Sharply increased insect herbivory during the Paleocene–Eocene Thermal Maximum

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The Paleocene–Eocene Thermal Maximum (PETM, 55.8 Ma), an abrupt global warming event linked to a transient increase in pCO2, was comparable in rate and magnitude to modern anthropogenic climate change. Here we use plant fossils from the Bighorn Basin of Wyoming to document the combined effects of temperature and pCO2 on insect herbivory. We examined 5,062 fossil leaves from five sites positioned before, during, and after the PETM (59–55.2 Ma). The amount and diversity of insect damage on angiosperm leaves, as well as the relative abundance of specialized damage, correlate with rising and falling temperature. All reach distinct maxima during the PETM, and every PETM plant species is extensively damaged and colonized by specialized herbivores. Our study suggests that increased insect herbivory is likely to be a net long-term effect of anthropogenic pCO2 increase and warming temperatures.

Bighorn Basin | paleobotany | plant-insect interactions | rapid climate change

During the 21st century, global surface temperature is expected to increase 1.8–4.0°C as higher atmospheric concentrations of greenhouse gases (especially CO2) are generated by human activities (1). Food webs incorporating plants and phytophagous insects account for up to 75% of modern global biodiversity (2), so their response to this anthropogenic change will have a profound effect on the biosphere. Experiments show that plants grown in elevated CO2 tend to accumulate more carbon and have a higher carbon:nitrogen ratio; they are, therefore, nutritionally poorer (3–5), leading to an average compensatory increase in insect consumption rates (6) as nitrogen becomes limiting. Modern insect herbivory and herbivore diversity are greatest overall in the tropics (7–10), implying a broad correlation between temperature and herbivory, and Paleocene–Eocene fossils show rapid shifts in the geographic ranges of insects in response to climate change (11). These existing data provide limited insight into future changes, however. The complexity of plant–insect food webs makes it difficult to generalize from experiments to the response of natural ecosystems over long time scales (12). Modern and Paleocene–Eocene plant biogeographic patterns have not been directly linked to pCO2 and do not document the response of plant–insect food webs to rapid increases in temperature and pCO2. Well preserved Paleocene–Eocene fossil angiosperm leaves show insect feeding damage and, therefore, can be used to investigate the net effects of increasing temperature and pCO2 on full plant–insect food webs over long time scales.

Beginning in the late Paleocene, global temperatures gradually warmed to the sustained Cenozoic maximum at ~53 Ma (13). The Paleocene–Eocene Thermal Maximum (PETM) is a transient spike of high temperature and pCO2 representing ~100 thousand years (ky), superimposed on a longer interval of gradual warming (14, 15); it is one of the best deep-time analogues for the modern time scale of global warming. The PETM is marked by a negative carbon isotope excursion, consistent with the release of a large amount of 13C-depleted carbon to the atmosphere and oceans (14). Atmospheric pCO2 levels are estimated to have increased by a multiple of three to four (16). Additionally, global mean surface temperatures rose at least 5°C over ~10 ky and returned to background levels after ~100 ky (16, 17). Significant changes in terrestrial floras and faunas have been documented from the PETM. In northwestern Wyoming’s Bighorn Basin, there was a transient increase in floral diversity and change in plant species composition, reflecting a northward migration of subtropical taxa (18). A major immigration of vertebrates from Europe and Asia across high-latitude land bridges also occurred (19).

In this study, the recent discovery of floras from the PETM in the Bighorn Basin of Wyoming (18, 20) allows us to evaluate the effects of atmospheric and climatic change on plant–insect associations at significantly shorter, and more ecologically and societally relevant, time scales (104–105 yr) than previously possible using the fossil record (106 yr; ref. 21). We conducted insect damage censuses on fossil angiosperm leaves at five sites in the Bighorn Basin positioned before, during, and after the PETM warming event (Table 1, and see supporting information (SI) Table 4 and Methods). Each censused leaf was scored for the presence or absence of 50 discrete insect feeding morphotypes (ref. 26 and Fig. 1), and the results were tabulated and analyzed, allowing us to determine changes in the diversity, frequency, abundance, and host species distribution of insect damage through the studied interval.

Results and Discussion

Damage diversity is low in the earlier late Paleocene (Tiffanian 4a and 5b), sharply increases in the latest Paleocene (Clarkforkian 3), peaks during the PETM, and then returns to intermediate values during the early Eocene. Both the bulk floras (Fig. 2) and species–site pairs (Fig. 3) show a similar pattern, as do analyses of only specialized damage morphotypes (made by insects that usually eat only one or a few plant species; ref. 27) or only mine morphotypes (Figs. 2 and 3).

