



Taphonomic experiments on damaged leaves: implications for interpreting insect-damaged leaves in the fossil record

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Abstract

Ancient interactions between plants and insect herbivores are primarily understood through investigations of insect feeding damage on fossil leaves. Such damage is assigned to a damage type on the basis of its morphology. The damage type system is a valuable tool for comparing insect herbivory between different sites; however, for such comparisons to be quantitatively robust requires that the fossilization process does not significantly alter the morphology of herbivore damage on leaves. Here we test the effect of decay in water on leaves with simulated hole or margin feeding damage through controlled laboratory experiments. *Crataegus intricata* leaves were artificially damaged with hole punches and then left to decay in river water for 50 days. The morphology of the damage was checked on days 0, 3, 5, 7, 10, 12, 14, 17, 21, 24, 27, 31, 34, 37, 44, and 50, and each leaf was assigned to a damage type. Although the leaves underwent many decay-related changes, the damage did not change in any noticeable way in any experimental replicate, and the assigned DTs did not change. These results indicate that decay in standing water does not alter the morphology of damage on leaves. Further studies are needed to assess if other components of the fossilization process, such as transport, decay in sediment, or diagenetic alteration can alter herbivore damage on leaves.

Keywords Taphonomy · Damage type · Plant-insect interactions · Herbivory · Experiment

Introduction

Preserved traces of insect herbivory on fossil leaves provide robust evidence for ancient plant-insect herbivore interactions (Labandeira and Wappler 2023). These interactions play a major role in terrestrial ecosystems (McCoy et al. 2021; Swain et al. 2022), making them an important component of paleoecology (e.g., Wing et al. 2009; Wappler et al. 2009, 2012; Currano et al. 2010, 2021; Labandeira et al. 2014, 2016; Donovan et al. 2014; Schachat et al. 2014; Xu et al. 2018; Maccracken and Labandeira 2020; Liu et al. 2020; Carvalho et al. 2021; Xiao et al. 2022; Labandeira et

al., 2023). Quantification of these herbivore traces became possible with the development of the damage type (DT) system, in which herbivore damage on fossil leaves is separated into seven broad functional feeding groups (FFGs) (Labandeira et al. 2007; Labandeira and Wappler 2023): hole feeding, margin feeding, skeletonization, surface feeding, piercing and sucking, oviposition, leaf mining, and galling (Labandeira et al. 2007). Damage is then further assigned to a unique DT based on the morphological characteristics of the damage (Labandeira et al. 2007; Labandeira and Wappler 2023). Any species of herbivore could in theory produce multiple DTs, and any DT could in theory be produced by multiple species of herbivore, so the DT system is somewhat decoupled from taxonomic diversity and rather represents ecological complexity (Swain et al. 2022). The DT system is a standardized way to quantify damage, and allows for quantitative comparison between fossil sites, or between fossil sites and modern ecosystems (e.g., Carvalho et al. 2014; Adroit et al. 2020; Carvalho et al. 2021; Donovan et al. 2020; Hazra et al. 2022; Swain et al. 2022; Labandeira et al. 2023).

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However, the DT system is used for direct quantitative comparisons between different fossil sites, even those that may have been formed under different taphonomic regimes (see examples of quantitative comparisons summarized in Labandeira et al. 2023). This approach therefore has the unspoken assumption, that decay, fossilization, and diagenesis do not meaningfully alter the morphology of herbivore damage. In other words, a specific numbered DT, for example DT81, has exactly the same meaning regardless of whether it is on a modern leaf or a leaf fossilized under one set of fossilization conditions, or a fossil leaf fossilized under a different set of fossilization conditions. There is some evidence to support this. For example, a study comparing damage on living leaves to damage on leaf packs found no meaningful differences, suggesting that the stages of taphonomy up to that point did not alter DTs on the leaves (Azevedo-Schmidt et al. 2022). However, there have been no controlled laboratory studies to assess if and how the stages of fossilization alter herbivore damage on leaves.

Here we test four hypotheses about the effect of decay in water on the morphology of leaf damage through controlled laboratory decay experiments. In this study, we are using the term ‘decay’ in the standard way it is used in taphonomic experiments (see e.g., Gupta and Pancost 2004) of meaning the physical and biomolecular changes that occur after an organism dies, and before its tissues stabilize or mineralize to produce a fossil.

Hypothesis 1 Decay in water will not alter the morphology and DT assignment, of damage on leaves.

Hypothesis 2 The shape of the damage will not affect whether the morphology and DT assignment of the damage changes through decay.

Hypothesis 3 The position of the damage on the leaf will not affect whether the morphology and DT assignment of the damage changes through.

Hypothesis 4 The damaged area will provide an additional opening for microbes to enter the leaf, so that leaf decay will start around the damaged region.

Materials and methods

Leaves for these experiments were collected from a *Crataegus intricata* (Copenhagen hawthorn) tree located in Milwaukee, WI, USA. Leaves were selected to fit within the experimental vessel, a 5 cm Petri dish, without folding or touching the sides. In addition, we picked leaves with no pre-existing damage (from insect feeding or other factors).

