Growth performance of *Populus* exposed to “Free Air Carbon dioxide Enrichment” during the first growing season in the POPFACE experiment

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(Received 2nd January 2001; accepted 6 July 2001)

\textbf{Abstract} – Stem diameter, total plant height and number of sylleptic branches of three poplar (*Populus*) genotypes were followed during the first growing season of a high density intensively cultured plantation (in Central Italy) both under ambient CO\textsubscript{2} (Control) and under elevated atmospheric CO\textsubscript{2} (550 ppm) using the FACE technique. The three poplar genotypes belonged to different species of *Populus alba* L., *Populus nigra* L. and *Populus x euramericana* Dode (Guinier). All three genotypes responded by an enhanced growth performance but the extent of their response to the FACE treatment was different. A stem volume index was calculated considering the stem composed by a truncated cone in the lower part and by a cone in the upper part. At the end of the first growing season, stem volume index was increased in the FACE treatment by 54\% to 79\% as compared to Control treatment, depending on the genotype. This increased stem volume index was caused by an increase of basal stem diameter rather than by an enhancement of plant height. Number of sylleptic branches was stimulated by more than 35\% in the *P. nigra* genotype. The results confirm the optimal performance of this new POPFACE experiment and show the positive response of this fast-growing tree species to elevated CO\textsubscript{2} conditions at an ecosystem scale even if considering the genotypic differences.

\textbf{Résumé} – Performance de croissance de plants de *Populus* exposés à une atmosphère enrichie en dioxyde de carbone durant la première saison de croissance dans l’expérimentation POPFACE. Le diamètre du tronc, la hauteur totale et le nombre des branches sylleptiques de trois génotypes de peuplier (*Populus*) ont été suivis durant la première saison de croissance d’une plantation de haute densité en culture intensive (en Italie Centrale), à la fois sous air ambiant (350 ppm, plantes témoins), et sous atmosphère enrichie en CO\textsubscript{2} (550 ppm) en utilisant la technique FACE. Les trois génotypes de peuplier utilisés font partie d’espèces différentes : *Populus alba* L., *Populus nigra* L. et *Populus x euramericana* Dode (Guinier). Les trois génotypes ont tous répondu au traitement FACE par une augmentation de la croissance, mais avec des intensité différentes. Un index de volume du tronc a été calculé en considérant le tronc comme étant composé d’un cône tronqué pour sa partie inférieure, et d’un cône pour la partie supérieure. À la fin de la saison de croissance, l’index de volume du tronc était supérieur de 54 \% à 79 \%, en fonction du génotype, pour le traitement FACE par rapport aux plantes témoins. Cette augmentation de l’index de volume du tronc est principalement due à l’augmentation du diamètre basal des troncs, plus qu’à...
l’augmentation de la hauteur des plants. Le nombre des branches sylleptiques a été augmenté de plus de 35 % par le traitement FACE, pour le génotype *Populus nigra*. Ces résultats, tout en illustrant le bon fonctionnement du nouveau dispositif expérimental POPFACE, confirment, à l’échelle de l’écosystème, qu’une atmosphère enrichie en CO₂ a pour effet une augmentation de la croissance de ces espèces ligneuses à croissance rapide.

CO₂ élevé / FACE / culture intensive de rotation courte / *Populus* / croissance

1. INTRODUCTION

There is growing awareness that trees and forests not only passively undergo global climatic changes, but that they are also driving actors that determine the course of climatic changes; for that reason, the scientific community aspires to assess and quantify the contribution of forests in the global climate change issue [12].

The current knowledge of the response of trees to an elevated atmospheric CO₂ concentration under different experimental conditions has been summarized in recent review papers [2, 13, 26, 34] and books [19]. Almost all experiments showed the positive effects of an increase in CO₂ concentration on growth parameters such as stem height, biomass and leaf area development, but in most cases the experiments were conducted only for a short time period and/or under controlled environmental conditions. Experimental techniques as open top chambers (OTCs) also have important limitations such as the change of microclimatic conditions around the plants and the dimensions of the trees [18, 26]. Besides large open top chambers that enclose portions of natural plant communities [8] or mature stands growing near natural CO₂ springs, the “Free Air Carbon dioxide Enrichment” (FACE) technique allows to investigate responses at the ecosystem level [16, 26]. Moreover, the FACE technology has been developed to minimize environmental disturbances between the CO₂ treated and the surrounding control plant communities. This technique is now being applied at different sites in the world on agricultural crops, but recently also on forest ecosystems such as a loblolly pine stand in North Carolina, USA [9], the AspenFACE in Wisconsin, USA [11], a sweetgum canopy in Tennessee, USA [27]. The POPFACE experiment [25, 36] aims to examine the response of a fast-growing poplar plantation to an atmospheric CO₂ increase.

