# Photosynthesis measurements on adult trees:
# a comparison between field and laboratory measurements

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## 1. Introduction

Photosynthesis is the most important physiological process on the level of individual plants. On a larger ecological level, from stand over region and even global scale, photosynthesis influences, directly or indirectly, several biogeochemical cycles on earth.

The influence on the carbon cycle is evident, as carbon is taken up from the atmosphere by the process of photosynthesis, and again released into the atmosphere by the process of respiration. This respiration process can be direct (autotrophic respiration) or after decomposition of the biomass produced by the photosynthesis process (decomposition of the litter fall or heterotrophic respiration).

Fifty percent of the uptake of carbon dioxide in all kinds of sinks takes place in forest and tropical grassland ecosystems (Enting and Mansbridge, 1991). On an annual basis this means a fixation of 4.3 Gt $CO_2$.

For this reason several authors tried to model the carbon cycle in forests (Mohren, 1994; Veroustraete, 1994, among others). In these models, beside modelling the light regime in the canopy, modelling the photosynthesis process is of the utmost importance.

Most authors conducted photosynthesis measurements on young seedlings or small trees (Ceulemans and Mousseau, 1994; Lootens, 1996). Others measured the carbon exchange between the ecosystem and the atmosphere (Wofsy *et al.*, 1993). Considering the first method, it is not sure that processes measured on the level of young trees can simply be scaled up to the level of mature trees. For the second method, no distinction can be made between the importance of soil, understorey and overstorey. The functioning of these different components will not be explained by this latter method.

Therefore, as an input in models trying to model the carbon cycle in forests, photosynthesis parameters determined on (adult) trees growing in the forest under study are necessary, because a better model performance could be expected (Baldocchi, 1993). Tree canopies are relatively inaccessible, and as a consequence, information of this kind of parameters is difficult to find.

If figures are found, most of the time they are the result of destructive measurements (after cutting of the branches) (Wang, 1996), because most research teams do not posses a measuring tower from which photosynthesis measurements can be conducted.

In this paper, photosynthesis parameters measured on adult trees *in situ* and on cut off branches are compared for several deciduous species. The measurements are repeated in time to see if possible relationships between the two methods are unique.

## 2. Material and methods

### 2.1. Site description

Field measurements of photosynthesis were conducted during the 1996 and 1997 growing season in a mixed deciduous forest, which can be divided in two vegetation types. The first type is an oak-beech forest, with oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) as dominating tree species. An ash plot, with ash (*Fraxinus excelsior* L.) as the dominant tree species, is the second forest type. The dominating trees of both forest types are all about 70 years old.
The field site is located in East-Flanders (Belgium) (latitude 50°58'35" N; longitude 3°49'30" E; elevation between 11 and 21 m above sea level). The canopy height is about 27 m, and a 35 m high measuring tower provides access to the leaves of a beech (at 7, 14 and 21 m) and an ash (at 21 m). In the discussion below, the different platforms at 7, 14 and 21 m above the forest floor are indicated as respectively level 1, level 2 and level 3.
More information about the site and the experimental set-up can be found in Samson *et al.* (1996).

### 2.2. Equipment

The measurements of the photosynthesis light response curves were performed using two different instruments. The first one was the phytotron of the Laboratory of Plant Ecology. Secondly a portable gas exchange instrument, a compact $CO_2/H_2O$ porometer (WALZ), was used. This portable apparatus was used in the field and in the laboratory. Both instruments were used in the differential mode, which means that the photosynthesis rate, at a certain light intensity, was calculated from the difference in $CO_2$ concentration between the incoming and outgoing air of the leaf cuvette.

