Food for Thought: Lower-Than-Expected Crop Yield Stimulation with Rising CO_2 Concentrations

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Model projections suggest that although increased temperature and decreased soil moisture will act to reduce global crop yields by 2050, the direct fertilization effect of rising carbon dioxide concentration ([CO_2]) will offset these losses. The CO_2 fertilization factors used in models to project future yields were derived from enclosure studies conducted approximately 20 years ago. Free-air concentration enrichment (FACE) technology has now facilitated large-scale trials of the major grain crops at elevated [CO_2] under fully open-air field conditions. In those trials, elevated [CO_2] enhanced yield by ∼50% less than in enclosure studies. This casts serious doubt on projections that rising [CO_2] will fully offset losses due to climate change.

Much effort has been put into linking models of climate and crop growth to project future changes in crop yields and food supply across the globe (1–4). Projections reviewed by the Intergovernmental Panel on Climate Change (IPCC) suggest that increased temperature and decreased soil moisture, which would otherwise reduce crop yields, will be offset by the direct fertilization effect of rising carbon dioxide concentration ([CO_2]) (5–7). The IPCC projections suggest that total crop yield may rise when averaged across the globe, but this net gain will result from generally lower yields in the tropics and increased yields in temperate zones. The accuracy of these projections and thus future food security depend critically on the magnitude of the CO_2 fertilization effect under actual growing conditions.

Atmospheric [CO_2] has risen from ∼260 parts per million (ppm) approximately 150 years ago to 380 ppm today (8). Yet [CO_2] is markedly uniform across the globe; so, in contrast to temperature and soil moisture, there is no consistent spatial variation on which to estimate yield responses to increasing [CO_2]. Similarly, it is not easy to alter [CO_2] experimentally around a crop in the field. As a result, most information about crop responses to elevated [CO_2] is obtained from studies in greenhouses, laboratory controlled-environment chambers, and transparent field chambers, where released CO_2 may be retained and easily controlled. These settings have provided the basis for projecting CO_2 fer-

tilization effects on the major food crops: maize, rice, sorghum, soybeans, and wheat.

Crops sense and respond directly to rising [CO_2] through photosynthesis and stomatal conductance, and this is the basis for the fertilization effect on yield (9). In C_3 plants, mesophyll cells containing ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) are in direct contact with the intercellular air space that is connected to the atmosphere via stomatal pores in the epidermis. Hence, in C_3 crops, rising CO_2 increases net photosynthetic CO_2 uptake because RuBisCO is not CO_2-saturated in today's atmosphere and because CO_2 inhibits the competing oxygenation reaction leading to photorespiration. RuBisCO is highly conserved across terrestrial plants, so instantaneous re-

sponses to increased [CO_2] may be generalized across C_3 plants, including rice, soybeans, and wheat. In theory, at 25°C, an increase in [CO_2] from the present-day value of 380 ppm to that of 550 ppm, projected for the year 2050, would increase C_3 photosynthesis by 38% (9). In contrast, in C_4 crops such as maize and sorghum, RuBisCO is localized to bundle sheath cells in which CO_2 is concentrated to three to six times atmospheric [CO_2] (10). This concentration is sufficient to saturate RuBisCO and in theory would prevent any increase in CO_2 uptake with rising [CO_2]. Although C_4 crops may not show a direct response in photosynthetic activity, an indirect increase in the efficiency of water use via reduction in stomatal conductance may still increase yield (9).

How have CO_2 fertilization factors been derived? Most models used to predict future crop yields, including those within the IPCC (5), are from two families: the Decision Support System for Agrotechnology Transfer (DSSAT) (6, 11, 12) and the Erosion Productivity Impact Calculator (EPIC) (13–15). Studies using DSSAT assume CO_2 fertilization factors based on the method of Peart et al. (3), which used summaries for soybeans (16), maize (17), wheat (18), and rice (18). Studies using EPIC (13–15) assume CO_2 fertilization factors based on the method of Stockle et al. (4), which parameterized a CO_2 response function to reproduce the mean yield stimulations reported for elevated [CO_2] by Kimball (18). Tracing DSSAT and EPIC methods back reveals that the magnitude of the CO_2 fertilization effects in these models is primarily based on data from three literature reviews from the 1980s (16–18). The CO_2 fertilization effects reported in these reviews for the major crops are given in Table 1

