A Review of Control Options and Externalities for Verticillium Wilts

Christine L. Carroll, Colin A. Carter, Rachael E. Goodhue, C.-Y. Cynthia Lin Lawell, and Krishna V. Subbarao

First author: College of Agriculture, California State University, Chico, CA 95929; second, third, and fourth authors: Department of Agricultural and Resource Economics, University of California, One Shields Avenue, Davis, CA 95616; and last author: Department of Plant Pathology, University of California, Davis, c/o U. S. Agricultural Research Station, 1636 E. Alisal Street, Salinas, CA 95616.

Corresponding author and email: C. L. Carroll and clcarroll@csuchico.edu.

ABSTRACT

Carroll, C. L., Carter, C. A., Goodhue, R. E., Cynthia Lin Lawell, C.-Y., and Subbarao, K. V. 2017. A review of control options and externalities for Verticillium wilts. Phytopathology 107:000-000.

Plant pathogens migrate to new regions through human actions such as trade, where they may establish themselves and cause disease on agriculturally important crops. Verticillium wilt of lettuce, caused by *Verticillium dahliae*, a soilborne fungus that was introduced to costal California via infested spinach seeds. It has caused significant losses for lettuce growers. Once introduced, Verticillium wilt could be managed by fumigating with methyl bromide and chloropicrin, but this option is no longer available. Growers can also manage the disease by planting broccoli or not planting spinach. These control options require long-term investments for future gain. Verticillium wilt can also be prevented or controlled by testing and providing spinach seeds with little or no V. *dahliae* infestation. However, seed companies have been reluctant to test or clean spinach seeds,

as spinach crops are not affected by Verticillium wilt. Thus, available control options are affected by externalities. Renters and other producers with short time horizons will not undertake longterm investments and seed companies do not take into account the effect of their decision not to test on lettuce producers. We review the recent research on the externalities that arise with shortterm growers, and between seed companies and growers due to Verticillium wilt. These externalities have important implications for the management of Verticillium wilt and, more broadly, for the management of migratory pathogens and the diseases they cause in agriculture in general. This review of interest to policy-makers, the producers, marketers, seed companies, and researchers.

Keywords: Verticillium dahliae, Verticillium wilt, economics, control options, dynamics, externalities, invasive species

1. Introduction

Species migrate into new regions through human actions, where they may become invasive and either cause disease in plants, animals or people, or out-compete the native flora and fauna. Species often invade as a result of trade, and invasive species in the United States cost over \$100 billion each year (Levine and D'Antonio 2003; Pimentel et al. 2005; Springborn et al. 2011). Invasive plant pathogens, including fungi, cause an estimated \$21 billion in crop losses each year in the United States (Rossman 2009). California, a major agricultural producer and global trader, sustains significant economic damage from such pathogens. We address a specific case of an invasive pathogen: *Verticillium dahliae* in California lettuce.

The value of California's lettuce (*Lactuca sativa* L.) crop, which represents the majority of the United States' lettuce production, was \$1.7 billion in 2013 (National Agricultural Statistics Service 2015). Further value addition accrues when lettuce is processed and sold as ready-to-eat salad

mixed with other leafy greens. Measured by value, lettuce ranks in the top ten agricultural commodities produced in California (National Agricultural Statistics Service 2015). Much of California's lettuce crop is grown in the Salinas Valley in Monterey County, where lettuce represents 27% of the county's agricultural production value (Monterey County Agricultural Commissioner 2015). Approximately 14,400 thousand hectares are planted to lettuce in Monterey County each season (spring, summer, and fall). Spinach, broccoli, and strawberries are also important crops in the region.

Even though lettuce has been grown in California since the early 1900s and *Verticillium dahliae*, a pathogen with a broad host range, was present in coastal California for most of this time (Atallah et al. 2011), lettuce had remained immune to Verticillium wilt caused by this pathogen. Remarkably, other crops grown in rotation with lettuce were highly susceptible to Verticillium wilt and the pathogen was present in these agricultural soils. Thus, despite being in the same niche, the host and the pathogen had failed to establish a host-pathogen relationship for most of the 20th century. This historical pattern altered with the dramatic appearance of Verticillium wilt on lettuce in 1995 (Subbarao et al. 1997) and its rapid spread through the Salinas Valley. Recent studies (Atallah et al. 2010, 2012; Short et al. 2015a, 2015b) have clearly established the role of exotic strains carried on spinach seed in including lettuce in the ever expanding list of hosts of *V. dahliae*. This paper discusses the economics of managing *V. dahliae*, a soilborne fungus that is introduced to the soil by infested spinach seeds that causes Verticillium wilt on lettuce crops that follow spinach.

Externalities are a common problem in pest management (Harper and Zilberman 1989; McKee 2009; Fuller et al. 2011; Ambec and Desquilbet 2011; Ceddia et al. 2011). An externality arises whenever the actions of one individual or firm affects the payoffs to another individual or firm not

involved in a specific transaction. When individuals or firms make their decisions, they generally do not account for any externalities they may impose on others, so their decisions may not be socially optimal. We discuss two externalities that arise due to Verticillium wilt and review our research in Carroll et al. (2017a,b) on these externalities.

2. Verticillium Wilt

Nearly 400 plant hosts, including major agricultural crops and ornamentals (Pegg & Brady, 2002), are susceptible to Verticillium wilt mainly in temperate climates of the world (Inderbitzin and Subbarao 2014; Pegg & Brady 2002). The fungus survives in the soil as microsclerotia, which are resting structures that are produced in infected plants. This allows the fungus to remain in the soil in the absence of a host for up to 14 years (Wilhelm 1955). Microsclerotia germinate and infect susceptible hosts through the root. Infection slowly progresses through the vasculature into the shoots (Fradin and Thomma 2006). The pathogen thus interferes with the water uptake and transport through the plant resulting in wilting symptoms, typically coinciding with host maturity (Isaac and Harrison 1968; Vallad and Subbarao 2008). In general, incidence of the disease is proportional to the density of microsclerotia in soil (Xiao and Subbarao 1998; Wu and Subbarao 2014). The threshold density of microsclerotia in the soil at which Verticillium wilt develops is host-dependent. Lettuce has a much higher threshold than most other crops, such as strawberries, artichokes, and cauliflower, with little or no disease developing when microsclerotial density is <100 per gram soil (Wu and Subbarao 2014). The disease appears just before harvest after all inputs have already been applied for crop production resulting in near-total economic loss.

Verticillium wilt first occurred on lettuce in California's Pajaro Valley in 1995 (Subbarao et al. 1997). Since then, the disease has spread rapidly through the Salinas Valley. By 2010, more than 150 fields with Verticillium wilt on lettuce were identified (Atallah et al. 2011), amounting

to more than 1,620 hectares. Although growers have resisted reporting the extent of the disease since 2010, it is likely that the number of affected production fields and hectares have expanded since.

Data are available regarding the impact of incorporating infected lettuce plants into the soil, planting repeated lettuce crops, and fumigation. Vallad and Subbarao (2008) show that several million microsclerotia are incorporated into the soil by tilling each infected plant. Figure 1 depicts the increase in microsclerotia per gram of soil following incorporation of the infected lettuce crop during the fall season. By the following spring, the density decreases and yet remains above the 150 microsclerotia per gram density required to cause significant disease in lettuce. There are approximately 370,500 lettuce plants per hectacre in a commercial field. Figure 2 shows that in a field with relatively low levels of microsclerotia, after just two harvests of lettuce crops microsclerotia levels increase to levels that warrants fumigation. Lettuce grown in fields with microsclerotia densities surpassing 600 microsclerotia per gram of soil is unlikely to result in harvestable yield.

From a sample of fifty-four lettuce fields in which Verticillium wilt occurred in coastal California, the level of disease incidence in the field was assessed and soil from these fields assayed for the density of microsclerotia (Atallah et al. 2011). As shown in Figure 3, the relationship between inoculum density (microsclerotia per gram of soil) and disease incidence (percentage of infected plants) is highly nonlinear. With a density less than 100 microsclerotia per gram, incidence is negligible and occasionally <10%. When the density is greater than 100 microsclerotia per gram, incidence increases rapidly, resulting in near total loss when the density is greater than 200 microsclerotia per gram soil (Wu and Subbarao, 2014). By contrast, most other

susceptible crops, including those normally grown in rotation with lettuce in California, suffer almost total loss when the density is less than fifty microsclerotia per gram, as shown in Table 1.

Verticillium dahliae is introduced to the soil in three possible ways. First, the pathogen can be spread locally from field to field by harvest crew or equipment or wind. Local spread is a relatively minor contributor, however, and growers have taken steps to mitigate this themselves, for example by cleaning equipment and having workers clean their protective equipment before moving between fields (Figure 4). The precise role of wind in disseminating infested soil to new fields has not been determined.

Second, it is introduced to the soil via infested lettuce seeds. However, studies of commercial lettuce seed lots from around the world show that fewer than 18% tested positive for *V. dahliae* and, of those, the maximum incidence of infestation was less than 5%, out of 265 total seed lots (Atallah et al. 2011). These relatively low levels do not cause Verticillium wilt in lettuce at an epidemic level. Models of the disease suggest that it would be necessary for lettuce seed to have an incidence of infection of at least 5% and be planted back to back for three to five seasons in order for the disease to appear, with at least five subsequent seasons required for the high disease levels currently seen (Wu and Subbarao, 2014).

Third, Verticillium wilt is introduced to the soil via infested spinach seeds. Spinach seeds have been shown to be the main source of the pathogen (du Toit et al. 2005; Short et al. 2015). The pathogen isolated from infected lettuce plants is genetically identical to the pathogen carried on spinach seeds (Atallah et al., 2010; Short et al. 2015a and 2015b). In a study of 75 spinach seed samples, 89% were infected, with an incidence of infected seeds per sample of mean 18.51% and range 0.3% to 84.8% (du Toit et al. 2005). Infested spinach seeds carry an average of 200 to 300 microsclerotia per seed (Maruthachalam et al. 2013). As spinach crops are seeded at up to nine

⁶

million seeds per hectare for baby leaf spinach, even a small proportion of infected seeds can introduce many microsclerotia into the production fields (du Toit and Hernandez-Perez 2005).