### 2.2.1. Description of the phytotron

Figure 1 gives a schematic diagram of the phytotron of the Laboratory of Plant Ecology. Air of the atmosphere is mixed by means of a ventilator in a buffer vessel to eliminate fluctuations of the $CO_2$ concentration. This homogenised air is brought in a gas cooling system, where the water vapour present in the air condenses. The resulting dry air is led to an evaporator. There, the air is re-wetted according to the dew point principle. (The air is saturated with water vapour at a chosen dew point temperature.)
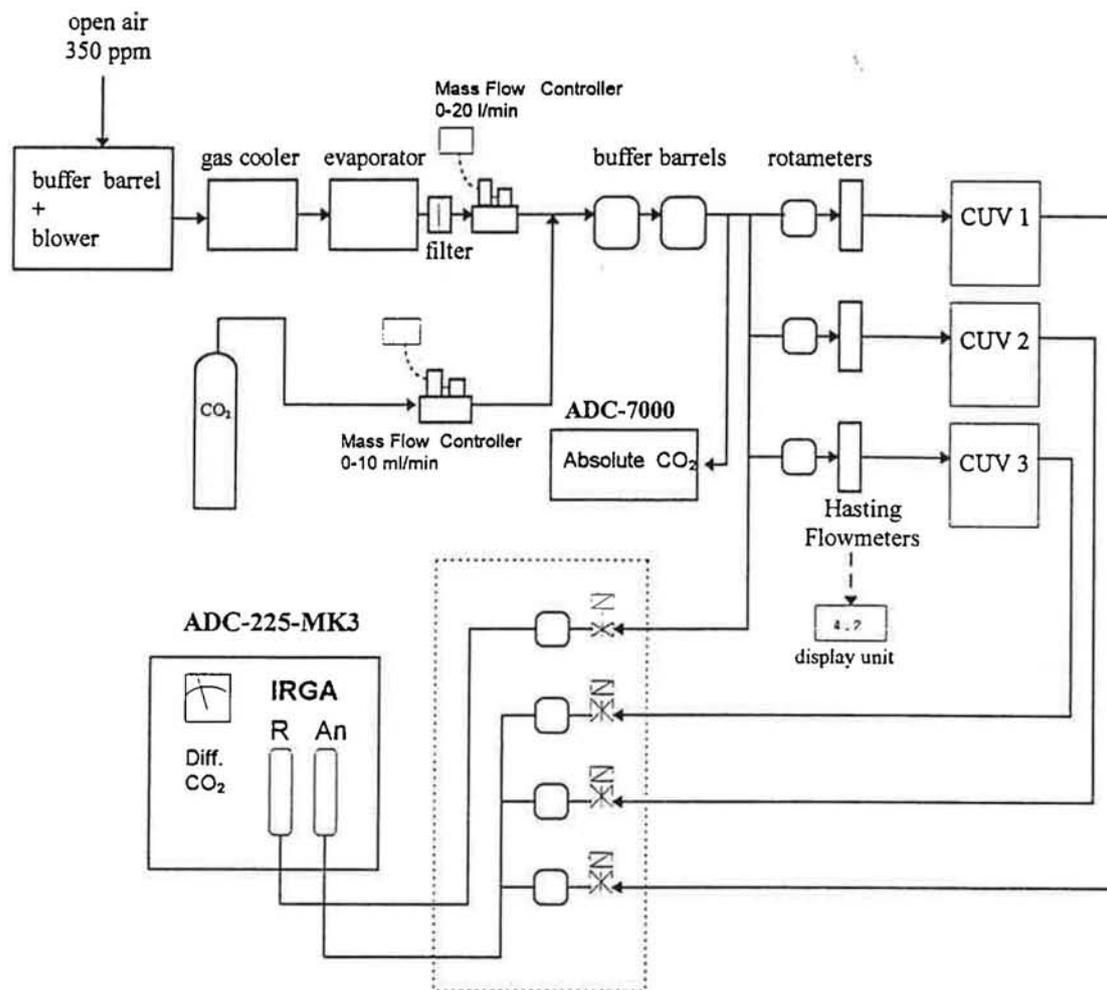
*Figure 1.*   *Schematic presentation of the phytotron of the Laboratory of Plant Ecology (Samson et al., 1997)*

Part of the air is sent to the reference tube of the differential $CO_2$-analyser. This $CO_2$-analyser is an IRGA (Infra-Red Gas Analyser - ADC 225 MK3). The other part of the air passes a flow controller and is led to three leaf cuvettes. The temperature in these cuvettes is controlled with a Colorawaterbath. Each cuvette has a ventilator, to diminish the boundary layer resistance of the leaf. The water mantle in the cover of the cuvette prevents the heating up of the cuvette due to the above placed halogen lamps and also filters out the IR radiation emitted by these lamps. The air coming out of the cuvette is led to the analyser tube of the differential IRGA where the $CO_2$ concentration is compared with the concentration of the reference tube. The difference in $CO_2$ concentration is measured for different light intensities. These different light steps are created by the halogen lamps, that hang horizontally above the cuvettes. A quantum sensor in the cuvette registers the PPFD (photosynthetic photon flux density).