By including only undamaged leaves from only one tree, the goal was to minimize variation that might influence decay. Although leaves are not often found as singletons but rather fossilized leaf litter (Burnham et al. 1992), and leaf-leaf interactions may influence the decay and alteration of damage, restricting our experiments to one leaf per vessel minimized variation between experimental replicates.

Water for the experiments was collected from the Milwaukee River to provide a natural source of microbes of a type which is likely to influence plant fossilization; leaves commonly fossilize in fluvial or lacustrine environments (Locatelli 2014). After the leaves and water were collected, they were relocated to the lab, where the experiments were set up within one hour of removing the leaves from the tree. The goal was to set up the experiments as quickly as possible, to minimize the time between plucking the leaves and damaging the leaves; however, each replicate took some time to set up and altogether it took about an hour.

Leaves were damaged using one of two hole punches, circular or oblong, in one of two locations, on the margin of the leaf or completely contained in the leaf, resulting in four treatment groups: circular edge, circular center, oblong edge, oblong center. Undamaged leaves were also used as a control group. There were seven replicates in each of the four treatment groups and in the control group, for a total of 35 experiments. By using hole punches rather than natural insect damage, we were able to produce identical damage for each experimental replicate in each treatment group, giving us more control over the experiment and removing the variability inherent in real insect damage. In addition, we could be certain that all damage was produced at exactly the same time.

The artificial damage for each treatment group was assigned a DT following Labandeira et al. (2007). In treatment group 1, the seven leaves were damaged using the round hole punch, ~6 mm in diameter, and the hole was fully surrounded by leaf tissue. This produced damage that can be categorized as damage type DT04 (Labandeira et al. 2007): “circular perforations > 5 mm in diameter.” In treatment group 2, the seven leaves were damaged using the round hole punch, ~6 mm in diameter, and the damage was on the leaf margin, resulting in almost perfectly circular damage subtending slightly more than a 180° arc. This produced damage that can be categorized as damage type DT81 (Labandeira et al. 2007): “almost or perfectly circular, > 180° of arc, can range from a cusped excision to a hole.” In treatment group 3, the seven leaves were damaged using the oblong hole punch, ~15 mm long and ~3 mm wide, and the hole was fully surrounded by leaf tissue. This produced damage that can be categorized as damage type DT08 (Labandeira et al. 2007): “parallel sided, rectilinear or curvilinear; length / width ratio > 2.5.” In treatment group 4, the

seven leaves were damaged using the oblong hole punch, ~15 mm long and ~3 mm wide, and the damage was on the leaf margin, resulting in damage that is only partially the length of the hole punch, ~7.5 mm long and ~3 mm wide. This produced damage that can be categorized as damage type DT15 (Labandeira et al. 2007): “An excision that is deeply incised or expands toward a primary vein.”

After being damaged, each leaf was placed in a petri dish and covered in water from the Milwaukee River. The experiments were stored in sealed Ziploc® bags in a fume hood to prevent them from drying out. In the event of water loss to evaporation in any petri dish, the dishes were replenished with additional Milwaukee River water.

The leaves were photographed over the course of 50 days, using a Samsung Galaxy S22® camera, on days 0, 3, 5, 7, 10, 12, 14, 17, 21, 24, 27, 31, 34, 37, 44, and 50. Using the photographs, the damage on the leaf (whether original or changed through decay) was assigned to a damage type (DT) (Labandeira et al. 2007) to determine if decay in water would alter the morphology of damage on a leaf to a large enough extent to change its DT. Representative photos from each treatment group at various times are presented in Fig. 1, and all photographs are available at <https://figshare.com/s/2756e7706b38257493be>.

Results

Control group

The undamaged leaves of the control group demonstrate the changes that develop in leaves that do not have insect damage after 50 days in water (Fig. 1A–D). These leaves stayed a bright, fresh-looking green color for the first few days of the experiments. By day 5, though, most of the leaves had started to develop spots and larger regions of light green, yellow, or light brown. These regions likely represent the first areas of decay, and their position is determined by where the decay microbes are able to infiltrate the leaf. There are no obvious patterns as to where these regions of initial decay are located on the leaves. By day 7, all the leaves were showing patches of decay, and in some, the surrounding water was turning brown. By day 10, the water around many of the leaves became brown, and in some cases there was a brown slimy material surrounding the leaf, which is likely a large amount of decay microbes, fungi, or a microbial mat. As the experiments progressed, the discolored, decayed patches on the leaves increased in size and became darker. By day 50, all of the leaves were a uniform dark brown or black (Fig. 1D). The overall shape of the leaf did not change noticeably, and no damage reminiscent of herbivore damage developed.

