International Journal of Paleopathology 4 (2014) 1–16

Contents lists available at ScienceDirect

International Journal of Paleopathology

journal homepage: www.elsevier.com/locate/ijpp

Invited Commentary

Plant paleopathology and the roles of pathogens and insects

Conrad C. Labandeira[a,b,c,d,*], Rose Prevec[b,1]

[a] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA
[b] Department of Geology, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa
[c] College of Life Sciences, Capital Normal University, Beijing, 100048, China
[d] Department of Entomology and BEES Program, University of Maryland, College Park, MD 29742, USA

ARTICLE INFO

Article history:
Received 1 June 2013
Received in revised form 25 October 2013
Accepted 26 October 2013

Keywords:
Bacteria
Fossil record
Fungi
Insects
Nematodes
Paleopathology
Pathogens
Plant–insect interactions
Plants
Vectors
Viruses

ABSTRACT

Plant pathologies are the consequence of physical and chemical responses by plants to invasive microorganisms or to imbalances in nutritional or environmental conditions. Many factors determine the potential for plant disease infection and disease, but the primary components are the terrestrial host plant, the pathogen, the environment, and occasionally a biological vector. Pathogens typically are one of four major causative groups: viruses, bacteria, fungi, and nematodes. The vector often is a passive abiotic agent such as wind, water or soil, but it also may be an insect that actively facilitates transmission of the pathogen to a plant. Pathogenic invasion of plants may require sophisticated structures for penetration of host tissues and can elicit a range of host responses such as production of defensive compounds, callus tissue, galls and necroses to seal wounded or infected areas. Fossil diseases primarily are diagnosed from surface leaf structures internal tissues, categorized into damage types (DTs), important for tracking the evolution of herbivore and pathogen attack and host-plant response in time, space and habitat. The fossil record is a useful, underappreciated, but accessible archive of plant damage. We present an overview of pathogens and life cycles that involve insects in the production of these disease symptoms in fossil plants.

Published by Elsevier Inc.

1. Introduction

If one mentions the term paleopathology among the biological or geological community, commonly the first thought that registers is the archeological record of human diseases reflected in various skeletal abnormalities (Ortner, 2011). The vertebrate fossil record also comes to mind, consisting of atypical, histological malformations that result from disease, growth anomalies, predation, or accidents incurred during life. Rarely considered is the broader compass of associations among other fossil organisms. Among these other associations are data from plant fossils that include insect herbivory from the compression–impression record which is becoming increasingly robust (Labandeira and Currano, 2013), as well as the more modest yet significant records of invertebrate animal–animal interactions. Examples of such relationships include the altered tissues of insect hosts by their nematode parasitoids (Poinar, 2012), and the healed wounds surrounding unsuccessful drill holes in the shells of marine mollusks by gastropod predators (Kelley and Hansen, 2003).

These paleopathological relationships occur in compression-impression or permineralized deposits. Compression fossils are the flattened, carbonized remains of organisms found in rock matrix. Related impression fossils are the remains of weathered compression fossils, essentially comprising a flattened mold of the original organism without any organic material remaining. By contrast, permineralized fossils are three-dimensionally preserved organisms typically in a silica or carbonate matrix, that result from mineralizing fluids perfusing the organic material at a cellular level.

Our application of the term "plant pathology," used here in reference to the fossil record, is therefore more eclectic than generally applied to the study of modern plant diseases. In extant plant pathology, biological damage to plants inflicted through the activity of insect herbivores is excluded. However, in the same way that paleopathological studies of fossilized vertebrates explore the origins of all healed wounds incurred during the life of the organism, we also include injuries acquired through herbivory within our concept of plant paleopathology. This is an essential modification in comparison to modern studies of plant pathology, as it is often impossible to distinguish in fossilized specimens between the symptoms of primary plant pathogens and organisms entering the host through wounds created during insect herbivory.

* Corresponding author at: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA.
Tel.: +1 202 633 1336; fax: +1 202 786 2832.
E-mail address: labandec@si.edu (C.C. Labandeira).
[1] Current address: Department of Earth Sciences, Albany Museum, Somerset St., Grahamstown, 6139, South Africa.

1879-9817/$ – see front matter. Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.ijpp.2013.10.002

Table 1
Insect-vectored pathogens likely to leave a fossil record on plant tissues.

