The Biology and Epidemiology of Fire Blight

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INTRODUCTION

Fire blight has been a mystery for scientists and fruit growers for most of the 200 years since the first symptoms were described in the New York Hudson Valley. Epidemics can develop rapidly in orchards with no history of the disease, destroying much of the current crop and killing many large limbs or whole trees within a few months. Epidemics also can be minor affairs, causing no significant economic damage, even in orchards that suffered severe blight the previous season. Between these extremes, variation in the incidence and severity of fire blight that seems to follow no particular pattern from season to season and orchard to orchard is characteristic.

The cause of fire blight remained elusive for another century after symptoms were first seen when it was proven to be a bacterial pathogen we now know as Erwinia amylovora. Despite the importance of this discovery, the mystery would continue for yet another century before we could predict certain infection events.. Use of the Maryblyt™ predictive programs in managing fire blight will be discussed later. The purpose of this discussion is to present an overview on the biology and epidemiology of fire blight as a basis for understanding its effective management in the orchard.

DISEASE CYCLE

Plant disease is a dynamic process, not a static condition. It develops as the result of a three-way interaction over time involving the host plant, the pathogen and the environment. The parallel development of the host plant as it begins growth and matures and the pathogen as it becomes available, multiplies and incites infections during any given season tends to be cyclic in nature. Infection events occur only when the host is in a susceptible condition, pathogen inoculum is adequate and environmental conditions (e.g., temperature, moisture, wind, etc.) are suitable. Disrupting these basic interactions at any point (host x pathogen, host x environment, pathogen x environment) prevents disease from occurring and is the essence of any good control program.

2.1 Overwintering Sources of Inoculum. The pathogen overwinters in living bark tissues surrounding some cankers formed at the base of spurs or shoots killed the previous season. They can also form in the bark surrounding cuts made to remove infected shoots during the growing season. There are two types of cankers: determinate and indeterminate. Determinate cankers have strongly delimited margins, often marked by a distinct crack or separation of the bark caused by an effective, early season resistance mechanism in which a barrier of suberized, corky

tissue isolates the pathogen from the surrounding healthy bark tissue. Determinate cankers seldom serve as sources of inoculum the following season. Indeterminate cankers lack this physical barrier zone so that their margins usually appear smooth and continuous with the surrounding healthy bark surface. Here, damage caused by the bacteria in the intercellular spaces withdrawing water from healthy cells appears to be halted only by the high carbohydrate reserves that develop in the bark during the mid- to late- season (e.g., after mid-June). The bacteria do not overwinter in the dead tissue of indeterminate cankers but in the living bark tissue that surrounds them.

Data obtained in developing the Maryblyt™ predictive model for fire blight suggests that bacterial multiplication and the renewal of infectious activity at indeterminate canker margins probably begins in the early spring at about 93 cumulative degree days (CCD) >550F after green tip which is about the time of the tight cluster to early pink stage on apples. This is an important event in the development of fire blight epidemics because it marks the time when the pathogen is probably first available for dispersal in the orchard.

2.2 Inoculum Dispersal and Colonization. Once the bacteria become available as droplets of sweet, sappy ooze on the surface of bark, many different species insects (mostly flies) are attracted and to the oozing canker sites and begin the casual dispersal of inoculum from tree to tree, leaving colonies of bacteria wherever they walk. E. amylovora is a competent epiphyte in that it is capable of surviving and multiplying on plant surfaces several weeks before flowering begins. The bacteria can also be dispersed by rain either by direct splashing or as aerosols carried on even modest winds. Once the first early opening flowers are colonized by bacteria, further dispersal is not only rapid but specifically directed at open flowers through the activities of honey bees and other pollinators. The five stigmas in the center and top of each blossom have a moist, nutrient-rich surface that supports their selective colonization by the bacteria to high levels even though infection has not yet occurred. As honey bees arrive to collect pollen, the bacteria are picked up on their body hairs and are then subsequently moved to other flowers in the orchard.

2.3 Multiple Infection Types. One of the most significant findings in our work to develop the Maryblyt™ program was the identification of five distinct types of infections that can occur over the course of a fire blight epidemic. These are identified as blossom, canker, shoot, trauma and rootstock blight. Of these, only canker blight occurs every year where fire blight occurred the previous year and the incidence and severity of the others will vary depending upon the prevailing weather conditions. These various types of infections differ in the sources of inoculum, the type of tissues invaded, and the weather conditions governing the infection process. While each type can be readily distinguished at the early stage of symptom development, once an epidemic gets under way, it is more difficult to separate all the various types. This is important because the types of control efforts we select and use against one type may not be effective against another, leading to costly investments in efforts that don't work.