The choice of poplar (*Populus*) species in this experiment is linked to the aim to study not only the effects of atmospheric CO₂ increase on growth and ecosystem behaviour, but also to quantify the carbon sequestration capacity of intensively managed tree plantations. In fact poplars are the most promising trees for “short rotation intensive culture” (SRIC) [15]. In recent years several experiments were already carried out on the effects of atmospheric CO₂ on poplars [1, 3, 7, 14, 20, 31, 32, 39], most of them for a limited duration of treatment (less than one year) and/or on individual plants.

A lot of the variability in elevated CO₂ effects can be explained by different environmental temperatures within studies and among studies as discussed by [24], but as important is the level of CO₂ concentration in the experiment. In the enriched treatment of POPFACE a CO₂ concentration of about 550 ppm is used, representing the expected CO₂ concentration in the atmosphere near the middle of this century [37].

The objectives of this paper are to report the results on the first year growth performance of the POPFACE experiment answering to some specific questions like: will poplars (*Populus*) grow more under elevated CO₂ at field conditions and which will be the most productive poplar genotype in a high density, intensively cultivated plantation?

2. MATERIALS AND METHODS

2.1. Site description

The experimental plantation and FACE facility are located in an agricultural region of Central Italy, near Viterbo (Tuscania; 42°22’ N, 11°48’ E, alt. 150 m). In spring 1999, after a detailed soil analysis, six experimental areas, generally called “plots” (30 m × 30 m) were selected within a field of about 9 ha. Three of these areas, representing the “Control” treatment, were left under natural conditions whereas in the other three, representing the “FACE” treatment, a polyethylene ring (22 m diameter), parallel to the ground and including about 350 trees, was established [25]. In order to avoid cross contamination between FACE and Control, the minimum distance between plots is 120 m. Pure CO₂ is released through laser-drilled holes in the polyethylene ring mounted on telescopic poles. Meteorological information used to control the release of CO₂ is obtained from an automatic station located at the centre of each ring. Di-
rectional release of gas along the ring is controlled, according to wind direction, by shut-off valves located before the point of injection; the released quantity of gas is established, according to wind speed, using an algorithm developed for the facility and based on a 3-D gas dispersion model. The system, that is controlled by a computer, is set to reach a concentration of about 550 ppm inside the treated plots. A detailed description of the set-up and performance of this FACE facility is given by Miglietta et al. [25].

2.2. Plant material and plantation lay-out

Before planting, the land was ploughed and then crumbled twice using a miller to remove weeds and to improve soil structure since it had been previously used for wheat culture. The poplar plantation was established during the second half of June 1999 using hardwood cuttings, length 25 cm, selected for size, bud status and vigour uniformity.

The entire field was planted with *Populus x euramericana* genotype I-214 at a planting density of 5000 trees per ha (spacing 2 m × 1 m). The six experimental plots were planted with three different poplar genotypes at a planting density of 10000 trees per ha (spacing of 1 m × 1 m) in order to have a sufficient number of experimental trees and a closed canopy already after the first year. The three genotypes were *P. x euramericana* Dode (Guinier) (= *P. deltoides* Bart. ex Marsh. × *P. nigra* L.) genotype I-214, a genotype of *P. nigra* L. (Jean Pourtet) and a local selection of *P. alba* L. (genotype 2AS11), as shown in table I. Each plot is divided into two parts by a physical resin-glass barrier (1 m deep in the soil) for future nitrogen treatments in the two halves of each plot. Each half plot is further divided into three sectors for the different genotypes. No nitrogen treatments were applied during the first year of the experiment.

