A review of Phytophthora root rot in blueberry

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Background

All species of Phytophthora are plant pathogens, many of which can cause serious disease across a range of important food crops including soy, potato and tomato. There are more than 800 identified species of Phytophthora which are capable of causing root rot in more than 900 plant species worldwide (Yeo et al., 2017). Some species include those with associated quarantine and statutory plant health risks such as *P. ramorum* as well as *P. cinnamomi* which are both important pathogens capable of affecting trees, the prominence of which continues to rise in the UK. Some species also cause significant damage above ground such as foliar blight and dieback, rather than just affecting the roots and these include, among others, *P. ilicis* and *P. kernoviae*.

The genus Phytophthora has played a significant role in both human history and the history of plant pathology. During the 1840s, an “unknown agent” caused epidemics of late blight in potatoes across the United States and Europe. That pathogen was later identified as *P. infestans* which resulted in the devastating Irish potato famine in 1845 (Bourke, 1991). More than 150 years later, and still potato late blight remains a major constraint for potato production worldwide with losses of up to $5 billion per annum due to associated control measures and yield losses (Fisher et al., 2012; O’Brien et al., 2009).

Pathogenic species of the soil borne oomycetes, Phytophthora and Pythium, can often affect a wide range of crops resulting in discoloured and necrotic roots, stunted growth, pale yellow or reddish leaves, premature defoliation and in many cases, plant death. Phytophthora root rot was first observed in blueberry 60 years ago following above ground symptoms discovered in plants which affected leaves, crown, and stems. *P. cinnamomi* was discovered as the pathogen in question and has since been isolated as the cause of blueberry root rot throughout America and across Europe (Raniere, 1961). Root rot is now considered a major disease in blueberries.

Summary of main findings

- Phytophthora can infect all parts of the plant but usually attacks roots and stems.
- Symptoms are generally seen above ground first e.g., discolouration and wilting of foliage.
- Phytophthora can survive in plant debris and soil for many years.
- Contaminated water, soil, farming or personal equipment can hold and spread the pathogen so good hygiene practices are imperative.
- Wider placed drip lines, further away from the crown can help to slow down the spread of infection.
- Inspect new plant material, monitor, and isolate if possible before planting, and clean tools between pruning plants or taking any cuttings.
- Plant cultivars with known tolerance if contamination of soils is suspected.
- Plant blueberries on ridges and try and maintain good drainage.

Approach

This desk study was commissioned to fill a knowledge gap in our understanding of factors influencing phytophthora root rot in highbush blueberries (*Vaccinium Corymbosum*) and how management regimes may influence these. The study was undertaken by performing literature searches of Web of Science, Google Scholar and the websites of grower organisations (e.g. AHDB, Defra, Fera), using search terms such as blueberry root rot, phytophthora, oomycete and pathogenicity.

The study summarises information gathered from these literature searches from mechanisms of infection, identification and detection and susceptibility of blueberry cultivars. Finally, the study summarises additional crop management and control strategies that could be used to reduce the impact of root rot and maintain healthy, vigorous crops.

Introduction

Blueberry is a key crop with great potential for UK production, but current supply only meets around 15% of the UK market. Demand for blueberries is at record levels with UK fresh sales valued at £450 million in 2020 representing growth of over 11% year on year. As the cost of production for the fresh market is high, and labour is increasingly difficult to secure, there is a significant requirement for cultivars which are quick to establish and consistent in yield and quality to be developed. The changing UK climate presents additional challenges to plant growth, particularly for woody perennial species like blueberries.

Regarded as plant destroyers from the Greek word *Phyton* meaning plant and *Phthora* meaning destruction, Phytophthora species have become one of the most widespread, invasive and destructive plant pathogens worldwide (Webster and Weber, 2007). *Phytophthora cinnamomi* was first isolated from lesions of stripe canker present on the bark of cinnamon trees (*Cinnamomum burmannii* Blume) in a plantation in Sumatra by Robert Delafield Rands and subsequently cultured in 1921 (Zentmyer, 1980). There are many plant hosts of *P. cinnamomi* and these include species such as Cupressaceae, Ericaceae, Fragaceae and Lauraceae (Zentmyer, 1980). Of greatest concern within Europe are pathogens affecting avocados (*Persea americana*) and worldwide, those affecting pineapple (*Ananas comosus*) in the form of root and heart rot.

