Late Blight Epidemics in the Columbia Basin

Dennis A. Johnson[1], Philip B. Hamm[2], Jeffrey S. Miller[3], and Lyndon D. Porter[4]

[1]Department of Plant Pathology, Washington State University, Pullman WA 99164-6430; [2]Department of Botany & Plant Pathology, Oregon State University, Hermiston Agricultural Research & Extension Center, Hermiston OR 978383; [3]Miller Research, Rupert, ID
[4]USDA-ARS, Vegetable and Forage Crops Research Unit, Prosser, WA

Abstract

Late blight was not originally expected to be a serious threat to potato in the semi arid environment of the Columbia Basin. However, the disease has occurred every year at various severities since 1990. Migration of *Phytophthora infestans* into the Columbia Basin in the 1990's is well documented. The US-1 strain predominated in 1992 and several unique isolates were discovered in 1993, which were likely the result of genetic recombination. The recombinants were ephemeral and were not found in 1994. The US-8 stain was first observed in 1994 and came to predominate in 1995 and in subsequent years. Epidemics in the Columbia Basin have been traced to infected seed tubers, refuse tubers and volunteers. Late blight spreads in fields by foci with foci enlarging in size, producing daughter foci, and coalescing. The process continued as favored by the environment. Sporangia of *P. infestans* have the capability of surviving in water for extended periods of time after detachment from sporangiophores on potato tissue. Late blight has been successfully forecasted and managed regionally in the Columbia Basin. Early season rain is an effective indicator of late blight outbreaks because moisture is important for the build-up of inoculum in fields during the early stage of epidemics. Early in epidemics, moisture promotes transmission of *P. infestans* from infected seed tubers to emerged shoots in fields. Method of fungicide application affects fungicide distribution and cost. The alternate use of air application and chemigation provides good protection at a reduced cost compared to only air or ground application methods. Application of phosphorous acid to tubers after harvest and prior to storage can result in a reduction in post-harvest infection by *P. infestans*.

10.1 Introduction

The Columbia Basin of south-central Washington and north-central Oregon is a major potato-growing region in North America. Over 65,000 ha of potatoes are grown in the region annually, with mean tuber yields exceeding 74 t/ha in 2010. The region is isolated and nearly completely bordered by mountains; the potato production area extends for approximately 180 km, from Umatilla and Morrow counties in north-central Oregon to Grant and Adams counties in south-central Washington. Potatoes are mainly planted in March through April and harvested from August through October. The environment is semiarid and the potato

crop is irrigated mostly by center-pivot systems. The first center-pivot systems were introduced about 1956 and after 1973 quickly replaced surface irrigation by gravity flow (Easton 1982). An increase in seasonal occurrence of late blight occurred with the increased use of center pivot irrigation in the region (Johnson et al. 2003a; Easton 1982); an increase in the severity of late blight has similarly been associated with sprinkler irrigation in the arid environment of Israel (Rotem et al. 1970).

Phytophthora infestans, the oomycete that causes potato late blight, is dependent on a wet, humid environment with mild temperatures for sporulation and infection. Sporangia are sensitive to drying (Minogue 1981) and are disseminated most effectively from field to field during cloudy and rainy periods (Hirst 1960; Sunseri 2002). Late blight was not originally expected to be a serious threat to potato in the semi arid environment of the Columbia Basin. The disease was first identified in this region during the 1947 growing season when weather was unusually cool, cloudy, and wet (Easton 1982). It was next reported 27 years later in 1974 and was observed in fields 7 of 16 years between 1974 and 1989. The frequency of disease occurrence since then has greatly increased and late blight has been present in the Columbia Basin every year since 1990, with the most severe outbreaks occurring in 1993, 1995, 1997, 1998, 2004 and 2010. The monetary cost of managing late blight is high and approached $30 million for the Columbia Basin in 1995 (Johnson et al. 1997). The cost was $22.3 million in 1998 and included $19.8 million for fungicides and application, $1.1 million for canopy desiccation, and $1.4 million in losses due to tuber rot in storage (Johnson et al. 1998).

10.2 Migration

Phytophthora infestans is well known for global migrations from its center of genetic diversity in the Toluca Valley of Mexico to the United States and Europe in the 1840's. One of the earliest recorded outbreaks of late blight on cultivated potatoes occurred in the United States in 1843 (Stevens 1933). Affected areas included all of New England and states as far west as Illinois and Wisconsin by 1845. In June of 1845, late blight was observed on potatoes in Belgium (Bourke 1964; Bourke 1991). The pathogen radiated in all directions that summer and reached Ireland by September (Bourke 1964). Late blight devastated Ireland resulting in the Irish potato famine from 1845 through 1852. A million people died and at least 1.5 million immigrated as a result (Large 1940).

Additional pathogen migrations occurred in the 1970's and 1990's (Fry et al. 1993). Evidence for these migrations was shown by an increased diversity in *P. infestans* populations (Goodwin et al. 1994a). Prior to these migrations some evidence pointed to a single clonal lineage or strain as being responsible for epidemics outside the Toluca Valley of Mexico (Goodwin et al. 1994b). Subsequent genetic analysis from herbarium specimens contradicts this view (Ristaino et al. 2001). During the initial population evaluation work with *P. infestans*, strains were identified as multilocus genotypes based on the following characteristics: 1) compatibility or mating type, 2) metalaxyl sensitivity, 3) glucose-6-phosphate

(*Gpi*) and peptidase (*Pep*) allozyme genotypes, and 4) restriction fragment length polymorphism (RFLP) genotype (Goodwin et al. 1995). Strains were named consecutively based on the country in which they were first identified (e.g. US-1 was the first strain identified in the United States, CA-2 was the second strain identified in Canada, and PO-4 was the fourth strain identified in Poland).