Spinach seed production is not located in California. The majority of spinach seeds (approximately 70%) are imported from Denmark, the Netherlands, and a small number of other locations that provide photoperiods in excess of the 18 hours per day required to trigger flowering and seed set in spinach. The remaining proportion of spinach seed planted in California comes from the state of Washington in the United States. Seeds from all of these regions are likely to carry *V. dahliae*.

3. Control Options

Figure 4 shows the control methods available now and in the future: resistant varieties; fumigation with methyl bromide (or alternate fumigants) on strawberries; crop rotation; and testing and cleaning spinach seeds. We evaluate these options according to feasibility and cost effectiveness.

Verticillium species are best controlled by soil fumigation, but the most effective component of soil fumigation, methyl bromide, has been phased out due to environmental concerns (Enebak, 2012), compounding the problem caused by *Verticillium* species in agriculture. No effective treatment exists once plants are infected by the fungus (Xiao and Subbarao, 1998; Fradin and Thomma, 2006). Several methods can mitigate the impacts of this disease on the lettuce crop. When portions of this study were conducted, methyl bromide was still available so we include it as an option in our studies. Results obtained for methyl bromide may be applicable to alternate fumigants currently available which may similarly involve incurring costs in the present for future gain.

Due to the wide host range, including weeds (Vallad et al. 2005), and the length of persistence of microsclerotia in the soil, crop rotation is generally of limited use for Verticillium wilt management. The main options are rotations of lettuce in fields with high *V. dahliae* microsclerotia with strawberries following fumigation and with broccoli, both of which are already major crops in the region. Strawberry cultivars are highly susceptible to Verticillium wilt and therefore pre-plant fumigation with methyl bromide and chloropicrin had been a standard practice for strawberry production since the late 1950s (Wilhelm and Paulus 1980).

Historically, methyl bromide has been the most widely used fumigant to treat Verticillim wilt. The Montreal Protocol has eliminated methyl bromide use for nearly all pre-plant soil fumigation, including fumigation of ground intended for lettuce; however, strawberries have received criticaluse exemptions through 2016. Since pre-plant fumigation with methyl bromide in strawberries remains profitable under certain conditions, to some extent affected lettuce growers have relied on pre-plant fumigation on strawberry and the residual fumigation effects to grow 2-3 crops of lettuce before microsclerotia densities increase to prevent lettuce production in these fields (Atallah et al. 2011). The phase-out of methyl bromide as an ozone depleting substance was supposed to reach 100% in 2005, but critical-use exemptions have allowed the use of methyl bromide for certain crops at least through 2016 (California Department of Pesticide Regulation, 2010; United States Environmental Protection Agency, 2012b). Critical-use exemption requests through 2014 specify that up to one third of the California strawberry crop can be fumigated with methyl bromide, but actual use was much lower. The remainder of the crop is treated with alternatives such as chloropicrin or 1,3-Dichloropropene (1,3-D) (United States Environmental Protection Agency, 2012a). However, these alternatives (unless combined with methyl bromide) tend to be less effective for Verticillium wilt (Atallah et al. 2011). Other chemical fumigants either have not been

widely used due to township caps or are not yet registered and approved. The long-term availability of this solution is limited and uncertain.

Broccoli is not susceptible to Verticillium wilt, and it reduces the levels of microsclerotia in the soil (Subbarao and Hubbard 1996; Subbarao et al. 1999; Shetty et al., 2000). Some growers have experimented with this solution, but relatively low returns from broccoli in the region have prevented this option from becoming a widespread solution. Planting all infected acreage to broccoli may also increase total broccoli supply, reducing price. Figure 5 shows a lettuce - broccoli rotation effects on *V. dahliae* in soil. Incorporating broccoli residue following the commercial harvest reduces the microsclerotia density in contrast to lettuce crop following which microsclerotia density increases to approximately ten times as much (Figure 5).

Two races of *V. dahliae* affecting lettuce have been described (Vallad et al., 2006) and resistance has only been found against race 1, which is currently being incorporated into commercial cultivars (Hayes et al., 2007). Resistance has not yet been identified for race 2 despite extensive screening of lettuce germplasm. In tomatoes, resistant varieties helped solve Verticillium wilt caused by race 1, but race 2 soon became widespread (Vallad et al., 2006). A similar problem is anticipated in lettuce.

Finally, testing or cleaning spinach seeds is an important option for preventing *V. dahliae* from being introduced into a field. Although *V. dahliae* cannot be completely eliminated by seed cleaning, incidence levels in spinach seed can be significantly reduced (du Toit and Hernandez-Perez 2005). Very recent developments in testing procedures suggest that testing both spinach seed and soil for *V. dahliae* might soon be feasible on a commercial basis. The conventional test of inoculum density in soil (via soil plating on modified NP-10 medium; Kabir et al. 2004) can take six to eight weeks to complete, a significant impediment for growers to making planting decisions.

The new technique (Bilodeau et al., 2012) allows for sensitive, accurate (approximately one to two microsclerotia per gram of soil), and timely testing of fields. Another very recent innovation speeds up testing spinach seeds. Previously, testing for *V. dahliae* in spinach seeds took approximately two weeks and could not accurately distinguish between pathogenic and nonpathogenic species (Duressa et al., 2012). This new method takes only one day to complete, is highly sensitive (one infected seed out of 100), and can distinguish among species (Duressa et al., 2012).

Controlling Verticillium wilt through its main inoculum source, spinach seeds infested with *V*. *dahliae*, will have trade implications because seeds are imported, exported, and re-exported. Currently, the United States has no phytosanitary restrictions on spinach seed imports, but Mexico prohibits the importation of seeds if more than 10% are infected (IPC, 2003).

Summarizing, Verticillium wilt may be prevented or controlled by the grower by fumigating with methyl bromide if available, planting broccoli, or not planting spinach. These control options require long-term investment for future gain. Verticillium wilt can also be prevented or controlled by the spinach seed company by testing and cleaning the spinach seeds. However, as we explain below, all these control options generate externalities.

4. Previous Literature

Our work on the economics of managing *V. dahliae* builds upon several strands of existing literature.

4.1 Pest Management

The first strand of literature to which our paper relates is on the economics of pest management (Hueth and Regev, 1974; Carlson and Main, 1976; Wu, 2001; Noailly, 2008; McKee et al., 2009), which focused on pests for which treatment is available after crops are affected. In contrast, Verticillium wilt cannot be treated once crops are affected. Existing work on crop disease, such as

Johansson et al. (2006), Gomez et al. (2009), and Atallah et al. (2015) focused on spatial issues regarding the spread of the disease. In contrast, Verticillium wilt has only a limited geographic impact, and thus dynamic considerations are more important than spatial ones for Verticillium wilt.

Early economic analyses of pest management abstracted from important aspects of the complexity of the problem are focused on "rules of thumb" for farmers (Moffitt, Hall, and Osteen, 1984). More recently, more economically efficient methods for controlling pests have been determined. At first, this meant static models, such as Moffitt et al. (1984). Subsequently, dynamic bioeconomic models were developed. Olson and Roy (2002) included a stochastic variable describing the degree to which conditions are favorable to the pest. This recognized that a pest population is not deterministic. Wu (2001) compared static and dynamic models of herbicide use. When growers do not consider the future benefits of reducing the current seed bank, as in the static model, they do not control weeds sufficiently.

Moffitt et al. (1984) described an economic threshold for pest control under uncertainty. They employed a static profit maximizing problem to derive a decision rule for farmers based on observed pest pressure. This method improved on the "rule of thumb" recommendations, but ignored dynamic effects. When the current pest level determines the future level, a static model cannot incorporate all pesticide effects.

Chatterjee (1973) took one of the first steps in creating a dynamic model. He minimized the cost of a pest control program with repeated control actions (Chatterjee, 1973). The total cost included the cost of administration, crop damage, and damage from the control action (i.e., environmental damage from pesticide use). He derived functions to describe each component and included parameters describing the birth, death, and immigration rates of insect pests. This model

encompassed the elements of a basic bioeconomic model with feedback effects between the pest and the control action.

One method to solve economic problems with a time component is optimal control theory, a mathematical optimization method for deriving control policies (Dorfman, 1969). Kennedy (1981) extended this method to applications in agriculture, forestry, and fisheries. Many of the subsequent papers adopted this method (Zacharias and Grube, 1986; Harper et al., 1994; Cooke, Jones, and Gong, 2010).

Many models are either deterministic or model uncertainty only in terms of the variance such as in Moffitt et al. (1984), where they accounted for uncertainty but only consider different densities of pests and not the uncertainty that drives these densities. Olson and Roy (2002) explicitly modeled the uncertainty in pest populations. The random process $\{\rho\}_{t=1}^{\infty}$ is independently and randomly distributed on the interval $[\rho_m, \rho^M]$ with $0 < \rho_m \le \rho \le \rho^M < \infty$. A larger ρ means conditions are more favorable for the pest. The authors used their results to determine whether it is optimal to eradicate the pest, depending on the size of the population (Olson and Roy, 2002).

The purpose of modeling biological systems is to predict economic and welfare outcomes accurately. Invasive species damage the environment; they also impose damage on humans, including crop losses, decreased livestock grazing, loss of recreational use services such as hiking and fishing, and decreased navigability of rivers, canals, and other waterways (Eiswerth and Johnson, 2002). The authors estimated the damages from an invasive species when the population follows a logistic growth function and can be diminished by a management technology. Solving the model yields the optimal time path of control, which accounts for the pest level in the future being dependent on the current level and allows the agent to choose the level of control in every

period. Eiswerth and Johnson (2002) performed comparative statics and sensitivity analysis to show the influence of different parameters on the costs of control. This general model must be adapted to the specifics of a given problem; one example is discussed below.