Treatment group 1

In general, the decay of these leaves (Fig. 1E–H) followed the same pattern as the undamaged leaves, with discolored regions starting to develop by days 5–7. Of the seven leaves in this treatment group (leaves 8–14), the discolored, decayed regions developed around the damage in only two of the leaves, leaf 8 (Fig. 2A) and leaf 11. For leaves 9, 10, 12 (Fig. 2B), and 13, the decay originated somewhat randomly elsewhere on the leaf. For leaf 14, the decay started at the petiole, which was broken, and although it quickly appeared to encompass the hole damage, there was initially a non-decayed green region around the hole, indicating the damage did not start here (Fig. 2C). All leaves were very fragile and completely dark brown to black by day 50 (Fig. 1H). In addition, in these replicates, by day 3, a yellowish-brown to black rim started to develop around the damaged area in most of the leaves (Figs. 1E–H and 3a), which showed little further change throughout the course of the experiments.

Despite the changes in color and robustness of the leaves over 50 days of decay, the damage remained the same damage type, DT04, throughout the course of the experiments in all seven replicates (Fig. 1E–H). The one possible exception to this is leaf 14. By day 50, there was a transparent window extending out from the damage into the leaf, where the interior of the leaf appears to have decayed (Fig. 4). However, it is clear that the cuticle and veins still remain in this transparent window, and in a fossil, this likely would still have been assigned to DT04.

Treatment group 2

These leaves followed the same decay patterns (Fig. 1I–L) as the control group and treatment group 1, with discolored decayed regions developing in days 5–7, and all leaves entirely dark brown to black by day 50. Of the seven leaves in this treatment group (leaves 15–21), decay started around the hole-punched damage only in leaves 15 and 20. For the rest, the decay started elsewhere on the leaf. A dark rim started developing around the damage by day 3 (Figs. 1I–L and 3b) and showed little change throughout the course of the experiments. There was no change to the size or shape of the damage, and it remained DT81 throughout the course of the experiments (Fig. 1I–L).

Treatment group 3

These leaves followed the same decay patterns (Fig. 1M–P) as the control group and treatment groups 1 and 2. A dark rim started developing around the damage by day 3 (Fig. 3c) and showed little change throughout the course of the experiments. Discolored decayed regions developing in