Pythium spp. have also been associated with root rot in many plants of the Ericaceae family including Rhododendron and Azalea but are rarely associated with the disease in blueberry. Studies have however, shown the potential incidence and damage that *Pythium* spp. can have on blueberry production so should not be underestimated (Bryla et al., 2008). *P. citrophthora* has also been reported as a potential pathogen capable of causing root rot in blueberries on a global scale as well as affecting citrus, raspberry, and kiwi (Larach et al., 2009).

Life cycle and sporulation

Oomycetes form a group of diverse fungus like eukaryotic microorganisms often known as water moulds. *P. cinnamomi* is a water mould which infects and decays roots under the right soil conditions (warm and wet) which requires free water in order to survive and reproduce (Kamoun, 2003).

There are three types of asexual spores, chlamydospores, sporangia and zoospores and then there are overwintering oospores which are formed through sexual recombination which are capable of surviving for several years even in the absence of a host plant. Both chlamydospores and oospores germinate to form sporangia under wet conditions. Sporangia can release tiny single celled zoospores which can travel by “swimming” in available water either found on leaf surfaces or within soil. Zoospores contain flagella (long whip like structures) which aid their ability to “swim” through wet soils spreading from plant to plant and spores can move considerable distances via contaminated soils (Byrt et al., 1982**)**. Zoospores are attracted to plant roots through a chemotactic response to root exudates where they can then form cysts on contact. These cysts can then germinate to form hyphae which allows the pathogen to grow and infect the plant while obtaining nutrients in return. The cycle then continues with the production of additional chlamydospores, oospores and sporangia via either asexual or sexual reproduction (Figure 1.). Zoospore cysts can survive for at least six weeks in the soil while mycelium can survive for six years (zentmyer and Mircetich, 1966; Gubler et al., 1989).

