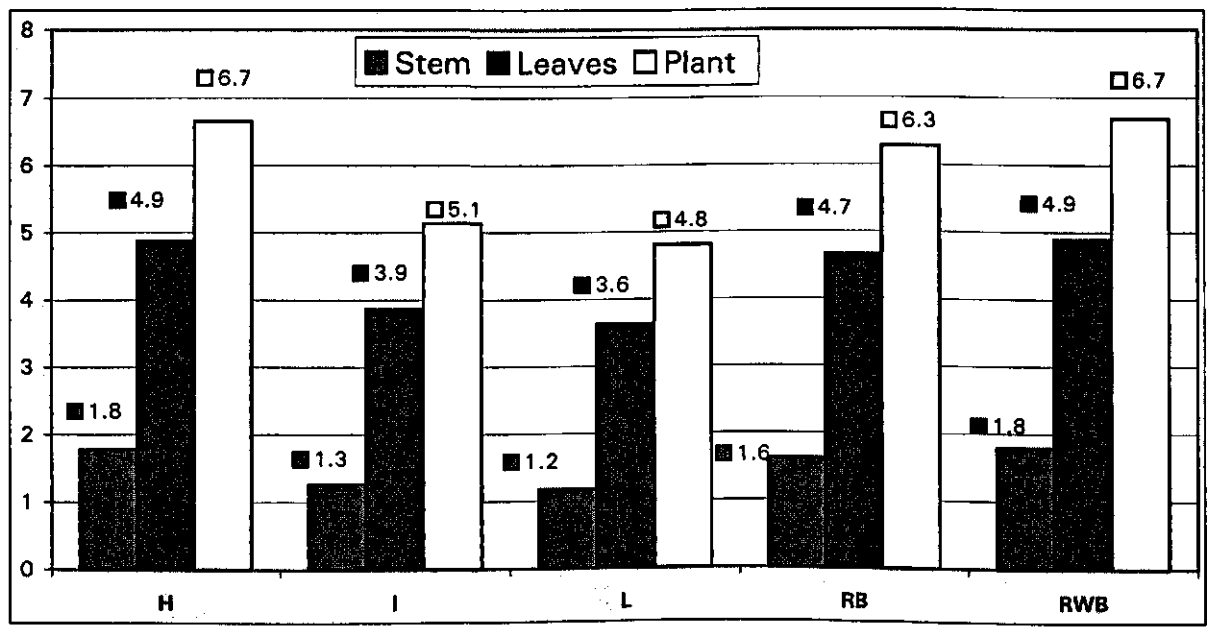


Figure 2 - Dry weights in g (averages) of plant, stem and leaf per treatment

APPENDIX 7: ROOT SYSTEM AND ORGANIC MATERIAL

Table 1: Rockwool cubes weight (saturated, dry and ignited,) fresh and dry roots weights and organic material weight in grams

