COMMENTARY

Insects take a bigger bite out of plants in a warmer, higher carbon dioxide world

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Carbon dioxide is a potent "greenhouse" gas. The dramatic increase in its concentration in the atmosphere as a result of human activities, beginning with accelerated fossil fuels combustion in the late 18th century, and perhaps even earlier, with modern agricultural expansion 8,000 years ago (1, 2), is driving a striking rise in global temperature (3). For the past 650,000 years, until relatively recently, the concentration of CO_2 in the atmosphere was 280 ppm or less; however, the current concentration exceeds 380 ppm and, on its present trajectory, will surpass 550 ppm by 2050 (3). The accumulation of CO_2 and other greenhouse gases in the atmosphere is forcing an elevation of global mean temperature; during the lifetime of child born today, the average temperature of the earth will increase by as much as $\approx$6°C (3). Working in concert, elevated temperature and CO_2 are redistributing plant and animal communities on the surface of the earth (4). Because of the direct effect of CO_2 and temperature on global food supplies, the influence of these changes on plant physiology and ecology is being actively studied (4–7). How these elements of global change may alter the interactions between plants and the insects that feed on them is relatively unknown. By bringing to light secrets contained in the fossil record, Currano *et al.* (8), published in this issue of PNAS, found that the amount and diversity of insect damage to plants increased in association with an abrupt rise in atmospheric CO_2 and global temperature that occurred >55 million years ago. If the past is indeed a window to the future, their findings suggest that increased insect herbivory will be one more unpleasant surprise arising from anthropogenic climate change.

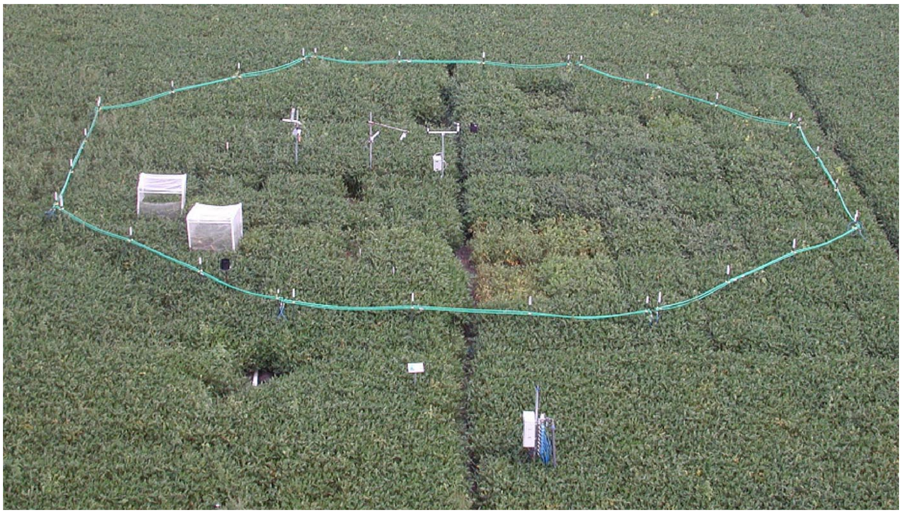

Fig. 1. The Soybean Free-Air Concentration Enrichment (SoyFACE) experiment at the University of Illinois (www.soyface.uiuc.edu), following a factorial design, exposes a soybean crop to the elevated levels of CO_2 and O_3 expected to occur in the Midwest by the middle of this century. The SoyFACE facility enables precise control of the atmosphere above the plant canopy under otherwise natural conditions, while permitting insects and pathogens unrestricted access. Equipment for sensing and controlling gas concentrations is located at the center of the plot. The tower at the upper left measures canopy temperature, and the caged subplots exclude canopy insects. Research at SoyFACE is supported by the Office of Science (BER), U.S. Department of Energy.

The intersection of the Paleocene and Eocene epochs 55.8 million years ago was marked by a sudden, transient elevation in atmospheric CO_2 and a corresponding rise in global temperature. During this Paleocene–Eocene Thermal Maximum (PETM), the concentration of CO_2 tripled, and surface temperatures rose by $\approx$5°C in 10,000 years. The speed with which temperature increased makes the PETM a powerful deep-time analog for contemporary anthropogenic climate change.

