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Management of Plant Disease Epidemics with Irrigation Practices

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Abstract

Adequate water provision to roots is essential to warrant sustainable harvests of agricultural crops globally. However, water applied in excess or in deficit may result in the development of many fungal and bacterial plant diseases, which compromise produce yield and quality. Leaf wetness duration, soil water tension and related water variables impact several aspects of different plant disease cycles, such as the sporulation, survival of pathogen propagules, their dispersal to new hosts, germination and infection. Irrigation is thus arguably the most important cultural practice in the management of plant diseases, especially in the context of the quest of a more sustainable, less chemically dependent agriculture. The technology of water application and method of irrigation have been profusely studied as to their direct relation to plant diseases. Irrigation management has a strong impact on the disease severity and epidemic progress rates of many plant pathosystems, ranging from leaf blights to vascular wilts. In addition, plant virus vector population levels and vector dispersal are also affected by the method of irrigation. This chapter reviews experimental data on the effect of different irrigation configurations and management systems on some representative plant diseases.

Keywords: bacteria, nematode, oomycetes, fungi, virus, leaf wetness, pathogen propagule, dispersion, water

1. Introduction

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Plant diseases are one of the main constraints for agricultural production, leading to great loses annually all around the globe [1]. Plant pathology evolved along with agriculture, starting with the earliest farmers competing against plant pathogens with religious, supernatural or other

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practices [2] to come to the modern era, where science is used to track the conditions which favors pathogens and consequently allows growers to how to avoid them on a rational basis.

The irrigation efficiency not only ensures the most efficient crop growth, but it is also essential for high-quality production of seeds, food, textiles and other produce with increasing perception of the economical and environmental impacts. It is estimated that 30–40% of the world food production is from irrigated agriculture [3, 4]. Its importance can be exemplified by reports on potato production which indicate that variations as low as 10% of the potato water need result in significant yield losses, either from water deficiency, leading to deformation and reduced tuber size, or excess, which increases the intensity of many diseases [5].

Choice of the irrigation system in itself, regardless of the volume of the water supply, affects plant development as well as disease onset, pathogen dispersal and rates of disease progress. For example, furrow irrigation which requires large amounts of water, usually demands higher rates of nitrogen fertilization which can predispose the plant to many diseases; in addition, soil borne pathogens easily spread in the irrigation furrows following water flow [6]. In areas infested with *Ralstonia solanacearum*, the furrow and some drip irrigation systems increased tomato wilt incidence and reduced yield, while conventional overhead sprinkler irrigation had much lower disease levels and higher yields [7, 8].

Drip irrigation, in addition to a more efficient water use, is usually recommended to avoid wetting of aerial plant parts and generally results in less foliar diseases [9]. On the other hand, the direct (mechanical) and indirect (environmental) effects of delivering irrigation water droplets onto the leaf surfaces have been demonstrated to significantly reduce powdery mildews on Cucurbitaceae [10], Fabaceae [11] and Solanaceae [12] while also depressing virus vector movement [13]. These two situations indicate that diseases vary as to their response to irrigation. Therefore, a precise determination of the disease frequency and intensity in a given area must be done before choosing the most adequate irrigation method.

The sprinkle irrigation systems usually allow for better water distribution to the crop, at reasonable economic costs. It is generally more efficient than furrow irrigation, but it promotes foliar wetting, required for many pathosystems, and is favorable to propagule dispersion, especially of bacterial and most fungal spores.

In addition to the choice of the irrigation method, other factors must be taken into consideration, such as irrigation timing. Most fungal plant pathogens produce spores during nighttime, being dispersed after dawn. Consequently, morning irrigations are prone to dislodge and disperse spores, also offering humidity and free water for germination at the leaf surface. Some fungal pathogens may form spores or propagules later in the day and are thus favored by afternoon irrigations, while night irrigation will reduce spore dispersion, as reported for *Phytophthora infestans* [14].

With exception of the members of the Erysiphales (Ascomycota), fungi and bacteria need free water on the leaf surface to initiate infectious processes. In fact, the leaf wetness duration has been considered the most determinant microclimatic variable for disease establishment and progress, and it is one of the main variables monitored in disease prediction systems [15].