Treatment	Rockwool cubes saturated weight		Fresh root weight	Rockwool cubes dry weight		Dry root weight	15/08 - Cut	Cubes ignited weight	Organic material weight
	16/jul	15/aug		16/jul	15/aug				
1 – H	534.32	529.92	-4.40	44.14	49.93	5.79	49.61	46.11	3.50
2 – H	533.75	574.13	40.38	44.18	48.94	4.76	48.71	43.89	4.82
7 – H	515.76	557.65	41.89	36.72	40.37	3.65	40.18	36.40	3.78
8 – H	450.66	570.32	119.66	34.55	38.26	3.71	38.19	34.43	3.76
3 – I	516.19	577.40	61.21	42.00	45.53	3.53	45.30	41.53	3.77
4 – I	506.99	578.95	71.96	44.08	44.72	0.64	44.51	39.94	4.57
9 – I	496.49	549.53	53.04	38.65	42.32	3.67	42.12	38.23	3.89
10 – I	535.49	554.16	18.67	37.61	40.71	3.10	40.34	37.24	3.10
5 – L	532.95	548.03	15.08	34.60	37.81	3.21	37.57	34.06	3.51
6 – L	516.10	563.55	47.45	36.16	39.21	3.05	39.09	35.92	3.17
11 – L	525.01	553.91	28.90	37.61	40.76	3.15	40.59	37.02	3.57
12 – L	503.71	571.75	68.04	38.83	41.84	3.01	41.60	38.19	3.41
13 – RB	521.43	559.25	37.82	39.23	41.89	2.66	41.62	38.47	3.15
14 – RB	507.15	570.42	63.27	39.17	42.06	2.89	41.84	38.23	3.61
15 – RB	428.48	531.01	102.53	35.09	37.59	2.50	37.43	34.14	3.29
16 – RB	525.53	564.50	38.97	37.79	40.47	2.68	40.29	36.82	3.47
21 – RWB*	384.10	598.16	214.06	45.32	49.31	3.99	45.71 (2.85)	41.97	3.74
22 – exRWB*	350.76	578.02	227.26	41.42	44.90	3.48	42.02 (2.47)	38.68	3.34
23 – RWB*	447.76	607.41	159.65	46.24	50.53	4.29	47.49 (2.70)	41.74	5.75
24 – exRWB*	330.85	566.85	236.00	41.71	45.01	3.30	42.51 (2.23)	42.32	0.19
25 – RWB*	416.29	606.98	190.69	46.79	52.22	5.43	47.85 (2.80)	41.52	6.33
26 – exRWB*	388.15	599.36	211.21	44.41	48.28	3.87	44.95 (2.87)	43.79	1.16
27 – RWB*	429.93	602.53	172.60	45.46	48.93	3.47	45.41 (2.75)	39.08	6.33
28 – exRWB*	415.59	597.99	182.40	44.84	48.45	3.61	45.20 (2.63)	43.51	1.69

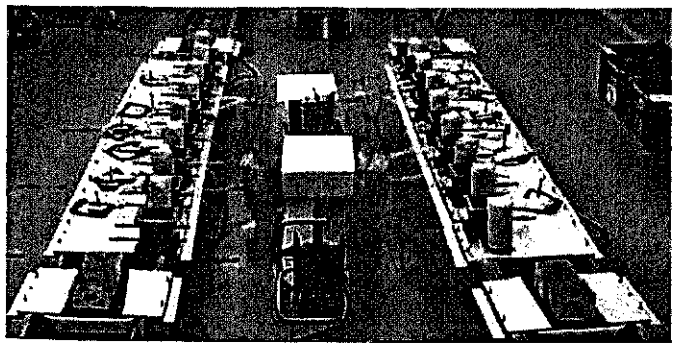
Values between parenthesis in 15-08 cut column was the weight of plastic which surrounded rockwool cubes.

Table 2 – Averages per treatment of fresh and dry root weight and organic material

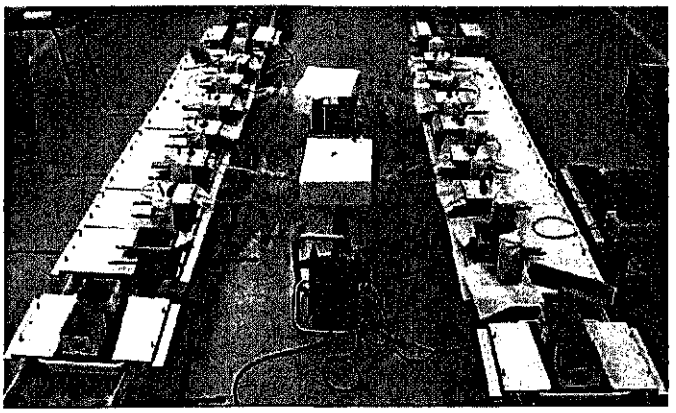
Treatment	Fresh root weight in g	Dry root weight in g	Organic material weight in g
H	67.3	4.0	4.1
I	62.0	3.5	4.1
L	39.9	3.1	3.4
RB	60.7	2.7	3.4
RWB	184.3	4.3	5.5

APPENDIX 8: PLANTS IMAGES

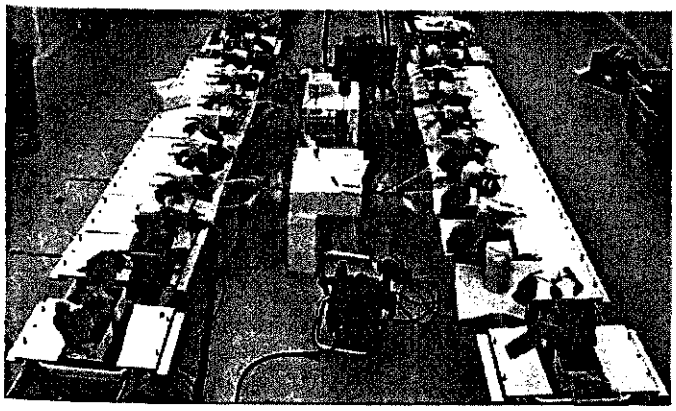
Figure 16-4 - General view of the cell at different dates



