and sequenced in four laboratories; the nucleotide sequence reported by Lochrie *et al.* (*24*) differs in many respects from the sequence reported by Tanabe *et al.* (*25*), Medynski *et al.* (*26*) or Yatsunami and Khorana (*27*). The differences in nucleotide sequences of α-transducin cDNA's may be due to differences between bovine strains (*24*). Alternatively, the species of α-transducin cDNA described by Lochrie *et al.* may be expressed in cones, whereas the species cloned by the other groups may be expressed in rods (*28*). Further work is needed to determine whether different genes for α-transducin are expressed in rods and cones.

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Technical Comments

Carbon Dioxide Enhancement of Tree Growth at High Elevations

The apparent acceleration of tree growth by increased atmospheric carbon dioxide shown by LaMarche *et al.* (*1*) must be put in perspective lest it be argued that stimulation of growth of natural vegetation by an increase in CO_2 has been confirmed and that future research need only determine how best to take advantage of that fact.

Widths of annual rings of bristlecone and limber pine trees near timberline in central Nevada were 106 percent greater in the decade ending in 1983 than in the years 1850 to 1859 at one site and 73 percent greater at another (*1*). The estimated increase in atmospheric CO_2 concentration during the same period was 26 percent. Plant physiologists agree that even under favorable laboratory conditions the growth response of plants exposed to elevated CO_2 is no more than about half the corresponding increase in CO_2, whereas the increase in ring width is three to four times the CO_2 increment.

Tree condition may explain the discrepancy. The small annual rings—0.5 mm per year compared with the 4 to 8 mm per year typical of vigorous young forests—suggest that the sampled trees were fully mature, even senescent. Old trees have a high ratio of cambial and root respiration to photosynthesis, so that most photosynthate is used for maintenance. Even a slight increase in photosynthesis, whether from CO_2 increase or from another cause, could add disproportionately to the small surplus of photosynthate available to form new wood.

LaMarche *et al.* argue that effects of CO_2 increase on plant growth are greater at high elevation than near sea level. The partial pressure of CO_2 within photosynthesizing leaves is nearly independent of elevation. The partial pressure of atmospheric CO_2 is, however, appreciably lower at high altitudes, so the atmosphere-to-leaf gradient is smaller at high elevations than at low ones. A given percentage increase in CO_2 would therefore enhance this gradient more at high elevations. Several factors seemingly reduce the significance of this effect.

The diffusion coefficient of CO_2 is known experimentally to be inversely proportional to pressure. Gale (*2*), in a study cited by LaMarche *et al.*, showed that faster diffusion of CO_2 at high elevation partially compensates for the smaller atmosphere-to-leaf gradient. The degree of compensation depends on the ratio of boundary plus stomatal resistances, which are pressure (diffusion coefficient) dependent, to mesophyll (or carboxylation) resistance, which is not. The higher the ratio, the smaller the elevation effect (*2*). Increased mole fraction of CO_2 increases the ratio, since stomatal opening, and hence leaf conductance, is inversely correlated with atmospheric CO_2 concentration. This further diminishes the effect of elevation on sensitivity to CO_2 increase.

Reduction of photorespiration, one of the principal mechanisms by which increased atmospheric CO_2 enhances net photosynthesis (*3*), is unaffected by elevation. The bifunctional enzyme ribulosebisphosphate carboxylase catalyzes oxidation of newly formed carboxylate before it can enter subsequent steps of the photosynthetic cycle. The balance between carboxylation and oxygenation depends on the proportions of CO_2 and O_2 in the atmosphere (*4*), which at any given time are constant at all elevations of biological interest.

Quantitative assessment of the ecological and economic importance of a CO_2 effect on natural vegetation awaits analysis of growth response in representative forest stands in diverse climatic and soil conditions.

CHARLES F. COOPER
Department of Biology,
San Diego State University,
San Diego, CA 92182

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LaMarche *et al.* (*1*) present tree ring data for trees growing at high altitude and suggest that apparent increases in growth from about 1850 to the present can be correlated with increasing concentrations of CO_2 in the atmosphere. They further argue that, at high altitudes, as a result of the lowered partial pressure of the atmosphere, CO_2 is less available; consequently any increase of the partial pressure of CO_2 would have a particularly large effect on photosynthesis. They correctly quote me as showing, in a theoretical paper (*2*), that the effect on photosynthesis of a reduction in partial pressure of CO_2 at high altitude is almost completely compensated for by an increase of the diffusion coefficient of the CO_2 gas at the lower absolute air pressure. They then go on to say that "his own [Gale's] research did not demonstrate a major counteracting effect." This is not so. On the contrary, I demonstrated (*3*) that, when stomatal closure as a result of dehydration was prevented, a reduction of the air pressure from 693 to 330 mmHg (equivalent to the atmospheric pressure at an altitude of 8000 m) resulted in only an 8 percent reduction in the photosynthesis of *Zea mays* and a 34 percent reduction in that of *Phaseolus vulgaris*. The latter effect was due to greater stomatal diffusion resistance. Both results were in close agreement with predictions from theory. At a simulated altitude of 3500 m, the altitude at which LaMarche *et al.* worked, the same experiments showed a reduction of photosynthesis of only 2 percent for the C_4 corn and 6 percent for the C_3 bean.

