HOW GLOBAL WARMING AFFECTS TROPICAL RAINFORESTS? A PALEOGENE PERSPECTIVE

Carlos Jaramillo

Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panamá: jaramilloc@si.edu

The consequences of global warming on tropical vegetation are unknown. Today, most tropical rainforest lives at temperatures below 27.5°C (Fig. 1). Many have argued that tropical communities live near their climatic optimum (Stoskopf 1981), and that a slight increase in temperature could be deleterious to them (Tewksbury *et al.* 2008). Empirical examples in earth history might help us understand the behaviour of tropical biota during past climate change.

Past tropical temperatures during the Paleogene for a fossil forest in northern Colombia named Cerrejón have been estimated using leaf margin analysis (Herrera *et al.* 2005) and snake morphology (Head *et al.* 2009). Leaf margin analysis, however, can give only a minimum estimate of paleotemperature for tropical forests, because the regression models used in the method lack a modern analogue for forest at temperatures above 28°C. Snake morphology suggests a temperature of 32°C for the middle Paleocene of Colombia (Head *et al.* 2009), which seems to agree with other proxies as well as with global circulation models for the Paleogene (Huber 2008).

The fossil record of the tropics shows overall that tropical biotas were able to cope with high temperatures over extensive periods of time (several millions of years). Paleocene tropical forests from northern Colombia were similar in composition to modern tropical forests (Wing

