

WHEAT RESPONSE TO CO<sub>2</sub> ENRICHMENT :  
CO<sub>2</sub> EXCHANGES TRANSPIRATION AND MINERAL UPTAKES

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## Introduction

In long term application of CO<sub>2</sub> enrichment ( i.e., from two to ten times the normal concentration) an increase in the dry matter production has almost always been observed. For C<sub>3</sub> plants the enhancement of dry weight ranges from almost a 5 fold increase for soybean <sup>1</sup> to barely a 1.2 fold increase for wheat <sup>2</sup>, <sup>3</sup>, rice <sup>3</sup> and tobacco <sup>4</sup> with many intermediate values (table I). Kramer's review <sup>14</sup> posed tentative generalization about growth responses of plants to enhanced concentration of CO<sub>2</sub> : I) large differences exist among various species ; II) responses are greater with indeterminate plants than determinate ones ; III) the largest response occurs in seedlings and decreases or ceases as plants grow older. The two first propositions are not strongly proved and studied and the effects of difference or not well defined conditions could explain much of observed variations. So, the Kimball's review <sup>15</sup> situates the average of stimulation coefficient of dry matter production, for a doubling of CO<sub>2</sub> level, in the moderate range of 30 - 40 %.

Ever since the Athens conference <sup>16</sup>, more attention has been paid to studying the crop and natural vegetation response <sup>17</sup> and to developing models predicting dry matter and yield enhancement. Progress in the crop studies was obtained by the experiments of Rogers et al <sup>18</sup> (with open-top chambers) and of Jones et al <sup>19</sup> (with day light growth chambers). But the discrepancy between their results concerning the dry matter enhancement factor (for example when doubling CO<sub>2</sub> one obtains 1.63 and 1.36 respectively for the same soybean plant) still remains to be explained.

As for proposition III) by Kramer, it was based on the decrease of the response to CO<sub>2</sub> enrichment with the length of treatment, as reported by Ford and Thorne <sup>6</sup> for barley, Neals and Nicholls <sup>22</sup> for wheat and Patterson and Flint <sup>12</sup> for soybean. It poses a problem for quantitative predictive models and asks questions for plant physiology : increase of

Matériel végétal	Réf.	Teneur en CO <sub>2</sub> (μl l <sup>-1</sup> )	Durée de traitement (j)	Rapport fort CO <sub>2</sub> /CO <sub>2</sub> normal	Nombre de plantes par échantillon	Eclairement (μEm <sup>-2</sup> s <sup>-1</sup> )	Température (°C)	Photo-période
Blé	5 *	490	140	1,32	20	LN (été)	21/16	8/16
	2 *	950	28	1,47	6 à 12	ca 1120 (a)	15°6 (a)	16/8
	8	600	17	1,30	10	360	22°5/20	20/4
	10 *	675-1000	24 47	1,13 1,90-2,16	10	600	26/20	12/12
Betterave à sucre	13	1000	10	2,80	10	320	28/22	16/8
	4	1000-3300	21 42	1,26-1,25 1,23-1,23	7 7	ca 330	20/15	16/8
	4	1000-3300	21 42	1,44-1,50 1,48-1,39	7 7	ca 330	20/15	16/8
Coton	12	640	40	2,00	5	LN (été)	32/20	
	7 *	630	110	2,10	9	LN (Mai-Août)		
Maïs (C4)	6	1000-3500	15	1,06-1,14				
	12	640	30	1,20	8	LN (été)	32/20	
	9	600-1000	12 24 45	1,17-1,21 n.s. - n.s. n.s. -0,86	8 8	650	28/22	14/10
	6	1000-3500	15	1,36-1,23	42	ca 330	20/15	16/8
Orge	4	1000-3300	21 42	1,44-1,61 1,28-1,24	42			
	6	1000-3500	15	1,24-1,23				
	6	1000-3500	15	1,24-1,23				
Riz	6	1000-3500	15	1,24-1,23				
	7 *	630	110	4,80	9	LN (Mai-Août)		
	9	600-1000	12 24 45	1,53-1,80 1,30-1,77 1,23-1,72	8	650	28/22	14/10
	1	1000	9-35	1,84	8	600	26/20	12/12
	3 *	1350	38	var. Chippewa : 1,51 var. Hark : 1,67	2	ca 280+LN(Fev-Av)	30/32	14/10
Tabac	11	1000	6-24 6-45 31-45	2,42 1,35 1,20	15 1	ca 780	26/22	9/15
	7 *	630	110	1,60	9	LN (Mai-Août)		
	7 *	630	110	1,60	9	LN (Mai-Août)		

Références : 1 : Clough et Peet 1981 (5)      2 : Combe 1981 b (9)      3 : Cooper et Brun 1967 (11)  
 col. 2      4 : Ford et Thorne 1967 (6)      5 : Gifford 1977 (10)      6 : Imai et Murata 1976 (3)  
 7 : Mauney et al. 1978 (1)      8 : Neales et Nicholls 1978 (2)      9 : Patterson et Flint 1980 (12)  
 10 : Sionit et al. 1981 d (7)      11 : Thomas et al. 1975 (4)      12 : Wong 1979 (13)  
 13 : Wyse 1980 b (8)

Table 1 : Effect of CO<sub>2</sub> enrichment on the dry matter production. The col. 4 gives the enhancement factor.

n.s. : non-significant effect ; (a) average on 4 weeks ; \* : until maturity ;

LN : natural light.

carboxylation is obtained at the expense of the oxidative photosynthetic carbon cycle. Measured by  $^{18}\text{O}_2$  uptake in  $\text{C}_3$  plants, this cycle consumes as much reducing equivalents as reductive carbon cycle <sup>20</sup>. It may have some physiological use for example by the well known coupling with nitrogen metabolism. When it is repressed, that can explain, together with many other already evocated processes <sup>16</sup>, the decrease with time of the growth efficiency.

Long term effect of  $\text{CO}_2$  enhancement also concerns research in the photorespiration genetics <sup>21</sup>, because the permanent change of  $\text{CO}_2$  exactly simulated a pure genetic change in the specificity factor of  $\text{CO}_2$  of the Ribulose biphosphate carboxylase/oxygenase.

Hence, to help understanding the physiological control of dry matter production posed in new and pertinent terms by  $\text{CO}_2$  effect studies, several experiments were performed on wheat, by integrating gas exchanges at the whole plant and canopy level <sup>22</sup>, <sup>23</sup>. Particular attention was paid to I) growth response from seedling to dense canopy situation <sup>24</sup> ; II) change in photosynthetic and photorespiratory characteristics at single plant or canopy level <sup>25</sup> ; III) water use efficiency in normal and limited watering ; IV) Relation between daily  $\text{CO}_2$  uptake and mineral uptakes. We'll report here typical results of this study, with emphasis on data which are not yet published.

## MATERIAL AND METHODS

### Plant material and growth conditions

Wheat seeds (*Triticum aestivum* L., var. Capitole) were germinated between wet filter papers in the ambient conditions of our laboratory (temperature was  $20^\circ\text{C} \pm 1$ ). No chilling treatment was applied for floral induction ; so, tillering went on throughout the experiment. Three day-old seedlings were planted out in pots of 1.45 liter : 5 and 1 plant per pot in the high and low density experiment respectively. The plants were grown either on garden soil or sand.