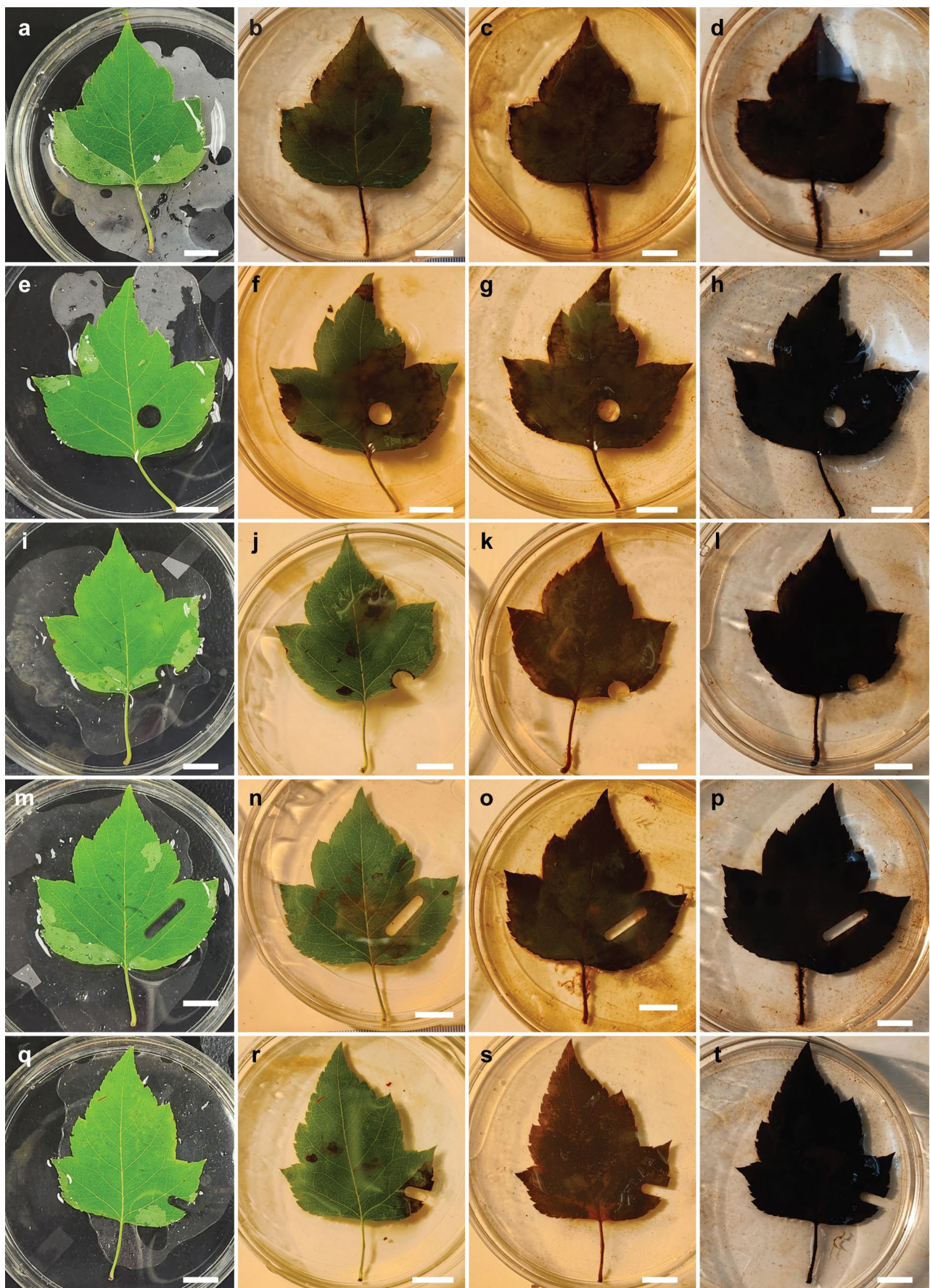


Fig. 1 Photos of one experimental replicate from each treatment group and the control group, at Day 0, Day 14, Day 34, and Day 50 of decay in river water. **a–d** Control group, leaf 2. **e–h** Treatment group 1, leaf 11. **i–l** Treatment group 2, leaf 16. **m–p** Treatment group 3, leaf 24. **q–t** Treatment group 4, leaf 33. Scale bars = 10 mm

days 5–7, and all leaves entirely dark brown to black by day 50 (Fig. 1P). Of the seven leaves in this treatment group (leaves 22–28), decay started around the hole-punched damage only in leaf 22. For the rest, the decay started elsewhere on the leaf. In leaf 26, the petiole was damaged, but the decay did not start from the petiole either. The damage remained DT08 throughout the course of the experiments (Fig. 1M–P).

Treatment group 4

These leaves followed the same decay patterns (Fig. 1Q–T) as the control group and treatment groups 1, 2, and 3. A dark rim started developing around the damage by day 3 (Figs. 1Q–T and 3) and showed little change throughout the course of the experiments. Discolored decayed regions developing in days 5–7, and all leaves entirely dark brown to black by day 50 (Fig. 1T). Of the seven leaves in this treatment group (leaves 29–35), decay started around the hole-punched damage only in leaves 29, 31, 33, and 35. For the rest, the decay started elsewhere on the leaf. The damage remained DT15 throughout the course of the experiments.

Discussion

Interpretation of the brown rim around the damage

Sometime within the first few days after the leaves were damaged, between the time the experiments were set up and our first photography session on day 3, a dark brown to black rim developed around the damage in every experimental replicate. This may represent wound reaction tissue. When a plant is damaged or wounded, this induces a number of responses, which can include the production of specialized, thickened tissue, composed of lignin, phenolics, and dead cells, around the wound to prevent further damage or infection (Savatin et al. 2014; Vega-Muñoz et al. 2020). Although the leaves had been removed from the tree before being damaged, the time gap was less than an hour. Harvested crops (e.g., cut lettuce leaves) are known to still exhibit wound reactions despite being removed from the rest of the plant (Iakimova and Woltering 2018). Although an alternative possible interpretation is that this dark rim is simply an initial decay front. However, all other decay patches on these leaves changed and expanded over the

course of the experiments; it seems unlikely that a region of decay would not change or expand over 50 days.

Hypotheses 1–3

The damaged leaves in these experiments exhibit qualitatively similar decay patterns to undamaged leaves. Moreover, up to 50 days of decay in water results in no change to the shape or assigned DT for damage on a leaf, regardless of the original shape or position of the damage. Therefore, the results of these decay experiments support our hypotheses 1–3: decay in water will not alter the morphology and DT assignment, of damage on leaves; the shape of the damage will not affect whether the morphology and DT assignment of the damage changes through decay; and the position of the damage on the leaf will not affect whether the morphology and DT assignment of the damage changes. However, these experiments do not encompass all morphologies and locations of insect damage on leaves or the entire leaf fossilization process.

Additional experiments would be needed to test the effects of decay in water on other morphologies of damage.

Hypothesis 4

Notably, decay, as indicated by discolored regions in the leaf, was not consistently initiated around damaged parts of the leaves. The results of this experiment, therefore, do not support our hypothesis 4: the damaged area will provide an opening for decay microbes to enter the leaf, so that leaf decay will start around the damaged region.