The pathogen success in establishing itself in the aerial plant parts is highly dependent on the duration of foliar wetting, which is directly affected by irrigation timing and other factors [16]. If the moisture provided by irrigation is enough to retain free water in the plant surface for the minimum time required for infection, it will lead to more intense disease epidemics. For many years, we have observed that processing tomato in Central Brazil display significantly lower incidence of diseases caused by *Phytophthora infestans, Septoria solani, Xanthomonas* spp. and *Alternaria* spp. under drip when compared to sprinkle irrigation.

In addition to water availability, the evaporation process must be considered. Evaporation is affected directly by relative humidity, air temperature, wind speed, air vapor pressure [4] and plant tissue position. For example, within Israeli climatic conditions, sprinklerirrigated tomato leaves take from 5 min (external leaves, strong wind, 36°C, 16% RH) to 4 h (internal leaves, no wind, no direct sun, 17°C, 16% RH) to dry. In the latter climatic conditions, the leaves may remain wet until dew formation at nighttime, completing a total 20 h of total humidity [17]. A similar phenomenon occurs in the dry season (April–September) in Central Brazil, when almost all processing tomato and potato crops are grown. Both crops are hosts of late blight (caused by the oomycete *Phytophthora infestans*) and early blight (caused by the true fungus, *Alternaria solani*). These pathogens have different resistance levels to dryness and widely different temperature requirements, serving as illustrative models for the discussion on infection and the influence of the leaf microenvironment on disease severity.

The way plant pathogens relate to irrigation and water availability depends on a diverse number of characteristics intrinsic of each group of microorganisms. In the present review, diseases and their respective causal agents were grouped according to their primary niche in the plant, either diseases of aerial plant parts or as crown and root diseases. Other divisions were made below for clarifying the effect of the water on each plant part or phase of the disease cycle. Oomycetes, for example, are very well adapted to the availability of free water, while other fungi, as the *Erysiphaceae*, (the powdery mildews) have a negative interaction resulting in damage of conidia when overhead irrigation is used. Bacteria are also highly dependent on water to prevent desiccation (which usually causes sharp decrease on their populations) and then to allow multiplication until they reach the threshold numbers necessary for invasion and infection. Fungi with a gelatinous matrix also respond differently when compared to other fungal groups: For instance, aerial transport by wind does not play an essential role for these organisms, whereas sprinkler irrigation typically provides the main dispersal method.

2. Diseases of the aerial plant parts

Fungi, oomycetes, virus and bacteria infect aerial parts of susceptible host plant (leaves, stem, flowers and fruits) resulting in diseases responsible for losses due to direct damage to the commercial produce or to yield reduction as a consequence of impaired photosynthesis and loss of photoassimilates.

These pathogens, different from the soil-habitant ones, must be resilient to adverse environmental conditions such as dehydration, large temperature fluctuations, nutrient scarcity in an epiphytic phase, incidence of UV light, among other physical, chemical or biological harmful factors [18].

While wind plays a critical role on the dispersion of plant pathogens, irrigation water and rain, provide conditions for spore germination, avoiding desiccation of fungal and bacterial cells or, in some instances, damaging propagules sensible to water.

Many reports have indicated that more frequent sprinkle irrigations increase disease incidence of several foliar diseases [6, 14]. The understanding of the dynamics of each pathosystem is therefore mandatory for choosing the method of irrigation to be implemented in a given situation.

While oomycetes, fungi, bacteria and viruses all infect aerial parts of plants and are affected by irrigation, the latter is indirectly influenced because water affects insects and other vectors which transmit them.

2.1. Oomycetes

The oomycetes, long treated as fungi and studied by mycologists due to their morphological, functional and ecological similarities with the Fungi Kingdom actually belong to the Chromista Kingdom and are more closely related to algae than to fungi [19]. They include Phytophthora wilts and blights, the downy mildews caused by the Peronosporales, the white rusts (genus *Albugo*) and root, crown and fruit rots by the genus *Pythium* and *Phytophthora*.