Table 1. Percentage increases in yield, biomass, and photosynthesis of crops grown at elevated [CO_2] (550 μmol mol^{-1}) relative to ambient [CO_2] in enclosure studies versus FACE experiments. Data for enclosure studies were summarized by Kimball (18), Cure and Acock (17), and Allen et al. (16) and in Fig. 2. Mean response ratios from these reviews were adjusted to an elevated [CO_2] of 550 μmol mol^{-1} by means of the nonrectangular hyperbolic functions for C_3 and C_4 species from Fig. 2. The values that summarize all chamber studies shown in Fig. 2 are given in the row entitled "enclosure studies." Percentage increases for FACE studies were generated by meta-analysis [see supporting online material (SOM) and table S2] (37).

Source	Rice	Wheat	Soybeans	C_4 crops
Yield				
Kimball (1983)	19	28	21	–
Cure and Acock (1986)	11	19	22	27
Allen et al. (1987)	–	–	26	–
Enclosure studies	–	31	32	18
FACE studies	12	13	14	0*
Biomass				
Cure and Acock (1986)	21	24	30	8
Allen et al. (1987)	–	–	35	–
FACE studies	13	10	25	0*
Photosynthesis				
Cure and Acock (1986)	35	21	32	4
FACE studies	9	13	19	6

*Data from only 1 year in Leakey et al. (30).

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after adjustment to estimate crop performance at a common [CO_2] of 550 ppm. Collectively, the fertilization factors averaged across the C_3 crops (rice, wheat, and soybeans) are 24% for yield, 27% for biomass, and 29% for photosynthesis. The responses for maize were lower except for yield, which was reported to increase by 27% (Table 1). All studies included in the reviews used enclosures, such as controlled environmental chambers, transparent field enclosures, or open-top chambers. Since the 1980s, many further chamber studies have been conducted. When these are compiled for wheat and soybeans, an even larger yield fertilization factor of 31% is suggested (Table 1). Although this is a wealth of data on which to project a CO_2 fertilization effect for crops across the globe, no agrochemical or plant-breeding company would base its business plan for a new chemical or variety solely on greenhouse studies without rigorous field trials ([19, 20]). Yet our current projections of future world food supply are based on such potentially inadequate data.

Why might chamber studies be inadequate for predicting future yields? Many chamber studies used plants grown in pots, which are now known to alter the response of plants to elevated [CO_2] ([21]). Most of the field studies used open-topped and transparent-walled chambers, up to 2 m in diameter. Despite being partially open to the atmosphere, important environmental differences remain. In a chamber carefully designed to minimize environmental differences, receiving ~75% of full sunlight, the temperature inside the chamber was 4.3°C warmer and the water vapor pressure deficit was 0.8 kPa higher ([22]) than outside the chamber. The transmission of sunlight into the chambers was lower and the ratio of diffuse to direct sunlight increased. Other chamber types would cause even greater perturbation of the natural environment. All chambers alter air flow and intercept rainfall. Access by pests and diseases is restricted, but if they gain access, higher humidity and more shelter may accentuate epidemics. As a result, the effect of the chamber on plants is often greater than that of elevated [CO_2] ([23]). In agronomic trials, buffer rows are used between treatments; typically the width of this zone is twice the height of the crop. Because of the small practical size of chambers, most or all of the treated crop will be within this zone, which could exaggerate the response to elevated [CO_2] ([23]). To overcome these limitations, free-air concentration enrichment (FACE) was developed.