Wu (2001) modeled the decision making process of a farmer maximizing the net present value of profits from growing grain over T years. The crop is subject to damage from weeds, which can be controlled by the farmer's choice of herbicide. Weeds, like microsclerotia, accumulate in the soil and require a dynamic approach to comprehensively model. The author compared the results of a static model with those of a dynamic model, and showed that the static model resulted in insufficient weed control because it ignored the benefits of reducing future seed density.

As *V. dahliae* persists in the soil for many years, a static model such as that proposed by Moffitt, Hall, and Osteen (1984) will not properly account for the future benefits of reducing microsclerotia in the soil. The dynamics of Verticillium wilt more closely fit the model by Wu (2001) that focused on the management of a weed seed bank. Uncertainty, as described by Olson and Roy (2002), also matters for Verticillium wilt. Weather is an example of uncertainty that affects the level of microsclerotia, the growth of lettuce plants, and the rate at which Verticillium wilt develops. Accounting for this stochastic element may result in different outcomes than using a deterministic model. None of the papers discussed here incorporate all the elements required to model the impact of Verticillium wilt, but each has contributed to the advancement of the pest management literature and specific aspects are applicable to the modeling of Verticillium wilt.

4.2 Pest Adaptation and Resistant Varieties

In the previous subsection, we focused on the persistence of microsclerotia over time; however, in addition to purely biological effects, the susceptibility of the host and the virulence of the fungus change in an interdependent way and as a result of human intervention. Specifically, lettuce

cultivars that resist colonization by *V. dahliae* have been developed for race 1 (although not yet commercially available) (Hayes et al., 2010), and based on evidence from other hosts, researchers expect race 2 to become more prevalent relative to race 1 when resistant varieties are planted (Subbarao, personal communication). The commonly recognized problem of pesticides that become less effective over time as pests develop resistance is an example of selection pressure. The first part of this section considers literature on the effects of declining pesticide efficacy; the second half introduces literature on research and development for resistant crop varieties.

Carlson and Main (1976) and Goeschl and Swanson (2003) modeled the returns received by developers of pesticides and resistant varieties, respectively. The value of innovation was reduced by pest adaptation in both cases. Noting the high and increasing costs of developing new genetic, chemical, and biological sources of disease control, Gilligan (2008) discussed the use of epidemiological approaches to minimize the spread of agricultural plant diseases and prolong the use of current technology.

Hueth and Regev (1974) used a discrete time optimal control model to maximize the difference between benefits and costs. They found a decision rule equating marginal costs, including the marginal user cost, with marginal benefits, consistent with the theory of exhaustible resources. The user cost results from increased future control costs as a result of using pesticide today and exhausting pest susceptibility. This is equivalent to the marginal user cost that is well known in the production of extractive resources. Hueth and Regev (1974) noted that their model does not account for uncertainty and that research and development for pesticides may be considered comparable to exploration costs in extractive industries. Hueth and Regev (1974) compared the loss of pest susceptibility to a model for extractive industries. For example, the oil industry must account for the marginal user cost. If the resource is consumed today, less is available for future use. The marginal use cost is the present value of these foregone profits. Similarly, if pest susceptibility is exhausted in the current period, less is available in the future.

Munro (1997) built on the work of Hueth and Regev (1974) to develop a model of pest evolution. This model consisted of three parts, one each to incorporate evolution, ecology, and economics. The model of evolution described how the resistance characteristic developed in an organism. The ecology component described the growth of the population. The economic model showed how human action changed the population growth rate and the resistance growth rate. Munro (1997) showed that if evolution is not considered, investment in research and development for control methods may be higher than optimal (Munro, 1997). Munro (1997) wass among the first economists to consider how human actions impact the evolution of biological species. Human economic activity has selected for adaptable pests—the others do not survive. Thus, the most adaptable pests survive and evolve. Noailly (2008) built on this model by adding a learning effect for growers. At first, they do not anticipate the effects their pesticide use has; later, they develop a strategy based on past experience with declining pest susceptibility to the pesticide.

Growers are only "boundedly rational"—they cannot fully anticipate or optimally respond to potential evolution by the pest. This was represented by a dynamic equation for the share of farmers using each pest management strategy. Along with dynamic equations for pest population and pest susceptibility, the system was solved for the steady states. The results defined several thresholds, in particular for the share of farmers that determined which steady state is achieved (Noailly, 2008). Noailly (2008) warned that considering these thresholds was key for policy makers, lest the system converged into an undesirable equilibrium from which it was difficult to recover.

McKee et al. (2009) describe a bioeconomic model of strawberries and the greenhouse whitefly, which provides an empirical example of the issues discussed in the previous papers. The greenhouse whitefly discussed by McKee et al. (2009) had previously overcome a number of chemical controls. As a result, the California Department of Pesticide Regulation manages the use of current chemicals to encourage the development of alternatives and delay the development of resistance to the insecticides. These restrictions were included in a bioeconomic model in which growers chose the dates for applying insecticide. McKee et al. (2009) found that the restriction, only two insecticide treatments per season, was binding on the growers' profit maximizing decision (McKee et al., 2009). Further, they noted that the regulations may be beneficial in the long-term to maintain susceptibility, even though they caused a loss in a single season.

When a solution to a widespread pest problem is developed, such as a new pesticide or crop variety, generally farmers will eagerly adopt the new technology. The more frequently the technology is used, the faster resistance becomes an issue.¹ Carlson and Main (1976) summarized the issues related to crop diseases and their associated economic losses. The use of resistant varieties is one such issue. "The longer a variety will last before it is replaced, for whatever reason, the larger the net returns to the owner of that variety" (Carlson and Main, 1976, pg. 390). The authors described a general theoretical framework for the value of a pesticide. The present value of the income from the pesticide is the sum of the income streams from *T* years in which the pesticide is useful. They posited that a capital budgeting model can represent the effect of reducing the useful life from *N* years to *T* years due to resistance. Unlike other work in which pests evolve, Carlson and Main (1976) believed resistance may be a renewable resource. If other methods of

¹ This problem is widely recognized in the medical field, where overuse of certain antibiotics has drastically reduced their efficacy.

control or other crops are planted, the susceptible population may eventually increase such that a particular control is effective again.

Economic models frequently include innovation or technological progress. Ordinarily, innovation is reasonably assumed to be cumulative. Goeschl and Swanson (2003) argued that in biotechnology (and its applications to agriculture), research and development effort is no longer durable or cumulative. The evolution of pathogens means that solutions are temporary. Widely used modern crop varieties have a life span of five to seven years as commercial products. New varieties must be constantly developed to replace their predecessors. This process is titled "adaptive destruction". Goeschl and Swanson (2003) modeled research and development investments for both a social planner managing the industry and private firms with the ability to patent their products. They found that the social planner increases investment as the biological adaptation rate increases. By contrast, private firms decrease investment because the patent protection they receive is undermined by adaptation, which reduces the usefulness of the innovation (Goeschl and Swanson, 2003). Yerokhin and Moschini (2008) further developed this model in the context of a duopoly, in which the firms compete to develop the innovation. The first firm to do so has a monopoly for that period.

Gilligan (2008) discussed durability, or how long a resistant variety or pesticide is useful. Given the cost of development and difficulty of registration, sustainable control is a major concern (Gilligan, 2008). Historically, resistance genes are quite variable in their durability. Resistant cabbage varieties have protected against cabbage yellows for more than ninety years. By contrast, rice varieties resistant to rice blast often last less than three years (Gilligan, 2008). Epidemiological models, particularly those that account for the differences in scale between a test plot and when the resistance gene is deployed commercially, can help prolong durability. Traditional benefit-cost

analysis of pest control methods focuses on the net benefits, but neglects irreversible costs, such as the pest overcoming resistance (Gilligan, 2008).

Resistant varieties will play an important role in the Verticillium wilt problem. In tomatoes, resistant varieties helped solved Verticillium wilt caused by race 1, but race 2 soon became widespread (Vallad et al., 2006). A similar problem is anticipated in lettuce. This suggests that the marginal user cost developed by Hueth and Regev (1974) is important, and their framework can be adapted to consider resistant varieties of lettuce as an exhaustible resource. McKee et al. (2009) demonstrated that an activity that is not profit maximizing in the short-term, such as planting broccoli, may be part of a profit maximizing strategy in the long-run. The expectation for the development of further races of V. dahliae that affect lettuce suggests a model along the lines of Munro (1997) and Noailly (2008). Evolution of the pest is expected. In addition, growers are unable to anticipate the precise path of evolution of the pests, as Noailly (2008) suggested. As such, new resistant varieties will be needed. The development of such varieties is time and resource intensive. Thus, the concerns of Carlson and Main (1976), Goeschl and Swanson (2003), and Gilligan (2008) are quite important. Accurately modeling the expected returns, as Carlson and Main (1976) did, and prolonging the use of resistant varieties, as suggested by Gilligan (2008) will be important, and has implications for grower cooperation in enhancing durability. On the developer side, Goeschl and Swanson (2003) discussed the difference between private firms and a social planner. As current research into V. dahliae resistance is both publicly and privately funded, the life span and returns generated by resistant varieties are also important.

Although resistant lettuce cultivars are the best alternative for managing Verticillium wilt in the future, other, complementary, solutions are necessary as well. The issues of plant and variety

resistance, pest resistance, and other types of pest evolution require that crop rotation and seed import controls be considered. None of these solutions suffices on its own.

4.3 Crop Rotation

The opportunity cost of crop rotation is the reduction in net income relative to producing the highest value crop, including the soil health benefits associated with crop rotation. This is particularly relevant for Verticillium wilt in lettuce, where broccoli reduces the density of microsclerotia, but provides a very low economic return, especially given the high land values in Monterey and Santa Cruz counties. Several papers, including Carlson and Main (1976) and Gorddard et al. (1995), discussed the link between crop rotation and pest management. Doole (2008) considered crop rotation between grain crops and pasture to delay herbicide resistance and mitigate salinity.

