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Productivity and compensatory responses of yellow-poplar trees in elevated CO_2

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INCREASED forest growth in response to globally rising CO_2 concentrations could provide an additional sink for the excess carbon added to the atmosphere from fossil fuels[1,2]. The response of trees to increased CO_2, however, can be expected to be modified by the interactions of other environmental resources and stresses, higher-order ecological interactions and internal feedbacks inherent in the growth of large, perennial organisms[3,4]. To test whether short-term stimulation of tree growth by elevated CO_2 can be sustained without inputs from other environmental resources, we grew yellow-poplar (*Liriodendron tulipifera* L.) saplings for most of three growing seasons with continuous exposure to ambient or elevated concentrations of atmospheric CO_2. Despite a sustained increase in leaf-level photosynthesis and lower rates of foliar respiration in CO_2-enriched trees, whole-plant carbon storage did not increase. The absence of a significant growth response is explained by changes in carbon allocation patterns, specifically a relative decrease in leaf production and an increase in fine root production. Although these compensatory responses reduced the potential increase in carbon storage in increased CO_2 concentrations, they also favour the efficient use of resources over the longer term.

Yellow-poplar trees were grown in ambient or elevated CO_2 concentrations in open-top chambers[5]. Open-top chambers allowed the experimental plants, which before outplanting had been grown from seed under the experimental CO_2 concentrations, to be exposed in the field under ambient light, temperature, precipitation and soil conditions. The CO_2 concentration in the six chambers was maintained day and night during the growing seasons at ambient (354.5 μmol mol^{-1}), ambient + 150 (502.9 μmol mol^{-1}) or ambient + 300 (655.6 μmol mol^{-1}). No fertilizer or supplemental water was provided during the course of the experiment. Five yellow-poplar saplings were harvested from each chamber after 28 months (2.7 growing season).

TABLE 1 Characteristics of yellow-poplar leaves in 1991

CO_2 enrichment (μmol mol^{-1})	Specific leaf area (cm^2 g^{-1})	Nitrogen (g m^{-2})	Chlorophyll (mg m^{-2})	Photo-synthesis (μmol m^{-2} s^{-1})	Respiration (μmol m^{-2} s^{-1})
+0	151 ± 6	1.52 ± 0.09	488 ± 54	7.4 ± 0.6	3.0 ± 0.2
+150	136 ± 5	1.30 ± 0.13	401 ± 82	10.8 ± 0.9	2.3 ± 0.2
+300	132 ± 5	1.18 ± 0.05	387 ± 32	12.3 ± 0.8	2.2 ± 0.1
P*	0.004	0.058	0.20	0.001	0.001

All data are means ±s.e. of five plants in each of two replicate chambers. Specific leaf area was determined at final harvest from total leaf area and total leaf mass. Nitrogen concentration was measured by near-infrared reflectance spectroscopy of oven-dried and ground leaves from leaf position 3–5 collected on 2 July. Chlorophyll concentrations were measured on 25 July in ethanol extracts of five 6-mm-diameter disks cut from one leaf per tree. Photosynthesis was measured with a closed gas-exchange system (LiCor 6200) on the fourth leaf from an upper branch apex. Measurements were made at midday under full sun on 1 July. Respiration was measured with the gas exchange system before sunrise on 5 July.

* Probability of a significant effect of CO_2 concentration, using sampling error in the F-test.

The accumulation of above-ground biomass was similar in all treatments throughout the course of the experiment, and although stem mass was usually lowest in ambient CO_2, there were no differences in stem mass that were statistically significant (Fig. 1*a*). Leaf area tended to decline with increasing CO_2 concentration in 1990 and 1991, and combining the stem growth and leaf area data provided a better (less variable, more robust) indicator of the response of above-ground productivity to CO_2 enrichment (Fig. 1*b*). Growth efficiency, the annual production of stem mass per unit leaf area, is akin to the term net assimilation rate used with herbaceous plants and is a good indicator of general tree vigour[6]. Growth efficiency in 1990 was 41% greater