The migration into the Columbia Basin is well documented and serves as an example for what happened in many areas of the world in the 1990's. The US-1 strain (characterized by the A1 mating type and metalaxyl sensitivity) predominated in 1992 (Fig. 10.1). This was the strain hypothesized to have been distributed globally outside Mexico prior to the migration in the 1970's (Goodwin et al. 1994a). The US-6 strain (characterized by the A1 mating type and metalaxyl resistance) was first observed that year, however. The frequency of the US-6 strain increased in 1993 and 1994, but was not found in 1995. Several unique isolates were discovered in 1993 and these did not fit any of the currently published strain descriptions, and were placed in an "uncategorized" group. Genotype data indicate that these uncategorized isolates were likely the result of genetic recombination (Gavino et al. 2000). The isolates representing these genotypes were ephemeral and were not found in 1994. The US-8 stain (characterized by the A2 mating type and metalaxyl resistance) was first observed in 1994 and came to predominate in 1995 and in subsequent years (*unpublished*).

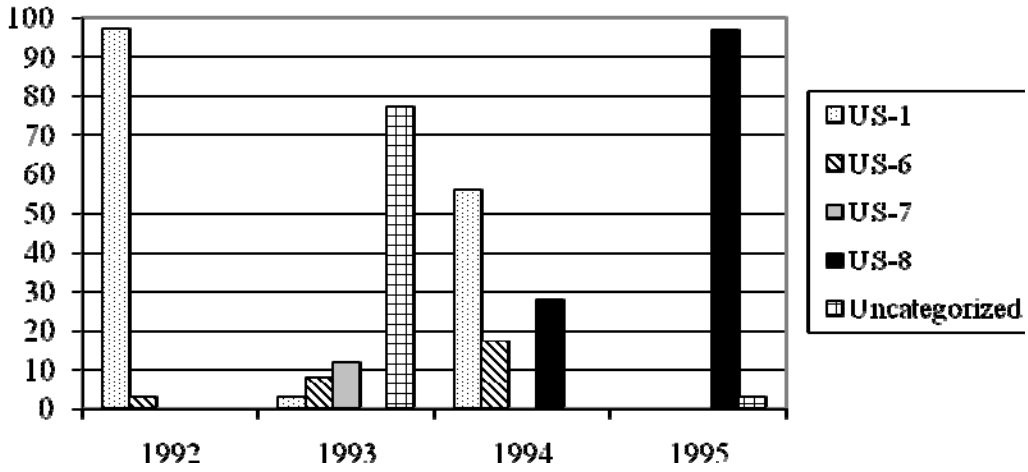

Figure 1. Distribution of *P. infestans* strains in the Columbia Basin of Washington and Oregon from 1992 to 1995 (adapted from Miller et al. 1997).

Resistance to metalaxyl may have influenced the shift from the older US-1 strain to newer strains. The US-6, -7, -8, and uncategorized isolates were all resistant to metalaxyl. More importantly, newer strains are more aggressive and have greater competitive fitness than the older US-1 strain. Detached leaf studies showed that US-8 isolates could produce more sporangia per lesion area and had a greater lesion expansion rate than US-1 and US-6 isolates (Miller et al. 1998). US-8 isolates infect young shoots from infected seed more readily than other isolates (Marshall and Stevenson 1996). Additionally, when US-1 and US-8 isolates were released into a small field plot with equal frequency, US-8 isolates were recovered with greater frequency (96%) than US-1 isolates (1%) (Miller and Johnson 2000). The remaining 3% were non-parental phenotypes. From 1995 through 2009, the US-8 strain has been the predominant isolate recovered from potato fields in the Columbia Basin (*unpublished data*).

10.3 Origin of epidemics - Oospores of *P. infestans* are not currently known to be a factor in overwintering in the Columbia Basin and a continuum of viable host tissue is essential for overwintering and transmission of the pathogen to new plant tissues in this region. The pathogen survives in infected tubers which may act as an inoculum source the following season (Melhus 1915; Van der Zaag 1956). However, infected tubers frequently rot during winter months and cease being a threat as an inoculum source when decomposed. Contemporary strains of *P. infestans* are highly aggressive and rapidly rot tubers, limiting the availability of viable host tissue (Kadish and Cohen 1992; Kirk et al. 2001). Epidemics of late blight characteristically start from low levels of initial inoculum originally arising from infected seed tubers, volunteer potato plants developing from infected tubers in the field, or from infected tuber refuse (Kadish and Cohen 1992; Johnson et al. 2003; Zwankhuizen et al. 1998). The relative importance of the three types of late-blight-infected tubers varies as inoculum sources and depends in part on microclimates, local conditions, and the extent of infection the previous fall (Davidse et al. 1989; Gigot et al. 2009; Zwankhuizen et al. 1998).

Epidemics in the Columbia Basin have been traced to infected seed tubers, refuse tubers and volunteers (Johnson et al. 2003). Observations in commercial fields and surrounding areas early in the course of epidemics revealed that volunteers are especially likely to pose a threat when potato plants in the field were infected the previous season, moreover, infected volunteers have been found in a field two years after an infected potato crop. Cull piles formed in late winter or early spring from tubers taken from storages can be a serious threat because infected tubers in storage are protected from external environmental variations in temperature and moisture, which may increase rot. Infected tubers may survive in cold storage at temperatures used to store seed tubers with little to no rot or symptom development (Johnson and Cummings 2009). Latent infections in seed tubers are a particular threat in generating new epidemics.