## 2.2.2. Description of the WALZ porometer

The portable $CO_2/H_2O$ porometer (WALZ) is used for measurements in the field and in the laboratory. The sequential scheme for differential measurements is shown in Figure 2. Only one cuvette (WALZ, PMK-10) is available, in contrast to the phytotron where three cuvettes are installed. For the measurements with the portable porometer, a lighting unit (WALZ, FL-400) is used to create the different light intensities. This unit hangs horizontally above the leaves in the cuvette. With the WALZ porometer, it is more difficult to control the temperature and the relative humidity in the cuvette, in comparison to the phytotron.
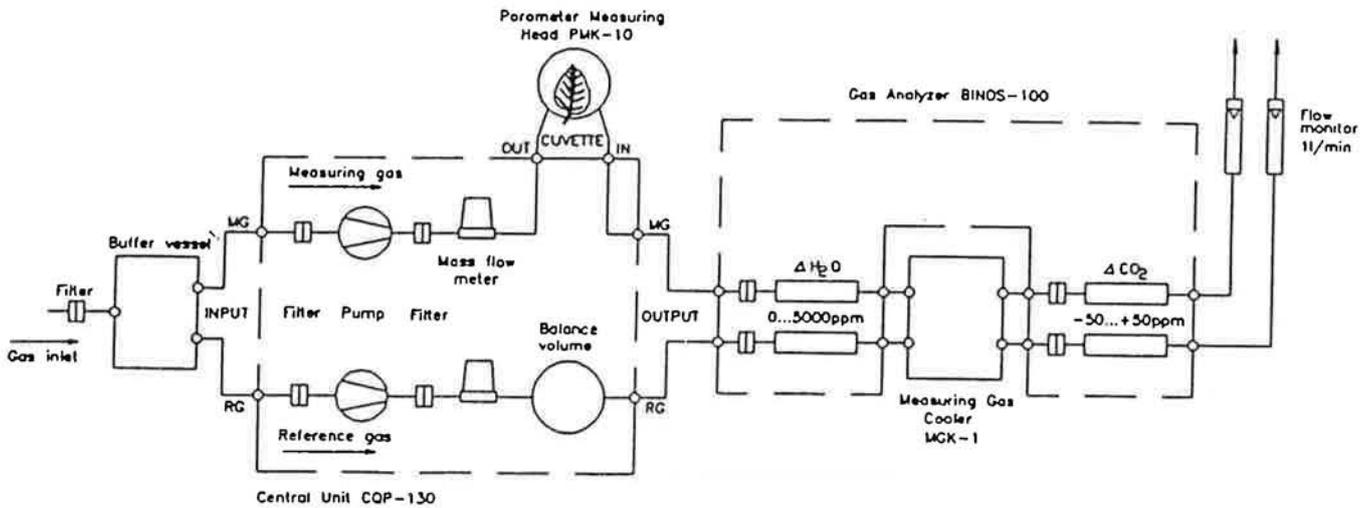


Figure 2.　Schematic overview of the WALZ porometer (WALZ, 1991)

## 2.3. Experimental set-up

The aim of the experiment is to compare the photosynthetic parameters of beech, ash and oak measured with two different methods. In the laboratory, beech leaves from the first, second and third level are studied, oak and ash leaves from the third level only. As oak is not easily accessible from the tower, only beech (level 2 and 3) and ash (level 3) are studied with the portable system. Several measuring campaigns took place. Table 1 gives a summary of the dates and the place where the measurements are performed.

Table 1.　Date and place of the measuring campaigns

|  | 26/8/1996 - 17/9/1996 | 1/7/1997 - 9/7/1997 | 18/8/1997 - 20/8/1997 | 26/8/1997 - 28/8/1997 |
|---|---|---|---|---|
| Phytotron | laboratory | laboratory | / | / |
| WALZ-porometer | / | / | field | laboratory |

For the measurements in the laboratory, a branch was cut off on the tower, and brought to the ground level. From this branch a piece of 15 centimetres was cut off under water, to avoid the penetration of air in the xylem. From this moment on, the section was never brought in contact with the air again. The branch was placed, until the end of the measurements, in a bottle filled with water, and transported to the laboratory where it was positioned in a way that allowed to bring one or several leaves in the cuvette. The cuvette was closed hermetically. A slight overpressure was created, to avoid air to enter the cuvette.

The photosynthesis rate of the leaves was detected for seven different decreasing light intensities (700, 450, 200, 100, 75, 50, 25, 0 $\mu$mol PAR photons m$^{-2}$ s$^{-1}$), allowing sufficient time for the steady-state rates of gas exchange to be attained (0.5-1h). The last step, 0 $\mu$mol PAR m$^{-2}$s$^{-1}$, was created by covering the cuvette with a black plastic bag. At this light intensity, the dark respiration was measured. After each measuring series, a 'Portable Area Meter' (LI-COR, LI-3000), coupled with a 'Transparent Belt Conveyer' (LI-COR, LI-3050 A), was used to measure the leaf area enclosed in the cuvette.

When using the phytotron, the air temperature in the cuvette and the relative humidity have to be chosen. For this study, an air temperature of 20°C was used, as this is close to the mean of the maximum month temperatures (for the months May until October) for the years 1984 to 1993 (Follens, 1997). The relative humidity was set at a value of 78% as this is the mean value for the months May until October for this region (the evaporator was set at a dew point temperature of 16.1°C).

For each measurement, following parameters were recorded : the temperature of the leaf, the temperature of the air in the cuvette, the PPFD, the difference in $CO_2$ concentration between the reference and the analyser tube of the IRGA, the rate of flow and the temperature of the evaporator. The air temperature and the relative humidity in the cuvette during the measurements are given in Table 2.

Field measurements were performed on leaves that were easily accessible with the leaf cuvette. The lighting unit hung horizontally above the cuvette. For the three lowest light intensities, a plastic cover was used to protect the cuvette from light coming from the environs. For the measurements with the WALZ-porometer, cuvette conditions were more difficult to control (Table 2).