How does FACE work? A typical FACE apparatus consists of a 20-m-diameter plot within the crop field (Fig. 1A), in which CO_2 is released just above the crop surface on the upwind side of the plot. Wind direction, wind velocity, and [CO_2] (or ozone concentration) are measured at the center of the plot. Fast-feedback computer control then adjusts the positions and amount of CO_2 released at different points around the plot. These systems have been engineered so that they can operate continuously from sowing to harvest and maintain [CO_2] within the plot to within ±10% of the target level, either 550 or 600 ppm, for ~90% of the time ([9, 24–26]) (Fig. 1B). Elevated [CO_2] decreases transpiration and therefore evaporative cooling, so that in sunlight the crop is warmer. This can serve to illustrate the uniformity of treatment (Fig. 1B).
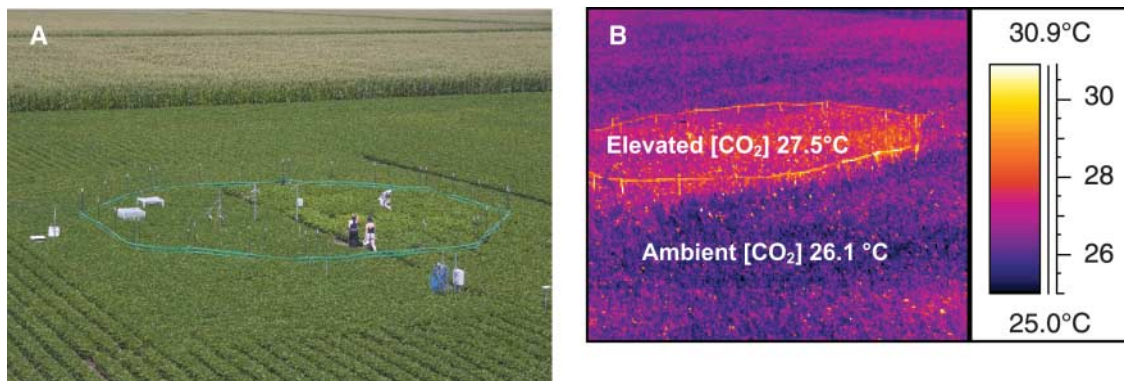
Mini-FACE systems as small as 1 m in diameter have been developed and have proved invaluable in ecosystem studies where the focus is on the effect of increased input of carbon ([27]), but they do not escape the problems of enclosures with respect to scale. Avoiding edge effects associated with small plots is critical when the objective is to determine an exact CO_2 fertilization factor for crops. Our analysis has therefore been limited to full-size FACE systems of plots >8 m in diameter, investigating the five major global food crops and managed pasture systems (table S1): wheat at Maricopa,

Arizona, USA, in 1992, 1993, 1996, and 1997; managed grassland at Eschikon, Switzerland, from 1993 to 2002; managed pasture at Bulls, New Zealand, from 1997 to 2002; sorghum at Maricopa, Arizona, USA, in 1998 and 1999; rice at Shizukuishi, Japan, from 1998 to 2000; and soybeans at Urbana-Champaign, Illinois, USA, from 2001 to 2005 and maize at the same location in 2002 and 2004 ([26, 28]).

What have we learned from the FACE experiments? The response of plant production to [CO_2] is approximately hyperbolic, increasing linearly at subambient concentration and saturating at around 800 to 2000 ppm. The ratio of yield at treatment [CO_2] to yield at atmospheric [CO_2] was calculated for over 340 independent chamber studies. Hyperbolas of the response of yield to [CO_2] were then fit for wheat, soybeans, and C_4 grains (maize and sorghum combined) (Fig. 2). Only one replicated FACE experiment was conducted with each of these crops, but these experiments were repeated over 2 to 5 years. It was notable that for each crop, the stimulation of yield observed in FACE experiments fell well below (about half) the value predicted from chambers (Fig. 2). This was apparent for total biomass and most marked for photosynthesis. Notably, the stimulation of photosynthesis by elevated [CO_2] in enclosure studies of rice was four times the value observed in the rice FACE experiment (Table 1). With so few FACE studies, it might be thought that these lower values are the result of chance. Table 1 shows that for three key production measures in four crops, only 1 of the 12 items is not lower than the chamber equivalent. The probability of this outcome being attributed to chance is remote ($P = 0.003$).

