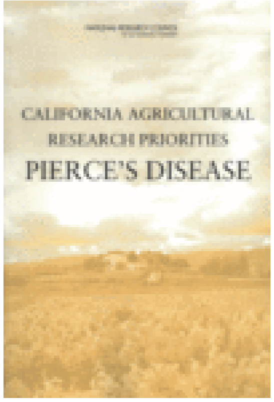

California Agricultural Research Priorities: Pierce's Disease

Committee on California Agriculture and Natural Resources, National Research Council

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CALIFORNIA AGRICULTURAL
RESEARCH PRIORITIES
PIERCE'S DISEASE

Committee on California Agricultural Research Priorities:
Pierce's Disease

Board on Agriculture and Natural Resources

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This report represents the integrated efforts of many individuals. The committee thanks all those who shared their insight and knowledge to bring the document to fruition. We also thank all those who participated in our public sessions.

The committee is grateful to members of the National Research Council (NRC) staff who worked diligently to maintain progress and quality in its work.

This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise, in accordance with procedures approved by the National Research Council's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following individuals for their review of this report:

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Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations nor did they see the final draft of the report before its release. The review of this report was overseen by R. James Cook, Washington State University. Appointed by the National Research Council, they were responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution.

Preface

Although Pierce's disease (PD), caused by the bacterial pathogen *Xylella fastidiosa (Xf)*, has been present in California vineyards for more than a century, it has not been considered a major problem for more than 40 years. The situation changed dramatically with the introduction of a new more aggressive vector, the glassy-winged sharpshooter (GWSS) *Homalodisca coagulata* (Say), a leafhopper of the Cicadellidae family. By the end of 2003, 15 counties in California were infested with this new vector, and in Riverside County alone PD damage estimates approached $13 million. Because of the high potential for GWSS to continue to move and transmit the pathogen within the state—and because of the tremendous value of grapes and grape products to California—this situation, understandably, created great concern. That worry is exacerbated by the facts that other strains of *Xf* can cause disease in other economically important crops, such as citrus and almond, and that GWSS is a voracious feeder, with tastes for a broad range of plants.

I can only imagine the frustration when this disease that historically had been confined to a relatively limited area of California first began to be spread farther and faster by the new vector. The old management strategies were insufficient by themselves, and it was not clear whether components of those strategies could provide some relief from the emerging problem, or whether entirely new paradigms for management of the disease and pest would be needed. Although pockets of solid and excellent research on PD, GWSS, and their interactions with grapevine existed, none were sufficient to provide conclusive answers to those questions.

Faced with this crisis, the relevant industry, university, and government groups rapidly established a funding program that solicited the badly needed research. The initial net cast for research projects was very broad and inclusive. Now, with the accumulation of several years of data, the funding network has realized the need to review research progress and to focus efforts in areas that are most likely to lead to management of the PD–GWSS problem. Identifying research areas with the most promise was the major challenge presented to the Committee on California Agricultural Research Priorities: Pierces' Disease, which has produced this report.

Although tragic in and of itself, the positive aspect of the PD–GWSS situation is that it calls attention to the need for models for coping with other emerging or introduced disease and pest problems of agronomic importance. Although the focus of the report is on PD–GWSS in grape in California, during its deliberations, the committee considered operational and research strategies in a much broader context. The intent is that the ideas and suggestions provided here will serve as a foundation for responses to future outbreaks.

Most of my career as a plant pathologist has been spent studying an annual crop species, where breeding for resistance is the most economically feasible and environmentally sound approach to disease management. Understanding the many complex facets of the PD–GWSS problem on grape was a particularly intriguing exercise. Breeding for resistance to PD in grapevine is not trivial for many reasons, not the least of which is the importance of the genetic identity of traditional cultivars used for wine making. The current social and political landscape in California restricts consideration of other options for disease management that might be acceptable elsewhere, including the use of transgenic varieties. These and many other considerations made for lively and thought-provoking discussions during committee meetings.

I particularly want to thank the committee members for their hard work in drafting, reviewing, and revising the document. It is particularly satisfying that the diverse expertise of the committee is positively reflected in the document, and I truly appreciate each member's willingness to consider and discuss freely the perspectives of others. The PD–GWSS research community was particularly helpful to our deliberations; they patiently answered our many questions and frequently provided unpublished information for our education and consideration. Special thanks are extended to the staff of the Board on Agriculture and Natural Resources of The National Academies, including Michael Kisielewski, Donna Wilkinson, Julie Coffin, Cindy Lochhead, Peter Rodgers, and Tanja Pilzak. I thank Dr. Kim Waddell, the study director, for his essential scientific insights, his tremendous tact and patience, and his tireless efforts. Finally, I thank Robin Schoen, who, due to changes in staffing, was brought into the preparation of this report just before the review process. Her fresh perspective, sound judgment, and superb organizational skills were critical in completing the document.

Jan E. Leach
Chair, Committee on California Agricultural Research Priorities:
Pierce's Disease

Contents

Tables, Figures, and Boxes

TABLES

FIGURES

BOXES

Executive Summary

Invasive species threaten agricultural ecosystems throughout the world. Within the United States, California has one of the most diverse and productive agricultural ecosystems. Because of its wealth of production systems, hospitable climate, and the ready movement of plants, animals, and microbes across its borders, California also is particularly vulnerable to invasive pests. Recent introductions of nonnative insect species into California, among them the olive fruit fly and the imported fire ant, are examples of invasive species that threaten ecosystems.

One significant threat to California agriculture in recent years has been the glassy-winged sharpshooter (GWSS) *Homolodisca coagulata* (Say) as a vector of *Xylella fastidiosa (Xf),* a bacterial pathogen that causes a range of diseases that threaten agricultural and horticultural crops. One disease is Pierce's disease (PD) of grapevines, which affects wine, table, and raisin grape production. In California, grape production covers over 880,000 acres and represents $33 billion dollars in economic value.