Before planting, cuttings of *P. alba* were treated with a phytohormone (IBA, 2000 ppm) to stimulate the formation of roots, notoriously difficult in this species. Moreover, additional cuttings were planted in pots, filled with the site soil, and put in the greenhouse to obtain a sufficient number of plants for possible replacements.

A drip irrigation system was installed both in the field and in the experimental plots to avoid drought stress. Rooting of the cuttings of *P. nigra* and *P. x euramericana* was nearly perfect (99%). For *P. alba* a partial replacement of plants (about 30%) was necessary in the first weeks after the plantation using the plants raised in the greenhouse.

The irrigation system was essential not only during the initial establishment phase, but also during the summer, characterised by high temperatures and long periods without rainfall. Weeds were removed manually or mechanically, whereas a limited use of insecticides was indispensable.

2.3. Growth measurements

From August 1999 onwards, stem height, basal stem diameter at 20 cm above the soil and number of sylleptic branches were measured or counted every two weeks.

All measurements were made on a sample of six adjacent plants selected within each sector of the

<table>
<thead>
<tr>
<th>Table I. Main characteristics of the poplar genotypes used in the POPFACE experiment.</th>
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<tbody>
<tr>
<td>Genotype name</td>
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<tr>
<td>Species name</td>
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<tr>
<td>Sex</td>
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<tr>
<td>Origin</td>
</tr>
<tr>
<td>Rooting</td>
</tr>
<tr>
<td>Branching habit</td>
</tr>
<tr>
<td>Apical control</td>
</tr>
<tr>
<td>Bud-burst***</td>
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<tr>
<td>Bud set***</td>
</tr>
</tbody>
</table>

* seed origin; ** origin of the selected hybrid; *** indicative dates for Central Italy.
experimental plots. Consequently, there were six experimental groups per plot, each of these including six plants. Each group of six adjacent plants, surrounded by at least one row of the same genotype (to avoid possible border effects) represented the Permanent Growth Plot (PGP) which was left undisturbed during the course of the study. Since no nitrogen treatment was applied during the first year, all growth parameters were measured on a sample of twelve trees per genotype in each plot.

At the beginning and at the end of the growing season height and diameter of 48 plants (including PGP plants) per plot and per genotype were measured to verify whether the PGP was representative for the entire population. At the end of the growing season also diameter of the main stem at 1 m above the soil was measured to determine the stem profile and calculate the volume index. All measurements of stem diameter were made using a digital calibre (Mitutoyo, type CD-15DC, UK) whereas for stem height measurements a graduated pole was used. Syllentic branches on the main stem, defined as branches that develop from axillary buds not undergoing a rest period [33], were counted.

2.4. Phenology

Near the end of the growing season visual observations of all PGP plants were made every two or three days looking at the apical bud formation to determine the date of bud set on the main stem. For all phenological observations, mean dates (± SE) were calculated. The large variation in the length of the growing season and the time of bud set, caused these visual observations to be carried out from September till the end of October.

2.5. Volume index

At the end of the growing season stem volume index was calculated for 48 plants per plot from total height and stem diameter measured both at 20 cm and at 1 m above the soil. To calculate stem volume index, each stem was considered as a combination of a truncated cone from the bottom to 1 m, and a cone from 1 m to the top of the main stem (figure 1). The volume of each part was calculated as:

\[
\frac{\pi}{3} H_1 (R_1^2 + R_1 R_2 + R_2^2)
\]

(truncated cone)

where \(H_1\) is the height of the truncated cone (100 cm) and \(R_1\) and \(R_2\) are the radii at the bottom and at the top of the truncated cone; and:

\[
\frac{\pi}{3} H_2 R_2^2
\]

(cone)

\(H_2\) is the height of the cone (difference between total height of the main stem and 100 cm) and \(R_2\) is the radius at the base of the cone (coincident with the upper base of the truncated cone). To avoid a considerable overestimation of the basal part, due to the normal stem enlargements, the lower diameter was measured at 20 cm above the soil. By doing so, a better estimation of stem volume could be achieved [30].

\[\text{Figure 1. Scheme of a poplar stem (not in scale) divided into a basal part, below 100 cm, considered as a truncated cone and the upper part, above 100 cm, considered as a cone. } R_1 \text{ is the radius at the base and } R_2 \text{ is the radius at the top of the truncated cone. } R_1 \text{ was measured at 20 cm above the soil to avoid the basal stem enlargements.}\]
2.6. Statistical analysis