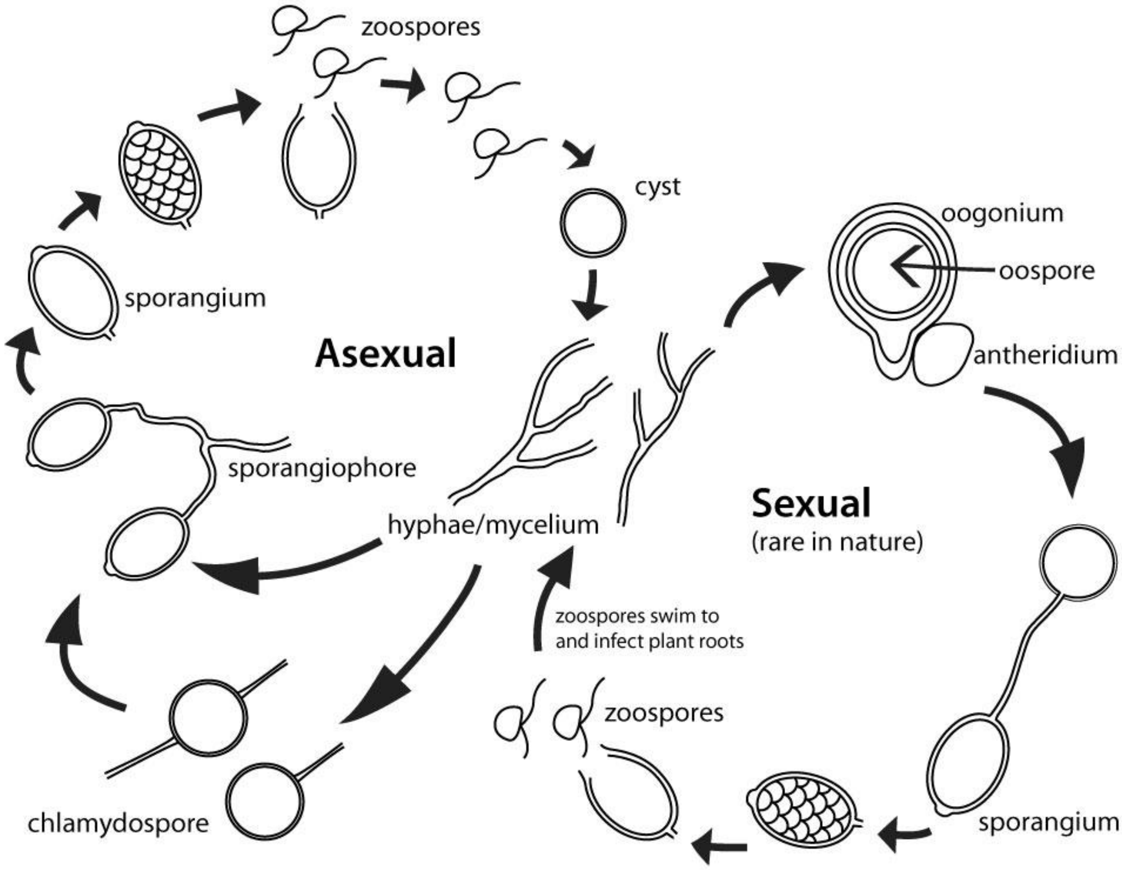

Figure 1. Life cycle picture showing the varying stages of both sexual and asexual spores in phytophthora. (Picture from Abad et al., 2019).

Mechanisms of infection by Phytophthora

Pathogenicity depends on the success or failure of a pathogen's ability to overcome host defence responses where it can then freely feed. Infection by *P. cinnamomi* tends to be more severe when soil temperatures rise above 25^{o}C, which can be reached early in the UK season especially when black weed matting is used for weed control (Yeo et al., 2017).

Plant defence systems are both sophisticated and complex and involve a number of signaling pathways. Spores can be physically transported in soil and infected material by animals, small feeding insects or through farming and nursery practices as well as extreme weather events. Once infections have been established hyphae begin to grow inter-cellularly. These hyphae continue to grow and extend into local cells where they digest cell walls and can acquire nutrients and, in some cases, suppress defence responses (Boevink et al., 2020).

Foliar symptoms then occur as a result of the inability of the diseased roots to uptake water and nutrients while additional stresses such as drought could hasten this onset.

Phytophthora root rot disease severity has been found to increase as a result of both soil wetness and saturation. Flooding instances will increase disease severity, allow the pathogen to spread and creates a greater risk of further contamination through movement of machinery and personnel who have come into contact with contaminated water or soil.

Characterisation and identification

Phytophthora root rot begins as spots or lesions which can be visible on susceptible plant roots. As the infection spreads the root decay advances resulting in severely decayed roots with no new root growth produced. This root infection then spreads into crowns and lower canes (Figure 2.). Symptoms are usually most severe on young plants. Initially, infected plants are stunted, appearing smaller than neighbouring healthy plants. The leaves can often be smaller, chlorotic and may turn red prematurely. Leaf scorch symptoms (necrotic leaf margins) can also develop as the root system becomes compromised. Severe infection leads to wilting and eventually death, particularly in younger plants. However, older plants with larger root reserves can survive for many years with a chronic infection and may never fully succumb to the disease. Lesions begin on small feeder roots which spread into main roots and then onto the crown (de Silva et al., 1999).