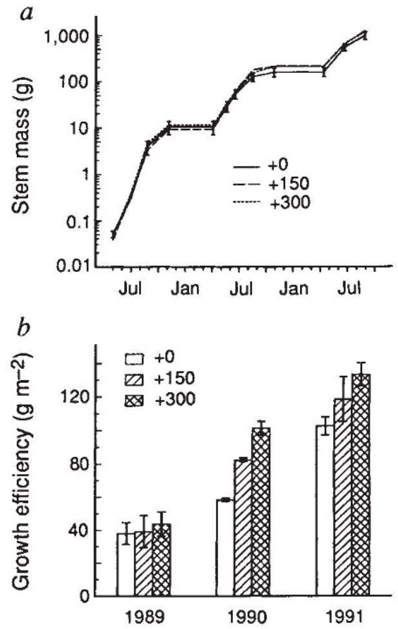

FIG. 1 Stem mass and growth efficiency of yellow-poplar saplings between May 1989 and August 1991 in ambient (+0), ambient +150, and ambient +300 μmol CO_2 mol^{-1}. All data are the means ±s.e. of five trees per chamber in two replicate chambers. *a*, Stem dry mass was estimated from periodic measurements of bole diameter (D) 10 cm from the ground and total height (H) of the bole, using a log–log regression between stem mass and D^2H. *b*, Growth efficiency was calculated as annual stem mass increment divided by leaf area at the end of the year. The effect of CO_2 on growth efficiency was significant at $P = 0.041$ in 1990, and $P = 0.002$ in 1991.

TABLE 2 Fine root mass and CO_2 efflux from the ground within open-top chambers

CO_2 enrichment (μmol mol^{-1})	Root mass density (g m^{-2}) Live	Dead	CO_2 efflux (μmol m^{-2} s^{-1})
+0	85.0 ± 22.3	51.6 ± 15.5	6.60 ± 0.53
+150	157.4 ± 31.3	61.3 ± 11.0	8.21 ± 0.72
+300	186.2 ± 53.6	51.0 ± 10.2	8.03 ± 0.55
P*	0.032	NS	0.150

Fine roots (<7 mm diameter) were quantified in five cores (10 cm diameter × 15 cm deep) per chamber collected 4 days after tree boles were removed. Data are the means ±s.e. of two replicate chambers. CO_2 efflux from 560 cm^2 of ground surface was measured on 11 August 1991 with a modified LiCor 6200 gas exchange system (P. J. Hanson, personal communication). Data are the means ±s.e. of three to four measurements per chamber.

* Probability of a significant effect of CO_2 concentration, using sampling error in the *F*-test. NS, not significant ($P > 0.20$).

in +150 and 74% greater in +300 relative to +0 chambers. From April to August 1991, growth efficiency was enhanced by 16% in +150 and 33% in +300, consistent with the expected response of plants to CO_2 enrichment[3,7].

Increased growth efficiency of yellow-poplar trees in CO_2-enriched atmospheres can be attributed to the sustained increase in photosynthesis we have observed in these trees. Light-saturated photosynthesis of upper canopy leaves on 1 July 1991 was 46% higher in +150 and 67% higher in +300 compared with that of leaves in +0 (Table 1); these values are representative of the response of photosynthesis throughout the experiment. The relative responses of photosynthesis to CO_2 enrichment were similar in older and shaded leaves from different parts of the canopy, and there was no effect of CO_2 on canopy longevity (bud break or autumn senescence). Stimulation of photosynthesis was sustained even though nitrogen concentration and chlorophyll concentration in leaves decreased with increasing CO_2 (Table 1). Coupling the increased photosynthesis with lower rates of foliar respiration (Table 1) implies a substantial increase in carbon uptake in elevated CO_2 concentrations[5].

The juxtaposition of increased carbon uptake and increased growth efficiency with no significant effect on stem mass is only partly explained by reduced leaf area (10% lower in +300); other changes in the patterns of carbon allocation to biomass and carbon losses from the plant are implied. When the trees were harvested in August 1991, however, we found no significant effects of CO_2 on the mass of the bole, primary or secondary branches, nor on the proportionate distribution of stem mass between the lower, middle and upper parts of the trees (Fig. 2). There were no indications that canopy structure of these yellow-poplar saplings was altered: tree height, diameter, the number and length of primary branches, and the ratio of branch mass to mass of the bole were similar in all treatments. The tap root was the only harvested component of the trees that significantly increased in mass in response to CO_2 enrichment, increasing 12% and 37% in +150 and +300 relative to +0 ($P = 0.072$). But there was no effect of CO_2 on total root mass or root-to-shoot ratio.

Leaf area ratio (leaf area divided by whole-plant mass) declined significantly and linearly with increasing CO_2. Leaf area ratio was 12% lower in +150 and 21% lower in +300 compared with +0. Leaf area ratio represents the balance between the assimilation capacity (leaf area) and respiratory demand (plant mass); relative growth rate will tend to decline as leaf area ratio declines unless there is a compensating increase in leaf efficiency (for example, photosynthetic stimulation). The maintenance or enhancement of growth in high CO_2 without a concomitant increase in leaf area represents a mechanism for increasing whole-plant water-use efficiency[4], a response that could improve environmental fitness over the long term.