Given the seriousness of the threat, the California Department of Food and Agriculture (CDFA), the U.S. Department of Agriculture (USDA), grape growers, and commodity and trade organizations have responded with directed efforts to slow the spread of the new insect vector and the disease. CDFA coordinates funding and provides oversight of the research effort through the Pierce's Disease Control Program. In 2001, CDFA and the University of California's Division of Agriculture and Natural Resources approached the National Research Council of the National Academies, requesting that the Council help monitor current and emerging issues in the state's agricultural research agenda, particularly for PD. In response, the Board on Agriculture and Natural Resources convened an ad hoc committee, the Committee on California Agricultural Research Priorities: Pierce's Disease, to address scientific and technical issues surrounding new and potential challenges to California agriculture with respect to PD. The committee was asked to monitor scientific advances in the areas of economically and environmentally important agricultural diseases and pests, including their vectors; respond to requests; identify emerging issues; provide independent analyses of scientific information and of state, federal, and international activities; and submit a rigorous and timely evaluation of scientific issues in response to identified areas of concern. The specific charge to the committee was as follows:

> The area of proposed study for the committee will be the current outbreak of agricultural diseases caused by *Xylella fastidiosa* and the disease vector, the glassy-winged sharpshooter. The committee will review the state of California's priorities for both short-term and long-term research and management efforts to control the glassy-winged sharpshooter, and identify a cure for Pierce's disease. It is anticipated that the committee will help to identify research priorities and needs, and will assist the state in coordinating with national and international program efforts to address the disease.

PIERCE'S DISEASE AND THE GLASSY-WINGED SHARPSHOOTER RESEARCH

Pierce's disease has affected grape production in California for more than a century, but until the introduction of GWSS in the past decade, neither the pathogen nor the insect stimulated significant and consistent research support. Because wine grape growers add significant value to their crops by making and selling wine, the wine industry has considerably greater resources than other agriculture commodity sectors do. The industry has been able to respond rapidly to the problems of PD–GWSS and to allocate significant resources for addressing the threat. The result is expanded research on the grape–PD–GWSS system and on identifying opportunities to control or manage the disease and vector.

Over the past 3 years, nearly $20 million has been set aside to fund 125 completed and continuing research projects. Support is provided by the PD/GWSS Board, CDFA, the University of California Pierce's Disease Research Grants Program, USDA's Animal and Plant Health Inspection Service and its Agricultural Research Service, the American Vineyard Foundation, the California Competitive Grant Program for Research in Viticulture and Enology, the California Citrus Nursery Advisory Board, the Almond Board of California, and the California Department of Transportation.

The research program that has emerged from the exchange of information, data, and experiences among growers, county and state officials, and academic researchers reflects the various interests of the stakeholders in the

PD problem. Projects within the program can be classified into nine areas of basic research:

- crop biology and ecology
- basic biology of the vector
- insect–plant interactions and vector population ecology
- genetics of *Xf*
- *Xf*–host and plant–insect interactions
- epidemiology of *Xf* diseases
- vector monitoring and action thresholds
- *Xf* monitoring and action thresholds
- economics

The program also supports applied research on management strategies for biologic and chemical control; cultural, physical, and behavioral control; and resistance to *Xf* diseases. The short-term objectives of the research are to produce tools and tactics that lead to methods of management of the bacterium and insect vectors; the long term goals are the prevention and cure of PD.

This report is being released as the research efforts are just beginning to deliver results from the initial investment. Although in some instances a clearer understanding of the remaining challenges is emerging, in general, management efforts are hindered by a lack of understanding of the biology of the organisms and their mechanisms of interaction, and by a lack of information about the costs and benefits of different approaches. Setting priorities is difficult, and, as part of the discussion about different research avenues, the committee had to consider experience with other diseases in other contexts to judge the likelihood that one or more approach for addressing PD would prove useful.

Nevertheless, the committee developed a clear picture of the foundation of information needed to build an effective response to PD–GWSS. The conclusion is that a well-conceived management program will be based on knowledge of the characteristics and interactions of the pathogen, the vector, and the host; the cultural and climate conditions under which the crop is grown; and the procedures available for disease control, including cultural, genetic, and chemical approaches. Management programs must be economically feasible, and their environmental and ecosystem effects must be kept to a minimum.

In general, the breadth of topics included in the program appears appropriate for building the foundation needed to address PD–GWSS, but because the community is still at an early stage of understanding the various components of the epidemic, management strategies, policies, and research programs will need to be adjusted to maximize the investment of limited financial resources as new information evolves. Those adjustments will be achieved by recognizing the varying pace at which information will flow from different projects and by assessing the relative value and quality of different types of information in leveraging progress across all elements of the program, so that some subject areas or projects can be emphasized relative to others as the overall research progresses over time. It also requires the selection of only those projects that meet the highest levels of scientific rigor. This strategic approach rests on the ability of the program to achieve significant coordination in project solicitation and selection and to maintain the flexibility to shift priorities as research results provide new information.

The current process of selecting and supporting research might not be the best one for implementing such a framework. Not all research approaches are valued the same by the involved parties. Industry is searching for a solution to the problem faced by its commodities, and much of the research community is focused on uncovering the basic biology and epidemiology of PD–GWSS. There are good reasons to pursue research on both kinds of questions, but disjointed selection of projects could hinder the opportunities to create synergies or to implement a logical progression of research. The selection and design of basic and applied research should be at least complementary, and even integrative, if possible; the goal is to accumulate data that will advance progress on all fronts.

The committee noted an absence of uniformity and communication in the process through which PD–GWSS research projects are selected, accepted, and funded. The greatest concern is that the scientific merit of the proposals is not receiving consistent scrutiny and attention. That could hinder the program's ability to move forward, because decisions about priorities and direction need to be made using solid, reproducible results. Consequently, the committee makes the following recommendation:

To ensure scientific rigor in and enhance coordination of the PD–GWSS research program, participating research sponsors should consolidate processes for proposal solicitation and review.

Consolidation would facilitate the identification of strategically critical projects and of critical areas that are not receiving funding, avoid redundancy in the selection of projects, reduce costs, and distinguish projects for which teams or consortia should be established from those appropriate for one or two principal investigators.