Table 2.    *Conditions of air temperature and relative humidity inside the cuvette during the measurements ($T_{cuv}$ is the temperature of the air in the cuvette; $RH_{cuv}$ is the relative humidity in the cuvette)*

| Tree species | Method | $T_{cuv}$ [°C] | $RH_{cuv}$ [%] |
|---|---|---|---|
| beech (level 1) | phytotron, laboratory 1996 | 20 | 78 |
| | phytotron, laboratory 1997 | 20 | 78 |
| beech (level 2) | phytotron, laboratory 1996 | 20 | 78 |
| | phytotron, laboratory 1997 | 20 | 78 |
| | WALZ, field | 25 | 74 |
| | WALZ, laboratory 1997 | 24 | 69 |
| beech (level 3) | phytotron, laboratory 1996 | 20 | 78 |
| | phytotron, laboratory 1997 | 20 | 78 |
| | WALZ, field | 28 | 65 |
| | WALZ, laboratory 1997 | 25 | 68 |
| oak (level 3) | phytotron, laboratory 1996 | 20 | 78 |
| | phytotron, laboratory 1997 | 20 | 78 |
| ash (level 3) | phytotron, laboratory 1996 | 20 | 78 |
| | phytotron, laboratory 1997 | 20 | 78 |
| | WALZ, field | 27 | 54 |
| | WALZ, laboratory 1997 | 25 | 75 |

## 2.4. Calculation of the net photosynthesis rate

If the temperature in the cuvette is called $t_{cuv}$ and the flow rate is $F$, then the rate of net photosynthesis per unit of leaf area is :

$$P_n = \frac{\Delta CO_2 \cdot F}{A} \cdot \frac{1}{22.414} \cdot \frac{273.15}{273.15 + t_{cuv}} \cdot \frac{P_r}{760} \cdot \frac{10000}{60} \tag{1}$$

with  $P_n$     :     net photosynthesis rate [$\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$];

$\Delta CO_2$     :     difference of $CO_2$ concentration [$\mu$l l$^{-1}$];

$F$     :     flow rate [l min$^{-1}$];

$A$     :     leaf area [cm$^2$];

$P_r$     :     atmospheric pressure [mmHg];

and  $t_{cuv}$     :     temperature in the leaf cuvette [°C].

In equation (1), following conversion and correction factors are charged :

1 / 22.414          = factor to convert litre to mol $CO_2$;

273.15 / (273.15 + $t_{cuv}$)     = correction for temperature (according to the universal gas law);

$P_r$ / 760          = pressure correction; and

10000 / 60          = conversion of [$\mu$mol cm$^{-2}$ min$^{-1}$] to [$\mu$mol m$^{-2}$ s$^{-1}$]

## 2.5. Determination of the functional photosynthesis parameters

Photosynthesis light response curves are derived from the $P_n$-values obtained for the different light intensities. Following functional parameters can be determined :

- **$P_{max}$** or the maximum rate of leaf photosynthesis : this is the maximum gross $CO_2$ uptake by the leaf for a situation of light saturation;
- **$I_c$** or the light compensation point : at this point the rate of $CO_2$ evolution is balanced by the uptake of $CO_2$, which means that net photosynthesis is zero;
- **$\alpha$** or the initial quantum efficiency : this is the initial slope of the curve (at $I_c$) which is a measure of $CO_2$ taken up per unit increase in irradiance [($\Delta CO_2$ uptake)/($\Delta$irradiance)];
- **$R_d$** or the dark respiration : this is the rate of $CO_2$ evolution from the leaf in the dark.

A non-linear regression was used to fit an exponential function to the measured $P_n$-values for the different light intensities. This exponential function is of the form (Thornley, 1976) :

$$P_n = P_{max} \cdot \left[ 1 - \exp\left( \frac{-\alpha \cdot I}{P_{max}} \right) \right] - R_d \qquad (2)$$

## 3. Results

### 3.1. Measurements with the phytotron

In Figure 3 the light response curves of beech measured with the phytotron in 1996 and 1997 at the 3 different levels are presented. The corresponding functional parameters are given in Table 3.

At level 1, the maximum photosynthesis rate $P_{max}$ is almost the same in 1996 and 1997. The initial light efficiency $\alpha$ is higher in 1997 than in 1996, and both are high in comparison with the theoretical maximum value of 0.125 (Landsberg, 1986; Lemeur, 1991).

At level 2 and 3, the net photosynthesis rates measured during the 1997 growing season are higher than the values obtained in 1996. This is reflected in the higher values of $\alpha$ as well as $P_{max}$ in 1997.

In 1996, the photosynthesis light response on level 2 is almost the same as the one on level 3. In '97 the photosynthetic activity is clearly higher on level 3 than on level 2, especially at high PAR irradiance.