To examine how the rapidly increasing CO_2 and temperature in the PETM affected insect damage to leaves, Currano *et al.* (8) unearthed >5,000 fossil leaves from the Bighorn Basin of Wyoming and measured the type, frequency, and extent of herbivory. The leaves revealed a dazzling array of damage types, from gaping holes inflicted by chewing insects with large, powerful mandibles and galls formed by wasp oviposition, to delicate mines created by larval moths and flies as they consumed nutritious leaf mesophyll, to the piercing damage caused by aphids and mites. As the elevation in CO_2 forced mean annual temperature to rise from 10.5° to 20.1°C, the percentage of leaves damaged increased from $\approx$38% to $\approx$57%, and the diversity of damage increased as well. The expansion in types and magnitude of leaf damage during the PETM may, in part, reflect fundamental changes in the interaction between plants and insects.

Although the pattern of increasing herbivory approaching the PETM is clear, the mechanisms governing the escalation in herbivory are elusive and represent a complex interplay of the effects of temperature and CO_2 on insects and plants. From the distribution and behavior of contemporary insects, it is reasonable to hypothesize that increased herbivory should follow rising temperatures. As with many taxa, the number of insects per unit area increases as one moves from cold, northern latitudes toward the warmth of the equatorial regions and from high peaks down to mountain bases (9, 10). Development time and growth rates accelerate, and the threshold temperatures for movement are exceeded earlier with warming temperatures for many, but not all, insects (11). The strength of these generalizations is, however, tempered by the close synchrony of insect life cycles with

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plant phenology and the great variation in the response to temperature among insects with widely divergent life history traits. Although the respiration rates and food consumption of insects may increase with temperature in the isolation of the laboratory, changes in the composition of the plant community (12, 13), or individualistic responses of plants and insects to temperature (14), may be the primary factors affecting herbivory in natural communities as the climate warms.

The mechanisms governing the amount of herbivore damage become even more complex when one considers the potential interactions with elevated CO_2. Many insects respond directly to CO_2 as a cue for identifying favorable oviposition sites or desirable food sources (15); however, the CO_2 concentrations producing this response are typically much higher than those expected from global change. The indirect effect of elevated CO_2 on leaf chemistry, and subsequently on the palatability of leaves to insects, likely will have the greatest influence on herbivory (16).

A rise in CO_2 generally increases the carbon-to-nitrogen ratio of plant tissues (17, 18), reducing the nutritional quality for protein-limited insects (19). Insects may accelerate their food intake to compensate for reduced leaf nitrogen content (19–21), although this is not always the case (22, 23). By exposing a soybean crop to elevated CO_2 under otherwise natural field conditions (Fig. 1), foliar damage inflicted by Japanese beetles (*Popillia japonica*; Fig. 2) more than doubled, and, when given a choice, both Japanese beetles and Mexican bean beetles (*Epilachna varivestis*) preferred to feed on high-CO_2 leaves (24). Recent results indicate that growth under elevated CO_2 compromises the ability of soybean plants to produce defensive proteinase inhibitors (C.L.C. and J. Zavala, unpublished data) and that consuming these poorly defended leaves increases the fecundity of Japanese beetles (25). Future elevated levels of atmospheric CO_2 will fundamentally alter the relationship between plants and insects, and accelerated feeding by insects may offset some of the predicted increases in agricultural productivity associated with greater levels of CO_2 in the atmosphere (5, 26).

Fig. 2. Japanese beetles (*Popillia japonica*) consuming soybean leaves. The Japanese beetle is a broadly polyphagous species introduced into the United States in 1916 that is now expanding its range throughout the Midwest (27). Japanese beetles are attracted to poorly defended, high-sugar soybean leaves that develop under elevated CO_2. Future increases in CO_2 and temperature may further the success of such destructive invasive species (28)

Understanding how these rapid anthropogenic changes in climate and atmospheric chemistry will affect the "goods and services" provided by native and agricultural ecosystems is one of the greatest scientific challenges of our time. By interpreting the "text" of the fossil record, Currano *et al.* (8) suggest that global change will result in greater insect damage to valuable crops and forests. Open-air experiments, such as SoyFACE (Fig. 1 and ref. 29), that combine precise experimental control with the opportunity for realistic ecological interactions will be instrumental in developing a mechanistic understanding of trophic interactions, as well as in devising the next-generation theory for predicting such interactions in the future.

1. Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshgi HS, Le Quéré C, Scholes RJ, Wallace DWR (2001) in Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the *Third Assessment Report of the Intergovernmental Panel on Climate Change*, eds Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (Cambridge Univ Press, Cambridge, UK), pp 241–280.
2. Ruddiman WF (2003) *Clim Change* 61:261–293.
3. Intergovernmental Panel on Climate Change (2007) *Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Available at www.ipcc.ch/ipccreports/assessments-reports.htm.
4. Parmesan C (2006) *Annu Rev Ecol Evol Syst* 37:637–669.
5. Long SP, Ainsworth EA, Leakey ADB, Nosberger J, Ort DR (2006) *Science* 312:1918–1921.
6. Long SP, Ainsworth EA, Rogers A, Ort DR (2004) *Annu Rev Plant Biol* 55:591–628.
7. Walther GR (2004) *Perspect Plant Ecol Evol Syst* 6:169–185.
8. Currano ED, Wilf P, Wing SL, Labandeira CC, Lovelock EC, Royer DL (2008) *Proc Natl Acad Sci USA* 105:1960–1964.
9. Gaston KJ, Williams PH (1996) in *Biodiversity*, ed Gaston KJ (Blackwell Scientific, Oxford) pp 202–209.
10. Wilf P, Labandeira CC (1999) *Science* 284:2153–2156.
11. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, *et al.* (2002) *Global Change Biol* 8:1–16.
12. Richardson SJ, Press MC, Parsons AN, Hartley SE (2002) *J Ecol* 90:544–556.
13. Roy BA, Gusewell S, Harte J (2004) *Ecology* 85:2570–2581.
14. van der Heide T, Roijackers RMM, Peeters ETHM, van Nes EH (2006) *Freshw Biol* 51:110–116.
15. Guerenstein PG, Hildebrand JG (2008) *Annu Rev Entomol* 53:161–178.
16. Bezemer TM, TH Jones (1998) *Oikos* 82:212–222.
17. Lincoln DE, Sionit N, Strain BR (1984) *Environ Entomol* 13:1527–1530.
18. Ainsworth EA, Davey PA, Bernacchi CJ, Dermody OC, Heaton EA, Moore DJ, Morgan PB, Naidu SL, Ra HSY, Zhu XG, *et al.* (2002) *Global Change Biol* 8:695–709.
19. Coviella CA, Trumble JT (1999) *Conserv Biol* 13:700–712.
20. Holton MK, Lindroth RL, Nordheim EV (2003) *Oecologia* 137:233–244.
21. Kooper BJ, Lindroth RL, Nordheim EV (2001) *Envrion Entomol* 30:1119–1126.
22. Knepp RG, Hamilton JG, Mohan JE, Zangerl AR, Berenbaum MR, DeLucia EH (2005) *New Phytol* 167:207–218.
23. Kopper BJ, Lindroth RL (2003) *Oecologia* 134:95–103.
24. Hamilton JG, Dermody O, Aldea M, Zangerl AR, Rogers A, Berenbaum MR, DeLucia EH (2005) *Environ Entomol* 34:479–485.
25. O'Neill BF, Zangerl AR, DeLucia EH, Berenbaum MR (2008) *Environ Entomol*, in press.
26. Fuhrer J (2003) *Agric Ecosyst Environ* 97:1–20.
27. Potter DA, Held DW (2002) *Annu Rev Entomol* 47:175–205.
28. Ward NL, Masters GL (2007) *Global Change Biol* 13:1605–1615.
29. Ort DR, Ainsworth EA, Aldea M, Allen DJ, Bernacchi CJ, Berenbaum MR, Bollero GA, Cornic G, Davey PA, Dermody O, *et al.* (2006) *Ecol Stud* 18:71–86.