The day after planting, 20 pots were distributed on a surface of  $0.5 \text{ m}^2$  in each of two C23A\* twin growth chambers <sup>26</sup>, <sup>27</sup>, <sup>28</sup>. The  $\text{CO}_2$  concentration was regulated at  $330 \pm 5 \mu\text{l l}^{-1}$  in the control chamber and at  $660 \pm 5 \mu\text{l l}^{-1}$  for the high  $\text{CO}_2$  treatment. The other climatic

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\*C23A= Chambres de Culture Automatique en Atmospheres Artificielles  
described by Andre et al in the session on International CELSS

conditions were the same in both chambers. The photon fluence rate, provided by 3 Osram HQI-T 400W/DV lamps, was  $600 \pm 90 \mu\text{moles m}^{-2}\text{s}^{-1}$  at a height of 30 cm from the bottom of the chamber. Air flow (rate of  $0.4 - 0.6 \text{ ms}^{-1}$ ) was vertical from a grid on the floor of the growth chamber. The temperature and the relative air humidity were respectively,  $24^\circ\text{C}$ , and 50% during 14 hours of light and  $18^\circ\text{C}$  and 85% during 10 hours of darkness. The four walls of the chambers were covered with polished Aluminium sheets in order to reduce the irradiance border effects. The homogeneity of climatic conditions inside each chamber had been tested previously <sup>29</sup>, <sup>30</sup> : on a horizontal plane the deviation was less than 4% for temperature and less than 15% for light. Four different treatments were carried out by crossing two  $\text{CO}_2$  concentrations (control and high) with two plant densities, in order to obtain different light availabilities (200 and 40 plants  $\text{m}^{-2}$  for high and low density respectively). The plants were grown in controlled conditions until almost 40 days after germination. The experiments described in this paper, constitute a part of a series of six, twin experiments on  $\text{CO}_2$  enrichment achieved in similar or identical conditions, at least for 25 days. At that stage the influence of a limiting water supply has been studied in part of them. These experiments included the inversion of the  $\text{CO}_2$  concentrations in the two chambers and showed the reliability of the system. Results were reproducible within 15% for  $\text{CO}_2$  gas exchanges for successive crops. The accuracy of relative measurements, between twin chambers, was better than 5%.

#### $\text{CO}_2$ gas exchange measurements

The  $\text{CO}_2$  concentration was measured with an infra-red gas analyser (Hartmann and Braun-URAS 2T). The  $\text{CO}_2$  uptake by photosynthesis and the  $\text{CO}_2$  release by respiration during the night were compensated respectively by calibrated  $\text{CO}_2$  injections and  $\text{CO}_2$  trapping with soda lime. The system has been previously described <sup>31</sup>. A computer (Télémécanique 1600) anticipated the compensation of the gas exchanges between two consecutive gas measurements (about every 7 minutes), in order to reduce the deviation from the set point. The same computer recorded the physical parameters (light, air and dew point temperatures) and the amount of  $\text{CO}_2$  injections or the time of  $\text{CO}_2$  trapping so that photosynthesis and respiration could be easily deduced. All the calculations were achieved with a Solar 16-40

mini-computer. During daytime the  $O_2$  concentration was kept normal (around 20.6%) in spite of the photosynthetic  $O_2$  release, by using a gas mixture of 80%  $N_2$  and 20%  $CO_2$  for the  $CO_2$  injections.

Photosynthesis (which included the  $CO_2$  uptake of shoots minus the  $CO_2$  evolution from the roots) and respiration were mean values of the  $CO_2$  gas exchanges of the canopy. A correction for soil respiration was applied when garden soil was used. This value was estimated from a preliminary experiment on pots without plants in the same chambers ( $9.0 \text{ mg } CO_2 \text{ h}^{-1}$  during the light period and  $6.1 \text{ mg } CO_2 \text{ h}^{-1} \text{ pot}^{-1}$  during the night). Over the whole period of growth this correction accounted only for 6% and 7.5% of the final dry weight at 660 and  $330 \mu\text{l l}^{-1}$  respectively.

Area of leaves and growth measurements.

During the high density experiment we harvested a sample of ca.15 plants randomly chosen at 23, 30 and 37 days after germination. In the low density experiment only two harvests took place at 23 and 38 days, of 5 plants each. After sampling the remaining pots were reorganized in order to avoid the formation of gaps in the canopy.

At each harvest, the length of the lamina was measured. A correlation curve between the length of the lamina and their surface (as determined with manual planimeter) had been established previously in order to obtain leaf lamina surfaces. These were taken as leaf surfaces. Leaf area index\* was calculated by the product of leaf area per plant by the number of present plants. A leaf was considered to be expanded when the ligule was visible. The plants were dried in an oven at  $65^\circ\text{C}$  during 60 hours before their different parts were weighted.

The continuous growth curves were obtained (without any fitting) by cumulating the net daily photosynthesis (PN) to the initial seed weight (52 mg). The factor relating the integration of PN expressed in mg of  $CO_2$  per plant to the dry weight in grams per plant, was determined by considering a dry matter carbon content of 44%.

Transpiration and mineral consumption

Methods previously described <sup>31</sup>, <sup>32</sup>, were performed with sample of 20 pots and in sand culture. The daily watering with nutrient solution (Hoagland and Arnon n°2) provided about twice as much water as was needed for transpiration. A device connecting each pot to an individual and

\* leaf area index (LAI)

calibrated reservoir, provided a good uniformity of the solution supply and allowed an easy control of the working of the watering. Tests of the system, with 40 pots, gave a maximum deviation of 4% from the wanted volumes. Weighting of the water, condensed in the cooling system kept at the accurate wanted dew point, gives the daily transpiration.

The collected overflow of watering was also weighted, pH controlled and kept in fridge for analysis. Nutrient uptake of  $\text{NH}_4 - \text{NO}_3 - \text{P} - \text{K}$ , was obtained from multichannel Autoanalyser Technicon data. Computer monitoring and data processing made comparison with fresh solution, calibrations with standard solutions and calculations of uptakes take into account input/output of volume and concentrations <sup>27, 32</sup>.

## RESULTS AND DISCUSSION

### Growth rate analysis

Continuous monitoring of  $\text{CO}_2$  exchange provided continuous growth curves of carbon accumulation (Fig.1) and accurate relative growth rate data reported elsewhere <sup>24</sup>. The main results for growth models was that : I) a little effect of  $\text{CO}_2$  on RGR was noticeable in first 14 days but then disappeared ; II) The expected exponential amplification of  $\text{CO}_2$  effect <sup>33, 16</sup> was not observed. Quasi exponential kinetics was observed but related by constant ratio and so, with same R.G.R. at the same time ; III) Reciprocally a consequence is that the R.G.R. comparison (as for example Ruffy's study <sup>35</sup>) is not the pertinent measure of a growth stimulation ; IV) Higher apparent stimulation effect in early stage previously reported <sup>23</sup> was, after analysis, attributable to the artefactual seed matter respiration : when, from negative figure, the carbon balance begins positive, a little advantage of one treatment can give an infinite ratio of stimulation. This effect was corrected <sup>24</sup> and the stimulation factor naturally rises from 1 (initial status of seeds) to finite values (Figure 1) (only in that phase R.G.R. was little stimulated).

### Effect on carbon accumulation.

In order to follow the time-evolution of the effect of  $\text{CO}_2$  enrichment on dry matter production, we plotted in figure 1 the ratio of high  $\text{CO}_2$  to control growth curves as deduced from  $\text{CO}_2$  exchange measurements.