The indeterminate nature of leaf production in yellow-poplar provides the opportunity for continuous adjustments in carbon allocation patterns to optimize the use of limiting environmental resources. In these trees, as in many forest trees, nitrogen was a limiting resource, and the concentrations of nitrogen and chlorophyll in leaves declined with CO_2 enrichment (Table 1). A common response to nitrogen limitations is a shift in allocation from leaf production to root production[6]. The mass of live fine roots (<7 mm diameter) increased significantly with CO_2 enrichment (Table 2). Yellow-poplar fine roots turn over rapidly, accounting for a significant loss of fixed carbon from the system[8]. CO_2 efflux from the soil (including lateral roots) in the chambers was indeed higher in elevated CO_2 (Table 2). Hence, the compensatory response in carbon allocation between leaf and fine root production, which may be associated with an enhancement in resource utilization, may effect short-term reductions in carbon storage by the system.

The results of this experiment, the longest so far in which any forest tree species has been exposed to elevated CO_2, show that the short-term responses of yellow-poplar seedlings to increased CO_2 (ref. 4) can be sustained over several growing seasons under field conditions: photosynthesis and growth efficiency remained significantly higher in CO_2-enriched saplings during the third year of enrichment. Nevertheless, there was no significant enhancement of tree dry mass (carbon storage) in this system. The leaf-level gas-exchange responses, and the more integrative response of growth efficiency, did not effect an increase in whole-plant carbon storage because of the changes in carbon allocation patterns between above-ground (leaf production) and below-ground (fine-root production) processes. This shift in allocation represents a trade-off between potential carbon acquisition versus water and nutrient acquisition, as well as a shift from carbon storage in perennial tissue versus production of the more ephemeral fine roots.

These results contrast with the more spectacular response of irrigated and fertilized sour orange trees (*Citrus aurantium*) to

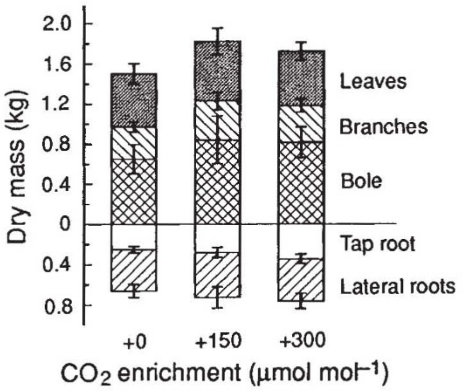

FIG. 2 Mass of components of yellow-poplar saplings when harvested in August 1991. Data are the means ±s.e. of five plants in each of two replicate chambers per CO_2 concentration. The only component for which there was a statistically significant effect of CO_2 was tap root ($P = 0.07$). Harvesting involved separating the stems and associated leaves into the bole, primary and secondary branches . Branches arising from the lowest 1 m of the trunk were cut off and processed first, followed by branches from the second metre of trunk, and then the topmost length of bole and its branches. The remaining bole was then cut off at the ground and separated into two 1-m sections. Leaves and stems were oven-dried (70 °C) and weighed. The tap-root system was excavated by digging a cylinder around the stump of ~25 cm in diameter, then severing all lateral roots to a depth of 25 to 30 cm. The tap root was then pried out of the ground with little breakage. The tap root and all broken roots in the cylinder of soil were washed free of adhering soil. The diameter of each lateral root was measured at the point where it left the excavated cylinder. Eight lateral root systems, ranging in initial diameter from 4 to 26 mm, were excavated, washed and oven-dried to establish a regression between dry mass and diameter, from which the mass of lateral roots of each tree was calculated.

elevated CO_2, from which conclusions about the response of the global forest have been drawn[9]. Such extrapolations from a single species growing under conditions uncharacteristic of a forest are neither justified nor particularly relevant to global carbon cycling. Our yellow-poplar responses provide evidence that the dramatic increases in tree growth reported for sour orange trees will not occur in all systems, but it should not be concluded from this that forests cannot provide a larger sink for increasing concentrations of atmospheric CO_2. Increased growth efficiency in elevated CO_2 implies that the trees may be better able to withstand environmental stresses because less leaf area is required to sustain the same growth rate. The compensatory responses in leaf and fine root production should also favour efficient use of resources over the long term. The potential for a forest ecosystem to provide a sink for atmospheric carbon may depend more on reactions to environmental stresses and resource availability than on the direct responses of growth rate to CO_2 concentration. Recent simulations with a forest stand succession model show that when the indirect effects of elevated CO_2 on carbon, nitrogen, and water dynamics are considered, considerable potential exists for increasing carbon storage in forest ecosystems (W. M. Post, personal communication). These results with yellow-poplar trees, then, emphasize the importance of resource interactions and feedbacks in the analysis of forest responses to rising CO_2 concentrations. □

