

## DYNAMICS OF PLANT – INSECT HERBIVORE INTERACTIONS DURING LATE PALEOCENE AND EARLY EOCENE ENVIRONMENTAL PERTURBATIONS IN THE BIGHORN BASIN, WYOMING, USA

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The Paleocene–Eocene sediments of the Bighorn Basin, Wyoming, USA, record a time of significant variation in climate, biodiversity, and floral and faunal composition. Beginning in the Late Paleocene, global temperatures warmed to the Early Eocene Climatic Optimum (EECO) 51–53 Ma (Zachos *et al.* 2001). Superimposed on this gradual warming are the abrupt temperature and CO<sub>2</sub> increase at the Paleocene–Eocene Thermal Maximum (PETM, 55.8 Ma) and an Early Eocene cool period (Röhl *et al.* 2000; Wing *et al.* 2000; Zachos *et al.* 2003). Although many studies have analyzed the responses of individual taxonomic groups to climate change during this interval (e.g. Chew 2009; Gingerich 2006; Wing 1998), very few have focused on interactions among organisms (Currano *et al.* 2008). Here, we examine the effect of climate fluctuations that are well documented and

well-placed stratigraphically in the Bighorn Basin on the plant-insect herbivore system there. In particular, we ask whether plants and herbivorous insects responded synchronously to environmental changes.

It is important to understand the dynamics of plant–insect interactions because these two groups dominate modern non-microbial terrestrial biodiversity. Today, 70% of herbivorous insect species are oligophagous or monophagous (Bernays and Chapman 1994), making the majority of plant-insect herbivore interactions highly species specific. Therefore, we predict that plants and herbivorous insects responded to climate change synchronously and in the same manner. Alternatively, the relationship between plants and insects could be destabilized by the effects of temperature changes, particularly the abrupt PETM event.

A decoupling of this sort has been observed following the Cretaceous–Paleogene extinction (Wilf *et al.* 2006).

To test these predictions, we examined insect feeding damage on angiosperm leaves from the Bighorn Basin of Wyoming, USA. We conducted insect damage censuses at nine stratigraphic levels ranging in age from 59 to 52.5 Ma (Table 1). These floras occur during the Late Paleocene warming, PETM, Early Eocene cool period, and beginning of the EECO. A total of 9071 fossil angiosperm leaves belonging to 107 species were examined for the presence or absence of 71 insect feeding damage morphotypes (DTs; Labandeira *et al.* 2007). Here, we focus on the turnover of plants and DTs as represented by first and last appearances. Turnover

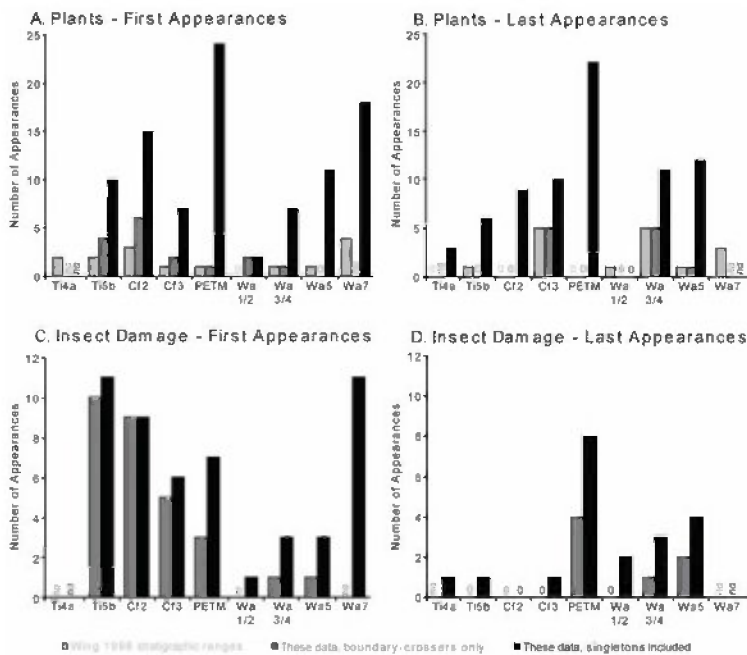


Figure 1 First and last appearances of plants (A, B) and insect damage morphotypes (C, D) at each stratigraphic level. The data are fully described in the text. First or last appearances cannot be calculated for some intervals, and these are labelled “na.” Intervals with no first or last appearances are labelled “0.”

of DTs is not directly equivalent to herbivorous insect turnover because some DTs can be made by many different insect groups and some insect groups make multiple DTs. However, our preliminary extant observations (unpublished) show that the DTs on individual host plants correlate at least approximately to real insect species.