Carlson and Main (1976) described a linear programming model of cropping patterns. Usual components of such models include constraints on land, labor, capital, water, etc. Their model added another set of constraints related to rotation length, e.g., growing a crop more than once in *n* years results in a reduction of crop yield or quality. They showed that for crops with equally high value substitutes, the cost of crop rotation is minimal, but if no suitable substitutes exist, crop rotation imposed costs even for low value crops. Optimal pest management improves gains from resistant varieties and reduces losses in land value due to disease (Carlson and Main, 1976).

Gorddard et al. (1995) incorporated both land use and pest problems. They modeled weed management with herbicide resistance. The farmer chooses the level of herbicide, the level of nonchemical control, and when to stop growing the crop (wheat) and convert the land to pasture. The authors measured the economic cost of herbicide resistance. In testing different scenarios, the authors found that the non-chemical control option significantly decreased resistance; the

conversion to pasture land took place in year seven without a non-chemical control whereas with a non-chemical control, it took place in year twelve. A shortcoming of the model is that the land remains a pasture forever once conversion takes place.

Building on Gorddard et al. (1995), Doole (2008) modeled the management of a wheat field with herbicide resistant weeds in Western Australia. Phase crop rotation to pasture land is an option to control weeds. An additional benefit to the pasture land is that it mitigates salinity issues in the region. The author used a regime-programming algorithm to solve for the optimal trajectory, including the length of the phase rotation. When herbicide resistance exists, it is optimal to employ the pasture; however, it is not profitable to do so without herbicide resistance. Pasture land is important for salinity mitigation, but it is not profitable for this reason alone.

Due to the widespread susceptibility of crops to Verticillium wilt, crop rotation is of limited use in managing the disease; however, broccoli can reduce levels of microsclerotia in the soil. Non-host cover crops have been tried elsewhere to manage Verticillium wilt, but *V. dahliae* reproduces even on non-hosts (Malcolm et al. 2013) but not on broccoli. Currently, there are no cover crops that are used in coastal California for managing Verticillium wilt. Updating the theoretical models described by Carlson and Main (1976) and applying them to the empirical case of Verticillium wilt will help farmers and policy makers reduce losses due to this disease. Gorddard et al. (1995) provided a theoretical basis that we use by combining a bioeconomic model of pest pressure with a crop rotation model. Doole (2008) brought in the additional factor of salinity mitigation, which is analogous to broccoli's role in reducing microsclerotia. Planting broccoli is generally not highly profitable, but if microsclerotia levels are sufficiently high, and growers need to prolong the durability of resistant varieties, this method of control may be profitable in the long-run.

4.4 Import Controls and Cleaning Technology

As invasive species introductions have increased with greater levels of trade, pest prevention and management should be based on broader economic analyses that extend beyond a single decisionmaker (Levine and D'Antonio, 2003). Countries protect their citizens, animals, and plants from invasive species. Members of the World Trade Organization (WTO) are bound by the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS Agreement), which states that in protecting human, plant, and animal health, a country must use the least trade restricting policy possible to achieve the desired level of protection. This agreement corrects externalities and market inefficiencies caused by invasive species (Olson, 2006). Policy options include tariffs, quarantines, and export certifications. Most of the research regarding trade, trade policy, and invasive species damage focuses on calculating the expected marginal damage from invasive species and using tariffs to internalize the related externalities (Springborn, Romagosa, and Keller, 2011). Mérel and Carter (2008) discussed the optimal two-part tariff to cover the cost of inspections and the cost of damages from contaminated goods. An alternative to tariffs is quarantine, as in James and Anderson (1998). Brennan et al. (2004) provided an example of the impacts of a quarantine, in which growers lose access to the wheat seed export market as a result of a Karnal bunt outbreak. Batabyal and Beladi (2007) considered the incentives of the firm, and whether export certification can encourage firms to comply with quality requirements. Each of these papers focused on the interaction between the government and importing firms.

A single tariff is not the optimal way to correct domestic distortions, in particular when a cleaning technology is available (Mérel and Carter, 2008). The rate of contamination of imports is endogenous because of the cleaning technology. The model showed that a two-part tariff with inspections is the first best efficient solution. The home country imports foreign goods and has no

domestic production. Contaminated goods cause irreversible damage. Solving this problem gives the optimal levels for the two tariff rates. The import tariff covers the cost of inspection only. The penalty tariff covers the expected damage from all contaminated units. The government could administer a similar program for contaminated seeds, but translating the theoretical model into an empirical application requires that a cleaning technology is available and that the infected seeds can be detected easily and quickly at the border.

Beyond tariffs, another method to control invasive species at the national or regional level is quarantine. James and Anderson (1998) considered the effects of a quarantine with a comparative static partial equilibrium model for a single commodity market. They assumed the costs of the quarantine, e.g., inspection, are charged to the importer. Without an externality, the ordering of social surplus levels is such that free trade is preferable to quarantine which is preferable to an import ban, as expected. With the possibility of importing the pest, the ordering is no longer certain, but depends on the cost and effectiveness of the quarantine (James and Anderson, 1998). The partial equilibrium approach neglects secondary effects and changes in the industry, but showed the challenges the government faces with an uncertain externality. These challenges include determining the appropriate level of protection, effectiveness and efficiency of quarantine; apportioning the responsibilities, benefits and costs of the program; and cost recovery for its expenses in administering the program (Mumford, 2002).

Brennan et al. (2004) considered the effect of Karnal bunt, a seedborne disease affecting wheat. They estimated the costs of a hypothetical Karnal bunt outbreak in the European Union. Beyond the costs of yield and quality loss and the costs of control measures, growers lose access to the wheat seed export market. Brennan et al. (1992) showed that evaluating the costs and benefits of diseases and control measures that affect trade is quite complicated and may result in the adoption

of policies that are not economically sound. Although direct effects on yield and quality are too small to justify the cost of control measures, the reaction costs (i.e. indirect costs associated with the market reaction to the detection of the disease), such as downgrading wheat or loss of export markets, are large enough to justify substantial control measures.

The above models have simplified or ignored the incentives of foreign firms exporting to the home country; the following two papers considered how importers react to invasive species prevention efforts. Batabyal and Beladi (2007) showed that the threat of a penalty duty on imports can ensure that firms certify their goods as pest free. Ameden, Cash, and Zilberman (2007) compared the responses of a firm to different enforcement strategies.

An export certificate provides importing nations with reasonable assurance about the quality of the certified goods, from food safety, to environmental regulation compliance, to inspection for pests (Batabyal and Beladi, 2007). Certification is costly to the firm; in the authors' example, the firm must screen the container cargo before loading and shipping it. Costly action requires an incentive. The authors assumed that Home and Foreign firms compete in Bertrand competition over two periods. They also assumed differential pricing, where the price for certified goods is higher than that of uncertified goods. The enforcement mechanism is an *ad valorem* duty in period two, whenever the first period import price, p_1 , is less than p^2 , the government's best guess of the price of the inspected goods. The foreign firm's profit is $\pi^*(\tau_2)$ when the duty is imposed and profit is $\pi^*(0)$ without a duty. Solving the first order conditions revealed that the first period import price increases with the threat of penalty and thus the firms certify their products (Batabyal and Beladi, 2007). A credible threat ensures export certification. This model showed that changing the incentives of the firm internalizes the externality. Much of the literature focuses only on one method of control. Ameden et al. (2007) compared the response of a firm, in terms of output exported and pre-entry treatment, when contaminated shipments are either destroyed or treated. Optimal output decreases in both scenarios as inspection rates, tariffs, and penalties increase; however, the magnitude of the firm's response varies, and is greater when shipments are destroyed than when they are treated (Ameden, Cash, and Zilberman, 2007).

Because the production of spinach seeds requires long, cool days, they are not grown in California but produced in the Pacific Northwest or imported from other countries. Thus, trade policies are important. The SPS Agreement provides a legal basis for preventing the importation of contaminated seeds; however, only Mexico has taken this step with regard to spinach seeds. All of the methods described above, including tariffs, quarantines, and export certifications, require that the product can be tested. Only recently have quick, efficient tests been developed to detect *V. dahliae* in spinach seed. Further, the method described by Mérel and Carter (2008) required that contaminated seeds be cleaned. Du Toit and Hernandez-Perez (2005) tested hot water and chlorine for their potential to eliminate or reduce the effect of *V. dahliae* and other pathogens on spinach. Further work in this area could lead to significant reductions in the amount of *V. dahliae* carried by seeds.

4.5 Dynamic Models of Agricultural Management

Dynamic models have been used to analyze many agricultural management problems. Weisensel and van Kooten (1990) used a dynamic model of growers' choices to plant wheat, use tillage fallow to store moisture, or use chemical fallow to store moisture. Growers are assumed to maximize the present value of their net returns. The authors solved the model to obtain the optimal agronomic decision for various scenarios (depending on price, discount rate, and erosion rate).

They found that compared to prevailing fixed crop rotations, flexible cropping (with fallow periods) can reduce the rate of soil erosion.

In a related paper, van Kooten et al. (1990) explicitly included soil quality in the farmer's utility function and the trade-off between soil quality (which may decline due to erosion) and net returns. Similarly, growers concerned about *V. dahliae* face tradeoffs between maximizing returns and preventing or reducing the pathogen infestation in their production fields.

4.6 Dynamic Structural Econometric Modeling

Our paper builds on the literature on dynamic structural econometric modeling. Rust's (1987; 1988) seminal papers developed a dynamic structural econometric model using nested fixed point maximum likelihood estimation. This model has been adapted for many applications, including bus engine replacement (Rust, 1987), nuclear power plant shutdown (Rothwell and Rust, 1997), water management (Timmins, 2002), agriculture (De Pinto and Nelson, 2009; Scott, 2013), air conditioner purchases (Rapson, 2014), wind turbine shutdowns and upgrades (Cook and Lin Lawell, 2016), and copper mining decisions (Aguirregabiria and Luengo, 2016). This type of model incorporates several of the important factors, including accounting for the dynamics of Verticillium wilt and allowing for individual field level decisions, in estimating a crop and fumigation choice model for Verticillium wilt in lettuce.