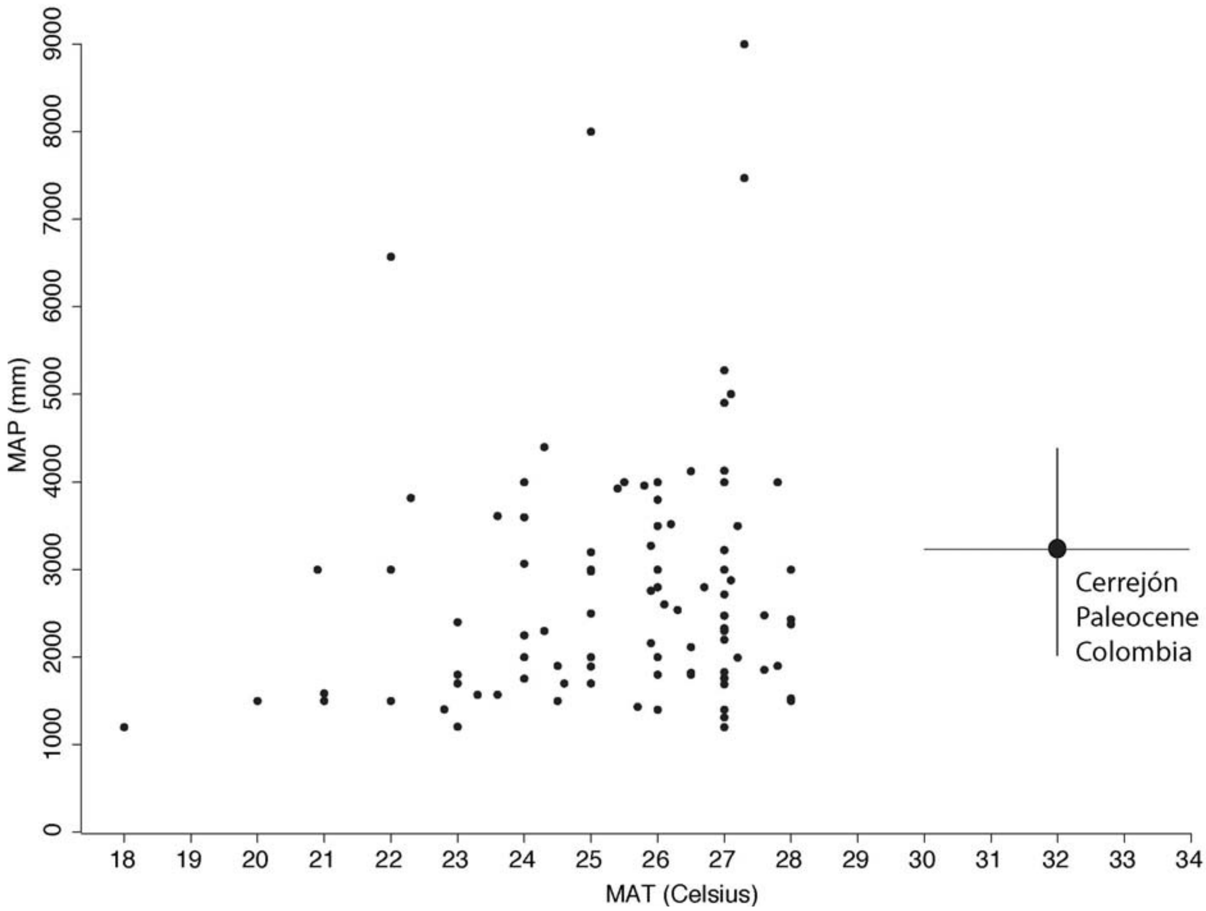

Figure 1 Mean annual precipitation and mean annual temperature for 99 tropical rainforest sites across the tropics. Note how all of the tropical rainforest are below 28°C today. The fossil site from the Paleocene of Colombia, Cerrejón, does not have a modern analogue in mean annual temperature. Cerrejón site shows the error bars for the estimation of temperature (Head *et al.* 2009) and precipitation (Herrera *et al*. 2008b).

et al. 2004). Most of the plant families that are abundant in the neotropical rainforest today were also abundant in the Paleocene, including legumes, Malvaceae, palms, Araceae, and Menispermaceae (Doria *et al.* 2008; Gomez *et al*. 2009; Herrera *et al.* 2008a; Jaramillo *et al.* 2007; Ramirez 2009). The forest also supported a rich fauna that included mammals, giant snakes, crocodiles, and giant turtles (Bloch *et al.* 2008; Cadena and Jaramillo 2006; Hasting *et al.* 2009; Head *et al.* 2009). Moreover, a subsequent warming, the long-term Eocene thermal maximum with temperatures in the tropics reaching 36– 37°C, correlates with an increase in tropical plant diversity (Jaramillo *et al.* 2006).

In contrast, modern experimental studies have shown than plants suffer several deleterious effects under maximum daily temperatures associated with mean annual temperatures of 32–33°C. Some of those effects include a decrease in the rate of photosynthesis, a decrease in net production, an increased risk of photoinjury, and an increase in isoprene emissions (e.g. Lerdau and Throop 1999; Stoskopf, 1981). How, then, to explain the Cerrejón forest thriving at 32°C?

The solution could rely on a combination of high CO_2 and elevated precipitation. The Cerrejón fossil forest lived under high precipitation regimes — about 3.2 m of rain a year (Herrera *et al.* 2005, 2008b) — and CO_2 levels much higher than those of today (Royer 2006). Experiments in greenhouses have shown that plants deal better with high temperatures under high levels of CO_2 and precipitation (Aber *et al.* 2001; Berry and Bjorkman 1980; Niu *et al.* 2008). Perhaps, then, rainforest lineages already have the genetic variability to cope with elevated temperatures if they are living in high levels of CO2 and high rates of rainfall, as during the Paleogene.

ACKNOWLEDGMENTS

This project was supported by the Smithsonian Paleobiology Endowment Fund, the Fondo para la Investigacion de Ciencia y Tecnología Banco de la Republica de Colombia, the Unrestricted Endowments Smithsonian Institution Grants, National Science Foundation, and Carbones del Cerrejón LLC. Special thanks go to M. I. Barreto for her continuous support, and ideas.

REFERENCES

Aber, J.; Neilson, R.; McNulty, S.; Lenihan, J.M.; Bachelet, D.; Draper, R.J. 2001: Forest processes and global environmental change: Predicting the effects of individual and multiple stressors. *BioScience* 51: 735-751.

Berry, J.; Bjorkman, O. 1980: Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* 31: 491-543.