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Growth was followed in two distinct ways : by harvesting plant

\* relative growth rate (RGR)

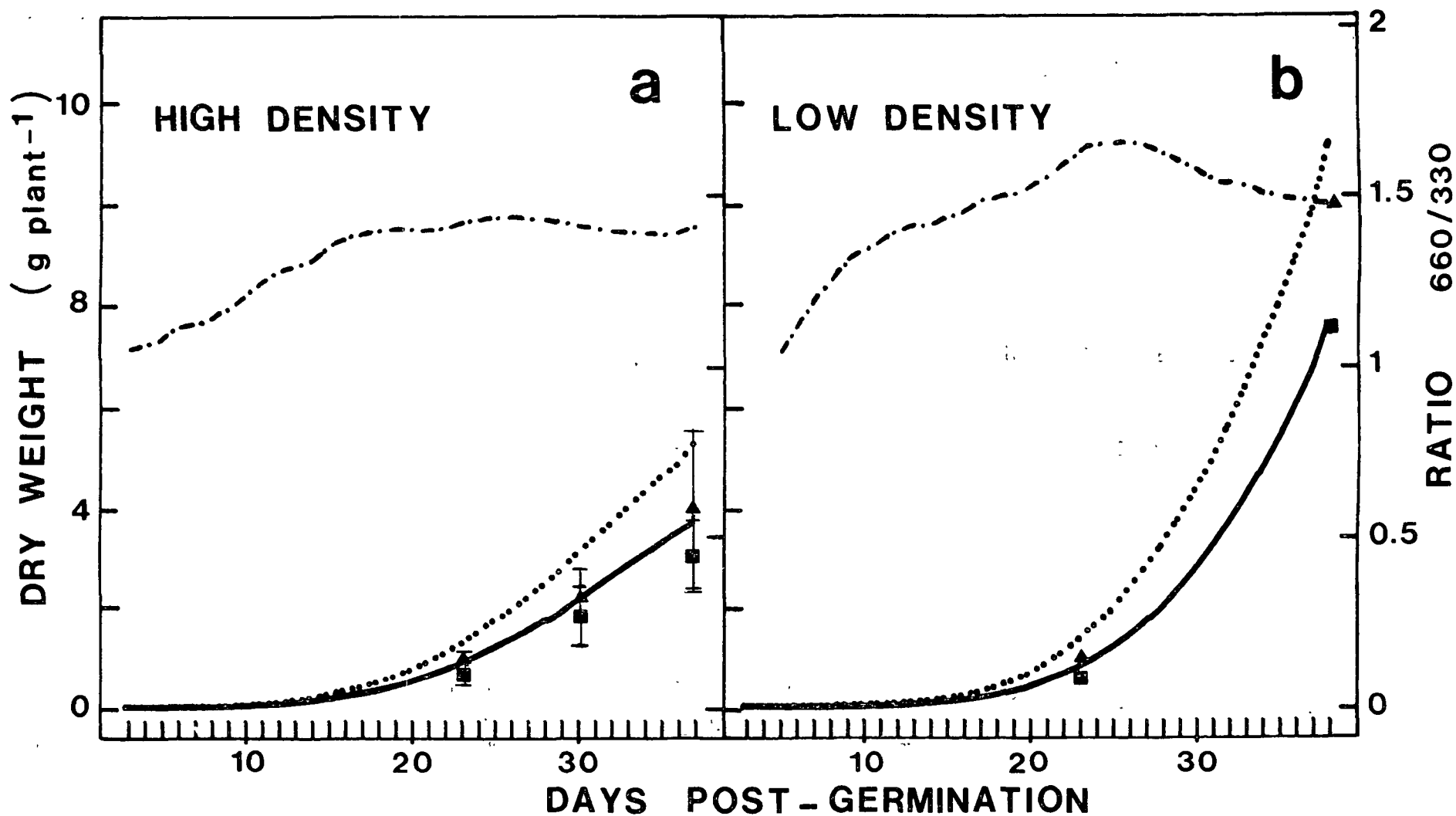


Figure 1 : Continuous growth curves obtained from the integration of the net daily  $\text{CO}_2$  uptake of whole canopies :

(—)  $330 \mu\text{l l}^{-1} \text{CO}_2$  and (.....)  $660 \mu\text{l l}^{-1} \text{CO}_2$ . Ratio of high  $\text{CO}_2$  to control growth curves (-.-.-) ; dry weights from harvests (samples of 15 and 5 plants respectively in the high and the low density experiment) :

(■)  $330 \mu\text{l l}^{-1} \text{CO}_2$  and (▲)  $660 \mu\text{l l}^{-1} \text{CO}_2$ . bars : standard deviation.

a :  $200 \text{ plants m}^{-2}$ . b :  $40 \text{ plants m}^{-2}$ .

material at time intervals, and continuously by the daily net carbon uptake. As shown in figure 1, the results did not exactly agree. Part of the global deviation might be ascribed to the uncertainty about the real carbon content of the dry matter.

The ratio between the continuous growth curves of both CO<sub>2</sub> treatments (Figure 1) was higher and more constant than those obtained from dry weight measurements. The most probable explanation for the discrepancy, was the large variability of the dry weight measurements, even with the largest samples (10 to 15 plants) and in spite of the attention paid to a good uniformity of the growth conditions inside each chamber. As a consequence, even the difference between samples from the two CO<sub>2</sub> levels was not always statistically significant. So, we will prefer the data obtained from CO<sub>2</sub> exchanges to discuss the factor of stimulation.

At both densities this ratio rose during the first 15 days up to a level of ca. 1.45 for the high density and ca. 1.50 for the low density. For the high density it then remained almost constant until the end of the experiment. However, for the low density, the ratio rose significantly (up to 1.65) until 23 days, stabilized a few days. That was due to the compound of two effects: relative increase of surface (by 20%) and promoting effect of CO<sub>2</sub> on photosynthesis. When leaf area increased (mainly due to tillering), the advantage of surface decreased. The ratio dropped again from the 26th day to ca. 1.50. In spite of a subsequent rise of LAI to 9.4 at 330  $\mu\text{l l}^{-1}$  CO<sub>2</sub> and to 10.3 at 660  $\mu\text{l l}^{-1}$  CO<sub>2</sub>, the ratio was maintained at this level until almost 70 days.

Thus final effect of the high CO<sub>2</sub> treatment on dry weight per plant (1.45 for high density and 1.50 for low density) was not much influenced by the plant density.

The promoting effect of CO<sub>2</sub> enrichment on dry weight of wheat seedlings showed no decreasing tendency with time (Fig.1). In contrast, Neales and Nicholls<sup>2</sup> found a progressive decrease of the stimulation of biomass at high CO<sub>2</sub> for young wheat plants too. The discrepancy might be explained by the difference in our respective photoperiods. Neales and Nicholls<sup>2</sup> applied a very short night (4 Hours) which might have resulted in a subsequent increase of the concentration of assimilates in the leaves, especially for the high CO<sub>2</sub> treated plants. A reduced photosynthetic capacity has often been observed in such conditions (Neales and Incoll<sup>3</sup>).



For both densities, the final enhancement of dry weight by CO<sub>2</sub> enrichment (1.45 at high density and 1.50 at low density) was in the same order of magnitude as the results reported for wheat by Gifford (1977), Combe <sup>9</sup>. However, the low density experiment showed a transient stimulation of 1.65 at 23 days for a LAI below 1, i.e. for strictly isolated plants. In the same way Sionit et al <sup>7</sup> found a two fold increase of dry weight with 675  $\mu\text{l l}^{-1}$  CO<sub>2</sub>. Even if no plant density was mentioned in that paper, we can assume that plants did not drastically interact. In the same way, the difference of behaviour between an isolated plant and a canopy might explain some discrepancies in the literature about CO<sub>2</sub> enrichment evocated in introduction. For instance, Rogers et al <sup>19</sup>, reported at either 620 or 815  $\mu\text{l l}^{-1}$  of CO<sub>2</sub>, respectively a 1.63 and a 1.77 fold increase of soja biomass in field experiments with a density estimated around 7 plants m<sup>-2</sup>. In contrast, Jones et al <sup>19</sup> obtained a stimulation of 1.36 and 1.53 respectively at 600 and 800  $\mu\text{l l}^{-1}$  of CO<sub>2</sub> in out-door chambers but with 50 plants m<sup>-2</sup>. It seems probable that the former observed the effect on relatively isolated plants when the later better simulated a crop canopy.