ESTABLISHING PRIORITIES

The committee's goal in providing advice on research priorities was to focus on strategies that would culminate in the development of effective control mechanisms. Several guiding themes emerged from deliberation on how to characterize the most desirable research outcomes. First, effective mechanisms can be defined as those that interfere with one or more of the three interactions involving PD–GWSS: between the host and the vector, between the vector and the pathogen, and between the host and the pathogen. Any successful "interference" could break the chain of events that ends with a plant succumbing to PD. By identifying a specific mechanism, researchers eventually could provide growers with tools or strategies to minimize the risks to or effects of the disease in their agricultural production systems. (The concept of interference gave the committee a logical way to organize its work. In the report, separate chapters are dedicated to research on each of the three interactions.)

A second guiding theme is that, because measures that keep the disease in check are more realistic than are attempts to cure or eradicate PD, it is better to focus on management strategies instead of cures, keeping in mind that different strategies will be useful for some parts of the grape industry and not for others and that management approaches will depend on the environment. Management tactics at the northern limit of the GWSS in California might be different from those used in the center. Third, although disease can be potentially controlled with one procedure, better management usually is achieved by means of a set of methods. Different measures are likely to provide incremental benefits; the goal should be to develop a complementary suite of approaches. Fourth, consideration should be given to the potential of any method to damage the environment and ecosystem; therefore, research that leads to ecologically based pest management (EBPM) strategies should be encouraged. Many board-spectrum synthetic chemical pesticides kill not only arthropod and pathogen pests but also beneficial organisms that serve as natural pest control systems. There also is a risk of dependence on chemical pesticides to which pests may eventually become resistant. EBPM systems are built on an underlying knowledge of the managed ecosystem, including the natural processes that suppress or augment pest populations. The practices will be supplemented by biological-control organisms and products, resistant plants, and narrow-spectrum pesticides.

Evaluation Framework

With the guiding principles in mind, the committee developed a framework for examining elements of the current and prospective PD–GWSS research program. The framework consists of two sets of evaluation criteria, and a system for grouping current and prospective research projects into categories that reflect differences in certainty, cost, and relative effectiveness.

The first criterion assesses the ability of projects to achieve successful management of the PD–GWSS problem. The second addresses the important notion of sustainability of the strategies or products.

1 **Feasibility:** Considering technical barriers and practical limits (including cost), what is the likelihood that the research will result in tools for effective management of PD–GWSS?
    a. **Time**: What period is required for the research to deliver an effective strategy, approach, or tool?
    b. **Effectiveness:** What is the likelihood that the research product will deliver a strategy that will improve the PD–GWSS situation? Because the degree to which a given strategy or product will change the situation will vary, it must be

determined whether the degree of change is better or worse than that achieved by other management measures and whether the strategy or product is sufficiently effective to warrant funding.

   c. **Cost**: What will it cost to accomplish the research objectives?

2 **Sustainability:** Is the approach or product biologically adaptable and affordable? Will it remain useful? Efforts to manage disease or pest outbreaks in agriculture often promote research that results in effective short-term solutions, but because diseases and pests are dynamic and evolving, those control measures are often not sustainable solutions. What is the likelihood that the proposed research will lead to management strategies that can be affordably implemented over the long term?

With information from the first criterion for any given research strategy, the committee classified each research strategy into one of four categories:

- **Category 1:** The research option holds reasonable promise of generating successful tools for management of PD–GWSS, either in the short term or in the long term.
- **Category 2:** The research approach looks promising, but either because of insufficient data or because of inconclusive results, it is difficult to predict whether it will lead to successful applications for management.
- **Category 3:** The research can produce data and results that are promising for successful management of PD–GWSS, but because of its complexity and the technology required, it would be prohibitively expensive for any one funding source to manage.
- **Category 4:** The research approach does not show promise, even in the long term, for PD–GWSS management.

Assignment of projects to those categories provides a way to examine options for the research program as a whole. In considering how projects might be selected from several categories or within any particular category, the committee returned to the criterion of sustainability, concluding that, because many short- and medium-term control options are unlikely to be sustainable, a mixture of projects should be considered.

Research priorities should be developed using the two criteria—the predicted feasibility that an approach will contribute to PD–GWSS management and its sustainability. The committee recommends a balance among short-, medium- and long-term research projects to ensure the development of sustainable management approaches.

KEY RECOMMENDATIONS

The research strategies recommended here are the result of the committee's evaluation process, and are designated by category. Many potential research avenues are promising but lack the data required to inform a convincing prediction of success; those strategies fall into Category 2. The committee recommends that a mixture of projects be pursued, but above all that projects of the highest scientific quality in rationale, scope, and design be selected. A small number of research efforts are under way that the committee would assign to categories 3 and 4. They are discussed but not highlighted in the recommendations. Although in the full report the committee discusses the interactions of host, vector, and pathogen in two dimensions—that is, host–vector, host–pathogen, and pathogen–vector—it is important to recognize that the reality is a dynamic three-way interaction. Therefore, many of the recommendations in the report exhibit overlap in approach. To reflect the nature of these interactions, in this Executive Summary we consolidate several of the report's recommendations. A full list is given at the end of the Executive Summary.

Several factors, apart from purely scientific considerations, will influence the decision to pursue or implement a management strategy. For example, the cooperation of growers of unaffected crops might be required to implement some control measures; if those measures are to be effective, a continuing dialogue must be fostered about PD within agribusiness. Some factors that affect the pursuit of one or another management strategy are related to sustainability, which, in addition to scientific issues (such as the vector's development of pesticide resistance), includes regulatory uncertainties or public acceptance, which could change. Some strategies will work in some cases and not others. For example, maintaining unique lineages of grapes results in the production of distinctive varieties of wine, such as chardonnay and cabernet sauvignon, which add value to grape production. But it also severely limits opportunities for crop improvement strategies that focus on breeding for disease or insect resistance by the conventional methods used for many other crop species. Breeding approaches might be useful for table grapes or raisins, however. Although the process of placing research options in categories focused on the potential effectiveness, time, and cost of a particular approach, the report mentions issues of sustainability and other factors when applicable.