To determine the main effects of CO₂ treatment and genotype, both fixed factors, data were analysed by nested Analysis of Variance (ANOVA). Plot, nested within CO₂ treatment, and the interaction between plot and genotype, were included as random factors in the design to account for between plot variation. Significance of this interaction was tested with the Likelihood ratio test. Analysis of stem diameter was performed separately for each measuring date. All statistical analyses were done in SAS (SAS Institute, Cary, NC) using the mixed procedure. Satterthwaite’s procedure was used to obtain the denominator degrees of freedom. Where the ANOVA F-test indicated an interaction between CO₂ treatment and genotype, a posteriori comparison of means was done, using parameter estimates as given by SAS. The Bonferroni method was applied to correct for multiple comparisons. Differences between parameter means were considered significant when \( p < 0.05 \).

3. RESULTS

Owing to their successful and vigorous rooting, *P. x euramericana* and *P. nigra* established very fast, reaching a diameter that was almost twice the value of *P. alba* two months after planting. This was particularly evident in the FACE treatment where trees of *P. nigra* and *P. x euramericana* reached at the end of August a value of stem diameter of 14.01 mm and 14.10 mm respectively, compared to 8.15 mm for *P. alba* (figure 2). Besides these differences among genotypes, the CO₂ treatment had a significant effect on growth. This was especially evident for *P. x euramericana* and *P. nigra* with a stimulating CO₂ effect by 40% and 30%, respectively, whereas for *P. alba* the CO₂ stimulation effect on diameter was only by 13% (table II).

The effect of the FACE treatment on stem height was much smaller (between 8% and 11%) with end-season values ranging from 140 cm for *P. alba* in Control treatment to 186 cm for *P. nigra* in FACE treatment (table II).

It should be underlined that stem height of the three genotypes increased not in parallel during the growing season because of the different growth rate and the different bud set dates of the genotypes. The first genotype that stopped height growth was *P. x euramericana*, which set bud on September 10 in both treatments. *P. nigra* set bud on October 3 in the Control treatment and on October 10 in the FACE, whereas *P. alba* set bud on October 25 and 26 in the Control and FACE treatments, respectively. As a result of this, the slower growing genotype *P. alba* was much lower in the early stages of the experiment but recovered part of the differences in comparison with the two other genotypes because of its longer growing season.

The end of the growth in stem diameter was more uniform among the three genotypes and was observed around the middle of October (as demonstrated by figure 2).

Larger and significant differences between CO₂ treatments and among genotypes were observed when comparing stem volume indices (table II). At the end of the season the maximum volume index value was reached by *P. nigra* in the FACE treatment with 289 cm³, whereas very small was the value reached by *P. alba*. In the Control treatment volume index values were always smaller for all genotypes highlighting a CO₂ stimulation effect ranging from 79% to 54% (table II).
For *P. nigra* there were on average 46 sylleptic branches produced near the end of the growing season in the FACE treatment whereas only 34 in the Control treatment. *P. alba* showed a very minor difference between CO₂ treatments with values of 15 and 14 sylleptic branches per tree, respectively for FACE and Control treatments. The number of sylleptic branches for *P. x euramericana* was 9 in the FACE treatment and 4 in the Control treatment showing a large effect of the CO₂ treatment (that is, however, also more pronounced by the very small numbers).

### 4. DISCUSSION

At present the POPFACE experiment is the only one of its kind in the world, together with the AspenFACE [11], where a short rotation, high-density culture of fast growing poplar trees is exposed under natural conditions to elevated atmospheric CO₂ conditions. The results illustrate the large response of the poplar genotypes to the CO₂ treatment. During the establishment year of this new FACE experiment a significant increase by elevated CO₂ was found in stem diameter (table III) ranging from 13 to 40%. Showing a rather tight relation between basal stem diameter and height, trees grew taller in the FACE treatment showing a relative increase by about 10%. This is within the range of growth enhancements reported for trees in controlled chambers and open top chambers [23]. For various hybrid poplar genotypes, growth enhancements of either stem diameter or plant height between 5 and 33% have been reported in response to elevated CO₂ treatments [4, 10]. However, in chamber studies on small *Populus tremuloides* genotypes [22] and *Populus grandidentata* [6] no significant growth responses were observed. The volume index, which is a useful indicator of stem biomass [30], was enhanced by FACE treatment by 79%, 77% and 54% for *P. nigra*, *P. x euramericana* and *P. alba* respectively, mainly caused by an increase in diameter. Norby et al. [26] reviewed tree responses of above-ground woody dry mass and reported a mean relative increase of 73% under elevated CO₂.