The difference between the response of an isolated plant and a canopy to CO<sub>2</sub> enrichment can be explained by the growth components involved in the buildup of the gain of carbon. In the case of an isolated plant (or LAI below 1), the stimulation of dry matter production results from promoted Net Assimilation Rate (NAR) and leaf area. Furthermore, the impact of the gain of leaf area on dry matter production depends on the duration of the phase in which LAI stays below 1. Therefore we found no such transient of high level of stimulation in the high density experiment.

In contrast, for a closed canopy (LAI beyond 2-3) the response of crop assimilation (per unit of ground area) to the increase of LAI is almost saturated <sup>24</sup>. The stimulation factor no longer depend on leaf area increasing. It depends only on the response of the canopy (considered as a big leaf) to the CO<sub>2</sub> enhancement. Only the second order processes (i.e. change of stomatal conductance, regulation of carboxylation rate, photorespiratory and respiratory changes) can intervene.

Comparison of long-term with short-term responses of photosynthesis

Daily Photosynthesis and respiration of cultures with and without

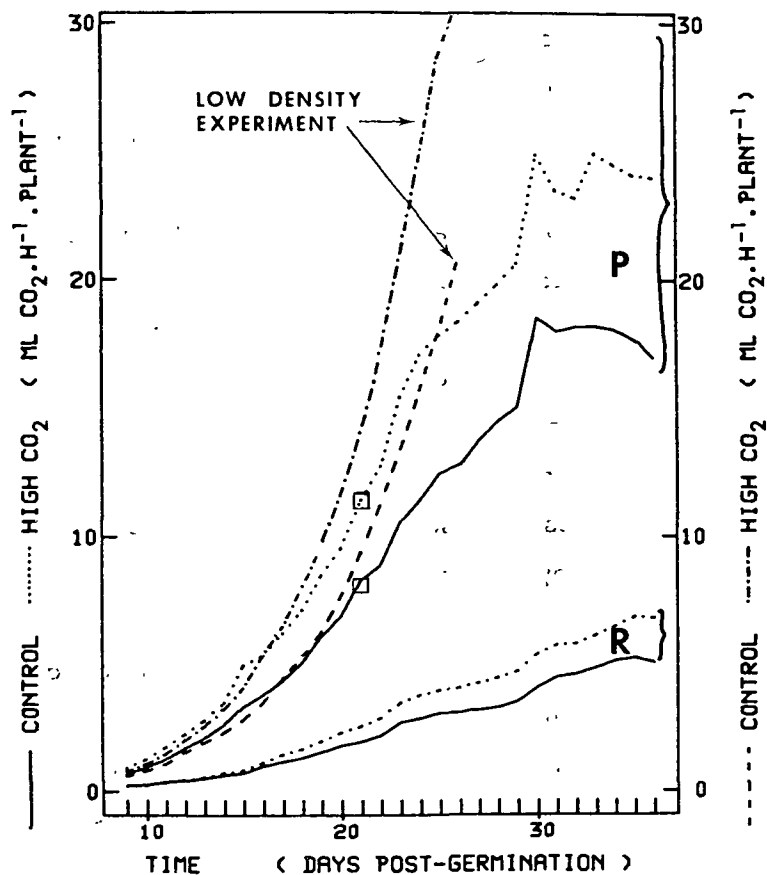


Figure 2 : Long term effect of CO<sub>2</sub> enrichment on daily photosynthesis (P) and respiration (R) expressed in mean rate of 14 hours of light period, and of 10 hours darkness respectively. High density experiment (—) 330 and (----) 660 μl l<sup>-1</sup> of CO<sub>2</sub>. P of low density experiment (----) 330 and (—) 660 μl l<sup>-1</sup> of CO<sub>2</sub>.

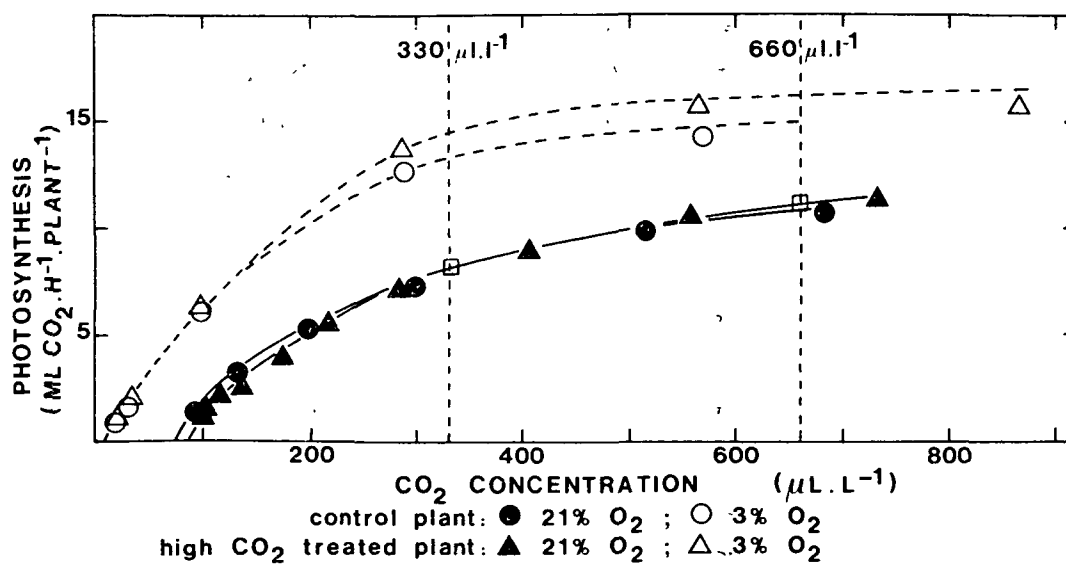


Figure 3 : Typical short term response of the photosynthesis of wheat canopies. Measurements were made at midday of the 21th day in the high density experiment of Fig. 2. Rates of photosynthesis were very similar for both canopies (LAI around 2) and particular values (□) well correspond to average values of Fig. 2.

CO<sub>2</sub> enrichment are shown in Fig.2. They were used to calculate the long-term effect of CO<sub>2</sub> on dry matter production discussed above. Second order effect can be estimated if one permutes the atmosphere or if one plots (Figure 3) the short term photosynthesis response of each canopy to the CO<sub>2</sub> concentrations. Such curves were systematically obtained in both crop densities when LAI was equal or above 2. At first they indicate that the photosynthetic characteristics (for normal O<sub>2</sub> pressure) of the two crops were similar (same big leaf) and therefore the second order of regulation processes were neglectible or compensated each other. Crossing the atmosphere gave also the same photorespiratory rate <sup>25</sup>. Only a careful analysis of photosynthesis (corrected to correspond to exactly the same LAI) suggests a second order effect which reduces the photosynthetic capacity by about 5 to a maximum of 10 per cent <sup>22, 24</sup>.