In general, oomycetes are greatly dependent on high humidity levels for all stages of the life cycle, including sporangia formation [20], and especially so for the indirect germination of sporangia in the form of zoospores, a process of great epidemiological consequence which requires not only high humidity levels, but actual free water [21]. High relative humidity (RH) can be achieved in several ways, including the method of application of irrigation water, high plant density and reduced plant spacing [22]. Shtienberg [23] also warned about the use of polyethylene mulch as a means to increase irrigation efficiency by reducing water evaporation.

Irrigation may also be responsible for the short or long-distance introduction of oomycete inoculum into new growing areas, which was reported for the first time in 1921 [24]. Ranging from 6 to 45 days, the survival of plant pathogen propagules on irrigation water varies accordingly to the pathogen species, other abiotic conditions (temperature, pH, etc.) and especially with the propagule type [25, 26].

Free water on leaves, generally reported as leaf wetness duration, is a combined consequence of rains, irrigation events and microclimatic conditions prevailing in the plant canopy. Due to the strong dependence of oomycetes to leaf wetness, the ones infecting aerial plant parts can be controlled by the choice of irrigation method in favor of the systems that reduce leaf wetness. This has been shown for *Peronospora sparsa*, the causal agent of the blackberry downy mildew [22]. Mildew severities of 97% were recorded in the sprinkler overhead irrigation, compared to less than 10% in the drip system. Greater severity was associated with larger periods of time of leaf wetness durations, in the sprinkler irrigated treatment.

Other oomycetes can be controlled by drip irrigation, as for *Phytophthora infestans* infecting greenhouse-grown tomatoes [27], or even in tomato field crops, planted in the dry season in the Brazilian Midwest (unpublished). *P. infestans* requires 2 to 6 h of leaf wetness (depending on temperature); nevertheless, high humidity levels inside the greenhouse (due evaporation) may favor disease development, stimulating spore germination [23, 28].

2.2. Gelatinous matrix fungi

Fungus is one of the most diverse Kingdoms, with many species pathogenic to plants. Most fungi do not require water for spore dispersion, being easily dispersed in the dry air. However, numerous fungi, including important plant pathogens, are dependent on water splash for the dissemination. Commonly, this kind of fungi produces conidia associated to a gelatinous matrix in asexual sporulation structures such as picnidium (*Ascochyta, Phoma, Septoria*) or acervulus (*Colletotrichum*).

If one fungus species requires water splash for dispersion, again the type of irrigation has a strong effect on such group of pathogens. The size and amount of the water drops may alter its capacity of spore dispersion, since smaller drops are unlikely to dislocate and disseminate spore from one spot to another [29].

An example of the effect of irrigation method on fungi dissemination are the high severities of gummy stem blight (*Didymella bryoniae*) and anthracnose (*Colletotrichum gloeosporioides* f. sp. *cucurbitae*) of watermelon irrigated by overhead sprinkler, which presented reduced productivity and fruit quality. When shifting overhead to furrow irrigation, both diseases were drastically reduced [6]. These changes were associated with strong reductions of the foliar and fruit wetness periods, resulting in less dispersion and germination of spores. The same pattern was seen for anthracnose (*Colletotrichum acutatum*) in strawberry, when drip irrigation leads to very low disease incidence, postponing disease onset, and, therefore, reducing loses [30]. The same pattern has been observed for sweet pepper anthracnose, caused by *Colletotrichum* spp. (unpublished) and *Septoria lycopersici* on tomato [31]. For the septoria leaf spot, disease progress rates varied widely in the sprinkler, microsprinkler, drip and furrow irrigated plots, and severity increased most in treatments that kept leaves wet the longest.

The concept of leaf wetness is also an issue for *Glomerella cingulata* in apple. This pathogen requires high RH (>99%) and foliar wetness duration of 2.76 h, for significant germination of conidia. Additionally, the spore release from the acervuli and subsequent dispersal need rain or irrigation water for the splash-dispersal effect. Therefore, in the absence of these conditions, lesions are sparse and do not spread, even within a single host plant [15].

2.3. Dry propagule fungi

Several species in the Fungi Kingdom reproduce asexually by producing dry conidia, with no gelatinous matrix, and may or may not be affected by irrigation management.