4.7 Externalities

The literature on externalities (Meade, 1952; Arrow, 1969) dates back at least to Pigou's *The Economics of Welfare*, originally published in 1920. Pigou (1920) defined social and private net products, whereby a firm maximizing its own objective function does not account for external social costs or benefits, thus leading to a potentially socially inefficient welfare solution. Arrow (1969) discussed externalities as a failure to reach Pareto efficiency. Classical microeconomic

theory states that intervention by a government (social welfare maximizing planner) may increase social welfare and correct externalities (Meade, 1952). For many years, Pigouvian taxes (or subsidies) dominated externality theory, supporting the idea of government intervention to correct market failures. Coase (1960) argued that this problem was reciprocal, i.e., in acting against either party, the opposite would be harmed. Without transaction costs, when rights are well defined and a legal system exists to enforce them, the parties can bargain with one another effectively. Yet, high transaction costs may bar an otherwise efficient solution. Others (Mishan, 1971; Mumey, 1971; Regan, 1972) have pointed out additional flaws, such as the "holdout" problem.

The current situation in coastal California exhibits these classic features of an externality. California lettuce growers and spinach seed companies require an effective plan to manage Verticillium wilt, which explicitly defines rights and responsibilities. Contracts are one means of doing so.

There exists an extensive literature on contract choice in agriculture in both developed and developing country contexts. In part, this literature focuses on why multiple types of contracts exist at the same time in the same place, among relatively homogeneous groups. Allen and Leuck (1992) compared cash rent versus cropshare contracts in the American Midwest. They found that a large portion of contracts are cropshare contracts and hypothesize that this type of contract offers risk sharing benefits between the landlord and the tenant. Another potential benefit of cropsharing is that tenants have less incentive to overuse the inputs supplied by the landlord, for example, soil quality. A cash rent contract may cause farmers to over-extract from the soil. The results show that for farmers in the Midwest, cropshare contracts are more likely when the cost of dividing the crop is low and when tenants can negatively affect the soil quality, but that risk sharing is not an explanation (Allen and Leuck, 1992). Although this model is far more complicated than the one

we choose, this is analogous to the idea of soil contamination we use to explain the problem caused by Verticillium wilt.

Similar results are obtained in the developing country context regarding contracts and land fertility in the Philippines (Dubois, 2002). This model incorporated the dynamics of soil fertility: the tenant's actions in a given season affect future production because land fertility is the result of an investment function of the previous period's fertility and the effect of the tenant's actions. Similarly, Verticillium wilt contamination is a function of previous contamination and the level of caution exercised by the grower, as well as the biological nature of the fungus. Dubois (2002) presented a principal-agent problem with moral hazard regarding the fertility of the soil. Results showed that the optimal contract depends on risk aversion, land fertility, and production technology. For example, landlords choose fixed rent contracts more often for more fertile, valuable land. This provided a rationale for suggesting that tenant influence on land quality can be a factor in land contract choices.

Although they considered franchising rather than agricultural contracts, Bhattacharyya and Lafontaine (1995) explained how double-sided moral hazard affects contracting. When both franchisor and franchisee participate in production (or in our case, tenant and landlord), potentially both agents have an opportunity for moral hazard. Their results showed that in general, linear rules for profit or revenue sharing can be the optimal second-best contract in the face of double-sided moral hazard.

5. Externalities

An externality arises whenever the actions of one individual or firm affects the payoffs to another individual or firm. When individuals or firms make their decisions, they generally do not account for any externalities they may impose on others, so their decisions may not be optimal for a societal point of view. In this paper, we discuss two externalities that arise due to Verticillium wilt and review our research on these externalities.

4.1.Intertemporal Externality that Arises with Short-Term Growers

As stated above, because the options for controlling Verticillium wilt require long-term investments for future gain, an intertemporal externality arises with short-term growers, who are likely to rent the land for only a short period of time. Renters, therefore, might not make the longterm investments needed to control Verticillium wilt. As a consequence, future renters and the landowner may suffer from decisions of previous renters not to invest in control options. Thus, decisions made by current renters impose an intertemporal externality on future renters and the landowner.

In Carroll et al. (2017b), we analyze the factors that affect the crop choice and fumigation decisions made by growers and consider how the decisions of long-term growers (whom we call 'owners') differ from those of short-term growers (whom we call 'renters'). We examine whether existing renter contracts internalize the intertemporal externality that a renter's decisions today impose on future renters and the landowner, and analyze the implications of renting versus owning land on the spread of the disease and welfare.

To analyze these issues, we developed and estimated a dynamic structural econometric model of growers' dynamic crop choice and fumigation decisions and compared the decision-making of long-term growers ('owners'), who have an infinite horizon; with that of short-term growers ('renters'), who have a finite horizon. The structural model generates parameter estimates with direct economic interpretations. We then use the parameter estimates to simulate counterfactual scenarios regarding renting and owning.

We used a dynamic model for several reasons. First, the control options (fumigation, planting broccoli, and not planting spinach) are investments (although not investments in the traditional sense, each of these actions requires spending money or foregoing profit in the current period in exchange for possible future benefit) that require long-term planning for future gain. Second, these investments take place under uncertainty. The investments are irreversible, there is uncertainty over the reward from investment, and growers have leeway over the timing of investments. Thus, there is an option value to waiting which requires a dynamic model (Dixit and Pindyck, 1994). A third reason to use a dynamic model is that long-term growers and short-term growers have different planning horizons, implying that short-term growers may be less willing to make the long-term investments needed to control Verticillium wilt. A dynamic model with different time horizons for long-term and short-term growers' best enables us to compare these two types of growers.

When it is costly for the renter to prevent Verticillium wilt, and costly for the landowner to observe the renter's actions, a contract may not suffice to internalize the intertemporal externality. Furthermore, if contracts that include stipulations to control Verticillium wilt are not the norm in the area, highly restrictive contracts may be less desirable and receive lower rents.

Although we do not have data on contracts, it is a testable empirical question whether existing renter contracts internalize the intertemporal externality imposed by renters on future renters and the landowner. We compare the results from short-term growers with those from long-term growers, and also compare results from short-term growers early in the time period (1993 to 2000) with those later in the time period (2001 to 2011). Verticillium wilt was not identified on lettuce until 1995 and the likely sources of the inoculum were not known until years later. If contracting internalized this externality, we would expect to see more evidence in the later period.

We apply our dynamic structural econometric model to Pesticide Use Reporting (PUR) data from the California Department of Pesticide Regulation. Our data set is composed of all fields in Monterey County on which any regulated pesticide was applied in the years 1993 to 2011, inclusive. Additional data on prices, yields, and acreage come from the Monterey Agricultural Commissioner's Office.

According to our results in Carroll et al. (2017b), spinach is not a desirable crop to plant for reasons that are not fully captured by its price, which is consistent with the conclusion that Verticillium wilt is a problem. Fumigating with methyl bromide and planting broccoli are both effective control options, but involve incurring costs or foregoing profit in the current period for future benefit. For short-term growers, existing rental contracts that may be in place do not reward short-term growers for either fumigating with methyl bromide or planting broccoli, and therefore do not fully internalize the intertemporal externalities imposed by renters on future renters and the landowner.

In the later period of our data set, when Verticillium wilt is more of a problem, short-term growers benefit from having methyl bromide history on their field, but incur costs if they fumigate with methyl bromide themselves. There may therefore be an intertemporal externality imposed by renters on future renters and the landowner, since methyl bromide is costly to use and not rewarded by contracts, but leads to future benefits for future renters and the landowner.

Similarly, in the later period, when Verticillium wilt is more of a problem, short-term growers benefit from having broccoli history on their field, but incur costs if they plant broccoli themselves. There may therefore be an intertemporal externality imposed by renters on future renters and the landowner, since planting broccoli is costly and not rewarded by contracts, but leads to future benefits for future renters and the landowner.

We find in Carroll et al. (2017b) that average grower welfare per grower-month is higher in the earlier time period than in the later time period for the long-term growers. Average grower welfare per grower-month is higher for the long-term growers than for the short-term growers over the entire period as well as in both the early and later time period.

To analyze how differences in grower welfare relate to differences in the data, differences in time horizon, and differences in parameter estimates, we simulate seventy-two scenarios, each a different combination of data type (owner or renter), data time period (all, early, or late), time horizon (infinite or finite), parameter type (owner or renter), and parameter time period (all, early, or late), or late). For each simulation, we calculate and compare welfare and crop and fumigation choices.

By using the results of our structural model to simulate owners on renter fields and renters on owner fields, our counterfactual simulations also enable us to address any concerns that the owners and renters in our data set may have differed in their characteristics, in the conditions they faced, and/or in the quality of their fields.

According to our results in Carroll et al. (2017b), the long-term decision-making of long-term growers yields higher average present discounted value of per-period welfare and more use of the control options, likely due to differences in incentives related to future time orientation faced by owners versus renters, differences in the degree to which the intertemporal externality is internalized by owners versus renters, the severity of Verticillium wilt, the effectiveness of control options, and rental contracts; as well as due to a longer planning horizon.

We find that although methyl bromide fumigation and broccoli can both be effective control options, growers with a short time horizon have no incentive to commit to such actions. Although contracts can be a potential method for internalizing an externality between different parties, our empirical results show that existing contracts do not fully internalize this externality. This outcome

may be because of the relatively recent development of the disease and knowledge of its causes, more restrictive contracts not being the norm, the possibility of land unknowingly being contaminated before rental, or difficulty in enforcing or monitoring aspects of the contract such as whether boots and equipment are washed between fields.