Transmission of *P. infestans* from infected tubers to plant tissues the next season may occur during seed-tuber handling, cutting and planting (Lambert et al.

1998) or in the field (Hirst and Stedman 1960; Melhus 1915). For secondary infection to occur during seed tuber handling and cutting, the pathogen must survive in intact tubers during the winter, sporulate, be dispersed, and infect additional tubers or foliage. Temperature and humidity within piles of cut seed tubers often favor sporulation, and sporangia have been observed on infected seed pieces within 19 hours of cutting (Porter et al. 2001). Sporangia are readily transmitted by direct contact from infected tubers or seed pieces to noninfected seed pieces (Dowley et al. 1991). Tubers infected prior to planting may be more likely to produce viable shoots than those infected in the field near harvest because of less time for rot to develop before shoot emergence. Under experimental conditions, transmission occurred from tubers to shoots when tubers were inoculated in the spring before planting, but not when tubers were inoculated in the fall (Gigot et al. 2009). Infection during seed-tuber cutting and handling increases the threat of late-blight outbreaks on foliage in the field. Fungicide seed piece treatments potentially reduce transmission from infected seed tubers (Inglis et al. 1999; Powelson et al 2002).

The exact pathway by which *P. infestans* progresses from planted, infected seed tubers to plant foliage has been disputed (Andrivon 1995; Boyd 1974; Melhus 1915). De Bary originally proposed that the pathogen spread by mycelial growth within infected seed tubers and advanced contiguously or followed growing shoots to produce lesions and sporangia on above-ground stems (De Bary 1876). However, the validity of De Bary's work on vegetation of the pathogen was questioned when not duplicated by other researchers as described by Melhus (1915). A moist environment plays an important role in the expression of transmission of the pathogen from infected seed pieces to shoots (Johnson 2010) and many of the studies contradicting De Bary's observations were done in relatively dry seasons or environments. Additionally, continuous lesions are not always observed on the below-ground stem between the infected seed piece and the resultant lesion on the above-ground stem (Johnson 2010) and mislead some of the previous researchers. No necrotic tissue or only slight streaking of reddish brown discolored tissue may be observed on below-ground stems when *P. infestans* is transmitted by mycelia growth within internal tissues (Fig. 10.2). De Bary's proposed pathway has been validated (Melhus 1915; Van der Zaag 1956) and was recently confirmed when *P. infestans* was detected in asymptomatic shoots emerging from infected tubers with the aid of the polymerase chain reaction (Appel et al. 2001; Hussain et al. 2007) and when sporangia and lesions developed on asymptomatic shoots placed in a moist environment (Johnson 2010).

Emergence of infected shoots from infected seed pieces is often low and infected seed tubers frequently result in a reduced stand due to tuber rot and preemergence blighting of shoots (Boyd 1980; Melhus 1915). For example, over five consecutive years only 21 of 3260 (0.64%) infected seed tubers planted produced infected above ground shoots capable of sporulating (Hirst and Stedman 1960). In experiments in Oregon and Washington (Partipilo et al. 2000**)**, transmission from artificially infected seed pieces to emerging shoots was 1.9 to 3.8% of the inoculated seed piece depending on the cultivar. In western Washington, tuber-to-sprout

transmission was as high as 25 % on plants held at 60 to 90% relative humidity in the greenhouse and transmission was greater with a US-8 than US-11 isolate (Gigot et al. 2009). Transmission is promoted in a moist environment (Johnson 2010). In a field experiment, transmission to emerged shoots did not occur from inoculated seed pieces until shortly after a rainy period following row closure. Eighty inoculated cut seed pieces were planted and late blight lesions developed almost simultaneously above the soil level on two separate main stems (Fig 10.3). One of the two lesions occurred about 8 cm above the soil level. Sporangia formed with the developing lesions.

The transmission rate from an infected seed tuber to foliage does not need to be very high for a late blight epidemic to develop given the explosive polycyclic capabilities of *P. infestans* and the large amount of potato seed tubers planted in major production regions (Hirst and Stedman 1960; Vanderplank 1963; Van der Zaag 1956). For example, in the Columbia Basin in 2010 the number of seed pieces that was planted was over 2.625×10^9 with a total weight of 156,300 metric tons. Only a few infected tubers are needed to initiate an epidemic (Hirst and Stedman 1960; Vanderplank 1963; Van der Zagg 1956) and a few infected shoots arising from infected seed pieces in a commercial field is below the perception threshold and will not likely be noticed during the early stages of epidemics. Inoculum originating from infected seed tubers in commercial fields can be especially devastating because of the potential earliness of the initial inoculum, the rapidity with which it can be produced, and the proximity of inoculum to the crop. In addition, the moist conditions favoring emergence of infected shoots also favor sporulation and repeated infections in the field (Harrison 1992; Johnson 2010). As many as 300,000 sporangia can be produced from a single lesion demonstrating the explosive reproductive capabilities of the pathogen (Fry 2008). In addition, weather conditions in the Columbia Basin are usually the least stable in May and June, with greater likelihood of rain events, further encouraging the development of primary inoculum, spore movement and new infection.

10.4 Spatial patterns of epidemics - Spatial variation of late blight-infected foliage is distinctive in the pattern of disease foci (concentrated area of diseased foliage) in commercial fields. Initial foci are generally circular to asymmetrical and clearly defined, and daughter foci are associated with, but separated from parent foci. Daughter foci are often scattered over the field. Late blight is also generally more severe in particular locations of a potato circle. The disease frequently occurs earlier and is often more severe near the center of the pivot where more irrigation water is delivered and the time of leaf wetness is greater than elsewhere in the circle (Johnson et al. 2003a). Disease foci also frequently develop in areas of the field where surface water tends to accumulate such as in field depressions, in places where pivots or sprinkler systems overlap and along wheel lines where the soil is compacted resulting in long term water reservoirs. These areas favor late blight due to higher humidity and more free water on plant

surfaces and are the areas most severely infected in fields when the epidemic is not severe throughout the field.