Table 3.     *Photosynthesis parameters of the different tree species*

| Tree species | Method | $\alpha$ [µmol $CO_2$ µmol $PAR^{-1}$] | $P_{max}$ [µmol $CO_2$ m$^{-2}$ s$^{-1}$] | $R_d$ [µmol $CO_2$ m$^{-2}$ s$^{-1}$] |
|---|---|---|---|---|
| beech (lvl1) | phyt., lab. 1996 | 0.088 + 0.004 | 5.47 ± 0.17 | 0.31 ± 0.06 |
| | phyt., lab. 1997 | 0.110 ± 0.006 | 5.09 ± 0.39 | 0.27 ± 0.11 |
| beech (lvl2) | phyt., lab. 1996 | 0.094 ± 0.004 | 5.67 ± 0.46 | 0.26 ± 0.02 |
| | phyt., lab. 1997 | 0.098 ± 0.005 | 7.08 ± 0.01 | 0.50 ± 0.19 |
| | WALZ, field | 0.067 ± 0.002 | 8.53 ± 2.62 | -0.32 ± 0.09 |
| | WALZ, lab. 1997 | 0.055 ± 0.002 | 7.18 ± 0.35 | -0.28 ± 0.09 |
| beech (lvl3) | phyt., lab. 1996 | 0.071 ± 0.008 | 5.79 ± 0.49 | 0.40 ± 0.04 |
| | phyt., lab. 1997 | 0.075 ± 0.015 | 8.94 ± 1.62 | 0.54 ± 0.02 |
| | WALZ, field | 0.068 ± 0.002 | 7.75 ± 0.22 | 0.11 ± 0.37 |
| | WALZ, lab. 1997 | 0.053 ± 0.001 | 9.64 ± 0.14 | 0.33 ± 0.16 |
| oak (lvl 3) | phyt., lab. 1996 | 0.076 ± 0.008 | 11.10 ± 1.97 | 1.09 ± 0.09 |
| | phyt., lab. 1997 | 0.033 ± 0.001 | 25.10 ± 7.31 | 0.40 ± 0.31 |
| ash (lvl 3) | phyt., lab. 1996 | 0.110 ± 0.007 | 11.90 ± 1.03 | 1.38 ± 0.16 |
| | phyt., lab. 1997 | 0.046 ± 0.011 | 11.10 ± 1.77 | 1.05 ± 0.09 |
| | WALZ, field | 0.066 ± 0.006 | 12.90 ± 0.17 | 0.14 ± 0.12 |
| | WALZ, lab. 1997 | 0.046 ± 0.006 | 11.00 ± 0.75 | 0.14 ± 0.24 |

Comparing the results for oak, there is an enormous difference between the values obtained in 1996 and 1997. The quantum efficiency for 1997 is half the value for the 1996 growing season, while the maximum photosynthesis rate of 1997 is more than double the value of the year before.

A comparison of the photosynthesis light response curves of ash, measured in the growing season '96 and '97, is shown in Figure 4.
The maximum photosynthesis rate of ash is almost the same for both years. The $\alpha$ is lower in July 97 than in September 1996.

Comparing ash and beech in 1996 (Figure 5), the photosynthesis light response of ash is higher than the curve of beech, which is also found in the higher values of $P_{max}$ and $\alpha$ for ash than these for beech.