The PETM is also distinct in terms of the frequency of damage on its leaves: 57% of PETM leaves are damaged, compared with...
Table 1. Sampling summary

<table>
<thead>
<tr>
<th>Site collection no*</th>
<th>Epoch</th>
<th>Mammal zone</th>
<th>Age, Ma*</th>
<th>MAT, °C*</th>
<th>Leaf specimens</th>
<th>Leaf species</th>
<th>Leaf species rarefied to 800 leaves†</th>
</tr>
</thead>
<tbody>
<tr>
<td>USNM 42395-42399‡</td>
<td>Eocene</td>
<td>Wasatchian 2</td>
<td>55.2</td>
<td>16.4 ± 2.7 (25)</td>
<td>1,008</td>
<td>6</td>
<td>5.1 ± 0.5</td>
</tr>
<tr>
<td>USNM 42384‡</td>
<td>PETM (Eocene)</td>
<td>Wasatchian 0</td>
<td>55.8</td>
<td>20.1 ± 2.8 (20)</td>
<td>995</td>
<td>29</td>
<td>26.9 ± 1.3</td>
</tr>
<tr>
<td>USNM 41643‡</td>
<td>Paleocene</td>
<td>Clarkforkian 3</td>
<td>55.9</td>
<td>15.7 ± 2.4 (25)</td>
<td>857</td>
<td>16</td>
<td>15.9 ± 0.3</td>
</tr>
<tr>
<td>USNM 42042 (22)</td>
<td>Paleocene</td>
<td>Tiffanian 5b</td>
<td>57.5</td>
<td>10.5 ± 2.9†</td>
<td>1,362</td>
<td>16</td>
<td>14.7 ± 0.9</td>
</tr>
<tr>
<td>USNM 42041 (22)</td>
<td>Paleocene</td>
<td>Tiffanian 4a</td>
<td>58.9</td>
<td>10.5 ± 2.9†</td>
<td>840</td>
<td>7</td>
<td>6.9 ± 0.2</td>
</tr>
</tbody>
</table>

*Complete locality information is available in SI Table 4.
†Determined by using the stratigraphic framework of Secord et al. (23), Wing et al. (18), and Clyde et al. (24).
‡Errors are ±1σ.
§Errors indicate 95% confidence intervals on the rarefaction.
¶New collection.
‖New paleotemperature estimate for the late Tiffanian, using leaf margin analysis on all published Tiffanian Bighorn Basin floral lists.

15–38% for the Paleocene sites and 33% for the post-PETM site (Table 2). Individual PETM plant species have 45–94% of their leaves damaged, and all but two have >65% of leaves damaged (Fig. 4, and see SI Table 5). Tiffanian 4a species range from 28 to 48% of leaves damaged, Tiffanian 5b 10–48%, Clarkforkian 25–65%, and post-PETM 33–34%. Additionally, 7.3% of the PETM leaves have four or more types of damage, compared with 0.4–2.6% for the Paleocene sites and 1.4% for the post-PETM (Table 3).

To examine changes in damage composition and distribution through time, we performed a two-way cluster analysis (29) of the seven functional feeding groups’ relative abundances on those 29 species–site pairs having at least 20 specimens per site (Fig. 4). Feeding on the individual Clarkforkian and PETM plant species (cluster 2) is distinct from that on the Tiffanian species (cluster 1) because of the rarity of the more specialized feeding groups (surface feeding, mining, galling, and piercing and sucking) in the Tiffanian. Mining and surface feeding are particularly abundant during the PETM, causing the majority of the PETM taxa to form a distinct cluster (2b) from the Clarkforkian taxa (2a). Thus, the increased diversity and frequency of damage in the PETM occurs on all plant species and is not driven by increased feeding on one particular host. All but one of the PETM plant taxa analyzed here have at least one insect mine morphotype (Fig. 1), compared with three of seven in the latest Paleocene and one at each of the remaining three sites. The only abundant PETM species not mined is a small legume (dicot sp. WW001) whose leaflet area rarely exceeds 225 mm². Mines also occur on three of the rare PETM taxa not shown in Fig. 3.

Because the PETM plant species are not found at the other sites, we tested whether their leaves had significant structural differences that would make them more palatable to herbivores. Leaf mass per area (LMA) is linked to a variety of important plant ecological traits, including lower nutrient concentrations and thicker and tougher leaves (30, 31). Therefore, leaves with higher LMA are generally less palatable to herbivores and have less insect damage (30, 32). Fossil LMA can be estimated by using an extensive modern calibration set that demonstrates a robust scaling relationship between petiole width, squared, and leaf mass, normalized for leaf area (32). The theoretical explanation is that a wider petiole has a greater cross-sectional area that scales to support a heavier leaf. Critically, there are no site-level differences in LMA (Fig. 5; an ANOVA of LMA by sites yielded an F value of 0.15 and P = 0.96, 4 degrees of freedom), indicating no significant differences in leaf

![Fig. 1. Representative insect damage diversity on PETM leaves.](image-url)
properties between the PETM species and the species found at the other sites. Nearly all plant species from all five sites have low estimated LMA that would be consistent with high palatability (Table 5 and Fig. 5).