Interactions of Host, Pathogen, and Vector

When this study began, the committee noted significant gaps in knowledge about the characteristics and biology of pathogen and insect and how they interact with each other and the host plant. Through the funding program coordinated by CDFA as well as other national and international institutions, significant, albeit in insufficient, strides are being made to remedy that lack of information. This is especially evident for *Xf.* The internationally coordinated research effort that recently released the genome sequence for *Xf* provides fundamental information for development of testable hypotheses. For example, genes selected based on their relationships to genes with known functions in other pathogenic bacteria can be tested directly to determine whether they function in virulence to grapevine, survival in the environment, and interactions with the insect vector. Those hypotheses can now be accurately tested because of the development of standardized and reliable plant inoculation and molecular assays for measuring disease and defense responses and because of the development of new tools for genetic modification of the pathogen. The information will identify targets for interference, and thus for management. Therefore, the committee makes the following recommendations for research:

- **Determine the genetic, biochemical, and physiologic base of *Xf* virulence, pathogenicity, transmission, and survival.** This **Category 2** research includes *Xf* colonization in grapevine and in GWSS and the production and delivery of *Xf* virulence factors in grapevine.

The complex nature of the GWSS has hindered progress in the elucidation of its interactions with *Xf* and with the diversity of plants that can serve as hosts for the vector. Several aspects of the insect's interactions with the pathogen and with plants need focused attention, including the biology of GWSS feeding, acquisition and transmission of *Xf*, host-finding behavior, host plant preferences, factors that influence reproductive success, and the importance of entomosymbionts (microbes that inhabit insects). To address those questions, the committee recommends the following research objectives:

- **Determine genetic, biochemical, and physiologic basis for GWSS herbivory and disease vectoring.** This **Category 2** research includes GWSS feeding and host–finding behavior, host plant preference, performance on different hosts, and influences of natural enemies. Also included are the effects of *Xf* on GWSS behavior and on survivorship, fecundity, population growth rates.

Knowledge of the host plant responses to GWSS feeding or to colonization by *Xf* could help guide breeding programs or vegetation management practices. Both *Xf* and GWSS target the plant xylem, so information about the composition of the xylem before, during, and after feeding or pathogen introduction is needed. Recent studies are beginning to unravel how GWSS feeds on xylem, and how, once introduced, *Xf* moves within and between vessels. However, little is known about how the xylem and surrounding tissues respond to insect feeding or to pathogen ingress or about whether modifications in the xylem structure or content enhance resistance or susceptibility. The committee makes the following research recommendations:

- **Determine the genetic, biochemical, and physiologic basis for host plant factors that influence attraction, repulsion, survival, or inhibition of**

GWSS or *Xf*. The studies must include an analysis of the criteria for assessing host plant responses and the means of *Xf* acquisition by GWSS from, and inoculation to, alternative hosts or dormant grapevines. This **Category 2** research will benefit from a multifaceted approach, and it should include combinations of biochemical, physiologic, genetic, and genomic analyses. The analyses must be statistically rigorous so the results will be reliable.

Host Plant Resistance to Pathogen and Pest

Host plant resistance is a core element of disease–pest management strategies for many crop species, including grape, and it should be emphasized as a component of ecologically based management of PD–GWSS. Plants that are resistant either to GWSS or to *Xf* can be developed through selection and breeding for resistance or by transgenic technologies. Although the plants mechanisms of resistance to the pathogen or pest could differ, the strategies for mapping, cloning, and manipulating resistance or defense response genes are the same.

The introduction of disease resistance in wine grapes by breeding is complicated by the complex and subtle gene combinations that contribute to grape quality and by the resistance of consumers, producers, and retailers to altering the genetic nature of the vines through the sexual process of breeding. One approach to reducing the disruption of complex trait combinations is to introduce useful genes by means of transgenic technologies. However, many consumers and producers are opposed to the use of transgenic technologies and there are significant regulatory requirements that must be met in introducing transgenic plants. Moreover, the assumption of introducing useful genes and minimizing disruption of desirable complex trait combinations currently is reasonable but can only be predicted, not assured. Thousands of transgenic plants will be discarded before one is found to have the desired traits. Nonetheless, the technology is a powerful research tool to further our understanding of the genes involved in pest and disease resistance. Although the transgenic plants might not be introduced into the field, the information gained through the research will be valuable.

Regardless of the approach taken to develop it, the nature of resistance to GWSS or PD must be better understood. Therefore, the committee recommends the following research:

- **Determine the genetic and mechanistic bases for grapevine resistance to *Xf* and GWSS.** This **Category 2** research would attempt to characterize the genetic loci and the biochemical and physiologic mechanisms responsible for host plant resistance to facilitate the development of resistant plants.

- **Develop and improve methods for manipulating grapevine resistance to *Xf* and GWSS**. This **Category 2** research is necessary both for experimental use (to identify and study resistance traits) and for possible commercial production. The methods should include various breeding practices and genetic transformation technologies. Transgenic approaches are essential to advancing our understanding of the genetic, biochemical, and physiologic bases for plant resistance to insects or pathogens.

It is worth pointing out separately that some kinds of research—especially genome based projects—are very expensive and will require consortium efforts and investments. Funding of genome-based projects (particularly those involving hosts) by public agencies such as CDFA and private-sector stakeholders, such as the PD/GWSS Board, should be considered supplemental funding, and the investments should be made when the potential for solving specific commodity problems appears to be within reach. This is **Category 3** research.

Biological Control

Biological control, or the use of living natural enemies to manage GWSS or *Xf,* is an appealing strategy because it is considered to be more environmentally benign than some other approaches. However, biological control must be rigorously evaluated to determine effectiveness in managing a pest or pathogen. Given approaches also must be proven to be environmentally benign and economically feasible.