Powdery mildew, for example, caused by a number of species on the *Erysiphaceae* (Ascomycota), can infect several hosts, and is characterized by the presence of a whitish growth (mycelium, conidiophores and conidia), mainly in the adaxial leaf surface. Still fairly dependent on

humidity as several other pathogens, its development may increase until a maximum of 80% RH as reported for *Uncinula necator* in grapevine [32]. Nonetheless, different from other fungal diseases, sprinkler irrigation is harmful for powdery mildews disease progress. The mechanical impact of water droplets harms the fungal structures, hindering disease progress. This phenomenon was previously found by Ruppel et al. [33] who observed lower disease incidence on sprinkler-irrigated sugar beet fields when compared to furrow irrigated ones. The effect of free water in powdery mildew conidia was analyzed by Shomari and Kennedy [34] in conidia of *Oidium anacardii*, a pathogen of cashew, by immersion of infected leaves in water, exhibiting a significant reduction on spore germination: after that phase, leaf wetness does not influence any further on the host tissue colonization.

Other examples of the irrigation effects over powdery mildew may be seen with *Leveillula taurica* in tomato, which displays a critical increase of incidence when the crop is drip-irrigated, due to the absence of free water on leaves [27]. On pumpkin, powdery mildew is progressively reduced with increasing water volumes applied by the conventional overhead sprinkler irrigation system [10].

Conversely, *Alternaria solani*, the causal agent of tomato and potato early blight, does not suffer any negative effects of sprinkler irrigation. In fact, *A. solani*, as the great majority of plant pathogens that form dry propagules, benefits from the increased leaf wetness duration delivered by irrigation systems that wet aerial plant parts. Processes such as spore production and germination rates are favored. Reduced amounts of water may not markedly affect the development of *Alternaria* diseases, since its dark, thick-walled, multicellular spores are resilient to desiccation. In addition, germination of *A. solani* can take place with the only source of moisture deriving from nighttime dew, without need for irrigations [6].

Fusarium head blights (*Fusarium graminearum, F. culmorum, F. avenaceum*) of maize, wheat and other Poaceae, are economically devastating diseases not only for the direct losses of reduced grain yield but also for the accumulation of mycotoxins in the produce. Timing of irrigation is determinant for avoiding the occurrence of these diseases, and water should be avoided before anthesis and early grain fill periods [35]. Irrigation or rain water stimulates spore production, dispersion and germination of the *Fusarium* and of its sexual form (*Gibberella zeae*). High humidity levels (>94%) are also a requirement for most of the disease cycle phases [36, 37].

2.4. Bacteria

Bacteria, single-celled prokaryotes (1–2 μ m in size) which reproduce by binary fission, are natural inhabitants on the rhizosphere or plant surfaces where they are mostly harmless as residents or epiphytes. The plant pathogenic ones will cause problems to a susceptible host only when conditions are favorable for their establishment, infection and multiplication. These conditions include high humidity and poor air circulation around plants. A film of free water on the leaf surface is the right condition for bacterial multiplication. Since they are microscopic, their presence is noticed only in large quantities, such as colonies in laboratory culture media or as viscous substances oozing from plant vessels and biofilms, or upon manifestation of symptoms of the diseases they induce.

As for the diseases caused by oomycetes and true fungi, bacterial diseases in plants may occur in the aerial plant parts, including leaves and fruits, causing several symptoms such as cankers, pustules, blights, spots and specks. The symptomatology may vary with plant variety, host age and climatic conditions [38].

Bacterial diseases are strongly affected by irrigation. Water, because it is necessary for the epidemiological processes of dispersal, infection and colonization, is considered one of the most, if not the most, important inputs that move bacterial disease expression on most crops.

Leaf wetness is essential for bacterial infection and colonization of aerial parts of the plants. Bacteria penetrate through wounds or natural openings such as stomata and hydathodes. From diseased plants, bacterial cells are dispersed within and among fields through aerosols, insects, windblown soil and sand particles, movement of plant propagules and water flow.

For instance, bacterial spot (*Xanthomonas euvesicatoria*) is a recurrent disease that can devastate pepper fields whenever warm, wet weather is present. The pathogen is seed borne and is responsible for the formation of leaf spots that harbors large number of bacterial cells. Upon impacting on lesions, droplets from rain or overhead irrigation disperse bacterial cells through many micro-droplets from infected plants to neighboring healthy plants, especially under windy conditions. In addition, when foliage is wet, farm operations allow bacterial cells from infected plants to be carried to healthy plants within or between field areas [39].