Bloch, J.; Cadena, E.; Hasting, A.; Rincón, A.; Jaramillo, C. 2008: New vertebrate faunas from the Paleocene sediments of Colombia, northwestern South America. In Society of Vertebrate Paleontologists Annual Meeting: Cleveland, USA. The Society of Vertebrate Paleontology.

Cadena, E.; Jaramillo, C. 2006: New Podocnemididae fossil turtles from the late Paleocene Cerrejon formation, Guajira Peninsula, Colombia. In 66th Annual Meeting of the Society of Vertebrate Paleontology, Ottawa, Canada.

Doria, G.; Jaramillo, C.; Herrera, F. 2008: Menispermaceae from the Cerrejon formation, middle to late Paleocene. *American Journal of Botany* 95: 954-973.

Gomez, N.; Jaramillo, C.; Herrera, F.; Wing, S.L.; Callejas, R. 2009: Palms (Arecaceae) from a Paleocene rainforest of northern Colombia: *American Journal of Botany*: in press.

Hasting, A.; Bloch, J.; Cadena, E.; Jaramillo, C. 2009: A new small short-snouted Dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of northeastern Colombia. *Journal of Vertebrate Paleontology*: in press.

Head, J.; Bloch, J.; Hasting, A.; Bourque, J.; Cadena, E.; Herrera, F.; Polly, P.D.; Jaramillo, C. 2009: Giant boine snake from a Paleocene Neotropical rainforest indicates hotter past equatorial temperatures. *Nature* 457: 715-718.

Herrera, F.; Wing, S.; Jaramillo, C.A. 2005: Warm (not hot) Tropics during the Late Paleocene: First Continental Evidence. In AGU, E.T. ed. AGU Annual Meeting, Volume 86, Fall Meet. Suppl., Abstract PP51C-0608.

Herrera, F.; Jaramillo, C.; Dilcher, D.; Wing, S.L.; Gomez, C. 2008a: Fossil Araceae from a Paleocene Neotropical rainforest in Colombia. *American Journal of Botany* 95: 1-16.

Herrera, F.; Wing, S.L.; Jaramillo, C.; Gomez, C.; Dilcher, D.; Wilf, P.; Labandeira, C.C. 2008b: Fossils from Colombia reveal tropical rainforest in the Paleocene greenhouse world. *Terra Nostra* 2008-2: 113.

Huber, M. 2008: A Hotter Greenhouse? *Science* 321: 353-354.

Jaramillo, C.; Pardo-Trujillo, A.; Rueda, M.; Harrington, G.; Bayona, G.; Torres, V.; Mora, G. 2007: Palynology of the Upper Paleocene Cerrejon Formation, northern Colombia. *Palynology* 31: 153-189.

Jaramillo, C.; Rueda, M.; Mora, G. 2006: Cenozoic plant diversity in the Neotropics. *Science* 311: 1893-1896.

Lerdau, M., T.; Throop, H., L. 1999: Isoprene emissions and photosynthesis in a tropical forest canopy: Implications for model development. *Ecological Applications* 109: 1109- 1117.

Niu, S.; Wu, M.; Han, Y.; Xia, J.; Li, L.; Wan, S. 2008: Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist* 177: 209–219.

Ramirez, M. 2009: Afinidades taxonómicas de una Malvaceae del Paleoceno Superior (58–60 Ma) en el norte de Colombia [Undergraduate Senior Thesis]. Medellin, Universidad de Antioquia.

Royer, D.L. 2006: CO2-forced climate thresholds during the Phanerozoic. *Geochimica et Cosmochimica Acta* 70: 5665–5675.

Stoskopf, N. 1981: Understanding crop production: Upper Saddle River, New Jersey. Prentice-Hall. 433 p.

Tewksbury, J.J.; Huey, R.B.; Deutsch, C.A. 2008: Putting the heat on tropical animals: *Science* 320:

Wing, S.; Herrera, F.; Jaramillo, C. 2004: A Paleocene flora from the Cerrejon formation, Guajira Peninsula, northeastern Colombia. In International Organization of Paleobotany, Seventh Quafrennial Conference, Argentina, Volume Abstracts: 146-147.