Spatial variation of late blight in potato fields is aggregated and dynamic as the disease spreads within fields during epidemics. An aggregated rather than random or regular pattern is expected for late blight because after introduction of the disease into a field, new infections are more likely to occur near a previously infected plant (Miller and Johnson 2000). The pattern depends on the stage of late blight epidemic and the nature of primary infection. In epidemics in the Columbia Basin, late blight-infected plants were aggregated during epidemics in commercial fields. Aggregation increased as disease incidence increased in the early and mid-phases of epidemics in fields. A field where initial inoculum likely originated from infected seed tubers exhibited less initial aggregation than the other fields, perhaps due to the source of primary inoculum. In all fields examined, disease foci were sparse and scattered at low diseases incidences and became larger and more clumped as disease incidence increased. Disease foci were quite large at high incidence of disease. Consequently, late blight was observed to spread by foci with foci enlarging in size, producing daughter foci, and coalescing. The process continued as favored by the environment. Disease aggregation was found to decrease in some cardinal directions but continued to increase in other directions as disease incidence increased to the highest levels toward the end of epidemics (Johnson et al. 2003). In contrast, disease aggregation was theoretically expected to rapidly decrease as disease incidence increased to relatively high levels (Ristanio et al. 2001). Few reports with quantitative data have been published concerning the degree of disease aggregation over the course of actual epidemics and quantitative data from the Columbia Basin is useful in evaluating existing theory on the spatial spread of disease.

10.5 Survival of Spores - Survival of zoospores and sporangia of *P. infestans* is an important variable of late blight epidemics, especially when overwintering oospores of *P. infestans* have not been found in the Columbia Basin. Many factors impact the survival of sporangia and zoospores including solar radiation (Mitzubuti et al. 2000; Rotem and Aust 1991; Rotem et al. 1985; Sunseri et al. 2002), temperature (Crosier 1933; Larance and Martin 1954; Martin 1949; Mizubuti and Fry 1998; Sato 1994), moisture (Crosier 1933; Glendinning et al. 1963; Warren and Calhoun 1975), soil chemistry (Andrivon 1994a,b,1995; Ann 1994; Boguslavskaya and Filippov 1977; Hill et al. 1998), soil microorganisms (Kostrowicka 1959; Lacey 1965; Zan 1962) and spore physiology (Blackwell 1930; De Weille 1964; McAlphine 1910; Rosebaum 1917; Rotem and Aust 1991).

Survival of sporangia of *P. infestans* in air, water and soil has been observed in natural and controlled environments. Sporangia of *P. infestans* under ambient conditions during cloudy weather rarely survive for more than 3 to 4 hours and in direct sunlight survival is rare beyond 1 hour (Glendinning et al. 1963; Mitzubuti et al. 2000; Sunseri et al. 2002). Spores of isolates of *P. infestans* collected from the Columbia Basin survived in surface water between 14 to 21

days under ambient conditions (Porter and Johnson 2004). Therefore, spores of *P. infestans* have the capability of surviving in water for extended periods of time after detachment from sporangiophores from sporulating potato tissue. Overhead center-pivot irrigation on potato in the Columbia Basin makes a rotation every 18 to 24 hours during hot weather. Spores surviving in surface water in the wheel tracks during a three-week period could be dispersed approximately 56 times (504 hours/18 hours x 2 wheels per tower) by the wheels, providing opportunities for surviving spores to be possibly deposited on the top and under surfaces of adjacent potato plant tissue where infection can take place. Incidence of late blight tuber rot is often high in wet areas of fields and is also likely influenced by the survival of spores in surface water (Johnson et al. 2003) or the movement of zoospores in these areas. Irrigation water is sometimes reused and spores could be transported to neighboring fields through infested water.

Zoospores are capable of surviving 10 days, sporangia 42 days, and mycelia 28 days *in vitro* in non-sterile soil at 22ºC (Zan 1962). The maximum survival of sporangia *in vitro* in non-sterile soil was 70 to 80 days (King et al. 1968; Larance and Martin 1954; Rotem et al. 1985; Zan 1962). Survival of *P. infestans* propagules under natural environmental conditions in naturally-infested soil and in artificially-infested soil in pots was 21 to 32 days dependent on soil type and moisture level (Lacey 1965; Murphy 1922). New clonal lineages of *P. infestans* from the Columbia Basin that were metalaxyl resistant survived under natural environmental conditions in soil between 23 and 30 days dependent on the soil type and moisture level (Porter and Johnson 2007).

An important means of survival is the overwintering of *P. infestans* in infected tubers. The effect of tuber depth, soil type and soil moisture on potato tuber infection by sporangia/zoospore inoculum was assessed in greenhouse studies for four soil types (Quincy fine sand, Quincy loamy fine sand, Quincy medium sand and Shano silt loam) commonly found in the Columbia Basin potato growing region (Porter et al. 2005). The majority of all infections were to tubers found at the soil surface and infected tubers were rarely found at 5 cm or deeper for all soil types. A Shano silt loam was effective at preventing any infection of tubers at 2 cm below an intact soil surface. Likely, this protection is due to the small pore size of the silt loam which prevents sporangia or zoospores from moving through the soil (Porter et al. 2005). However, additional factors such as oxygen concentrations (Cook and Papendick 1972; Uppal 1926; Zan 1962), microorganisms (Cook and Papendick 1972; Murphy 1922), negative geotaxic tendencies of zoospores (Cameron and Carlile 1977; Carlile 1983) and tendency of zoospores to encyst on impact with foreign objects (Carlile 1983) are all factors that could be limiting spore movement and infection of subterranean tubers. Sporangia of *P. infestans* do not readily wash through soil and less than 1% of sporangia are found deeper than 5 cm in sandy soil (Jensen 1887; Murphy and Mckay 1925). Increased moisture levels were not a factor increasing the depth of tuber infection in the Columbian Basin soils that were assessed (Porter 2005).