The genotypes used in this study differ in physiology and morphology at the leaf, tree and canopy levels. We observed significant genotypic effects both on main growth parameters and on the display of syllepsis (table IV). Height growth of *P. alba* continued until the end of October as emphasized by the delayed bud set, whereas *P. x euramericana* stopped growth in September. Anyway it is well known that bud set is not only determined by genotype but also depends very much on photoperiod and mean temperature [29]. For this reason the high temperatures registered in October could have influenced the bud set in the first year.
Another relevant difference among the three genotypes is the number of sylleptic branches produced on the main stem. This is important because the significant differences in stem volume (table IV) are just related to the different tree architecture of the various genotypes, together with differences in total leaf area and consequently photosynthetic production. *P. nigra* for example is characterised by a fast and numerous production of sylleptic branches whereas the syllepsis phenomenon is much weaker in *P. x eurameriana*. In particular, the inherent syllepsis phenomenon of *P. nigra* could influence the responses to CO₂ enrichment. Plants with an indeterminate growth habit like poplars show higher growth enhancements under elevated CO₂, presumably because of differences in sink strength [28] and acclimation would be less likely to occur [2, 21]. The results of the present study on three different *Populus* genotypes are in agreement with earlier data of Dickson et al. [10] who

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**Table III.** ANOVA results for the effects of CO₂ treatment, genotype and their interaction on stem diameter, stem volume index and number of sylleptic branches of three *Populus* genotypes. *F*: *F* value; *p*: probab. level.

<table>
<thead>
<tr>
<th>Time</th>
<th>Source of variation</th>
<th><em>F</em></th>
<th><em>p</em></th>
<th>Genotype × plot (treat)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stem diameter</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Aug.</td>
<td>CO₂ treatment</td>
<td>5.26</td>
<td>0.0833</td>
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<tr>
<td></td>
<td>Genotype</td>
<td>81.62</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Treatment × genotype</td>
<td>3.49</td>
<td>0.0324</td>
<td></td>
</tr>
<tr>
<td>Sept. I</td>
<td>CO₂ treatment</td>
<td>11.44</td>
<td>0.0277</td>
<td></td>
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<tr>
<td></td>
<td>Genotype</td>
<td>128.51</td>
<td>0.0001</td>
<td></td>
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<tr>
<td></td>
<td>Treatment × genotype</td>
<td>6.19</td>
<td>0.0024</td>
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<tr>
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<td>CO₂ treatment</td>
<td>10.18</td>
<td>0.0332</td>
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<tr>
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<td></td>
<td>Treatment × genotype</td>
<td>2.77</td>
<td>0.1213</td>
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<tr>
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<td>CO₂ treatment</td>
<td>15.82</td>
<td>0.0167</td>
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<td></td>
<td>Treatment × genotype</td>
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<td>0.0654</td>
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<td>17.21</td>
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<td>Genotype</td>
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</tr>
<tr>
<td></td>
<td>Treatment × genotype</td>
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<tr>
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<td>Genotype</td>
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<tr>
<td></td>
<td>Treatment × genotype</td>
<td>3.02</td>
<td>0.105</td>
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<tr>
<td>Nov.</td>
<td>CO₂ treatment</td>
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<td>Treatment × genotype</td>
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<tr>
<td><strong>Stem volume index</strong></td>
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<tr>
<td>End of season</td>
<td>CO₂ treatment</td>
<td>33.8</td>
<td>0.0044</td>
<td>X</td>
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<tr>
<td></td>
<td>Genotype</td>
<td>51.62</td>
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<tr>
<td></td>
<td>Treatment × genotype</td>
<td>5.35</td>
<td>0.0335</td>
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<tr>
<td><strong>Sylleptic branches</strong></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>End of season</td>
<td>CO₂ treatment</td>
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<td>X</td>
</tr>
<tr>
<td></td>
<td>Genotype</td>
<td>195.52</td>
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</tr>
<tr>
<td></td>
<td>Treatment × genotype</td>
<td>4.69</td>
<td>0.0451</td>
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</table>
observed the greatest response at elevated CO₂ was shown by the fastest growing or most productive genotypes. Moreover, since the POPFACE plantation is situated in a Mediterranean climate with an ample supply of water and nutrients (Van Dam, personal communication), we can assume that there were no environmental growth constraints.