There may be a causative relationship between increasing world CO_2 levels and tree ring growth. However, if there is a larger effect at higher altitudes, it is probably related to higher levels of radiation (increasing the response to CO_2) and not to the lower availability of CO_2 for photosynthesis.

JOSEPH GALE
Blaustein Institute for Desert Research,
Ben Gurion University of the Negev,
Sede Boqer Campus, 84 990 Israel

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Cooper offers a useful hypothesis that tree age and phenology may help explain the disparity in the ring width increases that we observed relative to increased CO_2. It may also signal the value of the environmentally stressed sites and trees on which we focused and partially explain why a CO_2 effect may not have been as discernible in ring widths of vigorous young trees growing in unstressed sites. Cooper's discussion of the reduction of photorespiration is pertinent and broadly supportive of our work, as the process is unaffected by elevation. We agree that the proportions of CO_2 and O_2 at any given time remain constant. Nonetheless, an increase in CO_2 over time will change these proportions at all altitudes and should promote a net increase in carboxylation over oxygenation. Despite the absence of an elevational effect on the photorespiration process, there remains an important elevational trend in other aspects of the net photosynthetic response to CO_2. Thus, we should still expect to find differences in those responses at different elevations over time with increased global CO_2.

Before quantitative assessment of the ecological and economic importance of a CO_2 effect on natural vegetation can be made, it is necessary that our hypothesis continue to be tested in terms of broader geographic and elevational detection of a CO_2 effect and separation of this effect from other climatic and ecological signals (*1*).

We appreciate Gale's concluding statement that the increased radiation levels at high altitudes may represent another factor that could enhance high-altitude tree growth in response to increasing global CO_2 concentrations. However, we (*2*) have not misinterpreted his published work, either theoretical or experimental, on the effects of the altitudinal decrease of air pressure on photosynthetic efficiency of C_3 plants.

Gale states that his experiments demonstrate that beans showed only a 6 percent reduction of photosynthesis in an atmospheric pressure equivalent to that at an altitude of 3500 m, compared with an atmospheric pressure equivalent to that at an altitude closer to sea level (800 m). This percentage is apparently based on the results shown in his figure 5 (*3*), which were obtained with warm, moist air (25°C and 80 percent relative humidity). From the same graph, we estimate the reduction to be 16 percent. The results shown in his figure 3, with dryer air, gave a 22 percent reduction. The latter percentage is most relevant to this discussion.

In support of our argument, we cited the experimental work of Mooney *et al.* (*4*), which was based on studies of high-altitude shrubs, woody perennials, and herbs. They had concluded that the photosynthetic rates of plants growing at an altitude of 3900 m in our field area in the White Mountains, California, were 30 percent lower than the sea level value as a result of the altitude effect. Interpolating to our tree ring sample altitude of 3500 m, we estimate a 27 percent reduction in net photosynthesis in *Pinus longaeva*. Gale's dry-air experiments indicating a 22 percent reduction are relevant because our field area is cool and dry in summer, when the pines are actively photosynthesizing. Average precipitation in June is only 9 mm, and we estimate the relative humidity to be about 15 percent at 14°C in mid-afternoon from nearby meterological data (*5*). Thus, Gale's experimental results with dry air—a reduction of 22 percent in photosynthesis over an altitude range of 2700 m—compare closely with our estimate of 27 percent over a range of 3500 m. In short, the rate of change of photosynthetic efficiency is about the same in both cases.

Furthermore, our figures also agree well with those predicted from Gale's theoretical calculations (*6*). In his table 1, values are given for the predicted effect of altitude on photosynthesis. For the case of a dry adiabatic lapse rate, extrapolation from the table yields a 23 percent reduction of photosynthesis at an altitude of 3500 m for plants of low photosynthetic efficiency (such as C_3 beans and pines). Gale (*6*, p. 496) states that "the dry adiabatic lapse rate is an extreme case" and that "temperatures do not fall this rapidly with increasing height." He therefore concludes that "*except* under conditions of rapid drop in air temperature with increasing height, the availability of carbon dioxide for photosynthesis falls with increasing elevation at a much lower rate than would be expected . . ." (italics ours). The dry adiabatic lapse rate *does* apply in our case. It is well established (*7*) that the gradient of surface air temperature in the White Mountains in summer is 9.1°C per 1000 m, very close to the dry adiabatic rate of 9.6°C per 1000 m.

In summary, we find no substantial disagreement between Gale's work, Cooper's comments, and our interpretation of the cause of increased growth rates in high-altitude arid-site conifers and the relation of those increased growth rates to increasing global atmospheric CO_2.

VALMORE C. LAMARCHE, JR
DONALD A. GRAYBILL
HAROLD C. FRITTS
MARTIN R. ROSE
Laboratory of Tree-Ring Research,
University of Arizona, Tucson 85721

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