Fungicides impact the ability of spores of *P. infestans* to survive and infect tubers in the soil. Viability of sporangia/zoospores in soil previously treated with fungicides was determined using buried healthy whole tubers and by assaying infested soil applied to freshly cut tuber disks (Porter et al. 2006). Mancozeb and metiram, both ethylene bisdithiocarbamates, were fungicidal to sporangia and zoospores of *P. infestans* and when applied to soil are capable of acting as a fungicide barrier preventing tuber infection, however this protection only lasted up to five days under natural conditions (Porter et al. 2006). Cyazofamid was the only non-EBDC fungicide identified with sporangicidal activity when applied to soil. The duration of this protection has not been determined. Fluazinam and fenamidone were not sporangicidal when applied to soil; however, these fungicides significantly reduced whole tuber infections when applied to soil following an infestation of the soil with sporangia/zoospores of *P. infestans*. These two fungicides may disrupt mechanisms that enable sporangia/zoospores to find and/or infect whole tubers.

10.6 Improved Control with Resistance - Specific resistance, resistance that is expressed when genotypes of the host react differentially to different genotypes of the pathogen (Johnson and Gilmore 1980), has not been durable in potato against late blight (Fry 2008; Swiezynski et al. 1996). Partial or field resistance, resistance that reduces the rate of disease development, has been recognized and quantified in potato infected with *P. infestans* (Guzman-N 1964; Hodgson 1961; Thurston et al. 1962) and appears to be general and a durable type of resistance (Colon et al. 1995; Inglis et al. 2007). However, the development of potato cultivars with partial resistance has not received emphasis because of the relative convenience of selecting for specific resistance (Fry 2008), the availability of affordable late blight fungicides and because partial resistance is not always easily identified and can be modified by the environment (Johnson and Gilmore 1980). Combining partial resistance with integrated control tactics that reduce initial inoculum and the rate of disease development will be the most economic and stable management strategy for potato late blight (Stevenson et al. 2007). In contrast, growing susceptible and especially very susceptible late blight cultivars will aggravate the late blight situation in a region due to an increased production of inoculum. Late blight is often found first in the Columbia Basin on the very susceptible and early maturing cultivar Russet Norkotah.

Foliage of the commonly grown potato cultivars in the Columbia Basin is susceptible to *P. infestans* (Inglis et al. 1996; Porter et al. 2004). Fortunately, tubers of Umatilla Russet, Alturas, Gem Russet and a few others are moderately resistant (Porter et al. 2001; Porter et al. 2004). Incidence and severity of infection are less in moderately resistant tubers and late blight is much easier to manage in storage for tubers of moderately resistant cultivars. During the same storage season, losses may not be encountered for tubers of moderately resistant cultivars whereas they can be high for tubers of the very susceptible cultivar, Ranger Russet (Johnson et al. 2000). Foliage and tubers of Defender have a high level of partial

resistance to *P. infestans* and the number of fungicide application can be reduced 3 to 6 times for successful control when compared to Russet Burbank. The mean economic returns associated with Defender were $6,196/ha; whereas they were only $4,388/ha for Russet Burbank (Stevenson et al. 2007).

10.7 Late Blight Forecasting - Late blight management has been augmented in regions of North America, Mexico and Europe by scheduling fungicide applications using predictive disease models (Beaumont 1947; Grunwald et al. 2000; Krause et al. 1975; Wallin 1962). Models developed in rain-fed agricultural regions that are based on leaf wetness or relative humidity and temperature in individual fields such as BLITECAST have not effectively predicted late blight outbreaks in the semiarid Columbia Basin and southern Idaho (Easton 1982; Henderson et al. 2007).

Late blight is forecasted and managed regionally in the Columbia Basin. This is because sporangia of *P. infestans* can become airborne in turbulent air currents and be quickly and widely disseminated within the region during cloudy and wet weather (Aylor et al. 2001; Sunseri et al. 2002), and when disease favoring weather of mild temperatures and rainy conditions occur, they usually prevail over the entire region. Additionally, the microclimate in fields can be similar throughout sections of the region after row closure. Row closure is when foliage between rows just touches and, for the main cultivars grown including Russet Burbank, generally extends from the second week of June in the southern Columbia Basin to the end of June in the northern Basin. Late blight has not been observed before row closure in the region. However, once row closure has occurred, microclimate conditions generally are favorable for late blight development whenever a field is irrigated (Easton 1982). Late blight is extremely difficult to manage once it is established in an irrigated field. For example, in a field with inoculum originating from infected seed tubers, incidence of late blight increased from 0.2 to 70% over a four-week period after row closure even with nine applications of efficacious fungicides (Johnson et al. 2003).