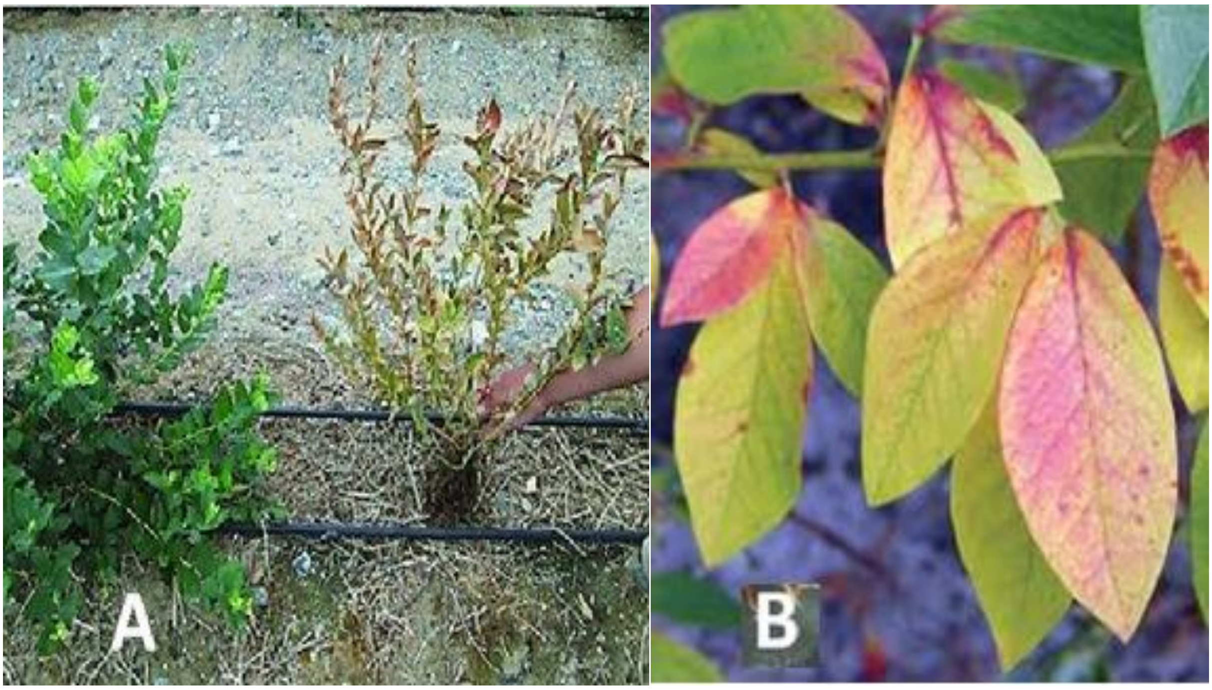

Figure 2. Above ground symptoms showing leaf discolouration as a result of poor water and nutrient uptake caused by the presence of root rot. Pictures from Huarhua et al., 2018 (A) and Ward, 2013 (B)

Above ground symptoms can often be seen without the need to expose roots (Figure 3.). Leaves will show yellowing or reddening before turning brown as a result of marginal leaf scorch and defoliation (de Silva et al., 1999). Damaged roots will result due to a lack of water uptake into the plant causing stunting, no new growth and terminal bud and leaf death which will lead to defoliation and dieback (Yeo et al., 2016).


Figure 3. The effects of Phytophthora root rot on blueberry plants can clearly be seen on the right-hand plant. Root mass is significantly reduced which results in limited shoot and leaf growth and a visibly

stunted plant. Leaves will be small, discoloured and no new growth will occur (Picture from Yeo et al., 2016b)

Detection and diagnosis

The high volume of plant germplasm which are currently transported between countries and continents continues to grow year on year as consumers demand new varieties of plants and flowers. Preventing the unintentional spread of Phytophthora therefore, will require the development of detection methods which are specific, sensitive, and robust (O'Brien et al., 2009). Isolates can often be obtained from the roots of plants suspected to be infected, washed and then cultivars obtained for identification. When grown on appropriate medium, isolates can then be further characterized with colony patterns after around seven days. Pathogenicity tests can then be conducted as well as molecular analysis to sequence and identify the species obtained.

There are many additional methods available today for the detection of Phytophthora and these include traditional methods such as baiting and direct isolation as well as the more rapid and specific methods of antibody and DNA based detection. Phytophthora ELISA (enzyme-linked immunosorbent assay) testing kits are available to screen for suspected cases which can detect the presence of a range of both Phytophthora and Pythium infections (O'Brien et al., 2009).

Baiting involves floating a susceptible piece of tissue on a soil-water slurry which, if infected can be grown on agar for subsequent morphological or sequence analysis. While up to 90% efficient, careful selection of bait tissue as well as soil composition and climatic conditions must be considered as these can affect the results (Marks and Kassaby, 1974,; O'Brien et al., 2009).

An immunological dipstick assay was developed for commercial use in the mid 1990's which was initially used in conjunction with baiting for greater levels of efficiency (Wilson et al., 2000). Commercially available ELISA tests, although quick to conduct can only identify to the genus level and not species level.

PCR analysis of DNA samples has rapidly become the method of choice due to higher degree of sensitivity, specificity and speed (Vincelli and Tisserat, 2008).

Susceptibility of blueberry cultivars

While all highbush blueberry cultivars are thought to be susceptible to Phytophthora infection there are some which appear to offer varying degrees of tolerance. While not immune by any stretch, some losses in both root and shoot biomass will still be evident compared to non-infected plants but these losses will be less than seen in more susceptible cultivars (Larach et al., 2009).

Many studies have shown significant differences in disease symptoms and severity across a range of highbush blueberry cultivars. Some of the cultivars which have been found with high levels of susceptibility include Bluecrop, Bluetta, Blue Ribbon, Cargo, Duke, Draper, Last Call, Top Shelf, Toro and Ventura. Susceptible cultivars show an inability of roots to grow into infected soils and typically have a low shoot and root mass (Yeo et al., 2016). These cultivars should be avoided in areas which are known to be infected with Phytophthora or poor drainage.