In this example, which applies to many other bacterial spot diseases, switching from overhead to drip irrigation will warrant necessary moisture accessible to the roots while keeping the foliage dry. It is necessary to keep in mind that, as discussed elsewhere in this chapter, other diseases and pests might be favored by one particular kind of irrigation. An overall analysis of the crop management is necessary for the decision-making process, in a way to cope with different diseases and obtain desirable yields.

2.5. Viruses

Viruses are intracellular pathogens not capable of reproducing outside a living cell but possessing the genetic means for the manipulation of the host replication machinery for such action.

Vectors of plant viruses have a major role on the epidemics of plant virus because they are needed for the transportation and introduction of the virus particles into the host plant cell [40]. Most plant viruses can be transmitted by one of several groups of insects. A minority may also be vectored by other organisms such as mites, nematodes and pseudofungi (as those from kingdom Protozoa) [41, 42]. Nematodes that disseminate plant viruses will be addressed below. In some cases, diseases of complex etiology combine damages from the nematode with the virus, compounding losses.

Irrigation water does not affect the several viral pre-infection stages that are found within the fungi and bacteria life cycles. When lacking or in excess, water and irrigation may cause physiological host changes, which may accentuate or attenuate symptoms or alter the relationship of the vector with the virus and the host plant [43]. In some cases, the virus may protect its host from severe drought by avoiding irreversible wilt, as reported by Xu et al. [44]. Another similar example is during the infection of wheat by the *Barley yellow dwarf virus*; when the host is stressed from severe drought, the survival of the infected plant is increased, and it offers a more favorable growth for the aphid vector, *Rhopalosiphum padi* [45]. Turnip plants suffering from water deficiency stress can increase the transmission of *Cauliflower mosaic virus* (CaMV) by 34%, while the transmission of the *Turnip mosaic virus* may be increased by 100%. The increase in transmission was not related to higher virus tittering but for a rapid response by CaMV in producing transmissible morphs [43].

The main effect of irrigation on plant virus diseases concerns its effects on the vectors. Irrigation may affect the vectors, by altering its feeding habits, the efficiency of virus acquisition from an infected host, and, especially, by physically removing or disturbing the feeding of the insect. This latter effect is most noticeable by the application of water by sprinkler irrigation, which can reduce the population when compared to other irrigation methods in experimental plots [46]. These findings were confirmed not only for whiteflies (*Bemisia tabaci*) [27, 47] but also for *Myzus persicae* [48], each of which are important vectors of numerous plant viruses worldwide.

3. Crown and root diseases

Crown and root diseases are caused by soilborne pathogens and usually result in great losses since control measures are more difficult because the "enemy" is protected by the soil layers. Frequently, soilborne pathogens lead to the abandonment of an infested field or make the whole farm improper for the cultivation of particular crops. These soil pathogens belong to different taxa in the fungi, oomycetes, bacteria and nematodes, and infect roots and crowns. They spend most of their life cycle in soil, with high resilience to changes in the physical environment and enhanced competitive skills. They are generally facultative pathogens, with good saprophytic activity. The dispersal of these pathogens is mostly associated to soil movement, adhered to implements and machines, even though spores of some may be dispersed by wind and water [49]. In tropical and subtropical conditions, these pathogens are favored, given the lesser oscillations in the soil physical parameters [50]. Soil is considered an environment that favors organisms which use water for movement, as the flagellate zoospores from oomycetes, flagellate bacterial cells, and nematodes that move in water films. Evidently, all these organisms may be passively transported even faster, and further, in flows of water.

The way irrigation methods affect crown and root diseases, and their causal agents vary accordingly to the group of microorganisms and other characteristics, such as the capacity for facultative anaerobiosis (in flooded or water-logged soil), which is conducive to soft rots caused by pectolytic bacteria.

Nematodes, mostly soilborne pathogens, are highly affected by water availability, typically by the aid of water for active movement in the root zone. Also, water allows for the passive movement following the water flow on soil, as when furrow irrigation is used.