The second observation (also consequence of previous consideration) was that, if we double the CO<sub>2</sub> concentration on the reference experiment growing at 330  $\mu\text{l l}^{-1}$ , we obtain the same photosynthesis as the high CO<sub>2</sub> adapted sample, and furthermore the values fit the daily average values (Fig.2) of the corresponding day. In other words, short term experiment can be used to predict long term response to CO<sub>2</sub> of the crop canopy production. If such behaviour is verified for other plants the consequence should be important to predict first order response of dry matter accumulation of vegetation in closed canopy. Experiment of Jones et al <sup>19</sup> in Soybean, by crossing the CO<sub>2</sub> level suggest similar conclusion in accordance with moderate enhancement factor and absence of a negative feed-back regulation.

The advantage given by CO<sub>2</sub> enrichment to obtain productive canopy (LAI > 1) faster than in normal conditions is neglectible in our case. The treated culture was only one or two days in advance in the kinetic of area increase.

#### Effect of CO<sub>2</sub> on transpiration

Transpiration rate at a given time were very similar for experiment without and with CO<sub>2</sub> enrichment (Figure 4). Taking into account the difference of leaf area (less than 20%) but also the non-linear relationship between transpiration and LAI (which forbid simple normalization by surface) a little effect of reduction of stomatal conductance (5%) was estimated for the same LAI<sup>22</sup>.

The water use efficiency was increased from 10 to 14 mg CO<sub>2</sub> g<sup>-1</sup> H<sub>2</sub>O (Fig. 5A) . . .

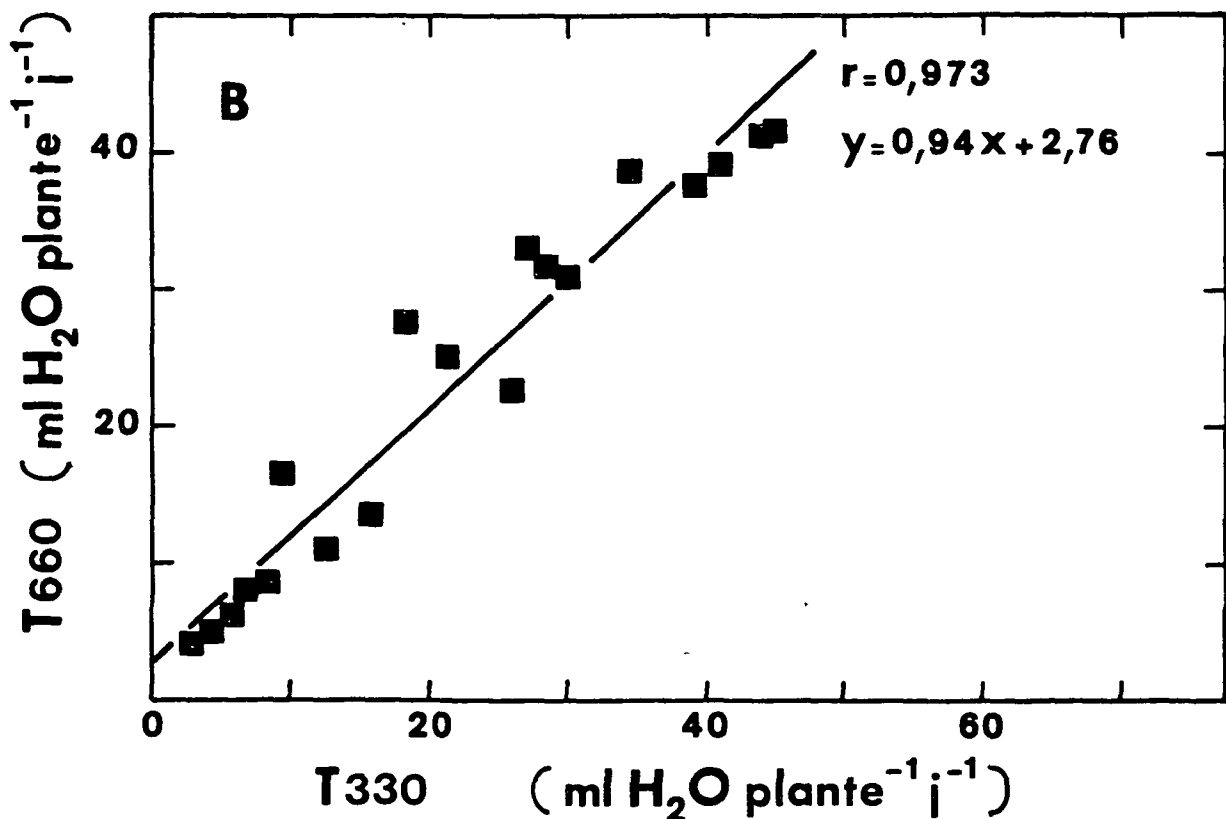
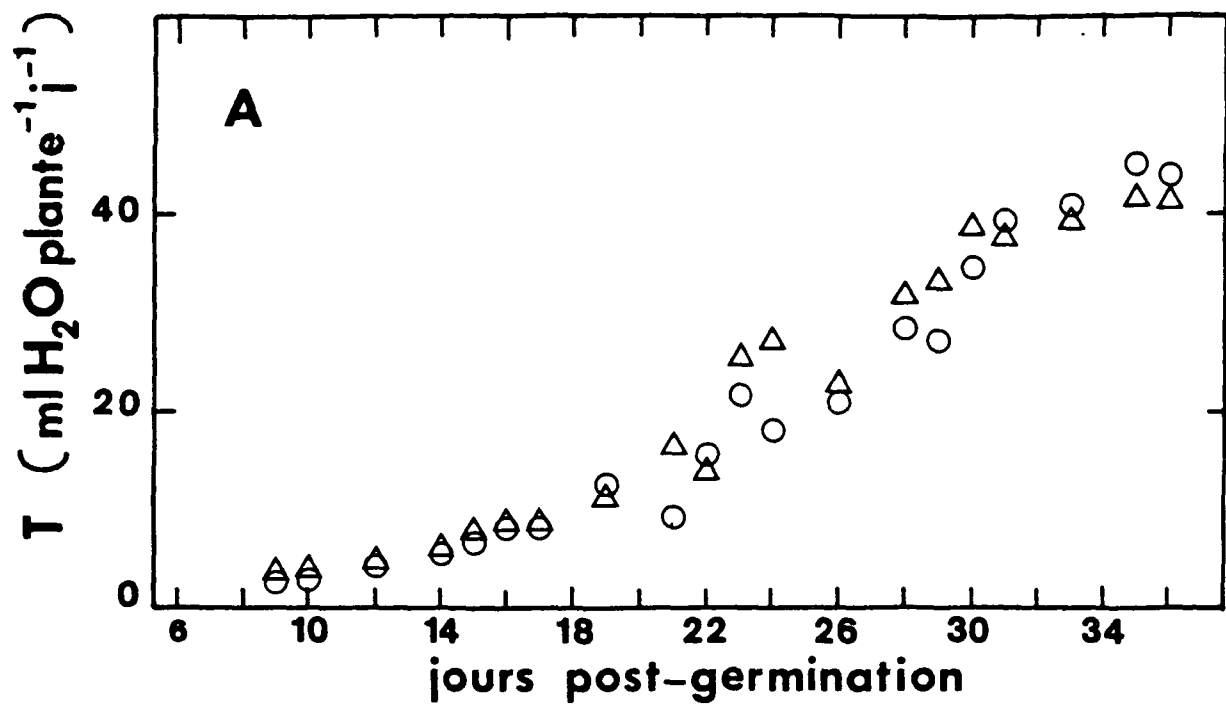


Figure 4 : Effect of  $\text{CO}_2$  enrichment on transpiration.