More resistant or tolerant cultivars include Aurora, Clockwork, Legacy, Liberty, Overtime and Reka. These more tolerant cultivars have been shown to have a reduced root mass compared to non-infected samples but still have enough root mass to continue to grow although with a reduced vigour. These are some of the cultivars which would be recommended should root rot be identified or suspected.

Increases in both yield and profitability can be achieved through the selection of cultivars with greater levels of resistance or at least tolerance. Genetic tolerance or resistance to root rot would be the target to reduce both crop and economic losses caused by the disease. Breeders would do well to include more tolerant parents such as Legacy, Liberty, Clockwork, Aurora and Reka in future selections and by applying phytophthora selective pressures in field trials could result in the development of new cultivars with both the fruit quality and disease resistance required (Yeo et al., 2016).

Crop management and control

Management requires an integrated approach beginning with cultural practices. While fungicides can occasionally slow down symptoms and suppress the disease, they do not cure the infection and are also prone to development of resistance in target pathogens. Throughout their life cycle, plants are subjected to many adverse environmental conditions including poor soil conditions, poor drainage or encountering a range of pest or diseases which can dramatically affect plant survival and limit productivity. To cope with such stresses, plants adjust metabolically and physiologically. Unanticipated variation in crop development is already in evidence in a range of crop cultivars resulting in yield instability with significant negative impacts on the rural economy, environment, and wellbeing.

Phytophthora can spread by means of tiny spores called zoospores which are capable of moving through water films towards plant roots which may be in response to chemical exudates from the roots serving as a signal or attractant to the zoospores. Heavy rain and method of irrigation can therefore affect infection rate with drip irrigation likely to have a greater impact than sprinkle irrigation due to a higher level of water content near the plant crown (Bryla and Linderman, 2007; Yeo et al., 2017).

It is important to therefore purchase disease free plants when establishing a new plot, avoid dark coloured roots and those which feel soft or mushy to the touch. Avoid waterlogged soil for planting and ensure good drainage by planting onto raised beds where possible. Heavy soils or poorly drained saturated soils are ideal conditions under which Phytophthora species can thrive. Planting blueberries on raised beds (at least 12 inches high), can increase drainage sufficiently which is especially important in low lying areas which can often be poorly drained in comparison to higher ground.

Disease suppressive cultural practices such as the use of organic mulches including sawdust or bark can help to suppress soil pathogen populations. The microbial activity (glucanase) found in the organic mulches have been associated with causing hyphal lysis and sporangial abortion through the breakdown of glucans in the cell walls of Phytophthora hyphae (Downer et al., 2001). High calcium levels in the soil can also suppress the progression of root rot by inhibiting both the motility and viability of zoospores in the soil (Messenger et al., 2000). High concentrations of calcium have also been shown to influence asexual reproduction in several Phytophthora species. It has been shown that calcium ions can cause rapid encystment of motile zoospores and immediate germination. The presence of these ions decreases the transport potential of zoospores through the soil leading to a reduction in pathogen persistence.

It is important to remember that while fungicides generally have the ability to slow the development and progression of the disease, they do not destroy the pathogen. Once fungicide activity declines the disease progression continues and the risk of developing resistance to fungicides increases. If prevention of infection is not possible then early identification and action are essential.

Conclusions and outlook

Cultural control methods aimed at alleviating high soil moisture and improving soil aeration by increasing drainage can help reduce potential losses as well as monitoring mineral nutritional content in soils (Stirling et al., 1992). Young plants are more susceptible to root rot, although mature plants can succumb under the right conditions. It can take several years for the presence of root rot to become obvious in plants which is why it is important for growers to monitor plant vigour especially during periods of warm temperatures as this is when disease development becomes prominent.

Once the presence of Phytophthora root rot has been confirmed the disease can be managed by avoiding planting in poorly drained areas, improving the drainage through tiling, selecting known tolerant cultivars and growing crops on raised beds. As with most diseases however, prevention is always better than cure and root rot is no exception.

Further work

1) Genetic resistance is a promising tool for minimising economic losses as a result of Phytophthora root rot. Identifying genes conferring tolerance in current blueberry cultivars would be a major step towards developing new breeding lines with significant tolerance and potential resistance to root rot in the future.

2) Comparing the performance of a wide range of commercial cultivars and how they can be grown for optimum vigour and resilience under UK conditions can help to guide growers in suitable cultivar selection.

3) Further work can be done to identify possible control measures for soil known to be contaminated with Phytophthora.

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