4.2. Supply Chain Externality between Spinach Seed Companies and Growers

Due to Verticillium wilt, a supply chain externality arises between companies selling spinach seed and growers growing lettuce. Although testing or cleaning seeds may prevent *V. dahliae* from being introduced into a field, spinach seed companies may not have an incentive to test or clean spinach seeds. In the absence of integration, seed companies and lettuce growers are unable to achieve a potentially more efficient equilibrium solution on their own, as contracting and price signals do not adequately internalize the supply chain externality, and as growers lack bargaining power in negotiating with seed companies. In Carroll et al. (2017a), we analyze the supply chain externality between growers and seed companies.

There are several reasons why the supply chain externality exists between spinach seed companies and growers. First, testing and cleaning spinach seeds is uncertain and potentially costly, and although testing or cleaning seeds may prevent *V. dahliae* from being introduced into a field, spinach seed companies may not have an incentive to test or clean spinach seeds, as they do not internalize the costs that infected spinach seeds impose on growers.

A second reason the supply chain externality exists between spinach seed companies and growers is that, owing to asymmetric information, the price signal for tested and cleaned spinach seed versus contaminated seed is weak.

A third reason the supply chain externality exists between spinach seed companies and growers is that Verticillium wilt in lettuce is an example of a market failure in which transaction costs

between seed companies and lettuce growers prevent them from reaching a potentially more efficient equilibrium solution. Transaction costs increase with the number of agents. There are a large number of growers attempting to bargain with a relatively small number of seed companies. Due to the small number of seed companies, some growers are hesitant to resort to legal means, such as working toward a seed testing or cleaning requirement from the County Agricultural Commissioner, lest seed companies decide to leave the market. Such transactions costs may also impede other possible solutions such as third party testing.

In Carroll et al. (2017a), we consider vertical integration of the industry as a solution to the supply chain externality problem. Williamson (1971) describes some of the cases in which vertical integration is an appropriate tool to mitigate an externality, via "substituting internal organization for market exchange". While in some cases vertical integration would capture a positive externality (Brewin et al., 2014), vertical integration would address Verticillium wilt by eliminating a negative externality.

In Carroll et al. (2017a), we analyze the supply chain externality between growers and seed companies. In our model, the seed company controls the spinach dummy coefficient, which captures the effects of spinach on the grower's per-period payoffs that are not internalized in spinach price, since the seed company's actions affect the contamination level of spinach seeds and therefore how spinach affects microsclerotia, which in turn affects lettuce growers.

We calculate the benefits to growers from testing and cleaning spinach seed by simulating growers' optimal decisions and welfare using different values for the spinach dummy coefficient. As expected, results in Carroll et al. (2017a) using data from the entire time period show that benefits to growers are the highest when the spinach dummy coefficient is equal to zero (i.e., the seed company tests and cleans the spinach seeds so thoroughly that planting spinach does not have

any significant negative effect on grower payoffs after controlling for spinach price) and decrease as the spinach dummy coefficient increases in absolute value (i.e., as less testing and cleaning is done).

We then estimate the spinach seed company's cost to testing and cleaning spinach seeds in order to reduce the level of microsclerotia, and compare the spinach seed company's cost to the grower's benefits. Because seed cleaning cost data are not available, we use several functional forms and parameters to estimate potential cost functions. We also determine the welfare maximizing level of seed testing and cleaning.

We compare the status quo, in which growers and seed companies are independent, to a vertically integrated industry, in which one company produces spinach seeds, as well as spinach, lettuce, and other crops. The vertically integrated industry would internalize the supply chain externality between growers and seed companies, and would choose the welfare-maximizing level of seed testing and cleaning.

According to results in Carroll et al. (2017a) using data over the entire time period, we find that in more than half of the cases, the socially optimal amount of spinach seed testing and cleaning is more than what arises when the externality is not internalized (the status quo). Significant welfare gains arise only when the seed company tests and cleans the spinach seeds so thoroughly that planting spinach does not have any significant negative effect on grower payoffs after controlling for spinach price. In other cases, even though it maximizes welfare, the socially optimal amount of spinach seed testing and cleaning does not yield any welfare gains.

Thus, depending on the functional form and parameters used to estimate seed company cost, the vertically integrated firm may choose not to test and clean seeds at all, may partially test and clean the seeds, or may test and clean seeds fully. In some cases, we find that vertical integration would not lead to more testing and cleaning of seeds than arises in the status quo. In most cases, however, vertical integration does lead to more testing and cleaning of seeds.

In the cases in which the social optimum would require more spinach seed testing and cleaning than the status quo, when the spinach seed company internalizes the externality and engages in the socially optimal amount of seed testing and cleaning, growers plant more lettuce, likely because Verticillium wilt then becomes less of a problem.

In Carroll et al. (2017a), we find that a cooperative solution would increase welfare, and in most cases, a cooperative solution would require that the spinach seed company engage in more spinach seed testing and cleaning than in the status quo. In particular, significant welfare gains arise only when the seed company tests and cleans the spinach seeds so thoroughly that planting spinach does not have any significant negative effect on grower payoffs after controlling for spinach price. Determining who pays for cleaning and testing the seed, or for future advances such as resistant varieties or replacement fumigants for methyl bromide, and determining how to divide the joint surplus are still complicated issues, but, nevertheless, cooperation among the different players can increase social welfare.

Our work in Carroll et al. (2017a) regarding the supply chain externality between seed companies and growers sheds light on how treatment of spinach seeds could potentially reduce externalities between seed companies and growers.

5. Conclusions

This paper discusses the economics of managing *Verticillium dahliae*, a soilborne fungus that is introduced to the soil via infested spinach seeds and that causes lettuce to be afflicted with Verticillium wilt. Verticillium wilt can be prevented or controlled by the grower by fumigating with methyl bromide, planting broccoli, or not planting spinach. These control options require

long-term investment for future gain. Verticillium wilt can also be prevented or controlled by the spinach seed company by testing and cleaning the spinach seeds. However, seed companies are reluctant to test or clean spinach seeds, as they are not affected by this disease. The control options therefore are characterized by externalities. We discuss our research on the externalities that arise with short-term growers (Carroll et al., 2017b) and between seed companies and growers (Carroll et al., 2017a) due to Verticillium wilt, which has important implications for the management of Verticillium wilt in particular, and also for the management of diseases in agriculture in general. The results of our research are of interest to policy-makers, the agricultural industry, and academics alike.

ACKNOWLEDGMENTS

We received helpful comments from seminar participants at the University of California at Davis and California State University at Chico, and from conference participants at the Heartland Environmental and Resource Economics Workshop, the Association of Environmental and Resource Economists (AERE) Summer Conference, the American Agricultural Economics Association (AAEA) Annual Meeting, the Giannini Agricultural and Resource Economics Student Conference, and the Interdisciplinary Graduate and Professional Student (IGPS) Symposium. We also benefited from valuable discussions with Tom Bengard, Bengard Ranch; Kent Bradford, Seed Biotechnology Center UC-Davis; Leslie Crowl, Monterey County Agricultural Commissioner's Office; Rich DeMoura, UC-Davis Cooperative Extension; Gerard Denny, INCOTEC; Lindsey du Toit, Washington State University; Thomas Flewell, Flewell Consulting; Hank Hill, Seed Dynamics, Inc.; Steve Koike, Cooperative Extension Monterey County; Dale Krolikowski, Germains Seed Technology; Chester Kurowski, Monsanto; Donald W. McMoran, WSU Extension; Marc Meyer, Monsanto; Chris Miller, Rijk Zwaan; Augustin Ramos, APHIS; Scott Redlin, APHIS; Richard Smith, Cooperative Extension Monterey County; Laura Tourte, UC Cooperative Extension Santa Cruz County; Bill Waycott, Monsanto; and Mary Zischke, California Leafy Greens Research Program. Funding provided by USDA NIFA grant (2010-51181-21069).

Literature Cited

- Aguirregabiria, V., and Luengo, A. 2016. A microeconometric dynamic structural model of copperminingdecisions.WorkingPaper,Availablehttp://aguirregabiria.net/wpapers/coppermining.pdf.
- Allen, D., and Leuck, D. 1992. Contract choice in modern agriculture: cash rent versus cropshare.J. of Law and Econ. 35:397.
- Ambec, S., and Desquilbet, M. 2011. Regulation of a spatial externality: Refuges versus tax for managing pest resistance. Env. and Res. Econ. 51:79-104.
- Ameden, H., Cash, S., and Zilberman, D. 2007. Border enforcement and firm response in the management of invasive species. J. of Agric. and Appl. Econ. 39:35–46.
- American Seed Trade Association. 2009. *Verticillium dahliae* and leafy greens information sheet. Available http://www.calseed.org/news.html.
- Arrow, K. 1969. The organization of economic activity: Issues pertinent to the choice of market versus nonmarket allocation. The Anal. and Eval. of Pub. Exp.: The PPB System 1:59–73.
- Atallah, S., Gomez, M., Conrad, J., Nyrop, J. P. 2015. A plant-level, spatial, bioeconomic model of plant disease, diffusion, and control: Grapevine leafroll disease. Am. J. of Agric. Econ. 97:199-218.
- Atallah, Z. K., Maruthachalam, K., and Subbarao, K. V. 2012. Sources of *Verticillium dahliae* populations affecting lettuce. Phytopathology 102:1071-1078.
- Atallah, Z. K., Hayes, R. J., and Subbarao, K. V. 2011. Fifteen years of Verticillium wilt of lettuce in America's salad bowl: A tale of immigration, subjugation, and abatement. Plant Dis. 95:784–792.