The focus of most current biological-control efforts for GWSS is on the use of native and introduced species of egg parasitoids (insect species that prey on the eggs). Although that strategy would prove useful in some environments and in combination with other management schemes (such as vegetation management), rigorous experimentation is needed to predict success. The experiments range from rearing and releasing natural enemies to those that examine the critical question of whether parasitoids can sufficiently reduce the abundance of GWSS. The latter point concerns the question of whether small numbers of GWSS can still transmit enough bacteria to cause economically significant disease. The committee makes the following recommendations:

Research is needed to advance the use of classical biological control (predators and parasitoids) of the insect. Management will be particularly relevant in commercial vineyards where there is minimal use of insecticides, in vineyards where selective insecticides that are nontoxic to natural enemies are used, or where the timing of insecticide use is such that mortality to natural enemies is minimal. It also will be relevant in areas or habitats where insecticide use can be severely limited or eliminated. Areas for study would include riparian habitats, watershed areas, wetlands, and some urban and suburban green areas. The research is classified as **Category 2**, and includes the following:

- **Establishment of protocols for the effective selection of natural enemies**
- **Development of strategies that will increase the success of inoculative releases of parasitoids**
- **Rigorous evaluation of the effectiveness of the released natural enemies.**

Other biological-control strategies for GWSS management, including insect growth regulators, biorational pesticides, biological-control agents other than parasitoids, mating disruption, behavior-modifying chemicals, sterile-male techniques, and mass trapping are discussed in Chapter 3. However, it is not clear whether those strategies would be effective for managing GWSS and PD.

For the pathogen, current research biological control is directed predominantly at identifying native endophytic (xylem inhabiting) or insect endosymbiotic (within insects) bacteria that might inhibit *Xf* or interfere with its interactions with the grapevine or the insect vector. Where limited control has been observed, it seems to be through competition for attachment sites in the hosts rather than through antibiosis. Thus, if any research is to be funded for biological control of *Xf,* it should be directed at identifying the factors involved in attachment and targeting organisms that compete for the same attachment sites. Such research elucidating the biology of the interactions between the target organisms could reveal important information about host–pathogen or host–vector interactions. However, biological-control strategies generally have not been highly effective for managing vascular pathogens (such as *Xf*), particularly in perennial crops such as grape. Thus, the committee views work involving biological control of the pathogen as **Category 4** research.

Because there is no way to confine an organism once it is released into the environment, no biological-control agent, whether to control the vector or to control the pathogen, should be considered for introduction without extensive study of its consequences for the ecosystem in general and more specifically for its effects on beneficial insects or microbes.

Vegetation Management

Vegetation management can be an important element in a comprehensive pest management system and has been effective for the control of insect-transmitted plant pathogens. Mixing host and non host species can lead to significant reductions in leafhopper abundance, which can also lead to lower prevalence of leafhopper-transmitted pathogens. Thus, GWSS populations, and therefore, the transmission of *Xf*, are likely to be influenced by the presence of ground covers in vineyards or through a mixture of plant species in riparian areas. However, the committee could not make clear recommendations for vegetation management to growers because information on leafhopper performance on, and preference for, a range of potential cover crops and alternative hosts is adequate, as is information on the potential of these alternative hosts to develop epidemiologically significant populations of *Xf.* Thus, the committee provides the following recommendations:

Research should advance the use of vegetation management to reduce populations of GWSS and *Xf.* This **Category 2** research would involve determining the potential of ground cover crops to develop epidemiologically significant populations of *Xf*; determining leafhopper performance on (survivorship, fecundity, development time) and preference for a broad range of potential ground cover crops; and investigating the use of carefully selected cover crops in vineyards to reduce insect colonization of grape plants.

Chemical Control

Currently funded research encompasses a range of approaches for PD–GWSS management, some of which will require years of study and field verification before commercial acceptance is possible. Until then, growers face an expanding infestation that promises serious economic consequences. Research on the use of chemicals or biocides offers the most cost-effective near-term solution to managing GWSS in California vineyards.

Many pesticides can be effective against GWSS eggs, nymphs, and adults. The insects predominate on different plants at different stages, so several types of pesticides with different application techniques or schedules are needed to effectively disrupt the their development. The best studied pesticides for control of GWSS include the systemic formulations, which move through the vascular system of the plant; the nonsystemics, which act after application to the surface of the plant; and inert compounds, which coat the plant surface to repel insects.

Although insecticides offer reasonably good short term management for such control to remain economically feasible and environmentally acceptable, the committee urges research on improved application mechanisms that will reduce drift and thus exposure of nontarget organisms. The committee also recommends the pursuit of additional narrow-spectrum chemical controls. The determination of the social and environmental effects of any recommended compound and the rigorous economic assessments of insecticide effectiveness within an EBPM scheme are also recommended. In general, research should identify management strategies or approaches that minimize the use of insecticides or that promote the use of narrow-spectrum, sustainable pesticides. Research on chemicals should focus on the following areas:

- **Identify and develop more efficient means of delivery of the chemical to the target.**
- **Identify novel pathogen targets for which highly specific chemicals can be identified or developed.**
- **Determine the social and environmental consequences of using these compounds.**

- **Conduct an economic assessment of insecticide effectiveness within an ecologically based pest management scheme.**

Although effective for GWSS, research has demonstrated that existing chemical controls do not provide effective, economically feasible management of *Xf* or of any other bacterial pathogen of plant vascular systems. Although not all available chemicals have been rigorously tested, chemical control does not appear to be a promising area for short-term management of *Xf* . This class of controls includes chemicals that do not directly affect the pathogen but which induce systemic resistance in plants. Thus, the committee views this as **Category 4** research. However, if research funding is directed at the study of chemical control the work should be directed toward the identification of novel targets in the bacteria for which highly specific chemicals can be identified or developed.

Economic Feasibility

The major factor driving research on PD–GWSS is the economic effect that results from the spread of the insect and pathogen in commercial agriculture but the true economic dimensions of the PD–GWSS problem are poorly defined. Economic analyses are needed in several areas, from studies of the relative cost of implementing control options to the prospective costs of management strategies currently in development. Because there is uncertainty about the spread of PD and GWSS to other parts of California, cost–benefit analyses of state policies on measures to control that spread should be undertaken.