Increases in insect damage diversity in the Bighorn Basin in the late Paleocene and early Eocene correlate positively with increasing temperature. The first significant change in insect damage composition and diversity occurs between the late Tiffanian and late Clarkforkian, a time when both plant diversity (Table 1) and many of the dominant floral elements remain constant despite rising temperatures (33). A contemporary increase in herbivory from the Tiffanian to Clarkforkian, also without significant plant turnover, has been observed in southwestern Wyoming (22). The late Paleocene and PETM increases in herbivory do not reflect a long-term radiation of insect herbivores because damage diversity decreases after the PETM, as temperature again declines. Therefore, increases in damage diversity, particularly of specialized feeding groups, may represent an influx of thermophilic herbivores to the midlatitude regions, rather than an in situ diversification and accommodation. Because the geographic ranges of plant species shifted significantly during the PETM, some insects may simply have followed their host plants to the Bighorn Basin. By the middle of the PETM, every plant species represented by at least 20 censused leaves had been colonized by specialized herbivores.

We attribute the peak in insect feeding frequency during the PETM to the estimated tripling of atmospheric $pCO_2$ and the associated abrupt temperature rise. The major increase in plant consumption is consistent with predicted effects of elevated $pCO_2$ on foliar nitrogen concentration. Additionally, our damage diversity and frequency data indicate that both insect diversity and population density probably increased with temperature, although populations may have been limited by the decrease in food quality. The dramatic rise in diversity and frequency of herbivore attack on all abundant plant species during the PETM suggests that anthropogenic influence on atmosphere and climate eventually have similar consequences.

Table 2. Percentage of leaves damaged in each flora

<table>
<thead>
<tr>
<th>Flora</th>
<th>Damage</th>
<th>Ti4</th>
<th>Ti5</th>
<th>Cf3</th>
<th>PETM</th>
<th>Wa2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No damage</td>
<td>65.5 ± 1.6</td>
<td>85.1 ± 1.0</td>
<td>62.2 ± 1.7</td>
<td>47.2 ± 1.6</td>
<td>67.0 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Damage</td>
<td>34.5 ± 1.6</td>
<td>14.9 ± 1.0</td>
<td>37.8 ± 1.7</td>
<td>57.3 ± 1.6</td>
<td>33.0 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Specialized damage</td>
<td>13.2 ± 1.2</td>
<td>0.8 ± 0.2</td>
<td>13.4 ± 1.2</td>
<td>21.6 ± 1.3</td>
<td>17.1 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>Mines</td>
<td>0.1 ± 0.1</td>
<td>0.1 ± 0.1</td>
<td>1.1 ± 0.4</td>
<td>1.8 ± 0.4</td>
<td>0.7 ± 0.3</td>
</tr>
</tbody>
</table>

Because leaves can either have damage or not have damage, sampling error can be quantified by using the equation for the standard deviation of binomially distributed outcomes (28). Errors are ±1σ.
Table 3. Percentage of leaves in each flora with a given number of damage types

<table>
<thead>
<tr>
<th>No of damage types</th>
<th>Ti4</th>
<th>Ti5</th>
<th>Cf3</th>
<th>PETM</th>
<th>Wa2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24.4</td>
<td>10.5</td>
<td>19.7</td>
<td>27.9</td>
<td>16.5</td>
</tr>
<tr>
<td>2</td>
<td>8.3</td>
<td>3.3</td>
<td>8.5</td>
<td>14.0</td>
<td>10.3</td>
</tr>
<tr>
<td>3</td>
<td>1.3</td>
<td>0.7</td>
<td>7.0</td>
<td>8.0</td>
<td>4.9</td>
</tr>
<tr>
<td>4</td>
<td>0.5</td>
<td>0.3</td>
<td>1.8</td>
<td>3.6</td>
<td>1.1</td>
</tr>
<tr>
<td>5</td>
<td>0.1</td>
<td>0.7</td>
<td>1.8</td>
<td>1.8</td>
<td>0.3</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>0.1</td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td></td>
<td></td>
<td>1.1</td>
<td></td>
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</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
<td>0.3</td>
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<tr>
<td>10</td>
<td></td>
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</table>
Estimation of LMA. Every fossil leaf that clearly showed the attachment of the petiole to the leaf blade and had a reconstructable leaf area was used in the analysis. Eighty-five leaves, representing 19 species–site pairs, fit these criteria. This fossil was digitally photographed and extracted from the matrix by using Photoshop (Adobe). Measurements were made using ImageJ (http://rsb.info.nih.gov/ij), and LMA (see SI Table 5 and Fig. 5) was calculated using the protocol of Royer et al. (32).

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