Two sets of forecasting models are used to regionally forecast the probability of late blight occurrence for the Columbia Basin. The first set of models identifies the probability of late blight occurrence early in the growing season and the second gives the probability of disease occurrence in midseason (Johnson et al. 1996; Johnson et al 1998). The models were derived empirically by examining the relationship of late blight occurrence in the region with meteorological variables at four vicinities in the Basin over 27 years using logistic regression analysis. Separate logistic regression models were derived for the early and mid-seasons for each of the four vicinities. Indicator variables for the early season logistic models include the presence of an outbreak during the preceding year and number of rainy days in April and May. Indicator variables for the midseason models include the presence of an outbreak the preceding year and either number of rainy days in July and August or number of rainy days in April and May and number of rainy days in July and August depending on the vicinity (Johnson et al. 1998). Variation in

number of rainy days in the spring occurs among the four vicinities and having more than one location or vicinity has been beneficial in making reliable disease forecasts (Johnson et al. 1998).

The models had high sensitivity (percentage of years with late blight outbreaks classified correctly) and specificity (percentage of years without outbreaks classified correctly) when validated. As with predictive models used for most diseases, a high sensitivity is desired for the models used in the Basin. All years with late blight outbreaks and 96% of the total of 27 years of data used to develop the logistic models were correctly classified using data from at least one of the four locations (Johnson et al. 1998). All 13 years since models were first developed in 1997 through 2010 have been correctly classified at each of the four vicinities.

The probability of late blight occurrence for a given season can be calculated on 1 June when the number of rainy days in April and May is known. However, the probabilities can be estimated in early May from the actual number of rainy days in April and a 30-day rain forecast for May. This is done and a late blight forecast is usually given in early May. Early May is several weeks before row closure and sufficient time for growers to implement late blight management tactics. The advanced knowledge is beneficial because fungicides used for late blight are mostly protective, and to achieve the maximum effect, the first application must be made before the pathogen is introduced into the crop (Hirst and Stedman 1960). In addition, sufficient time and applications are also needed for fungicides to be adequately distributed throughout the plant canopy after the initial application, especially if the application is made by air.

The probabilities of late blight occurrence from the logistic models are then coupled with weather forecasts for occurrence of rainy days for 1 to 15-day and 1 to 30-day periods for the four vicinities (Johnson 1998). The rain forecasts are obtained regularly throughout the growing season from a private weather forecasting group (Fox Weather, LLC, Fortuna, CA) and the short term (1 to 15-day) and long term (1 to 30-day) rain forecasts are derived independently. The probability of a late blight outbreak, weather forecasts, and crop canopy development are used to calculate a risk index and to determine initiation and intervals between recommended fungicide applications. Growers also use the late blight forecast to determine intensity of field monitoring for late blight. Late blight epidemiologists in Oregon and Washington provide oversight of the regional forecasting system. Fields are monitored for late blight throughout the growing season and the presence of any late blight in any fields is considered in scheduling recommended fungicide frequency and irrigation applications. Recommendations are available to growers via phone recordings, e-mails and a Website. Ambient temperatures are generally favorable for late blight development after row closure in the Basin and are not generally considered in scheduling disease management tactics.

A noted benefit of the late blight forecasting system used in the Columbia Basin is that growers have become more aware of environmental conditions that favor late blight outbreaks. Growers characteristically become lax in applying disease management tactics after several consecutive seasons with little or no disease.

The regional late blight forecasting models have been beneficial in alerting growers when disease threats are high. Another benefit is that fungicide distributors have an idea of how much fungicide may be needed in the region for a particular year. For example, early spring in 1997 late blight fungicides were not available in the Pacific Northwest because of decisions by fungicide manufacturers to ship them elsewhere. The late blight forecast for the Columbia Basin predicted a severe epidemic in the region and this was used to convince manufacturers to ship fungicides to the Pacific Northwest. A severe epidemic did occur that year and fungicides were available to reduce the effects of the disease.

Early season rain is an effective indicator of late blight outbreaks because moisture is important for the build-up of inoculum in fields during the early stage of epidemics. Early in epidemics, moisture promotes transmission of *P. infestans* from infected seed tubers to emerged shoots in fields. Transmission from seed tubers to shoots bearing sporangia can occur within 24 hours during rainy weather (Johnson 2010). Secondary infections will proceed almost immediately if a favorable environment with moisture continues. Moisture is also essential for effective dissemination of sporangia to additional fields. Additionally, solar irradiance is associated with incidence of late blight epidemics in the Columbia Basin (Johnson et al. 2009), but solar irradiance has not been incorporated in the late blight forecasting models.

10.8 Improved fungicide application for late blight management - Effective management of late blight with protectant fungicides requires the distribution of an effective fungicide at an effective concentration throughout the canopy and field. Season long fungicide protection is expensive because of the need of repeated fungicide applications. Method of fungicide application affects fungicide distribution and cost. Fungicides are applied by air, ground and chemigation. There are many kinds of aircraft, as there are many types of ground applicators; whereas, chemigation, the adding of fungicide to the water stream and using the irrigation equipment for dispersal, generally means the use of a center-pivot irrigation system. In the Columbia Basin, the specific type of aircraft or ground applicator used is not as important as a consistent and properly developed and applied, fungicide program. That includes the use of late blight prediction models (Johnson et al. 1996, 1998). Besides the general method used for application, other factors must be considered, such as how much water per hectare is used, frequency of application, time required to make an application, whether to add a spreader/sticker to the mixture, and fungicide rates. Cost of season long control can be significant, so choosing the appropriate application program is important (Johnson et al. 2000). Other considerations, dependent on method, include wind, humidity, droplet size, pressure, potential for skips, and nozzles. Each application method can provide adequate protection from late blight, but each has advantages and disadvantages. A discussion follows comparing application methodologies when using protectant fungicides to ultimately help in improving late blight control.