In 1997, the quantum efficiency $\alpha$ of ash is lower than the $\alpha$ of beech. The maximum photosynthesis rate of beech is lower than the one of ash, but the difference is less pronounced than in 1996.
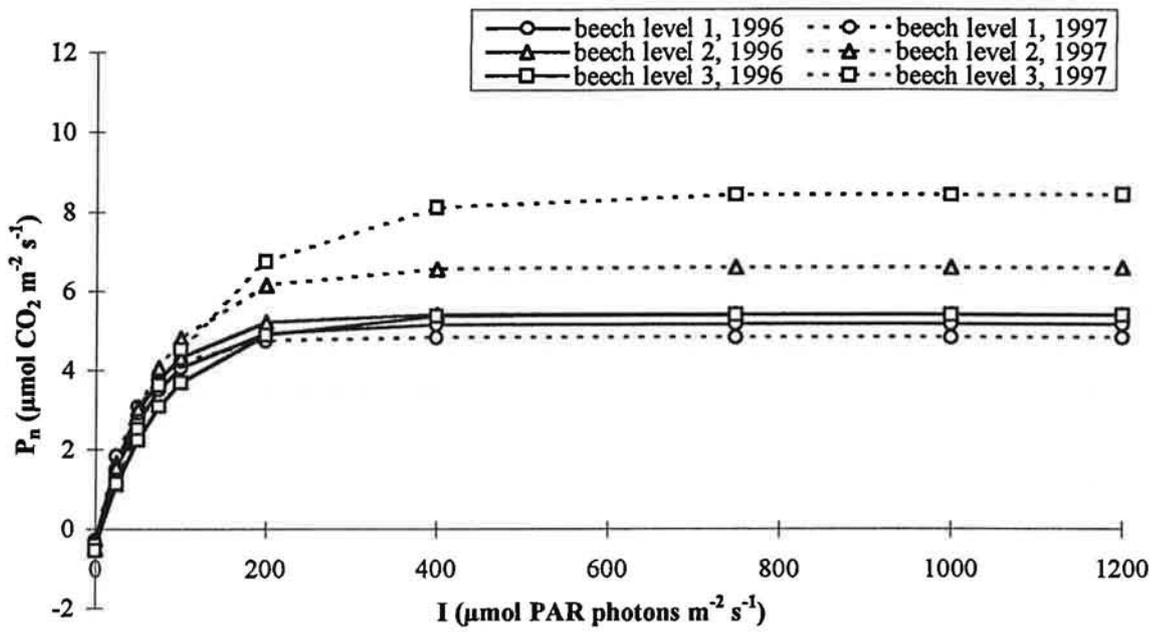
Figure 3.    Light response curves of beech, measured with the phytotron
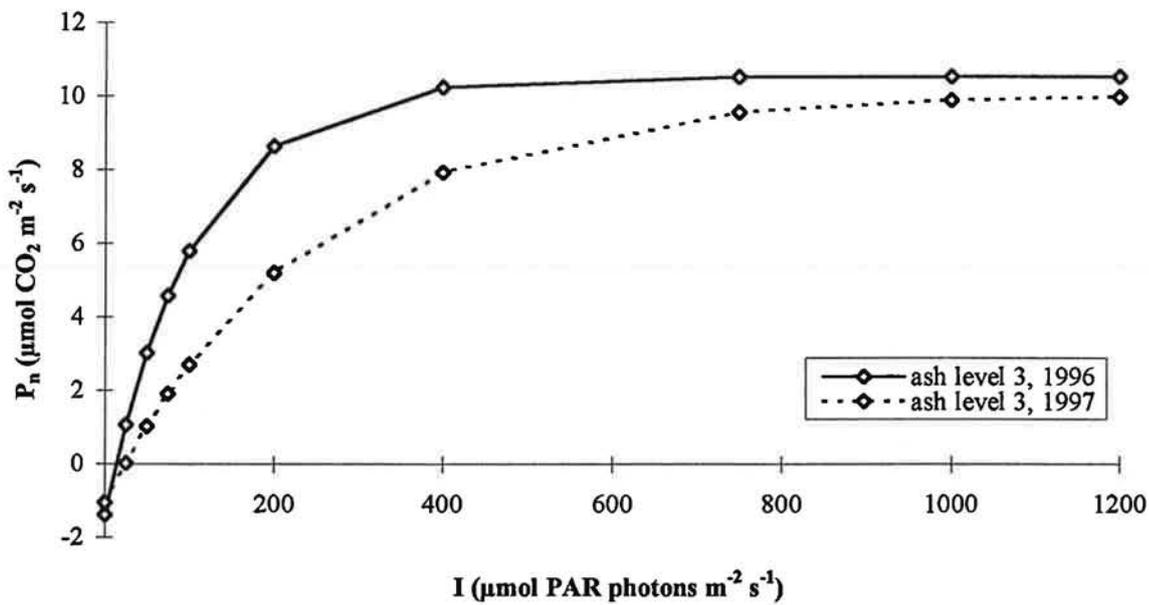


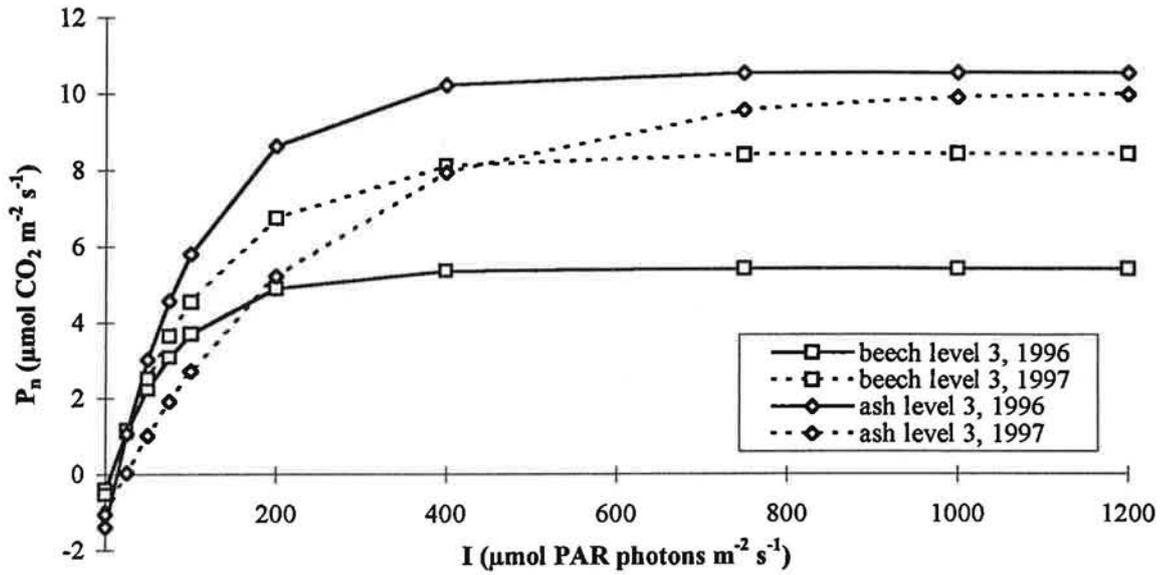Figure 4.    Light response curves of ash, measured with the phytotron