Holes in leaves, for example wounds or damaged areas, are potential entry points for pathogens and decay microbes, allowing them to bypass the protective exterior cuticle of the leaf and either infect the living leaf (Savatin et al. 2014; Vega-Muñoz et al. 2020) or decay a dead leaf (Gupta and Pancost 2004; Iniesto et al. 2018; Witkowski et al. 2022). Gupta and Pancost (2004), who experimentally decayed leaves in various conditions, found that decay-induced alteration (e.g., color changes, cracks in the cuticle, development of pits, etc.) was highest around stomata, suggesting that these openings allowed degradative elements to enter the leaf. Similarly, the lower surfaces of the leaves showed more decay than the upper surfaces, which they attributed in part to the higher number of stomata on the lower surfaces (Gupta and Pancost 2004). Iniesto et al. (2018) also observed more rapid decay in the lower side of fern pinnules (compared to the upper side of the pinnules), which they also suggested was due at least partially to the presence of stomata. In addition, Witkowski et al. (2022) observed fungal hyphae enter *Metasequoia* leaves through the stomata during decay experiments. In our experiments, when decay

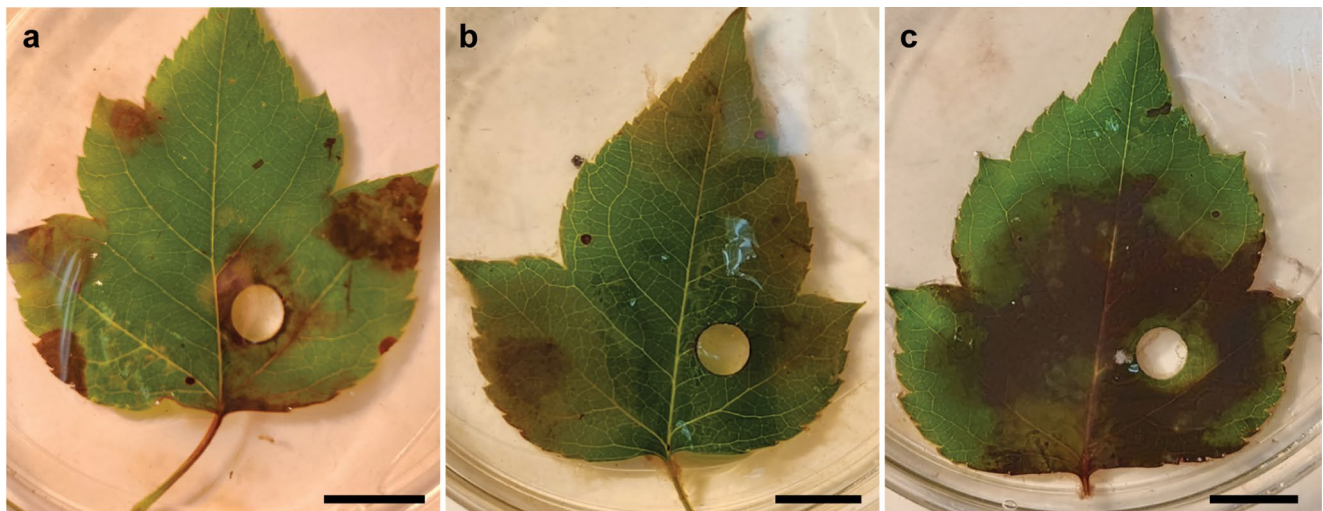


Fig. 2 Examples of decay starting at different parts of the leaf. All leaves are from treatment group 1 on day 12. **a** Leaf 8. **b** Leaf 12. **c** Leaf 14. Scale bars = 10 mm

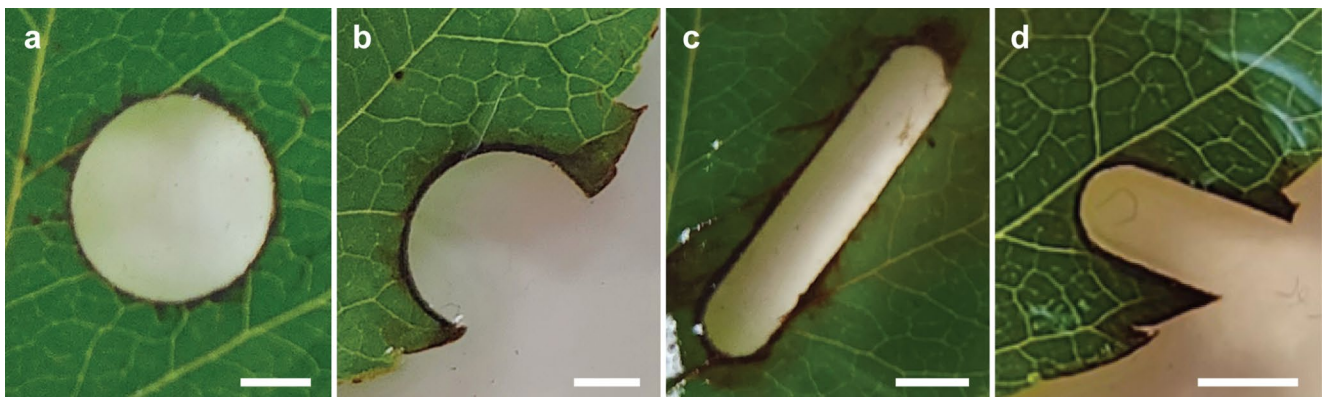


Fig. 3 Wound reaction tissue. **a** Leaf 9 from treatment group 1 on day 5. **b** Leaf 15 from treatment group 2 on day 5. **c** Leaf 22 from Treatment group 3 on day 10. **d** Leaf 34 from treatment group 4 on day 10. Scale bars = 2 mm

was initiated in an area with no visible wound or damage, the stomata are a likely entry point for decay microbes. Alternatively, wounds too small for the naked eye to see can allow pathogens to enter and infect the leaf (Vega-Muñoz et al. 2020) and presumably could allow decay microbes to enter the leaf as well.