In the following sections, the same group of pathogens addressed previously is discussed for the development root and crown diseases.

3.1. Oomycetes in soil

Many of the previously addressed factors in topic 2.1 can be applied for oomycetes causing disease in lower plant parts. The dependence on water still exists, although, different from the aerial organs, soil tends to be more stable for physical factors in general, and for temperature and humidity in particular, while it is a generally more competitive environment.

As for various pathogens, the epidemiology of a given oomycete is bound to irrigation or rainfall intensity and frequency. *Phytophthora capsici*, for example, during seasons of intense rainfall, causes much faster epidemics than when in conditions of moderate rainfall or irrigation [51].

Soil oomycetes are in general highly adapted to survive in soil, with varying times of survival accordingly to temperature and a few other abiotic factors. Irrigation water plays an especially important role on the dispersal of oomycetes, due to their flagellate zoospores. "True fungi" (those in the Kingdom Fungi) do not have flagellate spores, and so are less efficiently dispersed by soil water.

As discussed earlier, irrigation water and free soil water aid pathogens that are immovable, as non-flagellate bacteria which go with the water flux, but also for zoospores of oomycetes, flagellate spores that may dislocate in water [50]. Zoospores are also capable of host plant detection, allowing chemotaxis to the host and a quick attachment to the host tissue and the initiation of the infection process. *Phytophthora parasitica*, a pathogen of citrus, is one of those organisms that uses water for dispersal: irrigation spreads this pathogen not only within one field, but to an entire region, affecting growers that use the same water source [52]. The same pattern is found for *Phytophthora capsici*, in bell pepper, tomato and squash fields: for this pathogen, furrow irrigation has been shown to carry sporangia and zoospores to long distances. The number of infected plants along an irrigation line is attributed to the collection of secondary inoculum produced by the first infected plants [53]. *Phytophthora capsici* and *P. parasitica* were readily dispersed in furrow irrigation water up to 70 m from the point sources of inoculum in Solanaceae and Cucurbitaceae [54], and the mere reduction of furrow irrigation frequencies drastically reduced Phytophthora wilt on squash [53] and sweet pepper [55].

Frequent irrigations saturate soils and keep humidity for long periods of time, favoring propagule dispersal. Bowers et al. [56] and Ansani and Matsuoka [57] showed that in warm conditions (15–25°C), *P. capsici* resists for several days, even buried at several depths in the soil. In addition, soil moisture may render some hosts more predisposed to oomycete infection [58]. However, this has not been confirmed for all oomycete pathosystems, as for *P. capsici* in bell pepper [59]. Constant soil moisture at saturation or low saturation levels is not as positive for disease development as fluctuations of soil moisture [60]. Therefore, a lesser number of irrigation events are usually a form of disease control. For *Pythium aphanidermatum* in petunia, low and constant irrigation reduced plant infection, in contrast with constantly saturated soils or soils submitted to a cycling of wetting and drying [61].

Different irrigation methods may increase or reduce diseases caused by oomycetes in soil. Gencoglan et al. [62] showed that drip irrigation was the most efficient system to avoid *P. capsici*, with only 1.7% of incidence, versus 3.1% and 3.2% for furrow and sprinkler

irrigations, respectively, and lastly and most prejudicial, basin irrigation, which caused 93.9% dead plants. Several authors have confirmed that drip irrigation is the most efficient irrigation method for oomycete control [63, 64].

3.2. Fungi in soil

True fungi in soil must not only survive humidity and temperature fluctuations but also the competitive environment that prevails in the rhizosphere. The effect of irrigation is different from what is commonly seen on above soil plant organs, and here, diseases may be favored by drip irrigation due to the large availability of water next to the host roots and crowns.

Some plant pathogenic soil fungi have a complex relationship with the host, and infection may be hampered at low soil moisture, while high soil moisture may reduce symptom expression and improve yields. For example, the most effective management strategy to reduce Verticillium wilt, without decrease of dry matter production, is to irrigate at water deficit levels to the host during the vegetative stage and at 90% of soil capacity during the production phase (unpublished).