Pathogen system	Common name	Pathogen	Insect vector	Functional feeding group	Plant host	Organ(s) affected	Tissue(s) affected	Damage types[a]	Figure	References
Virus	Barley Yellow Dwarf	*Luteovirus* (barley yellow dwarf virus)	*Rhopalosiphum* spp. (Hemiptera: Aphididae)	Piercer-&-sucker	*Hordeum vulgare* and other cereals	Seed, stem and leaf	Endosperm, phloem	DT46, DT48, DT136	Fig. 1	Burnett (1989), Martin et al. (1990), Gray et al. (1993) and Agrios (1997)
Bacterium	Curcubit Bacterial Wilt	*Erwinia tracheiphila* (curcubit bacterial wilt virus)	*Acalymma vittata*, *Diabrotica undecimpunctata* – Coleoptera: Chrysomelidae	External foliage feeder	*Cucumis sativus* (cucumber) and other Curcubitaceae	Leaf, fruit	Xylem, phloem (vessels)	DT03, DT04, DT05, DT50, DT126	Fig. 2	Watterson et al. (1972), Goodman and White (1981) and Agrios (1997)
Fungus	Dutch Elm Disease	*Ophiostoma ulmi* (an ascomycete)	*Scolytus multistriatus*, *Hylurgopinus rufipes* – Coleoptera Scolytidae	Wood borer	*Ulmus americana* (American elm) & other *Ulmus* spp.	Stem (trunk), leaves as an effect	Xylem (vessels, wood), bark, fibers, tracheids	DT160, DT174, DT123, undescribed borings	Fig. 3	Pomerleau (1970), Brasier (1991), Smalley and Guries (1993) and Agrios (1997)
Nematode	Red Ring Disease	*Bursaphelenchus coccophilus* (an aphelenchoidid)	*Rhynchophorous palmarum* – Coleoptera, Curculionidae	Pith borer	*Cocos nucifera*, *Elaeis guineensis*, *Phoenix dactilifera* (coconut, date and oil palms)	Stem, foliage	Ground parenchyma, foliar mesophyll	DT160, DT174, DT221, undescribed borings	Fig. 4	Griffith (1987), Giblin-Davis (1990) and Agrios (1997)

[a] See Labandeira et al. (2007).

In this contribution, we therefore offer a more expansive and inclusive definition of paleopathology that extends beyond that of the vertebrate fossil record. Our intention is to recognize the types of pathogens and the effects that their life cycles have, in association with herbivorous insects, for the production of disease symptoms in fossil plants. To do this, we necessarily discuss examples of well studied and economically important pathogen life cycles from modern agriculture and forestry. Such an approach forms our concept of paleopathology as a discipline that seeks to understand the deep historical wealth of interactions between plants, their insect herbivores, and colonizing pathogens (Berry, 1923), but nevertheless is informed by modern plant pathology (Agrios, 2005). Plant paleopathology involves the presence of numerous substrates and opportunities for pathogenic invasion of plant tissues resulting from both the feeding activity of herbivorous insects as well as independent ingress of plant-host tissues. We will focus on plant diseases caused by pathogens of internal vascular-plant tissues that appear to have been related to insect feeding activities such as chewing, piercing-and-sucking, mining, galling, seed predation and penetrative oviposition during the past 420 million years (Labandeira, 1997; Labandeira et al., 2007; Prevec et al., 2009).

2. Plant pathology and insects in the fossil record

2.1. What are plant pathologies and pathogens?

A plant disease is a deleterious metabolic imbalance at the cellular level usually caused by microorganisms (Holiday, 1989). Plant pathogens consist of viruses, bacteria inclusive of mollicutes, parasitic green algae, parasitic higher plants, rare protozoans, fungi in the broadest sense, and nematodes (Agrios, 2005). Factors such as excesses or a surfeit of minerals and nutrients, extreme temperatures and humidity, and oxygen availability also cause disease symptoms in plants. Imbalances in these latter, abiotic, factors result in so-called “noninfectious plant diseases,” whereas maladies that are induced by biotic factors are termed “infectious plant diseases” (Agrios, 2005).

A pathogen is an organism that causes a disease (Falkow, 1977), and as a parasite, it lives on or in another host organism and exists at the expense of the host. Pathogenicity is the ability of a parasite to interfere with its plant host’s basic metabolic processes, and consequently cause disease (Lindgren et al., 1986; Casadevall and Pirofski, 1999; Shapiro-Ilan et al., 2005). Pathogens may be biotrophic parasites, deriving nutrition from living cells using strategies aimed at minimizing or delaying host responses, or they may be necrotrophic parasites, aggressively invading and killing host cells. Obligate (biotrophic) parasites can survive and reproduce only within a living host, whereas many other organisms are facultative, able to survive as either parasites or saprophytes that live on dead organic matter (Reis et al., 1999). The variety of plant hosts that a pathogen can attack may be monospecific, such as a single species, a particular organ or tissue, or oligospecific, a taxonomically less circumscribed group of related species, to broadly eclectic preferences of hosts that lack phylogenetic connection (Tsuchiya, 2004). Additionally, in the case of some fungal pathogens with complex life cycles, such as rust fungi, different life phases of the same species may exhibit specificity on different, alternate plant hosts. Typically there are three key factors that are involved in the development of infectious diseases, and their relationship is sometimes referred to as the “disease triangle” (Francl, 2001). The three sides of the triangle are (1), the plant host; (2), the pathogen; and (3), the environment. The plant host must be sufficiently susceptible both in its genetic predisposition and in its physical context. The pathogen must display acceptable levels of availability and abundance in order for propagules (dispersed