Applying fungicides by air allows for treatment of many hectares in a relatively short period of time. However, the cost of hiring a plane is moderately expensive, must be scheduled in advance, and should not be used under windy conditions and near natural or man-made obstructions such as trees, power lines and buildings. Care must be taken to accurately balance distance to canopy with pressure and nozzle orifice to ensure that droplet sizes are large enough to reduce evaporation during low humidity, so droplets containing fungicide reach the potato canopy (Jacobsen 1986), and are also of correct size to prevent off-site drift. Application skips used to be an issue prior to the use of GPS systems. The amount of water used per hectare (28-94 liters) is not particularly important (Geary et al. 2004) if environmental and droplet size are appropriately considered, though as the amount of water used per hectare increases, so does cost and time needed to complete an application. The deposition pattern in the potato canopy immediately following application and the days that follow is extremely important. Prior to row closure, application of fungicides by air is evenly distributed in the potato canopy (Geary et al. 2004). Once between row closure occurs, the dynamics of fungicide coverage in the canopy change and fungicides do not readily reach the lower canopy. When using air application, the greater the amount of water used per hectare the more droplets of fungicide reach the canopy if droplet size is constant, but with larger water volumes the concentration of fungicide in each droplet is reduced. Regardless of the type of air craft, fungicide amounts are applied at the highest levels in the upper canopy, less in the middle canopy and very little in the lower canopy of the potato plants (Hamm and Clough 1999). Essentially the upper leaves “catch” the fungicide so less fungicide reaches the mid and lower levels of the canopy. Therefore at the day of application and for a time beyond, the lower levels of the canopy have less fungicide. In the Columbia Basin, frequent crop watering is essential due to light sandy soils. The application of water re-suspends the fungicide in individual spots and redistributes the material across the leaves and down the canopy. After a 7 day period, the amount in the upper canopy (on leaves present at the last application) is low while the amount present in the lower canopy is now higher from redistribution (Geary et al. 2004; Hamm and Clough 1999). Hence the reason and time for the next application to recharge and apply to new foliage in the upper canopy, which also serves to maintain fungicide levels in the mid to lower canopy through the next week when irrigation water is applied. The loss of fungicide through the canopy due to redistribution is a reason why full label rates of protectant fungicides are needed and why spreader/stickers do not aid in late blight protection (Geary et al. 2004).

In contrast to air application, chemigation is a slow method to apply fungicides. Often approximately nine hours is required to apply fungicides to a 50.6 hectare field whereas air may only take an hour. Chemigation can be accomplished over many fields simultaneously, since field equipment already present is being utilized, but each field still requires 6-12 hours. Chemigation can be used under more windy conditions and costs are reduced since required equipment is already present in the field. Droplet and pressure balances are not as relevant, and

neither is humidity. Application skips are eliminated as long as sprinklers, the pump injecting the fungicide into the water stream and the center pivot system continues to operate throughout the application.

The major difference between chemigation, air and ground application is the amount of water used during application. Amounts of water used are generally 28-47 L/ha for air application, 94-187 L/ha for ground application, and under the best reduced water situations, approximately 0.25 centimeters/ha or 25,245 L/ha for chemigation. Compared to air, the use of this large amount of water during chemigation creates a much different application pattern in and through the canopy, redistribution need, and time requirement to provide adequate late blight control throughout the canopy (Hamm and Clough 1999). Immediately following application, nearly equal amounts of fungicide are present throughout the canopy. Leaves and stems are adequately protected. However, in contrast to air application where relatively little fungicide initially reached the lower canopy, during chemigation large volumes of water pass through the canopy, moving the fungicide through the canopy. While fungicide levels are nearly equal in all canopy levels (upper, middle, lower) the day of application, the total amount of fungicide present is much less than with air application. With each application of irrigation water, fungicide is again redistributed, but given that less is present there is a greater chance of residue levels falling below the concentration needed to control late blight before the standard recommendation of the next application a week later. This is particularly true in the Columbia Basin where frequent watering occurs, though this is less likely where heavier soil and other factors allow less frequent applications of irrigation water. The large use of water is why full label rates of protectant fungicides should always be used and why the use of spreader/stickers is not justified. Trials using a boom attached to a center pivot irrigation system that applied approximately 675 L/ha of water applied significantly more fungicide to the canopy compared to chemigation with normal water amounts (Geary et al. 1999). While using an attached boom was not directly compared to air or ground application, the benefit of higher residues has been shown to provide better late blight control (Geary et al. 1999). Costs of the attached boom are initially high, but long term would reduce application costs by allowing grower application while also allowing grower controlled scheduling. Regardless of chemigation method used, this method can be an effective way to control later blight if done correctly.

Applying fungicides using a ground applicator may be the most common application method for late blight management in many potato producing areas in North America, but is the least used method in the Columbia Basin. Several factors that contribute to this are the cost of equipment/application, the time required to apply and the damage that occurs to the crop. Purchase costs are high for a ground applicator, regardless of the model, and so is the cost of hiring a ground applicator. While not as slow as chemigation for a given field (only a single field can be treated at a time in contrast to multiple fields by chemigation), ground application still requires a significant amount of time and water (94 – 187 L/ha is

standard). Reduced yield occurs, either due to the wheel tracks causing soil compaction through the field or from planting skips specifically established for movement of ground equipment. Ground application is not as impacted by wind or evaporation compared to either air or chemigation, particularly if the appropriate balance between pressure and nozzles and boom distance to the canopy is used. Skips are easily prevented with careful observation of nozzles to confirm that they are properly working and with the use of GPS units.