2.3.1 Blossom blight. If rain or dew does not occur during bloom, the pollinated flowers will go ahead and set healthy fruit despite the presence of the bacteria. If rain or dew does occur during flowering, a gradient of several simple organic acids seems to form in water films between the stigmas and the nectarthodes in the base of the flower. Because the bacteria have flagella and,

attracted to this strong nutrient gradient, will follow it directly into the nectarthodes where over 90% of blossom infections occur. Below 600F, the bacteria, while still motile, lose the ability to move in a directed fashion following the chemical gradient. Above 600F, however, colonization and infection of the nectarthodes appears to occur within minutes. Once a blossom infection event does occur, symptoms of that specific event can be predicted accurately (usually + 1-2 days) using an interval of 103 CCD >550F from the date of the event. Since this threshold is temperature dependent the real time in calendar days for symptom development can range from 5-6 days under warm conditions to 30 days or more under cool conditions, a fact that explains the puzzling appearance of blossom blight as much as a month after petal fall.

The importance of blossom blight cannot be overstated, even when the number of overwintering cankers might be small. This is because blossom blight has the potential to develop explosively due to several key factors. First, primary inoculum is often dispersed from holdover cankers to surrounding trees and then throughout the orchards up to several weeks before bloom. Second, once the stigmas of the first open flower are colonized, the bacteria are spread quickly by pollinating insects to new flowers as they open and this can occur over a period of days before an infection event might occur. Third, under suitable temperature conditions, E. amylovora populations can double within 20-30 minutes so that with just 31 doublings, one bacterium gives rise to over a trillion, each of which is capable of initiating an infection. And, finally, when all conditions for blossom infection exist, infections probably occur within minutes. This 'quiet colonization' of the orchard and blossoms is perhaps best imagined by playing the sound track of the movie 'Jaws' from tight cluster until the first wetting event during bloom when the average temperature is 600F or above. When such an infection event occurs the number of new sources of secondary inoculum in the orchard can suddenly reach several hundred thousand or more, making efficient control over the rest of the season difficult.

2.3.2 Canker blight. Although the infectious activity of E. amylovora begins at the margins of overwintering cankers much earlier than bloom, the actual symptoms associated with this infection event usually do not become apparent until some time after bloom. Unlike the other infection types, canker blight can be expected to develop every year in orchards where overwintering indeterminate cankers remain from the previous year. The first symptom that can be detected can only be found by cutting into the bark at the canker margin and then appears as only a narrow zone (1-2mm) of water-soaked green or diffuse brown tissue at the margin between the necrotic tissue of the canker and the surrounding healthy bark. This occurs routinely with the accumulation of 196 CDD >550F after green tip. A second, more easily recognized and striking symptom of canker blight occurs 103 CCD >550F later (=299 CDD >550F after green tip) when the tips of vegetative shoots, especially water sprouts, close to active canker sites develop a distinct yellow to orange color and begin to wilt. At the same time the bottom few leaves on these shoots often show darkened mid-veins indicating that these shoots have been invaded from the base as the result of systemic infections arising at canker margins. Even without these tell-tale tip and basal leaf symptoms, close examination of new shoots arising near the margins of cankers will often show droplets of bacterial ooze on their stems.

Canker blight symptoms are often overlooked in the light of much more numerous and dramatic blossom infections or because of their similarity to the more familiar shoot tip (=shoot blight) infections that occur later. Because of the limited number of overwintering cankers in a well

managed orchard the significance of canker blight is often underestimated. Indeed, their importance is probably insignificant in terms of overall damage when blossom blight occurs. However, in years when blossom infection events do not occur or have been well controlled, active canker sites serve as the primary source of inoculum for a continuing epidemic of secondary shoot blight infections that can lead to major limb, fruit and tree losses. Such sources of inoculum can also be important for new orchards with no history of fire blight when they occur in older, surrounding orchards from which the bacteria can be moved into young orchards by wind, blowing rain and certain insect species.

2.3.3 Shoot blight. Shoot tip infections are common in areas where fire blight occurs and, as the name implies, are incited on the youngest 2-3 tender, un-expanded leaves at the tips of vegetative shoots. The symptoms of these shoot tip infections differ from those of the systemically invaded shoots associated with canker blight in that the shoot tips are usually still green (not yellow to orange) when they wilt and there are no symptoms on the basal leaf mid-veins. The significance of shoot infections is two fold. First, these infections tend to progress downward rapidly, often invading and destroying larger supporting limbs resulting in the loss of large portions of trees and a proportion of the total fruit bearing surface. Secondly, Al Biggs in West Virginia has evidence that the leading edge of up to 80% of shoot infections that occur after mid-June ends as an indeterminate canker suitable for the overwintering of the bacteria for the next season.