Taking these dimensions into consideration, the committee recommends examples of economic research projects needed. The first two are **Category 1** projects:

- **Assess the economic feasibility of specific biological and chemical control methods and strategies.** In addition the cost of crop losses, grape production costs can be incurred through biological or chemical controls. Growers need decision and cost models to guide their implementation of specific control regimes.
- **An economic analysis, including environmental impacts, should be for all potential management strategies and outcomes.** There are no economic analyses of research-based management strategies and outcomes that address PD–GWSS. Such analyses are needed both to help determine the outcomes that will be most economically practical for growers and to inform the research agenda.
- **The long-term research agenda should include economic analyses of policy regulations, incentives, and institutions to limit introduction and movement of PD vectors.** The current concern with PD in California is attributable to the introduction of GWSS, which arrived in California and spread from a single location as a result of human activity. The need to

manage invasive species, such as GWSS and others that could emerge as PD vectors, could become more significant in the years ahead. This is classified as **Category 2** research**.**

SUMMARY

Significant progress already has been made in elucidating the biology of the PD–GWSS problem. Plausible management strategies have been tested and either advanced to future studies or eliminated. However, there still are significant knowledge gaps in critical areas. This report identifies those gaps, provides guidance for setting priorities in the research needed to fill them, and describes mechanisms for improving funding and management. Areas that could benefit from research include economic feasibility; the biology of interactions among GWSS, *Xf,* and host plants; and various management strategies, including those that involve host plant resistance and biological and chemical controls. This and other reports, including those published by USDA's Agricultural Research Service and the American Vineyard Foundation, provide stakeholders with guidance to take on the remaining challenges in managing the PD–GWSS problem.

This report was developed early in the process of elucidating the mechanisms of GWSS–*Xf*–host interaction and early in the process of setting priorities for funding research. As new data emerge and as approaches and priorities are refined, research and management strategies will be adjusted. The process that has developed through this study can serve as a template for other emerging pest–pathogen problems not only in California, but in agricultural ecosystems in general.

RECOMMENDATIONS
(By Chapter)

2.1 To ensure scientific rigor and enhance the coordination of the PD–GWSS research program, participating research sponsors should consolidate the processes for proposal solicitation and review.

2.2 Research priorities should be developed according to their ability to meet two criteria: the predicted ability of the approach to contribute to PD–GWSS management and its sustainability. The committee recommends a balance among short-, medium-, and long-term research projects to ensure the development of sustainable management approaches are achieved.

2.3 An economic analysis including a study of environmental impacts should be conducted for *all* potential management strategies and outcomes (Category 1).

2.4 The long-term research agenda should include economic analyses of policy regulations, incentives, and institutions to limit introduction and movement of PD vectors (Category 2).

3.1 Studies that provide more information about sharpshooter feeding, host-finding behavior, host plant preferences, and the factors that influence reproductive success and natural-enemy-caused mortality are needed. The potential effects of *Xf* infection on sharpshooter behavior and performance should be included in those studies. Those factors must be examined with statistical rigor so that the results are reliable (Category 1).

3.2 All the modern chemical, molecular, ecological, and statistical tools available to scientists should be used to identify mechanistic bases of grapevine resistance to xylem-feeding leafhoppers. Studies should be done in the ecosystem and consider multitrophic interactions among plants, insect pests, and natural enemies (predators and parasites), and they should include both insect- and *Xf*-induced changes in plant quality (Category 2).

3.3 Host–plant resistance should be emphasized as a component of ecologically based insect management strategies in the grapevine–sharpshooter–*Xf* system. Methods for manipulating grapevine resistance should be developed for experimental use to identify key resistance traits and with an eye toward eventual commercial deployment. The methods should allow work with genetically transformed plant material, use of chemical or other elicitors, and cultivation practices (Category 2).

3.4 Detailed, quantitative studies should examine leafhopper performance (survivorship, fecundity, development time) on and preference for a broad range of potential ground cover crops (Category 2).

3.5 The feasibility of using carefully selected cover crops in vineyards to reduce sharpshooter colonization to grape should be investigated (Category 2).

3.6 Potential ground cover crops should be screened for the capacity to develop epidemiologically significant populations of *Xf* (Category 2).

3.7 Detailed, quantitative studies should examine leafhopper preference for potential host plants in the context of natural assemblages of hosts in the field. Studies of leafhopper performance on a broad range of potential host plants are essential to elucidate host ranges (Category 2).

3.8 The plant-to-plant movement of GWSS at multiple scales should be examined throughout the year to identify long-range seasonal and "trivial" movements that lead to disease spread (Category 2).

3.9 Sharpshooter host plants should be screened for their capacity to develop epidemiologically significant populations of *Xf* and examined for effective transmission rates from host to grape (Category 2).

3.10 After the epidemiologically important noncrop host plants of the vectors are identified, the ecological and socioeconomic barriers to removal of those plants from areas that influence disease prevalence in grapes should be explored (Category 2).

3.11 Basic and applied research should establish protocols for the effective selection of natural enemies, develop strategies to increase the success of inoculative releases of parasitoids, and rigorously evaluate the effectiveness of released natural enemies (Category 2).

3.12 Support for classical biological control (inoculative releases) is preferred over augmentation if inoculative releases result in self-sustaining populations and can be shown to be less costly than augmentation (Category 2).

3.13 Research should assess the economic feasibility of biological-control tactics and strategies (Category 2).

3.14 Biological-control tactics within EBPM schemes should be evaluated within the context of working economic thresholds (Category 2).

3.15 Research on the use of biological-control agents (predators and parasitoids) should be a priority in commercial vineyards where there is a minimal use of insecticides, the use of selective insecticides that are nontoxic to natural enemies are used, or where the timing of insecticide use is such that mortality to natural enemies is minimal. Similarly, research should be supported that advances the use of biological-control agents in areas and habitats where insecticide use can be severely restricted or eliminated. Areas for study could include riparian habitats, watershed areas, wetlands, and urban and suburban green areas (Category 2).

3.16 Control strategies should be pursued that limit the use of insecticides to sustainable formulations that are minimally incompatible with ecologically based approaches to pest management. A premium should be set on minimizing the negative consequences of pesticide use for human health and environmental quality.

3.17 Research should assess the economic feasibility of specific chemical control strategies and develop decision and cost models to guide growers in setting up chemical control methods for GWSS (Category 1).

4.1 A systematic analysis of *Xf* pathogenicity should be accomplished with a combination of biochemical, genetic, and genomic analyses. Such research lends itself to a collaborative approach (Category 2).