A) Time evolution of the daily transpiration of the high density culture with (○) 330 and (△) 660  $\mu\text{l l}^{-1}$  of  $\text{CO}_2$ . Same conditions as Fig. 1.

B) Correlation between the daily transpiration of the two cultures at the same time.

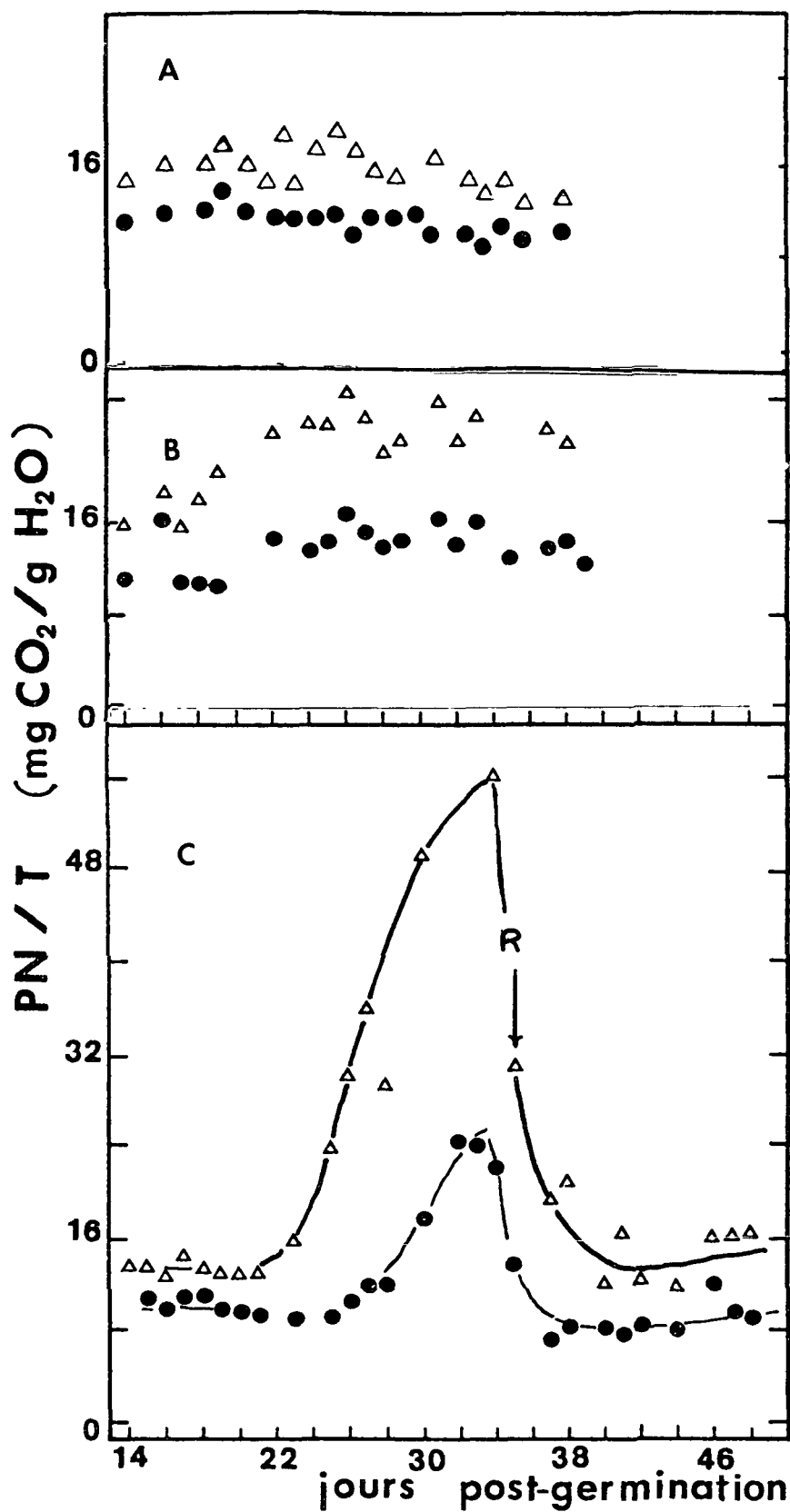


Figure 5 : Water use efficiency of two cultures at high density at ( ● ) 330 and ( Δ ) 660  $\mu\text{l l}^{-1}$ .

A) Without water limitation (average of two experiments)

B) With the limitation of 20  $\text{ml day}^{-1} \text{ plant}^{-1}$ , and (C) of 10  $\text{ml day}^{-1} \text{ plant}^{-1}$  of water (Experiment of Fig. 6)

(R) Rewatering.