Larger areas of damage, such as wounds induced by herbivores, or mechanical damage of dead leaves, can also allow pathogens and decay microbes to enter leaves (Gupta and Pancost 2004; Iniesto et al. 2018; Savatin et al. 2014; Vega-Muñoz et al. 2020). Decay, as indicated by a darkened region, has been observed at the base of the leaf when there is damage to the petiole (Gupta and Pancost 2004). Moreover, when leaves ripped or ruptured during the course of decay experiments (often because of how fragile leaves become after decay), these areas of damage allowed microbes to enter. Gupta and Pancost (2004) observed higher amounts of decay alteration around ruptures in leaves, as well as directly observed bacterial growth (using SEM) in ruptures.

Iniesto et al. (2018) observed fungal filaments growing into cracks in fern pinnules during their decay experiments. In contrast to these results, in our experiments, two of the leaves had broken petioles, but decay was only initiated at the base of the leaf in one of these. Similarly, 28 of the leaves were damaged using a hole punch, but decay was initiated around the damage in only nine of these (27%).

Potentially the difference between our results and previous results is the timing of the damage and the influence of wound reaction tissue. In our experiments, all leaves were damaged within one hour of removing them from the tree, and a dark rim visibly developed within a few days. If this dark rim is indeed wound reaction tissue, it may have inhibited the entry of microbes into the leaf. Wound reaction tissue, generally speaking, as well as other response such as immune system activation, plays a role in sealing wounds and preventing infection and infiltration of wounds by microbes (Savatin et al. 2014; Vega-Muñoz et al. 2020). In previous experiments in which microbes and fungi were

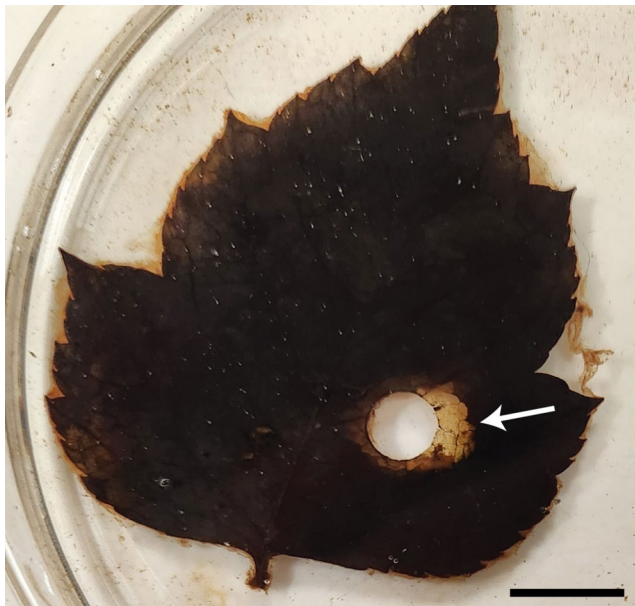


Fig. 4 Leaf 14 in treatment group 1 at day 50 of decay, showing the transparent rectangular window (arrow) extending from the hole into the leaf. Scale bar = 10 mm

observed entering damaged areas of the leaves, the ruptures and cracks happened after significant decay, when the leaves were very fragile, and there would not have been any wound reaction tissue forming after the leaf is so long-dead.

Wound reaction tissue and other wound responses by plants are not infallible at protecting against infection. For wound infection in plants, the timing of when pathogens are introduced to the wound (whether they are present before and during wounding, or only after) influences whether a pathogen will successfully infect a plant (Vega-Muñoz et al. 2020). For our experimental replicates in which decay did start at the wound, the microbes may have been present earlier, and able to infiltrate the leaf prior to extensive wound reactions. In terms of extrapolating these results to real-world herbivore induced damage, if the herbivore is the vector of the pathogen, then that would be introduced immediately to the wound and might initiate decay at the wound. Similarly, insect herbivores and pathogens have mechanisms to circumvent wound reactions (Vega-Muñoz et al. 2020), and these mechanisms may enhance decay around herbivore damage in leaves. However, even in our replicates where decay was most rapid and extensive directly around the damage, there were no changes to the assigned DT. Therefore, even if herbivore damage will more consistently be the region of initial decay in a leaf, it is unlikely to result in significant alteration to the morphology of the damage.