- Atallah, Z. K., Maruthachalam, K., du Toit, L., Koike, S. T., Davis, R. M., Klosterman, S. J., Hayes, R. J., and Subbarao, K. V. 2010. Population analyses of the vascular plant pathogen *Verticillium dahliae* detect recombination and transcontinental gene flow. Fung. Gen. and Biol. 47:416–422.
- Batabyal, A., and Beladi, H.. 2007. A dynamic Bertrand Gaus model of trade, threats, and export certification in alien species management. J. of Econ. Research 12:65–78.
- Bhattacharyya, S., and Lafontaine, F. 1995. Double-sided moral hazard and the nature of share contracts." RAND J. of Econ. 26:761–781.
- Bilodeau, G.J., Koike, S.T., Uribe, P. and Martin, F.N. 2012. Development of an assay for rapid detection and quantification of Verticillium dahliae in soil. Phytopathology 102:331–343.
- Brennan, J.P., F.S. Thorne, P.W. Kelly, and G.M. Murray. 2004. Defining the Costs of an outbreak of Karnal Bunt of wheat. 2004 Conference (48th), February 11-13, 2004, Melbourne, Australia No. 58382, Australian Agric. and Res. Econ. Society.
- Brennan, J.P., E.J. Warham, D. Byerlee, and J. Hernandez-Estrada. 1992. Evaluating the economic impact of quality-reducing, seed-borne diseases: Lessons from Karnal Bunt of wheat. Agric. Econ. 6:345–352.
- Brewin, D.G., M. Undi, S. Kulshreshtha, K. Wittenberg, M. Tenuta, and K.H. Ominski. 2014.
- Integration of forage, beef, and hog production systems in western Canada: An economic assessment. Agric. Sys. 127:1–8.
- California Department of Pesticide Regulation. 2010. Department of pesticide regulation announces work group to identify ways to grow strawberries without fumigants. Available http://www.cdpr.ca.gov/docs/pressrls/2012/120424.htm>.

- Carlson, G.A., and Main, C.E. 1976. Economics of disease-loss management. Annu. Rev. of Phytopathol. 14:381–403.
- Carroll, C.L., Carter, C. A., Goodhue, R.E., and Lin Lawell, C.-Y.C. 2017a. Supply chain externalities and agricultural disease. Working Paper, University of California at Davis.
- Carroll, C.L., Carter, C. A., Goodhue, R.E., and Lin Lawell, C.-Y.C. 2017b. The economics of decision-making for crop disease control. Working Paper, University of California at Davis.
- Ceddia, M. G., Bartlett, M., De Lucia, C., and Perrings, C. 2011. On the regulation of spatial externalities: coexistence between GM and conventional crops in the EU and the 'Newcomer Principle. Aust. J. of Agric. and Res. Econ. 55: 126-143.
- Chatterjee, S. 1973. A mathematical model for pest control. Biometrics 29:727–734.
- Coase, R. 1960. The problem of social cost. J. of Law and Econ. 3:1-44.
- Cook, J.A., and Lin Lawell, C.-Y. C. 2016. Wind turbine shutdowns and upgrades in Denmark: Timing decisions and the impact of government policy. Working Paper, University of California at Davis.
- Cooke, B., R. Jones, and W. Gong. 2010. An economic decision model of wild rabbit *Oryctolagus cuniculus* control to conserve Australian native vegetation. Wildlife Res. 37:558–565.
- De Pinto, A., and Nelson, G.C.. 2009. Land use change with spatially explicit data: A dynamic approach. Env. and Res. Econ. 43:209-229.
- Dixit, A.K., and Pindyck, R. S. 1994. Investment under uncertainty. Princeton, N.J.: Princeton University Press.
- Doole, G. J. 2008. Optimal management of annual ryegrass (*Lolium rigidum Gaud.*) in phase rotations in the Western Australian wheat belt. Aust. J. of Agric. and Res. Econ. 52:339–362.

- Dorfman, R. 1969. An economic interpretation of optimal control theory. The Am. Econ. Rev. 59:817–831.
- du Toit, L., Derie, M., and Hernandez-Perez, P. 2005. Verticillium wilt in spinach seed production. Plant Dis. 89:4–11.
- du Toit, L., and Hernandez-Perez, P. 2005. Efficacy of hot water and chlorine for eradication of *Cladosporium variabile, Stemphylium botryosum*, and *Verticillium dahliae* from spinach seed. Plant Dis. 89:1305–1312.
- Dubois, P. 2002. Moral hazard, land fertility and sharecropping in a rural area of the Philippines.J. of Dev. Econ. 68:35–64.
- Duressa, D., Rauscher, G., Koike, S. T., Mou, B., Hayes, R. J., Maruthachalam, K., Subbarao, K.V. and Klosterman. S. J. 2012. A real-time PCR assay for detection and quantification of Verticillium dahliae in spinach seed. Phytopathology 102:443–451.
- Eiswerth, M. E., and Johnson, W. S. 2002. Managing nonindigenous invasive species: insights from dynamic analysis. Env. and Res. Econ. 23:319–342.
- Fradin, E. F., and Thomma, B. P. H. J. 2006. Physiology and molecular aspects of Verticillium wilt diseases caused by V. dahliae and V. albo-atrum. Mol. Plant Pathol. 7:71–86.
- Fuller, K. Alston, J., and Sanchirico, J. 2011. Spatial externalities and vector-borne plant diseases:
 Pierce's disease and the blue-green sharpshooter in the Napa Valley. Annual Meeting, July
 Pittsburgh Pennsylvania. Available
 http://ageconsearch.umn.edu/bitstream/103865/2/BGSS%20AAEA%202011%2005%2003%
 20Final.pdf.>.
- Gilligan, C. A. 2008. Sustainable agriculture and plant diseases: An epidemiological perspective.Phil. Trans. of the Royal Soc. B: Biol. Sci. 363:741–759.

- Goeschl, T., and Swanson, T. 2003. Pests, plagues, and patents. J. of the Eur. Econ. Assoc. 1:561– 575.
- Gomez, M. I., Nunez, H. M., and Onal, H. 2009. Economic impacts of soybean rust on the US soybean sector. (Abstr.) Annual Meeting, Milwaukee, Wisconsin No. 49595, Agricultural and Applied Economics Association.
- Gorddard, R. J. Pannell, D. J., and Hertzler, G. 1995. An optimal control model for integrated weed management under herbicide resistance. Aust. J. of Agric. and Res. Econ. 39:71–87.
- Harper, C. R., and Zilberman, D. 1989. Pest externalities from agricultural inputs. Am. J. of Agric. Econ. 71:692-702.
- Hayes, R. J., Vallad, G. E., Qin, Q.M., Grube, R. C., and Subbarao, K. V. 2007. Variation for resistance to Verticillium wilt in lettuce (*Lactuca sativa L.*). Plant Dis. 91:439–445.
- Hayes, R. J., Maruthachalam, K., Vallad, G. E., Klosterman, S. J., Simko, I., Luo, Y., and Subbarao, K. V. 2010. Iceberg lettuce breeding lines with resistance to Verticillium wilt caused by Race 1 isolates of *Verticillium dahliae*. Working paper, USDA Agricultural Research Service and University of California, Davis.
- Hueth, D., and Regev, U. 1974. Optimal agricultural pest management with increasing pest resistance. Am. J. of Agric. and Res. Econ 56:543–552.
- Inderbitzin, P., and Subbarao, K. V. 2014. Verticillium systematics and evolution: How confusion impedes Verticillium wilt management and how to resolve it. Phytopathology 104:564-574.

IPC. 2003. International Phytosanitary Certificate No. 4051.

Isaac, I., and Harrison, J. A. C. 1968. The symptoms and causal agents of early-dying disease (Verticillium wilt) of potatoes. Ann. Appl. Biol. 61:231-244.

- James, S., and Anderson, K. 1998. On the need for more economic assessment of quarantine policies. Aust. J. of Agric. and Res. Econ. 42:425–444.
- Johansson, R.C., M. Livingston, J. Westra, and K.M. Guidry. 2006. Simulating the U.S. impacts of alternative Asian soybean rust treatment regimes. Agric. and Res. Econ. Rev. 35:116–127.
- Kennedy, J. 1981. Applications of dynamic programming to agriculture, forestry and fisheries: Review and prognosis. Rev. of Marketing and Agric. Econ. 49:141–173.
- Levine, J., and C. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Bio. 17:322–326.
- Maruthachalam, K., S.J. Klosterman, A. Anchieta, B. Mou, and K.V. Subbarao. 2013. Colonization of spinach by *Verticillium dahliae* and effects of pathogen localization on the efficacy of seed treatments. Phytopathology 103:268–280.
- Malcolm, G. M., Kuldau, G. A., Gugino, B. K., and Jiménez-Gasco, M. M. 2013. Hidden host plant associations of soilborne fungal pathogens: An ecological perspective. Phytopathology 103:538-544.
- McKee, G. J. 2011. Coordinated pest management decisions in the presence of management externalities: The case of the Greenhouse Whitefly in California-grown strawberries. Agric. Sys. 104L 94-103.
- McKee, G.J., R.E. Goodhue, F.G. Zalom, C.A. Carter, and J.A. Chalfant. 2009. Population dynamics and the economics of invasive species management: The Greenhouse Whitefly in California-grown strawberries. J. of Env. Management 90:561–570.
- Meade, J. 1952. External economies and diseconomies in a competitive situation. The Econ. J. 62:54–67.