Accumulation of water in soil due to irrigation is increased when field soil is compacted (e.g., as a consequence of intensive agrotechnical operations) and/or native pedosphere properties (e.g., texture heavier soils). Several pathogenic soil fungi are favored by this condition of reduced aeration, such as *Fusarium oxysporum* pv. *solani*, *F. oxysporum* pv. *phaseoli*, *Rhizoctonia* spp. and *S. sclerotiorum* [65]. For *Rhizoctonia* infections causing root dieback in *Pinus* nurseries, excessive water interacts negatively with the host due to lack of root aeration, reducing growth and favoring the fungal infection. The ensuing root decay and water accumulation further stimulates the development of other secondary plant pathogens [66].

Irrigation may also aid on the propagule dispersion and disease development. For example, Fusarium root rot (*Fusarium solani* f. sp. *phaseoli*) in beans is greatly reduced when sprinkler irrigation is used, contrarily to the negative effects of furrow or drip irrigations on the disease [67]. For *Sclerotinia minor*, the causal agent of lettuce drop, drip irrigation has a suppressive effect on the pathogen, while furrow increases substantially the sclerotial population. Irrigation not only provided humidity but also lowered the soil temperature, with furrow irrigation allowing the establishment of a more suitable temperature (18°C) for the fungus [68].

As several other group of pathogens, fungi can also enter a new area by means of irrigation water. Previous studies on *V. dahliae* in irrigated olives showed a great dispersion of propagules [69] while its survival is also remarkable, with reports of up to 15,000 propagules of per liter of water in ponds used for irrigation [70].

3.3. Bacteria in soil

Soil-associated bacteria are highly influenced by soil moisture. For most plant pathogenic bacteria, high humidity favors disease onset and development. Incidentally, bacterial wilt

(*Ralstonia solanacearum*) was first known as the "moisture disease" of potatoes, before the causal agent was identified [71]. In fact, the disease is prevalent during the wet summers, when high temperatures and high humidity are combined in a perfect condition for bacterial multiplication.

When comparing irrigation methods on bacterial wilt, Marouelli et al. [7] found that disease was significantly higher when processing tomato in Central Brazil was drip-irrigated, with an average of 42.5% wilted plants, 65 days after seedling transplant, in comparison with 5.0% incidence with sprinkle irrigation. Frequency of drip irrigation did not affect bacterial wilt incidence. It is believed that drip irrigation maintains the plant rhizosphere close to field capacity, thus favoring the disease, contrasting with the sprinkle irrigation, which provides periods of dry and wet conditions. Furrow irrigation was not studied, but it would most probably have an effect similar to the drip irrigation, or even more pronounced, if dispersion of the pathogen in the furrow is taken into account.

Contrasting with bacterial wilt, potatoes are affected by common scab, induced by *Streptomyces* spp. In this case, however, low soil humidity during tuber growth phase favors scab formation, what makes irrigation management recognized as one of the most efficient scab control measures. According to Wharton et al. [72], keeping soil moisture near field capacity for a few weeks at the beginning of tuberization substantially inhibits pathogen infection and disease development. The most likely explanation for this phenomenon is that the maintenance of high soil moisture is a condition that favors a more varied and competitive microbiota in the host rhizosphere, to the detriment of *Streptomyces* species.

Overall, because plant pathogenic bacteria may be viable in water for long periods of time, irrigation deserves special attention for two important epidemiological processes: survival and dispersal [73].

3.4. Nematodes

Nematodes infect root systems of a great number of plants species and are one of the most difficult plant pathogens to control. Some parasitize upper plant organs, causing galls or lesions on leaves and seeds. However, most nematodes are root pathogens that not only act as plant parasites, but also facilitate infections by other soil pathogens, that penetrate through lesions caused by the nematodes on the root systems.

Nematode populations usually keep a steady growth if a susceptible host is available, soil texture is ideal and irrigation is not excessive (reducing oxygen availability), or restricted (preventing movement), as reported for *Meloidogyne enterolobii* in guava [74].

The influence of water in this group of plant pathogens is mostly related to dissemination and movement in soil. Soil moisture, depending on the nematode species is essential to allow movement of juveniles and adults from colloid to colloid on water films around soil particles.