Figure 5.   Light response curves of beech and ash, measured with the phytotron
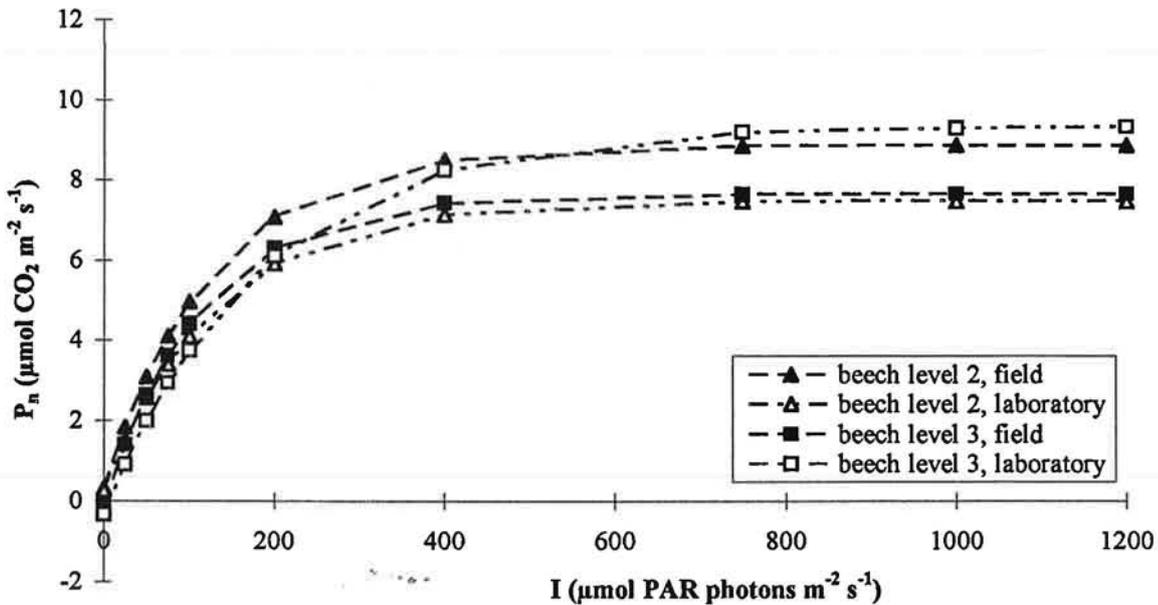


Figure 6.   Light response curves for beech, measured with the WALZ-porometer, in 1997

## 3.2. Measurements with the WALZ-porometer

To validate the destructive measurements in the laboratory on cut off branches, non-destructive field measurements were performed. Comparing field and laboratory measurements (Figure 6 and Table 3), it can be seen that $P_{max}$ and $\alpha$ measured at the field for beech (level 2) are higher than in the laboratory. For leaves growing at level 3 the opposite effect is noticed.

Fig. 7 shows that the photosynthetic light response for ash measured in the laboratory is lower than the one measured in the canopy. Related to this general response, laboratory measurements of ash (Figure 7) indicate a lower $\alpha$ and $P_{max}$ than the ones of the field measurements. This is opposite to the results for beech on level 3. Both the laboratory and the field measurements give higher net photosynthesis rates for ash than for beech.
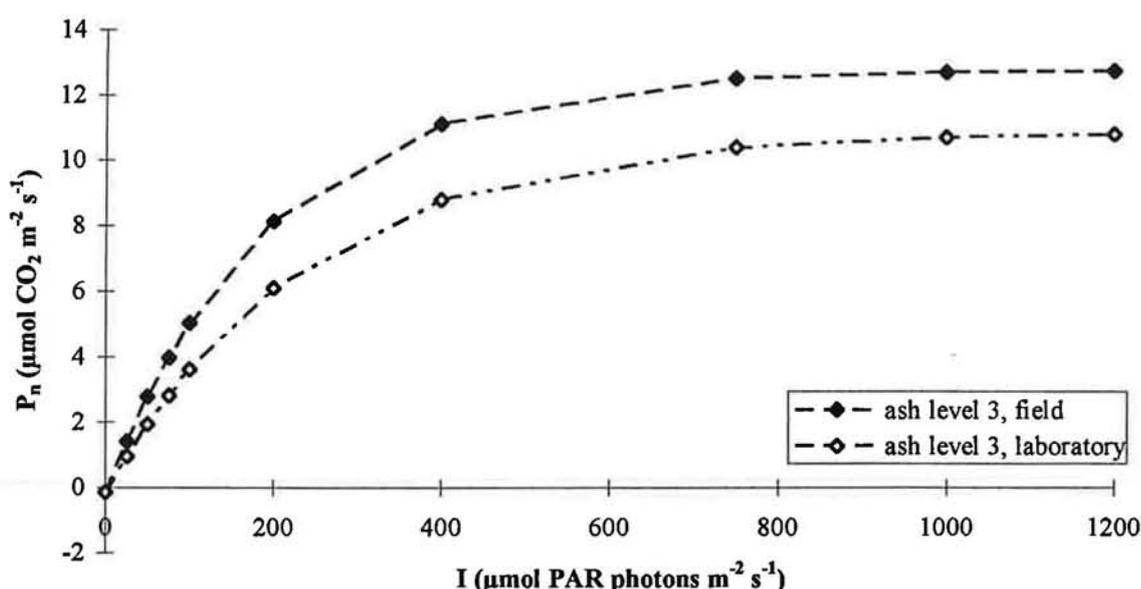