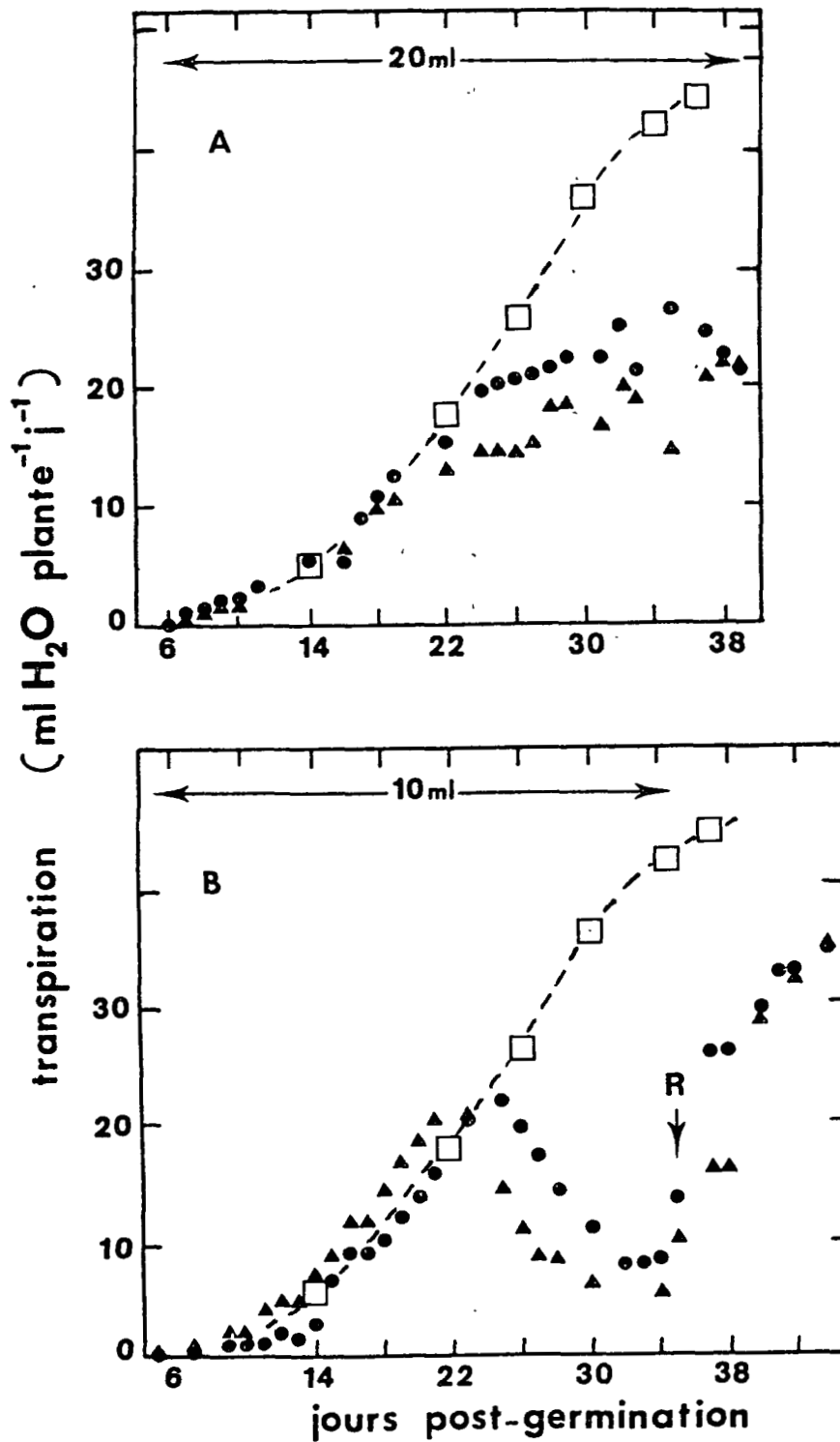


Figure 6 : Effect of moderate water stress on the transpiration rate of two cultures at high densities with (●) 330 and (Δ) 660 μl l<sup>-1</sup> of CO<sub>2</sub> ; (□) standard well watered experiment. The watering was limited to (A) 20 ml day<sup>-1</sup> plant<sup>-1</sup> and (B) 10 ml day<sup>-1</sup> plant<sup>-1</sup> until 37 days, then rewatered (R).

Water limitation.

When watering was limited to a given value (20 or 10 ml day<sup>-1</sup> plant<sup>-1</sup>) - simulating low but constant water availability - the dry weight production was reduced by 43% and the leaf area by 57% at day 35 in the later case. Figure 6 shows that the output of transpiration raises above the input of watering during the depletion of the water storage in the pot (estimated by weighting of 350 ml, sand and bottom reserve). The transpiration finally falls to reach the level of watering. So, at day 35, for the normal CO<sub>2</sub> experiment the transpiration was five times lower than the well watered experiments. Daily photosynthesis was only halved and water use efficiency was more than two times higher. With CO<sub>2</sub> enrichment the photosynthesis is less reduced and the water use efficiency raises up to 56 mg CO<sub>2</sub>.g<sup>-1</sup> H<sub>2</sub>O i.e. around five times the well watered standard (Fig. 5c).

In both cases during the water stress the xylem's hydric potential changes from - 3 to - 6 bars in normal CO<sub>2</sub> and from - 5 to -8 in high CO<sub>2</sub> level. The later one having a constant difference of potential in agreement with results of Sionit et al<sup>36</sup>.

These observations confirm, and quantitatively illustrate, the general agreement on this subject<sup>16</sup>. They respond to the need to link observations made on leaves - the most often reported - and the crop canopy behaviour.

Effect of CO<sub>2</sub> on Nutrient uptakes.

The daily measurement of mineral uptakes in large sample of plants was successfully performed. Figure 7 shows that at a given time the consumption of nutrients was similar in normal and high CO<sub>2</sub> culture. So, as the photosynthesis was higher, the mineral uptake was relatively lowered in the CO<sub>2</sub> enriched culture. The uptake was linearly correlated to photosynthesis in the first phase of growth, Figure 8. From the slopes of the regression lines, we calculated the percent decrease of the mineral uptakes : they was 38% for P, 29% for NO<sub>3</sub>, 28% for NH<sub>4</sub> and 25% for K uptake.

In low density experiments similar results were obtained. The effect was reinforced for nitrate uptake which was relatively depressed in comparison with the carbon uptake, by a factor of 1.7 at day 22 after sowing. Results are in accordance with observations of the decrease of nitrogen content of dry matter previously reported by Madsen<sup>37</sup>, Wong<sup>13</sup> and Allen et al<sup>38</sup>. Studies must be continued until the fructification

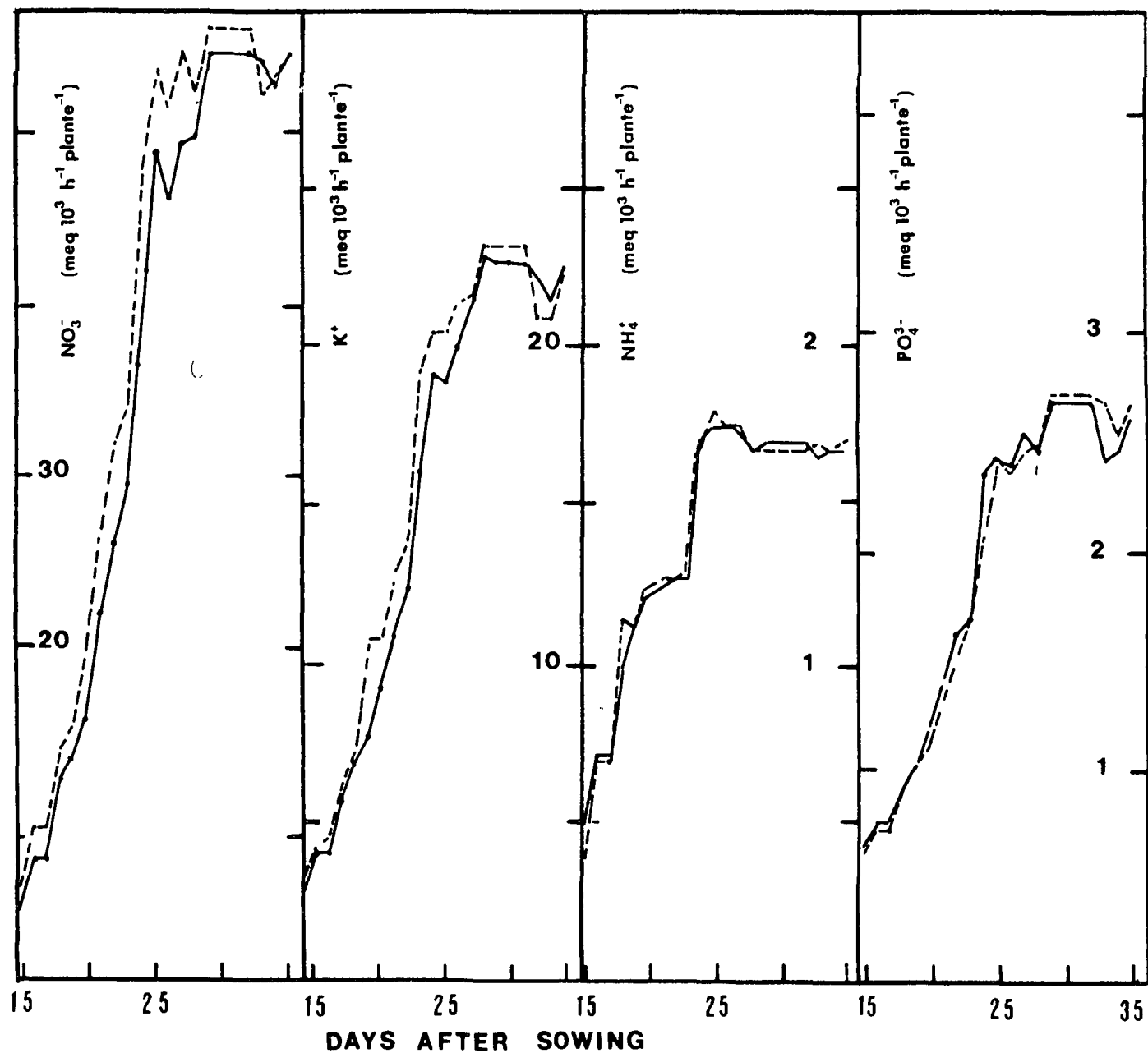


Figure 7 : Daily measurements of mineral uptakes obtained by quantitative monitoring of nutrient solution supply in two large samples of 100 to 60 plants of wheat cultivated with (—)  $330$  and (-----)  $660 \mu\text{l l}^{-1}$  of  $\text{CO}_2$ . The figure is a reprinting of curves directly plotted by the computer which monitors chemical analysis.