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Earliest known simian primate found in Algeria

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THE record of early fossil Simiiformes (Anthropoidea[1]) from the Late Eocene and Early Oligocene of Africa and the Arabian Peninsula has increased dramatically in recent years[2–6]. We report here the discovery of a new, diminutive and much older (Early or Middle Eocene) simian from an Algerian locality, Glib Zegdou. This species is smaller than any other living or fossil African simiiform. Derived similarities shared with *Aegyptopithecus* suggest that the new genus is more closely related to propliopithecines than to oligopithecines, implying that these two subfamilies differentiated during the Early Eocene. The new discovery confirms predictions about the great antiquity of Simiiformes[7–9] and emphasizes a long and endemic African history for higher primates.

Isolated mammalian teeth were recovered from the upper fossiliferous level of the Glib Zegdou section, which had previously yielded charophytes[10]. The Glib Formation is situated in the northern part of the Hammada du Dra, Algerian Sahara. The mammals include hyracoids, rodents, primates and other new taxa, probably condylarthrans. Five primate teeth have been recovered, of which two well preserved molars and one premolar represent the new simian, described below. The two others are less well preserved and represent a second, slightly larger and related species.

For the few mammals from other Glib Zegdou loci and from the nearby correlative Gour Lazib, a Middle Eocene age has been proposed[11,12]. Early and Middle Eocene mammals are poorly known in Africa, however. Charophytes (algal cysts) provisionally remain a better basis for a continental biostratigraphy. They have permitted estimation of an Early Eocene age for Glib Zegdou[10]. Work in progress (M. Feist and F. Mebrouk, personal communication) confirms a late Early Eocene age (46–50 Myr), which we favour here, but more evidence is still needed to exclude definitely a Middle Eocene (40–46 Myr) age.

Algeripithecus minutus gen. et sp. nov.

Holotype. Left upper molar M^2, GZC 1 (Oran University collection; Fig. 1*a*).

Referred material. Right lower molar M_3 (GZC 2; Fig. 1*b*) and right lower premolar P_3 (GZC 3).

Horizon and locality. A 50-cm sandstone bed at the top of the lower third of the Glib Formation at Glib Zegdou, Algeria.

Diagnosis. Small size (M^2: length, 1.66 mm; width, 2.63 mm. M_3: length, 2.08 mm; width, 1.37 mm). M^2 transversely elongated, bearing a large cuspidate hypocone, a lingual cingulum and an incipient pericone. Labial slope of paracone and metacone, and lingual slope of protocone and hypocone all very low (lower than in any known adapiform or omomyiform). M_3 broad, moderately high-crowned and bunodont. Trigonid open anteriorly, with a thin ventro-lingually oriented paracristid, and a shorter and much thicker premetacristid. Protoconid and metaconid close and connected by a high protocristid. M_3 buccal cingulid continuous from the hypoconulid to the anterior rim.

Although this material is fragmentary, its remarkable characteristics lend it far-reaching significance. Foremost is the very small size of the teeth, which are smaller than those of *Catopithecus* and *Proteopithecus*, recently described from the Fayum of Egypt[5], and slightly smaller than those of *Qatrania wingi* and *Biretia piveteaui*, the smallest previously known African simians[4,13,14]. We suggest a broad body weight estimate of 150 to 300 g, based on tooth size–body size regressions for generalized living primates[15] (mean weight from M_3 is 246 g, and mean from M^2 is 285 g). *Algeripithecus* hence was in the size range of New World callitrichids and small prosimians.

Among fossil Euprimates, species of similar size are known

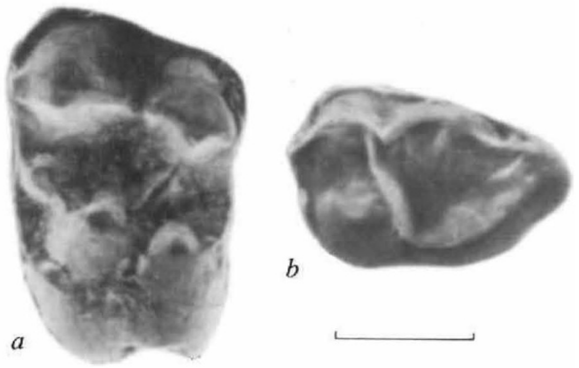

FIG. 1 Scanning electron micrographs of the two molars of *Algeripithecus minutus* gen. et sp. nov. from Glib Zegdou, in occlusal views. *a*, The type-specimen, left M^2 GZC 1; *b*, the right lower M_3 GZC 2; scale bar, 1 mm. (Micrographs by A. Rossi).