*Figure 7.    Light response curves for ash, measured with the WALZ-porometer, in 1997*

## 4. Discussion

### 4.1. Measurements with the phytotron

Measurements performed with the phytotron always yielded high $\alpha$ values. The theoretical maximum for $\alpha$ is 0.125 µmol $CO_2$ µmol PAR photons$^{-1}$, and the values found in this study range from 0.07 to 0.11 (exceptions are oak and ash of level 3 measured in 1997). In normal atmospheric conditions the quantum yield values are 0.050 to 0.054 µmol $CO_2$ µmol PAR$^{-1}$ at 30°C. However, the $\alpha$ is strongly temperature dependent (Landsberg, 1986).

The values found for the maximum rate of photosynthesis $P_{max}$ are comparable to values found by other authors. Landsberg (1986) gives an overview of different investigations. $P_{max}$ values of different tree species range from 5 to 17 µmol $CO_2$ $m^{-2}$ $s^{-1}$. Impens *et al.* (1992) found values between 2.9 and 11.4 µmol $CO_2$ $m^{-2}$ $s^{-1}$ for different poplar species. The only exceptional results found in this study are those for oak. As there is an enormous difference between the values of 1996 and 1997, it is recommended to repeat the measurements for this tree species.

The curves of ash always lay higher than the curves of beech. This is probably the result of the fact that ash is a light tolerant species, while beech is a shade tree species. Previous research indicated that there is a difference in photosynthetic behaviour of sun leaves growing in the top of the canopy and shade leaves found at a depth of several meters from the top of the canopy. Sun leaves have a higher light compensation point, and continue to respond up to typical values for full sunlight (Jones, 1992).

For beech of level 2 and 3, the $P_{max}$ was higher in 1997 than in 1996. Probably this is caused by the time of the measurements : in 1997, measurements were performed in June, while in 1996 these took place in September, when senescence of leaves already begun. De Pury and Ceulemans (1997) found that leaf photosynthesis declined with needle age in Scots pine (*Pinus sylvestris* L.).

De Pury and Ceulemans (1997), Harley and Baldocchi (1995) and Kull and Jarvis (1995) mention that leaf photosynthesis declines with depth in the canopy. Results of the measurements of beech seem to lead to the same conclusion.

## 4.2. Measurements with the WALZ-porometer

From Table 3, it becomes clear that the field measurements always give a higher $\alpha$ than measurements in the laboratory. In 2 of the 3 cases, the same conclusion can be made for the value of $P_{max}$. These results are in contradiction with Landsberg (1986) : he mentions that $\alpha$ values obtained from field measurements are lower than the ones obtained in the laboratory.

## 4.3. Comparison of the two methods

In the case of the phytotron, the temperature and the relative humidity in the cuvette are set on a constant value. However, these two parameters are not controlled while measuring with the WALZ-porometer. From Table 2, it is clear that the temperature in the cuvette was at least 4°C higher during the WALZ-measurements, and that relative humidity was always lower. These differences in environmental conditions can have influenced the results of the measurements, as photosynthesis is one of the most temperature-sensitive aspects of growth (Impens *et al.*, 1992; Jones, 1992).

Comparison of measurements with the phytotron and with the WALZ-porometer is possible for beech of level 2 and 3, and ash of level 3, both for the 1997 growing season (see Table 2). The value of $\alpha$ resulting from the measurements with the phytotron always exceeded the one found with

the WALZ-system. The opposite is observed for $P_{max}$ : the highest values are found with the WALZ-porometer.

Measurements performed with the WALZ-porometer on the field are expected to approximate the natural situation of the photosynthesis process as good as possible. When cutting off branches, this photosynthesis process is inevitably disturbed. In some cases, *f.e.* when leaves are not easily accessible, it may be necessary to cut off branches and to do measurements in the laboratory. The advantage of the phytotron in comparison with the WALZ-system is that temperature and relative humidity can be better controlled in the leaf cuvettes. The disadvantage of the phytotron on the other hand is that this system is unmovable, so plants or branches have to be brought to the laboratory. For forest trees, where branches are cut off and transported to the lab, this means that there will be a disturbance of the photosynthesis of the leaves. The method that will be used for measuring the photosynthesis parameters depends on the system available, on the accessibility of the leaves and the aim of the research (*f.e.* if you want to determine the photosynthesis parameters for different temperatures, then it is recommended to use the phytotron as you can set the temperature on a certain value). Nowadays, portable photosynthesis equipment is available, which allows better control of the cuvette microclimate. This allows to make better reproducible measurements on the field.

## 5. Acknowledgements

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