Results from FACE experiments with C_4 crops are consistent with CO_2 having no direct effect on photosynthesis, but there may be an indirect effect through the amelioration of drought stress by reduced stomatal conductance at elevated [CO_2] ([29–31]). This fits the theoret-

Fig. 1. (**A**) One of the 16 FACE plots of soybeans at the University of Illinois SoyFACE facility. CO_2 is released into the wind from nozzles in the green pipe, on the upwind side of the plot. Release rate is determined by wind speed and [CO_2], which is measured at the center of each ring. (**B**) The false-color infrared image provides a simple visualization of the uniformity of CO_2 treatment within a FACE plot. Here the atmosphere around a maize crop within the octagonal plot is maintained at 550 ppm [CO_2], whereas the rest of the field is at the current ambient [CO_2] of ~380 ppm. Maize growing inside an elevated [CO_2] plot was warmer in full sunlight than maize growing under ambient [CO_2] outside the plot at 15:30 on 15 July 2004. At that time, the average canopy temperature inside the four elevated [CO_2] plots at SoyFACE was 27.9 ± 0.2°C, significantly higher than canopy temperatures under ambient [CO_2] outside the plots (26.8 ± 0.3°C; $P = 0.03$). Because the pipes surrounding the plot are dry, they are warmer and so appear as white or light yellow. Greater canopy temperatures under elevated [CO_2] result from lower stomatal conductance, reducing latent heat loss by evapotranspiration and leading to lower crop water use, as described in Leakey *et al.* ([30]).

ical expectation that C_4 photosynthesis is CO_2-saturated at current atmospheric $[CO_2]$ (10); therefore, no yield increase would be expected for well-watered crops. Under drought, elevated $[CO_2]$ increased midday photosynthesis by 23% in sorghum (31). This failed to translate into a significant yield increase (32). On average, no significant yield increase has been observed for C_4 crops or C_4 wild grasses at elevated $[CO_2]$ in FACE studies (28). This is in sharp contrast to the large stimulation of yield for well-watered plants in chambers (Fig. 2B) used to parameterize models. This suggests that the consistent stimulation of C_4 crop yield by elevated $[CO_2]$ currently applied in models is inappropriate. At best, yield will in all probability be enhanced by elevated $[CO_2]$ only in times and places of drought.

Wheat and rice FACE experiments included nitrogen treatments. At the lowest [N] (15 to 70 kg of N ha^{-1}), the average yield increase with elevated $[CO_2]$ was only 9% (28), just over one-third of that of the chamber response (Table 1). Although this N input treatment was considered low by the standards of intensive agriculture in the European Union and United States, these levels exceed the world average and may therefore be closer to the stimulation factor for crop yields across the globe. Lower-than-expected yields under elevated $[CO_2]$ are not just confined to grain crops. For example, the major C_3 herbage grass, *Lolium perenne*, also showed a yield increase of only 9% at two locations; and at the lowest [N] (100 to 140 kg of N ha^{-1}), the yield increase was an insignificant 1% (table S2)

(28). Although the data here apply to a single species, *L. perenne* is one of the most important and widely grown herbage grasses in the temperate zone.

No FACE experiment has been conducted in the tropics, but two factors emerging from temperate studies have particular implications for tropical crops. First, the CO_2 fertilization effect may be small without large additions of N. Second, FACE experiments with the major grain crops of sub-Saharan Africa, sorghum and maize, have so far failed to show any yield increase from elevated $[CO_2]$. Parry *et al.* (7) projected that yield losses in these countries due to climate change could be 10 to 30% by 2050, but these would be ameliorated to only 2.5 to 5% when the CO_2 fertilization effect is added (7). The FACE experiments suggest that this amelioration may be far less than expected.

Rising surface ozone. Increased combustion of fuels will increase not only atmospheric $[CO_2]$ but also atmospheric nitrogen oxide concentrations, which, when coupled with climate change, will result in a continued increase in surface ozone concentration ($[O_3]$). Many rural areas in the temperate zone of the Northern Hemisphere, as well as in the tropics, are forecast to see increases in $[O_3]$ of ~20% by midcentury (8). Ozone is toxic to plants at concentrations as low as 30 parts per billion (ppb). Although chamber studies have shown large yield losses owing to elevated $[O_3]$ (33), these effects are not incorporated in current projections of future yields (2, 8).