4.2 As with the pathogen, systematic and global approaches to address host plant responses (disease or defense) to pathogen invasion are essential to identify important plant defense factors. However, until the sequence of the grape genome is available and until other tools, such as grapevine mutants for dissection of defense responses, are available, that approach should be viewed as a long-term and expensive effort (Category 3).

4.3 Host plant resistance to *Xf*, whether quantitative or qualitative, is important to long-term management of the disease. Immediate emphasis should be placed on identification and characterization of the genetic basis for resistance to *Xf* in host plants. Characterization of the genetic loci and biochemical mechanisms responsible for resistance will facilitate classical approaches (which use molecular markers) and transgenic breeding to create *Xf*-resistant plants (Category 2).

4.4 Improvements in tissue transformation systems and in the ability to regenerate plants from transformed tissue have made transgenic technology increasingly feasible, although the availability of genes of known function that could be introduced to target desired effects is limited. In the longterm, however, transgenic technology could hold promise for improving resistance to *Xf* (Category 2).

4.5 Long-term projects should focus on identification of pathogen targets for existing or novel chemical control approaches for means to stimulate or alter host defense response pathways (Category 2).

4.6 Research should determine the efficacy and the economic and environmental feasibility of manipulating alternative hosts for PD management (Category 2).

5.1 Research should be done on the transmission biology of the disease system, including acquisition from and inoculation to alternative hosts and acquisition from and inoculation to dormant grapevines (Category 2).

5.2 Research should be done on the determinants of transmission efficiency, including attachment and reproduction of *Xf* in GWSS (Category 2).

5.3 A subset of studies of the vector should explore the effects of *Xf* on vector survivorship, fecundity, and population growth rates (Category 2).

5.4 A subset of studies of the vector should explore the effects of *Xf* on vector behavior, including movement and attraction to infected hosts (Category 2).

Category 4 Research

Chapter 4: With existing chemistries and approaches, chemical control of *Xf* is not promising for short- term disease management. However, the identification of new targets in the bacteria for which highly specific chemicals could be developed has not been explored.

Chapter 4: Biological control of bacterial pathogens of plants' vascular systems, particularly in perennial crops, has generally shown limited success. Naturally occurring endophytes or attenuated strains of *Xf* have not been effective in control of PD. However, better understanding of *Xf* and of the endophyte genes required for colonization, establishment, and virulence or antagonism through genome analysis could identify target genes that would allow development of effective biological-control agents.

Chapter 5: It might be useful to consider the possibility of interference between two strains of *Xf* within the vector. Although that research is interesting from a biological perspective, the committee concluded that biological control of bacterial vascular pathogens, particularly in perennial crops, has generally shown little practical success.

Chapter 5: Genetic engineering bacterial symbionts of vectors to express and release transgene products that can damage the pathogen (paratransgenesis) would clearly be a very long-term strategy for managing PD, and one in which the likelihood of success is limited.

Research Lacking Sufficient Data to Categorize

Chapter 3: Several research options could not be categorized because information associated with the techniques in the context of PD is so preliminary. They include the use of biological-control agents other than parasitoids, insect growth regulators, biorational insecticides, mating disruption, behavior-modifying chemicals, sterile male technique, and mass trapping using a compound from a living organism.

BOX ES-1
Framework for Evaluating Research and Management Strategies

Category 1 The research holds reasonable promise of generating successful tools for short-term or long-term management of PD–GWSS.

Category 2 The approach looks promising but either because of insufficient data or because of inconclusive results, it is difficult to predict whether it will lead to successful applications for management.

Category 3 The research can produce data and results that show promise for successful management of PD–GWSS, but because of complexity and the technology required, the work will be prohibitively expensive for any one funding source to manage.

Category 4 The approach does not show promise even in the long term for PD–GWSS management.

Research also should be evaluated for its long-term sustainability and for nonscientific barriers to implementation.

1

Pierce's Disease and the Glassy-winged Sharpshooter: Their Biology and the Challenges of Their Management

In 2001, the California Department of Food and Agriculture (CDFA) approached the National Research Council of the National Academies, requesting that it help monitor current and emerging issues in the state's agricultural research agenda, particularly for Pierce's disease (PD), which threatens California's wine, table, and raisin grape industry, and several other agricultural commodities. In response, the Board on Agriculture and Natural Resources convened the Committee on California Agricultural Research Priorities: Pierce's Disease. The Committee was asked to monitor scientific advances in the areas of economically and environmentally important agricultural diseases and pests, including their vectors; respond to requests; identify emerging issues; provide independent analyses of scientific information and of state, federal, and international activities; and to submit a rigorous and timely evaluation of scientific issues in response to identified areas of concern. The specific charge to the committee was the following:

> The area of proposed study for the committee will be the current outbreak of agricultural diseases caused by *Xylella fastidiosa* and the disease vector, the glassy-winged sharpshooter. The Committee will review the state of California's priorities for both short-term and long-term research and management efforts to control the glassy-winged sharpshooter and identify a cure for Pierce's disease. It is anticipated that the Committee will help to identify research

> priorities and needs, and will assist the state in coordinating with national and international program efforts to address the disease.

In this report, the committee recommends ways to improve the development and implementation of a coherent research and management agenda to address Pierce's disease. Chapter 2 discusses the issue of setting research priorities and the process of selecting the best science, emphasizing the need for economic analysis to enable more thoughtful decision-making. Chapters 3, 4, and 5 examine potential research and management approaches for protecting plants from the disease and for controlling the pathogen, *Xylella fastidiosa* (*Xf*) and its insect vector, the glassy-winged sharpshooter (*Homalodisca coagulata* [Say], GWSS). The remainder of Chapter 1 provides an introduction to the biology of the disease and the vector and offers estimates of the costs of their management. The chapter concludes with an overview of the organizational and institutional stakeholders who are responding to the threat of the disease and with a brief discussion of factors that could directly or indirectly influence the feasibility or effectiveness of proposed management strategies.

PIERCE'S DISEASE

In 1892, Newton B. Pierce, California's first trained plant pathologist, characterized a disease that had been called "Anaheim disease" or "mysterious vine disease" that now bears his name. PD is caused by (*Xf*), a bacterial plant pathogen. Once transmitted to a plant by an insect vector, the bacteria multiply and generate a plaquelike substance within the xylem of the plant. Ultimately, water movement is blocked, and the plant dies.