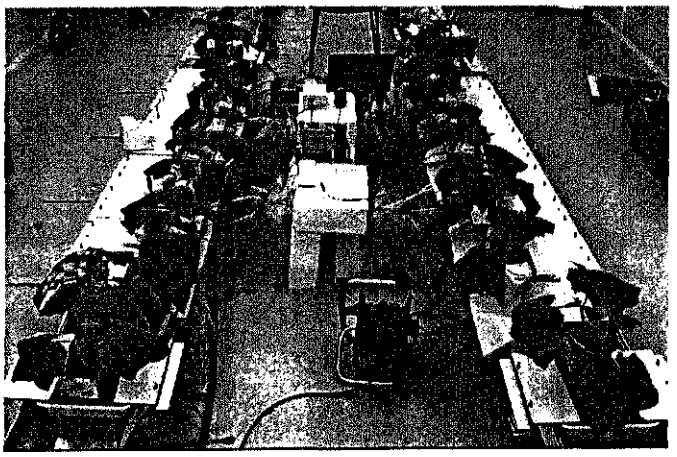
19th July 2001 – 2 days



24th July 2001 – 6 days, just after closing



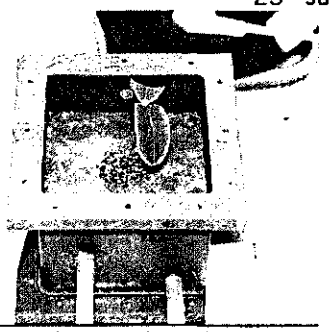
3rd August 2001 – 17 days



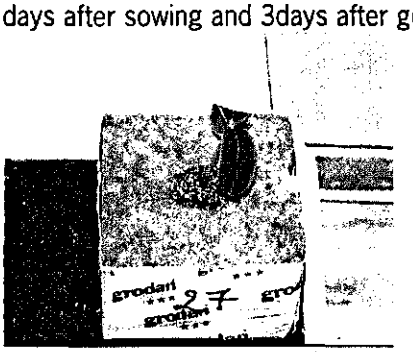
8th August 2001 – 22 days

Figure 5-15 - Photos of the different treatments at four dates

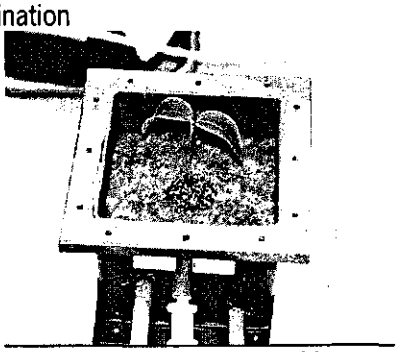
23rd July: 6 days after sowing and 3days after germination



Reference box (RB)



Reference without box (RWB)



Treatment (H, I or L)

3rd August : 17 days after sowing

Reference Box

Reference Without Box

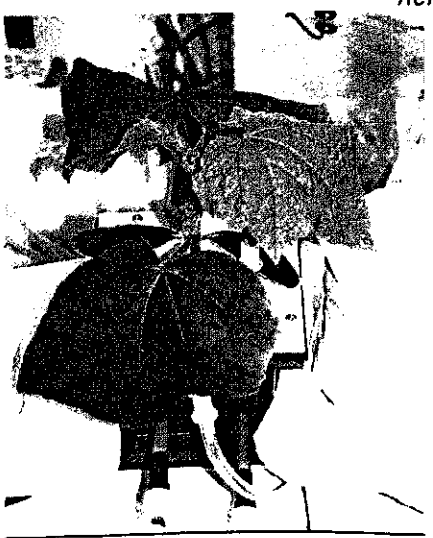
Treatments

8th August: 22 days after sowing

Reference box (RB)

Reference without box (RWB)

Treatment H



Treatment I

Treatment L