- Mérel, P.R., and C.A. Carter. 2008. A second look at managing import risk from invasive species. J. of Env. Econ. and Management 56(3):286–290.
- Mishan, E.J. 1971. The postwar literature on externalities: An interpretative essay. J. of Econ. Lit. 9:1–28.
- Moffitt, L., D. Hall, and C. Osteen. 1984. Economic thresholds under uncertainty with application to corn nematode management. Southern J. of Agric. Econ. 16:151–157.
- Monterey County Agricultural Commissioner. 2015. Crop reports and economic contributions. Available http://www.co.monterey.ca.us/government/departments-a-h/agricultural-commissioner/ forms-publications/crop-reports-economic-contributions>.
- Mumey, G.A. 1971. The "Coase theorem": A reexamination. The Quarterly J. of Econ. 85:718–723.
- Mumford, J. 2002. Economic issues related to quarantine in international trade. European Rev. of Agric. Econ. 29:329–348.
- Munro, A. 1997. Economics and biological evolution. Env. and Res. Econ. 9:429-449.
- National Agricultural Statistics Service. 2015. California agricultural statistics 2013 crop year. Available http://www.nass.usda.gov/Statistics_by_State/California/Publications/ California Ag Statistics/index.asp>.
- Noailly, J. 2008. Coevolution of economic and ecological cystems. J. of Evolutionary Econ. 18:1– 29.
- Olson, L. 2006. The economics of terrestrial invasive species: A review of the literature. Agric. and Res. Econ. Rev. 35:178–194.
- Olson, L., and S. Roy. 2002. The economics of controlling a stochastic biological invasion. Am. J. of Agric. Econ. 84:1311–1316.

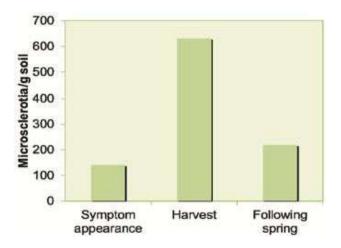
- Pegg, G. F., and Brady, B. L. 2002. Verticillium wilts. CABI Publishing, Wallingford, Oxon, UK.
- Pigou, A.C. 1932. The Economics of welfare, 4th ed. Edinburgh: R. & R. Clark, Limited.
- Pimentel, D., Rodolfo Zuniga, and Doug Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52:273-288.
- Rapson, D. 2014. Durable goods and long-run electricity demand: Evidence from air conditioner purchase behavior. J. of Env. Econ. and Management 68:141–160.
- Regan, D.H. 1972. The problem of social cost revisited. J. of Law and Econ. 15:427-437.
- Rossman, A. 2009. The impact of invasive fungi on agricultural ecosystems in the United States. Biological Invasions 11:97–107.
- Rothwell, G., and J. Rust. 1997. On the optimal lifetime of nuclear power plants. J. of Bus. & Econ. Statistics 15:195–208.
- Rust, J. 1987. Optimal replacement of GMC bus engines: An empirical model of Harold Zurcher. Econometrica: J. of the Econometric Soc. 55:999–1033.
- Scott, P.T. 2013. Dynamic discrete choice estimation of agricultural land use. Working Paper, Available http://www.ptscott.com>.
- Shetty, K. G., Subbarao, K. V., Huisman, O. C., and Hubbard, J. C. 2000. Mechanism of broccolimediated Verticillium wilt reduction in cauliflower. Phytopathology 90:305–310.
- Short, D. P. G., Gurung, S., Gladieux, P., Inderbitzin, P., Atallah, Z. K., Nigro, F., Li, G., Benlioglu, S., and Subbarao, K. V. 2015a. Globally invading populations of the fungal plant pathogen *Verticillium dahliae* are dominated by multiple divergent lineages. Env. Microbiology 16: doi: 10.1111/1462-2920.12789.

46

- Short, D.P.G., S. Gurung, S.T. Koike, S.J. Klosterman, and K.V. Subbarao. 2015b. Frequency of Verticillium species in commercial spinach fields and transmission of *V. dahliae* from spinach to subsequent lettuce crops. Phytopathology 105:80–90.
- Springborn, M., C.M. Romagosa, and R.P. Keller. 2011. The value of nonindigenous species risk assessment in international trade. Ecol. Econ. 70:2145–2153.
- Subbarao, K.V., and J.C. Hubbard. 1996. Interactive effects of broccoli residue and temperature on *Verticillium dahliae* microsclerotia in soil and on wilt in cauliflower. Phytopathology 86:1303–1310.
- Subbarao, K.V., J.C. Hubbard, and S.T. Koike. 1999. Evaluation of broccoli residue incorporation into field soil for Verticillium wilt control in cauliflower. Plant Dis. 83:124–129.
- Timmins, C. 2002. Measuring the dynamic efficiency costs of regulators' preferences: municipal water utilities in the arid West. Econometrica 70:603–629.
- United States Environmental Protection Agency. 2012a. Critical use exemption information. Available http://www.epa.gov/ozone/mbr/cueinfo.html.
- —. 2012b. The phaseout of methyl bromide. Available http://www.epa.gov/ozone/mbr/index.html.
- Vallad, G., Q. Qin, R. Grube, R. Hayes, and K. Subbarao. 2006. Characterization of race-specific interactions among isolates of *Verticillium dahliae* pathogenic on lettuce. Phytopathology 96:1380–1387.
- Vallad, G., and K. Subbarao. 2008. Colonization of resistant and susceptible lettuce cultivars by a green fluorescent protein-tagged isolate of *Verticillium dahliae*. Phytopathology 98:871–885.
- Vallad, G.E., R.G. Bhat, S.T. Koike, K.V. Subbarao, and E.J. Ryder. 2005. Weedborne reservoirs and seedborne transmission of *Verticillium dahliae* in lettuce. Plant Dis. 89:317–324.

- Weisensel, W.P., and G.C. van Kooten. 1990. Estimation of soil erosion time paths: The value of soil moisture and topsoil depth information. Western J. of Agric. Econ. 15:63–72.
- Wilhelm, S. 1955. Longevity of the Verticillium wilt fungus in the laboratory and field. Phytopathology 45:180-181.
- Wilhelm, S., and Paulus, A. O. 1980. How soil fumigation benefits the California strawberry industry. Plant Dis. 64:264-270.
- Williamson, O. E. 1971. The vertical integration of production: Market failure considerations. The Am. Econ. Rev. 61:112–123.
- Wu, B. M., and Subbarao, K. V. 2014. A model for multiseasonal spread of Verticillium wilt of lettuce. Phytopathology 104:908–917.
- Wu, J. 2001. Optimal weed control under static and dynamic decision rules. Agric. Econ. 25:119– 130.
- Xiao, C. X., and Subbarao, K. V. 1998. Relationships between *Verticillium dahliae* inoculum density and wilt incidence, severity, and growth of cauliflower. Phytopathology 88:1108–1115.
- Yerokhin, O., and G.C. Moschini. 2008. Intellectual property rights and crop-improving R&D under adaptive destruction. Env. and Res. Econ. 40:53–72.
- Zacharias, T.P., and A.H. Grube. 1986. Integrated pest management strategies for approximately optimal control of corn rootworm and soybean cyst nematode. Am. J. of Agric. Econ. 68:704–715.

Figure 1. Fluctuation in number of microsclerotia of *Verticillium dahliae* per gram of soil associated with infection of lettuce plants in coastal California fields. The number of microsclerotia generally increased after the incorporation of infected plant material following harvest. The level of inoculum remained high for the following crop unless plots were fumigated. Reproduced with permission from Atallah, et al. Hayes, and Subbarao (2011).



49

Figure 2. Fluctuation in number of microsclerotia of *Verticillium dahliae* per gram of soil detected in soil samples from an infested lettuce field in coastal California over two successive crops within a year, and requiring fumigation at the end of the second lettuce crop. Reproduced with permission from Atallah_et al. , Hayes, and Subbarao (2011).

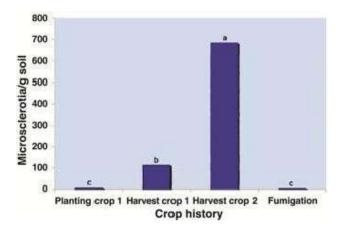


Figure 3. Relationship between *Verticillium dahliae* microsclerotia per gram and Verticillium wilt incidence. Reproduced with permission from Wu and Subbarao (2014).

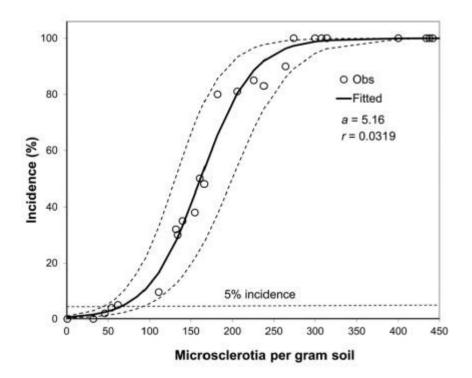


Table 1. Economic thresholds

Сгор	Threshold (microsclerotia (ms) per gram)	Approximate Loss
Lettuce (Iceberg)	150 ms/g	50%
Strawberry	3 ms/g	50%
Artichoke	5-9 ms/g	50%
Cauliflower	10 ms/g	50%
Cotton	19 ms/g	50%
Tomato	0.5 ms/g	50%

Sources: Xiao and Subbarao (1998); American Seed Trade Association et al. (2009); Atallah <u>et al.</u> , <u>Hayes</u>, and <u>Subbarao</u> (2011)

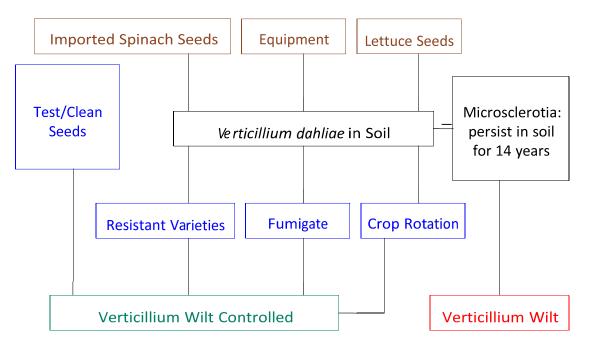


Figure 4. Verticillium wilt: Causes and control options

53

Figure 5. Impact of lettuce/broccoli rotation on number of microsclerotia of *Verticillium dahliae* from soil samples (expressed as microsclerotia per gram of soil). Broccoli cultivation suppressed *V. dahliae* populations in the soil, whereas lettuce cultivation significantly increased soil inoculum densities. Reproduced with permission from Atallah et al., Hayes, and Subbarao (2011).