Limitations of these experiments

Leaf fossilization is a complicated process, and decay in water is only one small part of it (Greenwood 1991; Spicer 1991; Burnham et al. 1992; Locatelli 2014). Moreover, variations in factors such as temperature, water and sediment composition, and composition of the microbiota can also significantly affect fossilization (e.g., Palmer et al. 2024, 2025). Leaf fossilization typically occurs in aquatic environments such as lakes, or rivers (Locatelli 2014), and so most leaves, prior to fossilization, spend some time floating in or being transported by water (Greenwood 1991; Spicer 1991). For deciduous leaves, the time spent in water is rarely more than a few days, so transport distances are short, although evergreen leaves may float for several weeks over longer distances (Greenwood 1991; Spicer 1991). The duration of the experiment presented here (50 days) covers all typical lengths of time that isolated leaves might be in the water column. Based on our experiments, the morphology and DT assignment of actual insect damage is unlikely to be altered by this portion of leaf taphonomy. After spending some time in water, leaves will eventually sink and get buried and will be subject to additional alteration such as further decay, scavenging, chemical alteration, or mineralization (Locatelli 2014). The goal of the experiments presented here is not to perfectly replicate the fossilization process, or even to test every variable of interest, but rather to provide a carefully controlled assessment of how one aspect of the fossilization process (leaf decay in water) may alter damage on the leaves. Additional taphonomic experiments, especially under more natural conditions, would be necessary to determine if these other aspects of the leaf fossilization process would alter the morphology or damage type assignment of insect damage on leaves.

Conclusions

Laboratory experiments testing the effect of decay in water on leaves with simulated hole feeding or margin feeding damage demonstrate no change to the shape or assigned DT of the damage. Decay in water therefore would not affect the interpretation of damaged fossil leaves. This adds to the body of evidence that fossilization does not affect insect damage on leaves, and therefore that quantitative comparisons are valid between fossil and extant ecosystems, and between fossil sites with different mechanisms of fossilization. However, additional studies are needed to similarly assess other types of damage and other aspects of the leaf fossilization process.

Data Availability

The photos of all experimental and control replicates at all time points are available at <https://figshare.com/s/2756e7706b38257493be>.

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Author contributions M.G. and V.E.M. conceived of and designed the study. M.G. and J.J.P. gathered materials and set up the experiments. M.G. photographed the experiments and assigned damage types at each stage of decay. M.G. and J.J.P. interpreted the results. M.G. and V.E.M. write the first draft of the paper. All authors reviewed the manuscript.

Data availability The photos of all experimental and control replicates at all time points are available at <https://figshare.com/s/2756e7706b38257493be>.

Declarations

Competing interests The authors declare no competing interests.

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References

- Adroit B, Zhuang X, Wappler T et al (2020) A case of long-term herbivory: specialized feeding trace on *Parrotia* (Hamamelidaceae) plant species. *R Soc Open Sci* 7:201449
- Azevedo-Schmidt L, Meineke EK, Currano ED (2022) Insect herbivory within modern forests is greater than fossil localities. *Proc Natl Acad Sci USA* 119(42):e2202852119. <https://doi.org/10.1073/pnas.2202852119>
- Burnham RJ, Wing SL, Parker GG (1992) The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18:30–49
- Carvalho MR, Wilf P, Barrios H et al (2014) Insect leaf-chewing damage tracks herbivore richness in modern and ancient forests. *PLoS ONE* 9:e94950
- Carvalho MR, Jaramillo C, de la Parra F et al (2021) Extinction at the end-Cretaceous and the origin of modern Neotropical rainforests. *Science* 372:63–68
- Currano ED, Labandeira CC, Wilf P (2010) Fossil insect folivory tracks paleotemperature for six million years. *Ecol Monogr* 80:547–567
- Currano ED, Azevedo-Schmidt LE, Maccracken SA, Swain A (2021) Scars on fossil leaves: an exploration of ecological patterns in plant–insect herbivore associations during the age of angiosperms. *Palaeogeogr Palaeoclimatol Palaeoecol* 582:110636
- Donovan MP, Wilf P, Labandeira CC et al (2014) Novel insect leaf-mining after the end-Cretaceous extinction and the demise of cretaceous leaf miners, great Plains, USA. *PLoS ONE* 9:e103542
- Donovan MP, Wilf P, Iglesias A et al (2020) Persistent biotic interactions of a Gondwanan conifer from cretaceous patagonia to modern Malesia. *Commun Biol* 3:708
- Greenwood DR (1991) The taphonomy of plant macrofossils. In: Donovan SK (ed) *The processes of fossilization*. Columbia University, New York, pp 141–169
- Gupta NS, Pancost RD (2004) Biomolecular and physical taphonomy of angiosperm leaf during early decay: implications for fossilization. *Palaios* 19(5):428–440. [https://doi.org/10.1669/0883-1351\(2004\)019%3C0428:BAPTOA%3E2.0.CO;2](https://doi.org/10.1669/0883-1351(2004)019%3C0428:BAPTOA%3E2.0.CO;2)
- Hazra T, Adroit B, Hazra M et al (2022) New discovery of rare insect damage in the pliocene of India reinforces the biogeographic history of Eurasian ecosystems. *Rev Palaeobot Palynol* 298:104589
- Iakimova ET, Woltering EJ (2018) The wound response in fresh-cut lettuce involves programmed cell death events. *Protoplasma* 255(4):1225–1238
- Iniesto M, Blanco-Moreno C, Villalba A, Buscalioni ÁD, Guerrero MC, López-Archilla AI (2018) Plant tissue decay in long-term experiments with microbial Mats. *Geosci J* 8(11):387. <https://doi.org/10.3390/geosciences8110387>
- Labandeira CC, Wappler T (2023) Arthropod and pathogen damage on fossil and modern plants: exploring the origins and evolution of herbivory on land. *Ann Rev Entomol* 68:341–361. <https://doi.org/10.1146/annurev-ento-120120-102849>
- Labandeira CC, Wilf P, Johnson KR (2007) *Guide to insect (and other) damage types on compressed plant fossils*. Version 3.0. Smithsonian Institution, Washington, D.C
- Labandeira CC, Tremblay SL, Bartowski KE, VanAller Hernick L (2014) Middle devonian liverwort herbivory and antiherbivore defence. *New Phytol* 202:247–258
- Labandeira CC, Kustatscher E, Wappler T (2016) Floral assemblages and patterns of insect herbivory during the permian to triassic of Northeastern Italy. *PLoS ONE* 11:e0165205
- Liu H-Y, Wei H-B, Chen J et al (2020) A latitudinal gradient of plant–insect interactions during the late permian in terrestrial ecosystems? New evidence from Southwest China. *Glob Planet Change* 192:103248
- Locatelli ER (2014) The exceptional preservation of plant fossils: a review of taphonomic pathways and biases in the fossil record. *Paleontological Soc Papers* 20:237–258
- Maccracken SA, Labandeira CC (2020) The middle permian South Ash pasture assemblage of North-Central Texas: coniferophyte and gigantopterid herbivory and Longer-Term herbivory trends. *Int J Plant Sci* 181:342–362
- McCoy VE, Wappler T, Labandeira CC (2021) Exceptional fossilization of ecological interactions: plant defenses during the four major expansions of arthropod herbivory in the fossil record. In: Gee CT, McCoy VE, Sander PM (eds) *Fossilization: Understanding the material nature of ancient plants and animals*. Johns Hopkins University, Baltimore, pp 187–220
- Palmer B, Karačić S, Low SL et al (2024) Decay experiments and microbial community analysis of water Lily leaf biofilms: sediment effects on leaf preservation potential. *PLoS ONE* 19:e0315656
- Palmer B, Karačić S, Liesegang M, Bierbaum G, Gee CT (2025) Microbial taphonomy of Ginkgo leaves in fine-grained substrates: how sediment type facilitates preservation. *Palaeontology* 68(6):e70037