A ground applicator is the most effective method for applying fungicide in a potato canopy. Nearly three times the amount of product can be found in the canopy the day of application compared to air, and many times more than chemigation. More material is found in the upper canopy, and reduced levels in the middle and lower canopy, but still much higher than that found in any canopy location compared to air or chemigation. Redistribution downward occurs as in air application, but through a 7 day period the fungicide levels are always higher at each canopy location compared to air. The level of fungicide in the lower canopy the day of the first application provides good protection but still requires at least one watering cycle to redistribute the fungicide from the individual fungicide spots, particularly in the mid to lower canopy levels, to provide complete coverage throughout the canopy. Given that irrigation water redistributes the fungicide, the use of spreader/stickers is not justified. However, a case could be made that reduced rates of fungicide could be used given the substantially higher levels that result from this application method. Seven day application schedules are still recommended due to the large amounts of new unprotected growth from the last application.

Long term in-season needs for fungicides equate to substantial application costs in the Columbia Basin given the long growing season and high late blight risk (Johnson et al. 2000). Given that, alternative methods to apply fungicides have been suggested that reduce costs while using the distinctiveness and effectiveness of air and chemigation methods. While air is expensive, the amount of fungicide applied to the canopy is high. Chemigation is the least expensive application method but also leaves the least amount of fungicide in the canopy. Trials have shown that beginning a 7-day application program using air, followed by chemigation, and continuing that alternation of methods effectively controls late blight with reduced costs in the Columbia Basin (Geary et al. 1999).

In summary, late blight can be successfully managed by applying fungicides with each of the application methods, but each method has advantages and disadvantages. If late blight protection is needed immediately, then any method may work, given the time constraints needed for each to complete application. Chemigation is the least expensive but fungicide levels may fall below threshold levels within 7 days, depending on frequency and amounts of irrigation water applied. Ground application delivers the most fungicide to and throughout the canopy but is slow, expensive and reduces yield because of soil compaction in the wheel tracks. Air application requires at least one watering to ensure redistribution of fungicide droplets throughout the canopy after the initial fungicide application.

The alternate use of air and chemigation provides good protection at a reduced cost compared to only air or ground application methods. Careful consideration and use of fungicide application methods as part of an integrated disease management program will help ensure season-long protection from late blight at the least cost.

10.9 Post-Harvest Fungicides for Tuber Blight Control - Typically post-harvest products are applied as a low-pressure, low-volume spray as potatoes are being conveyed into storage. Some post-harvest disinfestants are applied through the humidification system during the storage season. Post-harvest fungicides are specific to a particular organism or class of organisms whereas disinfestants are general biocides with a wide spectrum against both bacteria and fungi. Additional products such as inorganic and organic salts, aromatic oils, bacteria, and other biological products have also been evaluated for potential post-harvest disease suppression properties.

The late blight pathogen can spread from tuber to tuber as a result of contact that occurs during tuber handling (Dowley and O'Sullivan 1991). This exposure may occur as tubers are lifted from the soil on the belt of commercial potato harvesters, as tubers collide on the harvester belt, as tubers are piled into trucks for transportation, or when tubers are delivered from trucks to storages, packing, or processing plants. Healthy tubers can become wounded during any of these phases, increasing tuber susceptibility to pathogen infection. Inoculum in soil adhering to tubers or from infected tubers may be present in the form of viable spores or mycelium and may be transferred to healthy tubers during these processes. Applications of post-harvest disinfestants and/or fungicides are aimed at reducing the viability of these potential inoculum sources on the surface of the healthy tubers prior to infection.

Post-harvest fungicides and disinfestants can be applied to potatoes as a low volume aqueous spray as the potatoes are conveyed into storage. The spray boom is generally located in an area where the potatoes may roll, such as a startable or a drop from one conveyor to the next, to ensure adequate coverage of the tuber. Post-harvest applications may include one or multiple sets of spray nozzles. With all the post-harvest applied products, full coverage of the tuber is needed for optimal efficacy. The volume of product applied ranges from 0.25 gal to 1 gal/ton tubers. In general, 0.5 gal/ton is recommended to ensure adequate tuber coverage and to avoid excess water on the tuber surface and surrounding equipment.

The use of phosphite or salts of phosphorous acid was investigated as a post-harvest applied fungicide after research demonstrated that these products could control diseases on potatoes caused by Oomycetes Johnson et al. 2004). Application of phosphorous acid to tubers after harvest and prior to storage can result in a reduction in post-harvest infection by *P. infestans*. In experiments where tubers were submersed in a suspension of *P. infestans* sporangia/zoospores, applications of phosphorous acid-based fungicides (= phosphonate, phosphites) significantly reduced tuber blight (Miller et al. 2006). Phosphorous acid fungicides are

more effective for this purpose than general disinfestants such as hydrogen peroxide/peroxyacetic acid products (HPPA) or chlorine dioxide-based products.

Duration between the occurrence of inoculation and post-harvest treatment appears to impact the efficacy of the product applied. HPPA was effective in reducing late blight incidence when applied immediately after inoculation, but was not effective when treatment was made one hour or more after inoculation (Miller et al. 2006). Phosphorous acid applications were effective in significantly reducing late blight up to six hours after inoculation. Complete control of late blight was obtained with 12.8 fl oz/ton of phosphorous acid when applied in a larger scale trial (one ton of tubers stored for 77 days at 8.9°C; *unpublished data*). As a result of this work, phosphorous acid is now being used more commonly for post-harvest control of late blight and pink rot.

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Figure 1. Distribution of *P. infestans* strains in the Columbia Basin of Washington and Oregon from 1992 to 1995 (adapted from Miller et al 1997).

Figure 2. Streaking of reddish brown tissue on the below-ground stem where *Phytophthora infestans* moved internally in the below-ground stem from an infected seed piece to near the soil line and then formed a symptomatic lesion during a moist period.

Figure 3. Late blight lesion on an above-ground stem arisen from an infected seed piece planted in the field.