Figure 1 shows the number of first and last appearances of plant morphotypes (A, B) and DTs (C, D) in each flora. Plant stratigraphic ranges were determined using three different methods. First, the range for each morphotype was ascertained using both our data and Wing's (1998) compilation of plant data for hundreds of localities in the Bighorn Basin; first and last appearances were tabulated accordingly. However, insect damage has been measured only at the nine sites in this study. Therefore, the number of floral first and last appearances was also computed using only the data from the nine sites. In one case, only those morphotypes occurring in more than one flora (boundary-crossers) were included. This scenario minimizes the uniqueness of the

PETM flora, which is composed primarily of plants not found at any other time in the Bighorn Basin. A third scenario includes all morphotypes from the nine sites. Except when using the Wing (1998) compilation, the number of first appearances in the Tiffanian 4a flora and last appearances in the Wasatchian 7 flora cannot be determined.

Although many of the major changes in insect damage composition occur at times of major floral turnover, there are subtle differences between the turnover patterns for the two groups. The data show a steady addition of plant morphotypes during the Late Paleocene and a peak in last appearances at the end of the Paleocene (Cf3). Similarly, new DTs appear throughout the Paleocene, but the number of first appearances may be elevated due to edge effects (Foote 2000). Both plant and DT turnover are high during the PETM. This likely represents a northward migration by thermophilic plants and highly specialized insect herbivores in response to warming (Currano *et al.* 2008; Wing *et al.* 2005). A peak in floral last occurrences occurs during

USNM Locality Number	Epoch, Mammal Zone	Age (Ma)	Formation	Mean Annual Temperature (oC)	No. of Leaves in census
USNM 42400 - 42406	Eocene, Wasatchian 7	52.75	Willwood	22.2 ± 2 *	1821
37560	Eocene, Wasatchian 5	53.4	Willwood	15.8 ± 2.2 *	693
USNM 37654, 42407, 42408, 42409, 42410	Eocene, Wasatchian 3-4	54.2	Willwood	11.1 ± 2.8	491
USNM 42395 – 42399	Eocene, Wasatchian 1-2	55.2	Willwood	16.4 ± 2.7 *	1008
USNM 42384	PETM (Eocene), Wasatchian 0	55.8	Willwood	20.1 ± 2.8 ‡	995
USNM 41643	Paleocene, Clarkforkian 3	55.9	Fort Union	16.4 ± 2.9	843
USNM 42411	Paleocene, Clarkforkian 2	56.4	Fort Union	12 ± 3	1016
USNM 42042	Paleocene, Tiffanian 5b	57.5	Fort Union	10.5 ± 2.9 †	1364
USNM 42041	Paleocene, Tiffanian 4a	58.9	Fort Union	10.5 ± 2.9 †	840

Table 1 Sampling summary. The Wasatchian 7 and Wasatchian 1-2 levels have more than one USNM locality number because multiple quarries were dug within the same bed. Leaf fossils from the cool period (Wasatchian 3-4) are scarce, and those included here come from four quarries in the same bed (USNM 42407-42410) and an additional quarry that is 8.5 miles away but within 5 meters stratigraphically (USNM 37654). Temperature estimates are from the following sources:

\* Wing *et al.* (2000) || Currano (2008) ‡ Wing *et al.* (2006) † Currano *et al.* (2008)

the cool period (Wa2/3), followed by an increase in floral first appearances during the EECO (Wa7; Wing 1998). The insect damage data show a similar pattern, although there are more last appearances in Wa5 than Wa2/3, perhaps suggesting a lag between changes in floral and insect damage composition. This implies that plants and insect herbivores do not always respond synchronously to climate change.

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