- Savatini DV, Gramegna G, Modesti V, Cervone F (2014) Wounding in the plant tissue: the defense of a dangerous passage. *Front Plant Sci* 5:470. <https://doi.org/10.3389/fpls.2014.00470>
- Schachat SR, Labandeira CC, Gordon J et al (2014) Plant-insect interactions from early permian (kungurian) Colwell creek pond, north-central texas: the early spread of herbivory in riparian environments. *Int J Plant Sci* 175:855–890
- Spicer RA (1991) Plant taphonomic processes. *Taphonomy: Release Data Locked Fossil Record* 9:71–113
- Swain A, Maccracken SA, Fagan WF, Labandeira CC (2022) Understanding the ecology of host plant–insect herbivore interactions in the fossil record through bipartite networks—Corrigendum. *Paleobiology* 48:353–355
- Vega-Muñoz I, Duran-Flores D, Fernández-Fernández ÁD, Heyman J, Ritter A, Stael S (2020) Breaking bad news: dynamic molecular mechanisms of wound response in plants. *Front Plant Sci* 11:610445. <https://doi.org/10.3389/fpls.2020.610445>
- Wappler T, Currano ED, Wilf P et al (2009) No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. *Proceedings of the Royal Society B: Biological Sciences* 276:4271–4277
- Wappler T, Labandeira CC, Rust J et al (2012) 565 testing for the effects and consequences of mid paleogene climate change on insect herbivory. *日本花粉学会会誌* 58:255
- Wing SL, Herrera F, Jaramillo CA et al (2009) Late paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proc Natl Acad Sci U S A* 106:18627–18632
- Witkowski CR, Leng Q, Reid CW, Feng L, Yang H (2022) Tissue decay tested in modern metasequoia leaves: implications for early diagenesis of leaves in fossil Lagerstätten. *Rev Palaeobot Palynol* 304(104720):104720. <https://doi.org/10.1016/j.revpalbo.2022.104720>
- Xiao L, Labandeira CC, Dilcher DL, Ren D (2022) Arthropod and fungal herbivory at the dawn of angiosperm diversification: The Rose Creek plant assemblage of Nebraska U.S.A. *Cretac Res* 131:105088
- Xu Q, Jin J, Labandeira CC (2018) Williamson drive: herbivory from a north-central Texas flora of latest Pennsylvanian age shows discrete component community structure, expansion of piercing and sucking, and plant counterdefenses. *Rev Palaeobot Palynol* 251:28–72

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