In addition to active movement, eggs, juveniles and adult nematodes can be carried passively by irrigation water to short or long distances. Nematode spreads through large field areas, if water is collected from the same infested source [75]. Also, intensive irrigation is conducive to high nematode population levels, due to its effect on soil texture remodeling, altering abiotic conditions as aeration and particle arrangement creating new niches for protection [76]. Nematode locomotion depends on water, as studied for the J2 of *Meloidogyne incognita*, which could not travel against the water flow, limiting itself to resist the flow, trying to remain static. In sand substrate tests, when water percolated, the nematode moved with the water flow, resulting in the distribution of the nematode along irrigated areas [77].

Nematodes are already plant parasites *per se* but can also act as vectors for viruses as *Xiphinema index* (and other species) capable of transmitting *Grapevine fanleaf virus* into grapes [78]. Two nematode orders are known as vectors of plant viruses, Dorylaimida and Triplonchida [79]. For these nematode vectors, and several other species, soil is not required to be saturated, if humidity is kept at "normal levels" the parasite can survive and still act as a vector even 4 years in the absence of its hosts [80]. Also, *X. index* can be disseminated by contaminated irrigation water [81]. In some cases, these parasites are highly resistant to dehydration, in a survival strategy termed anhydrobiosis. Anhydrobiosis has been observed in many nematodes, such as among *Pratylenchus* (the lesion nematodes), one of the most important plant pathogenic nematode genera [82].

Differences among irrigation methods have not been very well explored for this group of plant pathogens. However, taking into consideration the effect of water flow and irrigation on the nematode's movement and displacement, drip irrigation could result in lesser dispersal and consequently, less infected plants in the fields.

4. Conclusion

The response of plant pathogens (fungi, oomycetes, bacteria, nematodes, viruses) to the range of irrigations methods and management configurations varies widely and must be addressed for each particular plant-pathogen system (Figure 1). Among furrow, overhead sprinkler, microsprinkler, and drip irrigation, there are a variety of management choices that may strongly affect propagule dispersion, induction of germination, biofilm formation, penetration and survival of each specific group of pathogens. For the oomycetes and bacteria associated to aerial plant organs, due to their strong dependency on free water and high humidity, drip irrigation might be the appropriate choice. Among the true fungi, the effects of the irrigation system and management differ, and species of dry and wet spores respond distinctly to each individual method. In some groups, such as the Erysiphales, free water may hamper disease progress. Nematodes and oomycetes need free water in the soil to be actively distributed in the crop. Viruses, accompanying their vectors, can be controlled by sprinkle irrigation water, which disrupts the contact of the insect with the plant. The knowledge of the causal agent and of the disease epidemiological components is essential when deciding the type of irrigation, frequency and water volume to be applied to manage one particular plant disease and is key to achieve good yields and high product quality.

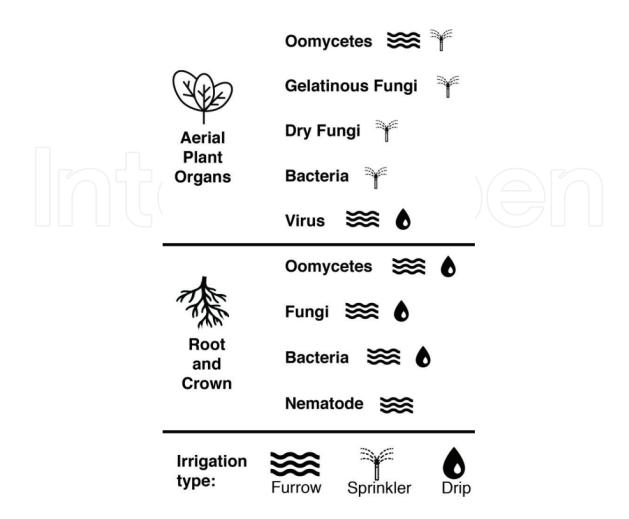


Figure 1. Schematic representation of irrigation methods which benefit disease development according to the plant pathogen group and affected plant organ. Furrow irrigation is conducive for oomycetes when aerial plant parts are in contact to the ground, as in processing tomato fields. Exceptions may exist for all groups.

Conflict of interest

The authors state no conflict of interest.

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