Until very recently, the only studies of the effects of elevated $[O_3]$ on crops were conducted

in chambers, and it was unclear whether similar losses would occur under conditions of normal canopy/atmosphere coupling in the field. Morgan *et al.* (34) used a FACE system adapted to elevate $[O_3]$ rather than $[CO_2]$ to examine whether the decreases in yield for soybeans in central Illinois projected from chamber experiments occurred in the open air. A 23% increase in $[O_3]$ from an average daytime ambient concentration of 56 to 69 ppb over two growing seasons decreased soybean yield by 20%. How does this compare with the expectations established from chamber studies? Based on a prior compilation of chamber studies (33), the expected decrease was 8%. If the effects of $[CO_2]$ and $[O_3]$ observed in FACE studies are additive, then the net effect of simultaneous increases in $[O_3]$ and $[CO_2]$, as forecast by the IPCC A1B scenarios, would be a 5% decrease in yield, compared with the 23% increase used to parameterize current models (Table 1). Chamber studies suggest that elevated $[CO_2]$ may provide some protection against elevated $[O_3]$ and therefore the effects will not be additive, but this has yet to be verified for any crop under open-air field conditions.

What is needed? The CO_2 fertilization effects, derived from chamber experiments, currently used in crop models forecast substantial increases in future crop production under conditions associated with climate change. The FACE experiments, conducted in open fields, are not without their limitations (26, 35), but represent our best simulations of the future elevated $[CO_2]$ environment. Our meta-analytic summary of the FACE experiments indicates that there will be a much smaller CO_2 fertilization effect on yield than currently assumed, and possibly little or no stimulation for C_4 crops.

The average yield increase at elevated $[CO_2]$ for crops in FACE studies fell well short of the
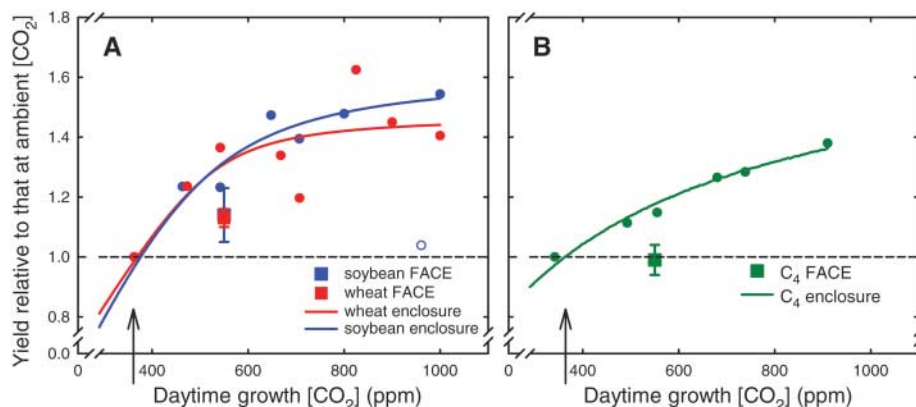
Fig. 2. Effects of elevated $[CO_2]$ on crop yield. Data are yields at elevated $[CO_2]$ relative to those at ambient $[CO_2]$ (arrow) for (**A**) soybeans in chambers (solid blue circles) and FACE (blue square, hidden behind red square) and wheat in chambers (red circles) and FACE (red square); and (**B**) C_4 crops (maize and sorghum combined) in chambers (green circles) and FACE studies (green square). Error bars indicate mean $\pm$ 90% confidence intervals around the means for the FACE studies. The chamber studies included 115 independent measures of soybeans (21), 211 of wheat (36), and 14 of maize and sorghum (table S3). These measures were divided into 10 classes of growth $[CO_2]$ in 100-ppm increments. Plotted values are the class means of growth $[CO_2]$ and yield. Solid lines are the least-squares fits for the nonrectangular hyperbolic response of yield to growth $[CO_2]$ from these enclosure studies of soybeans (blue line, $r^2 = 0.98$), wheat (red line, $r^2 = 0.88$), and C_4 crops (green line, $r^2 = 0.99$). The yield response of soybeans in chambers to growth $[CO_2]$ of 900 to 999 ppm [open blue circle in (A)] was an outlier and was excluded from the curve fitting. Full details of the meta-analysis methods and results from FACE are presented in the SOM and table S2.
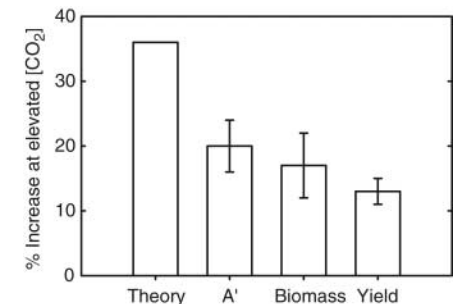
Fig. 3. Comparison of theoretical and actual changes in C_3 crop production parameters at an elevated $[CO_2]$ of 550 ppm relative to ambient $[CO_2]$. Theory, theoretical RuBisCO-limited photosynthesis at 550 ppm [(9) and SOM]; A', measured daily integral of carbon uptake; biomass, final above-ground biomass; yield, harvestable grain yield. Error bars indicate mean $\pm$ 90% confidence intervals. A', biomass, and yield were measured in C_3 crops exposed to elevated $[CO_2]$ in FACE experiments (table S2).