This might be also confirmed by the larger production of sylleptic branches in the FACE treatment for the different genotypes. The relative enhancement of the syllepsis phenomenon was most prominent for *P. x euramericana* (even if not significant) because this genotype is characterized by an inherently low production of sylleptic branches. Information about the response of the production of branches to elevated CO₂ is rather scarce. A stimulation of branch production under elevated CO₂ was observed for different *Populus* genotypes [5, 40] and for sour orange trees [17]. This is an important aspect not only for architecture but also because Scarascia-Mugnozza et al. [35] found in four genotypes of poplars that sylleptic branches had a high translocation efficiency and contributed a lot to the growth of the tree exporting carbon mainly to the lower stem and the roots. Nevertheless competition within and between genotypes might increase in a CO₂ enriched atmosphere and this would become even more pronounced in a dense poplar plantation.

The differences among genotypes and between CO₂ treatments observed at the end of the establishment year are very relevant because they will determine further growth during the next years. Especially in the present high density ecosystem study, it will be interesting to investigate how long the growth enhancement in the enriched CO₂ atmosphere will be sustained since competition might play an important role in the following years.

Differences among the poplar genotypes are also of major interest for SRIC and our results can provide relevant information about clonal performance under SRIC in general and future carbon enrichment in particular. The *P. x euramericana* genotype I-214, that is the most frequently used genotype in poplar plantations in Italy...
and widely used in many regions of the world, showed optimum rooting and good growth. The *P. alba* genotype 2AS11 confirmed known problems of rooting for this species [38] and showed a smaller production of biomass in spite of delayed bud set; *P. nigra* genotype Jean Pourtet performed best during the first growing season, considering optimum rooting and high growth during the entire growing season which lasted until mid-October. Moreover in terms of biomass production this genotype seemed to profit more than the others from the CO₂ enrichment considering also its large production of sylleptic branches. This aspect could increase the interest in this genotype especially for SRIC, where a large biomass production in very short rotations (3–10 years) is the ultimate goal. Also this *P. nigra* genotype could be very interesting in function of its large carbon sequestration capacity that might be indispensable for limiting increase of atmospheric CO₂ concentration.

5. CONCLUSIONS

In conclusion, the growth of three poplar genotypes was significantly enhanced under CO₂ enrichment in POPFACE, indirectly showing the validity of the FACE facility to study CO₂ effects on agro-forestry ecosystems. Additionally expected differences among genotypes were observed within separate treatments. This first-year response will undoubtedly influence future growth and assessing long-term responses of this man-made ecosystem will be crucial in understanding the behaviour, productivity and carbon sequestration capacity of this type of plantations.

Acknowledgements: This research is funded by the EC Fourth Framework Programme, Environment and Climate RTD Programme, research contract ENV4-CT97-0657 within the Terrestrial Ecosystems Research Initiative (TERI). The POPFACE is also a core project within the GCTE (Global Change & Terrestrial Ecosys tems) Elevated CO₂ Consortium of the IGBP (International Geosphere Biosphere Programme). The authors wish to acknowledge Dr T. Crowe (University of Southampton) for his recommendations concerning the statistical analysis and Arnaud Carrara for the translation into French. This research activity was also possible thanks to the assistance of Tullio Oro, Pierpaolo Pinacoli and Matilde Tamantini. The authors are in particular grateful to Giandomenico Cortignani, Ivan Janssens and Martin Lukac for their help during the field campaigns and to S. Van Dongen for practical advice about SAS. B. Gielen is a Research Assistant of the Fund for Scientific Research-Flanders, Belgium (F.W.O.-Vlaanderen).

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