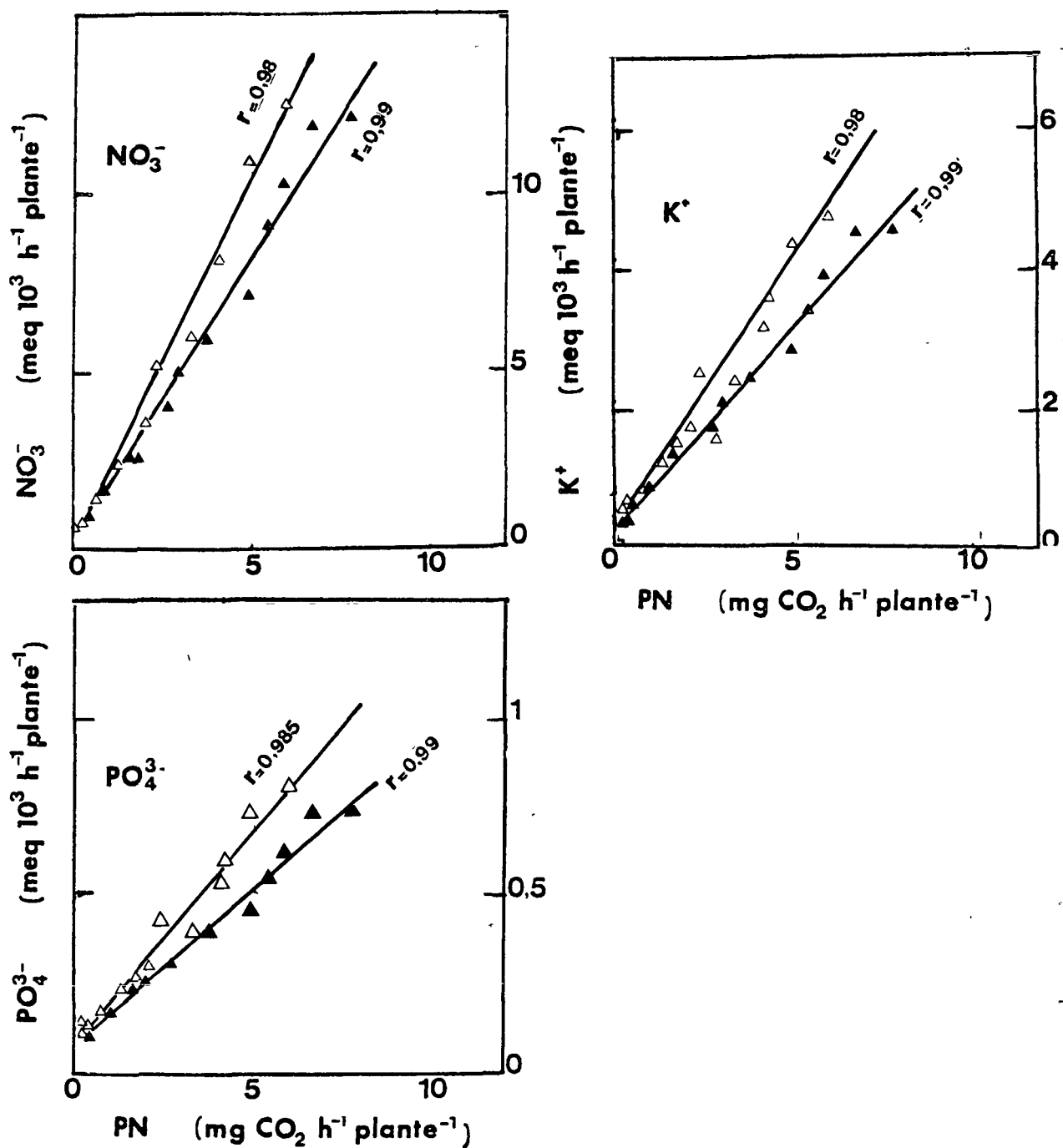


Figure 8 : Relationship between daily mineral uptakes and net daily photosynthesis for two cultures at high density with ( $\Delta$ ) 330 and ( $\blacktriangle$ ) 660  $\mu\text{l l}^{-1}$  of  $\text{CO}_2$ .

stage and the harvest to know if such difference disturb the grain accumulation in wheat.

#### Conclusion

When simulating canopies planted in varied densities, we have been able to demonstrate that increase of dry matter production by enhancing CO<sub>2</sub> quickly becomes independent of increase of leaf area, especially above leaf area index of 2; dry matter gain results mainly from photosynthesis stimulation per unit of surface (primary CO<sub>2</sub> effect). When crop density is low (the plants remaining "alone" a longer time), the effects of increasing leaf surface (tillering, leaf elongation here, branching for other plants etc...) was noticeable and dry matter stimulation factor reached 1.65. This "area effect" decreased when canopy was closed in, as the effect of different surfaces no longer worked. The stimulation of photosynthesis reached to the "primary" CO<sub>2</sub> effect. The accumulation in dry matter which was fast during that phase made the original weight advantage more and more neglectible.

Comparison with short term measurements showed that first order long term effect of CO<sub>2</sub> in wheat is predictable with a short term experiment, from the effect of CO<sub>2</sub> on photosynthesis measured on reference sample.

We obtained a noticeable stimulation of dry matter for wheat (40 - 50 %) but it never reaches the very high figures we mentioned above taken from literature. These figures cannot be applied to plants in field conditions.

Unlike in some other research works we have not noticed any decrease in stimulation factor due to some negative feed-back, when the experiment is lengthened. So, if one represses for quite a long time photorespiration rate, it does not seem to have any negative consequence for wheat on the photosynthetic apparatus in our conditions. But this, only during the vegetative phase, when the nitrogen metabolism is not as active as in fructification stage.

We should note that transpiration and mineral uptakes in our culture under best conditions, were not changed notably in a doubling of CO<sub>2</sub> whereas carboxylation increases. These result in increase of about 50 % in water use efficiency and a decrease in mineral uptake (-30 %) for

a given photosynthesis. Active research should be made in the consequences of the later point over the dry matter content especially in case of grain production.

During water limitations which reduces dry matter production by 20 to 40 %, in both canopies -with and without CO<sub>2</sub> enrichment -stimulation of matter production was maintained or even reinforced when strongly water limited. In that case water use efficiency reaches up to five times the standard figure.

These results emphasize the necessity to take into account simultaneously all the exchanges of the plant with its environment, in the shoot and at the root level as well.

We should like to make this point again, research without respect of density of planting cannot and must not be used in predictive models for field crops. Neither can they and must they be, in CELSS program whose density problem will be probably greater and crucial.

Acknowledgments - This work was partly supported by a grant of the Ministère de l'Industrie et de la Recherche (DGRST) in collaboration with Pr. B. SAUGIER. We thank the staff of the Agro-Physiologie Laboratory at Cadarache : A. Daguenet, A. Gerbaud, D. Massimino, J. Massimino; J. Vivoli

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