theoretically possible increase based on the well-defined properties of RuBisCO (Fig. 3). At 25°C, an increase in [CO$_2$] to 550 ppm should increase light-saturated photosynthesis by 36%. The average increase observed for C$_3$ crops in FACE was 20% for the daily integral of photosynthetic CO$_2$ uptake, 17% for total biomass, and just 13% for yield (Fig. 3). This suggests that a series of feedbacks operate in the field to constrain realization of the potential benefits of elevated [CO$_2$]. Only with a thorough high-priority R&D effort might we overcome these feedbacks and achieve the potential gains in food supply.

The FACE experiments clearly show that much lower CO$_2$ fertilization factors should be used in model projections of future yields; however, the present experiments are limited in the range of growing conditions that they cover. Scientists have not investigated the interactive effects of simultaneous change in [CO$_2$], [O$_3$], temperature, and soil moisture. Technological advances suggest that large-scale open-air facilities to investigate these interactions over controlled gradients of variation are now possible (*26*). Although we have projected results to 2050, this may be too far in the future to spur commercial R&D, but it must not be seen as too distant to discourage R&D in the public sector, given the long lead times that may be needed to avoid global food shortage.

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37. Materials and methods for meta-analyses are available as supporting material on *Science* Online. Full results from the meta-analyses summarized in Table 1 are presented in table S2 with references in appendix S1. C$_4$ crop yield responses to elevated [CO$_2$] are presented in table S3 with references in appendix S2.
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Frictional Afterslip Following the 2005 Nias-Simeulue Earthquake, Sumatra

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Continuously recording Global Positioning System stations near the 28 March 2005 rupture of the Sunda megathrust [moment magnitude (M_w) 8.7] show that the earthquake triggered aseismic frictional afterslip on the subduction megathrust, with a major fraction of this slip in the up-dip direction from the main rupture. Eleven months after the main shock, afterslip continues at rates several times the average interseismic rate, resulting in deformation equivalent to at least a M_w 8.2 earthquake. In general, along-strike variations in frictional behavior appear to persist over multiple earthquake cycles. Aftershocks cluster along the boundary between the region of coseismic slip and the up-dip creeping zone. We observe that the cumulative number of aftershocks increases linearly with postseismic displacements; this finding suggests that the temporal evolution of aftershocks is governed by afterslip.

Slip on faults occurs as a combination of relatively continuous aseismic creep and transient slip events. These transient events occur as earthquakes radiating seismic waves, and also as aseismic events with characteristic time scales of days to years. A better understanding of the physical factors that control the relative amounts and location of seismic and aseismic slip is a key goal in the study of fault mechanics and in particular can affect assessments of regional seismic and tsunami hazards. After a large earthquake, postseismic deformation may result from earthquake-induced slip along the plate interface, commonly referred to as afterslip, and as viscoelastic relaxation in the volume surrounding the fault rupture (*1*–*3*). Thus, well-positioned postseismic observations can probe the mechanical properties of subduction megathrusts and the media that surround them.

Geodetic and seismological investigations suggest that typical subduction megathrust earthquakes involve fault rupture at depths between ~10 km and ~50 km, and that rupture all the way up to the trench is rare (*4*). However, evidence for slip on the shallowest portions of a megathrust has been notoriously difficult to evaluate. We commonly assume that seismic slip decreases in both up-dip and down-dip directions, presumably bounded by regions where frictional behavior of the fault does not support stick-slip (i.e., seismic) rupture (*5*).

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