It now appears that as inoculum becomes abundant in the orchard, leaf surfaces are colonized by the bacteria (arriving from earlier blossom infections, active cankers or young shoots systemically invaded by bacteria from nearby cankers), but cause no harm so long as they remain on the surface. In the past, while we have often associated shoot blight outbreaks with insect activity, which insect species might be involved, if at all, is still being investigated. There is good evidence that green apple aphids and, probably, white apple leafhoppers are not important because of their peculiar feeding habits. Potato leafhoppers, however, which feed on shoot tips and often occur in high numbers may still play a role.

A more likely factor is wind and then not necessarily the high winds associated with storms. There is evidence from work published in the 1960s of a direct relationship between the incidence of shoot blight in apple nursery trees and their distance from Lombardy poplar wind breaks. More recent work in Germany provides clear evidence that the simple damage to leaf hairs along the midrib of pear leaves (only a few cells away from the xylem parenchyma and vascular tissues) provides suitable wounds for the bacteria to enter and to incite infections leading to typical shoot blight symptoms. Thus, the greatest number of shoot tip infections may well occur during days with gusty winds that might cause a whipping type injury to shoot tips leaves, an event that is, unfortunately, all too common in the temperate climates where apples and pears are grown.

2..3.4 Trauma blight. The incidence of severe fire blight associated with damage caused hail and high wind is well known by experience and has been well documented in the literature. Much like shoot blight, it appears that leaf surfaces already colonized by the bacteria are severely injured during hail and wind storms so that the bacteria have ready access to internal leaf tissues and the vascular system. A similar observation has been made following a late season frost <280F, where the bacteria may be drawn from surfaces into internal leaf tissues during the

thawing process. It is important to note that trauma blight is not limited to highly susceptible cultivars, but can also occur in more resistant Red Delicious orchards as well since the injuries seem to breech the normal defense mechanisms active in these trees

When such trauma-inducing events occur, the amount of fire blight that follows appears to be directly related to the amount of foliar colonization by the bacteria in the orchard, being heaviest near good sources of inoculum such as active blossom, canker or shoot blight symptoms or active cankers not previously removed. In one recent case in Maryland, a grower who had followed a rigorous fire management program in his apple and pear orchards for several years experienced a severe hail storm that struck his entire planting. The trauma blight symptoms that subsequently developed, however, were limited to less than 20 trees scattered in small clusters around the orchard where, in nearly all cases close examination revealed the presence of an overlooked active canker. Because of his previous good efforts at limiting the number and distribution of these primary sources of inoculum, this grower was able to cut out and remove all of the blighted wood in his orchards within a few hours after symptoms were discovered.

2.3.5 Rootstock blight. Rootstock blight can be especially damaging where M.26 and M.9 apple rootstocks are used for high density plantings. Here, we have shown that the bacteria from a single shoot infection can move rapidly down through the otherwise healthy superstructure of branches, limbs and trunk into the rootstock (or C-6 inter-stem) where the bacteria initiate a canker that quickly expands to girdle the tree causing the death of the whole tree. In the Midwest, Mid-Atlantic and Southeast part of the U.S., whole trees may collapse and die suddenly in June or July following an earlier bout with blossom, shoot or trauma blight. Additional trees show early fall red coloration in late summer to early autumn and still, more trees may not show symptoms until they begin to decline and die in the early spring following the infection. While not all trees showing infections in the scion ultimately succumb to rootstock blight, 5-10% tree loss per year for the first 5-6 years is not uncommon and can be as high as 20-40% or more in some orchards. In New York and New England, where summers are generally cooler, the mid-summer death of trees seems rare, but the losses from fall and spring deaths are about the same. Note, too, that such losses can occur even with relatively resistant apple varieties such as Red Delicious where scion infections can occur in trauma blight situations.

3. SUMMARY

As fire blight epidemics unfold, the symptoms that appear can be associated with up to five different types of infections, each determined by the source of inoculum and the conditions in the host and environment. Not all of these infection types occur every year in all orchards nor with the same intensity. Canker blight, while often limited to a few locations were overwintering cankers were not removed, occurs regularly and predictably every year, can serve to fuel a major epidemic of shoot blight or set the stage for serious damage following summer storms. Blossom blight may or may not occur in any given season and varies in its incidence and severity with the number of open flowers colonized by the bacteria, temperatures above 600F, and the thoroughness of wetting by rain or dew. Shoot blight outbreaks have been associated independently with both insect activity and modest wind damage where young shoot tips are already colonized by the bacteria. Trauma blight also requires a degree of foliar colonization by the pathogen and is triggered by the wounding that occurs with hail, high winds and late season

frosts. Rootstock blight is limited to apple cultivars planted on M.26 and M.9 rootstocks and can cause severe damage in young orchards where blossom, shoot or trauma blight events occur. At present, there is sufficient information regarding blossom, canker, shoot and trauma blight to allow for their accurate prediction in advance so that effective control measures can be taken. The conditions governing rootstock blight, however, have yet to be defined well enough to make prediction reliable.

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