Pierce's (1892) bulletin for the U.S. Bureau of Agriculture, *The California Vine Disease*, became the first comprehensive published description of the disease, which had caused significant problems for California agriculture up to that point and has continued to do so ever since: Between 1884 and 1900, PD destroyed more than 35,000 acres of grapevines in the Los Angeles basin (Gardner and Hweitt, 194). By 1921, the disease had become endemic throughout most of the grape-growing areas of California (Hewitt, 1970). It was observed in the Napa Valley in 1887, in the Livermore area in 1888, in the Sacramento and Santa Clara valleys in 1900, and in the San Joaquin Valley in 1921. Three major epidemics occurred in the twentieth century: Between 1914 and 1918, vineyards in the Santa Clara Valley were devastated. Then, between 1935 and 1940, more than 50,000 acres of grapevines in the San Joaquin and Napa valleys were destroyed (Gardner and Wewitt, 1974). The last major epidemic occurred in the Napa Valley between 1960 and 1962.

Twentieth-century PD epidemics renewed interest in research. Throughout much of the century, PD generally was believed to be caused by a virus (Hewitt et. al., 1949) because no bacterial or fungal pathogens had been identified and because PD was known to be transmissible by grafting (Hewitt,

1939) and by insect vectors (Hewitt et al., 1942). Researchers reported that numerous xylem-feeding insects could transmit the disease (Winkler, 1949) and that at least 76 species of plants in 28 genera were hosts of the pathogen (Freitag, 1951). In 1931, Weimer recognized alfalfa dwarf disease, which later was found to be caused by the same pathogen as PD. He demonstrated that alfalfa dwarf disease was graft-transmissible (Weimer, 1936), and he reported that the most consistent microscopic characteristic of alfalfa dwarf was the presence of "bacteria-like bodies" in xylem vessels. However, because Weimer observed bacteria in 75% of diseased plants, and because his bacterial isolations and subsequent inoculations failed to reveal a pathogen, he concluded that alfalfa dwarf most likely was a viral disease (Weimer, 1931). In 1941, Hewitt and Houston reported on the association of PD and alfalfa dwarf disease in adjacent plantings. Several years later Hewitt and colleagues (1946) demonstrated by grafting and by insect transmission that PD and alfalfa dwarf were caused by the same agent.

In 1967, researchers (Doi et al., 1967; Ishie et al., 1967) reported that mycoplasma-like organisms, now known as phytoplasmas, were associated with several diseases that previously had been thought to be caused by unidentified viruses. That discovery stimulated renewed interest in the cause of numerous plant diseases of unclear etiology. In 1973 a xylem-inhabiting bacterium was described independently in Florida (Hopkins et al., 1973) and in California (Goheen et al., 1973) in association with PD. The xylem-inhabiting bacterium was described as "rickettsia-like" because of its small size, susceptibility to tetracycline antibiotics, peculiarly rippled cell wall, arthropod transmission, and apparent obligate parasitism (Hopkins, 1977). Because the bacteria were not readily cultured on conventional media, light and electron microscopy were used to reveal their existence in plants. That finding dispelled the assumption that a virus caused PD, but it did not entirely solve the mystery surrounding the etiology of the disease. Auger and colleagues (1974) reported isolation in culture of the bacterium associated with PD; the bacterium was later classified as *Lactobacillus hordniae* (Latorre-Guzman et al., 1977). Purcell and colleagues (1977) later determined that *L. hordniae* was not the cause of PD, but that it is commonly associated with an insect vector of PD (Purcell et al., 1977).

Davis (1978) isolated the bacterium subsequently named *Xylella fastidiosa* (Wells et al., 1987) from grapevines with PD and conclusively proved that the *Xf* bacterium caused the disease. The PD bacterium was the first of numerous fastidious xylem-inhabiting bacteria to be isolated in special culture media that supports in vitro growth. Since that initial success, most of the known fastidious xylem-inhabiting bacteria have been cultured on the same or similar media derived from that media developed by Davis and colleagues, and in most cases the role of the bacteria as plant pathogens has been confirmed (Davis, 1991). Among the bacteria are numerous strains of *Xf* that cause "emergent" plant diseases (Hopkins and Purcell, 2002) (Table 1-1). Several of those diseases are found commonly from central Florida to the area near the Gulf of Mexico and the coastal plain of Georgia and South Carolina.

Table 1-1 Plant Diseases Caused by Different Strains of *Xylella fastidiosa*

Host plant	Strain and Disease	Reference
Almond (*Prunus dulcis*)	Almond leaf scorch disease	Davis et al., 1980; Goheen et al., 1973
Alfalfa (*Medicago sativa*)	Alfalfa dwarf disease	Mircetich et al., 1976; Thomson et al., 1978
Peach (*Prunus persica*)	Phony disease of peach	Davis et al., 1981; Hopkins et al., 1973; Goheen et al., 1973; Wells et al., 1981, 1983
Plum (*Prunus domestica*)	Plum leaf scald disease	French et al., 1978; Kitajima et al., 1975; Raju et al., 1982; Wells et al., 1981
Elm (*Ulmus americana*)	Elm leaf scorch disease	Hearon et al., 1980; Kostka et al., 1984; 1986a
Mulberry (*Morus rubra*)	Mulberry leaf scorch disease	Kostka et al., 1986b
Oak (*Quercus* spp.)	Oak leaf scorch disease	Chang and Walker, 1988; Hearon et al., 1980; Kostka et al., 1984
Periwinkle (*Littorina vinca minor*)	Periwinkle wilt disease	Davis et al., 1983; McCoy et al., 1978
Ragweed (*Ambrosia trifida*)	Ragweed stunt disease	Timmer et al., 1981
Red maple (*Acer rubrum*)	Leaf scorch of red maple	Sherald et al., 1987
Sycamore (*Platanus occidentalis*)	Sycamore leaf scorch disease	Hearon et al., 1980; Sherald et al., 1983
Oleander (*Nerium oleander*)	Oleander leaf scorch	Purcell et al., 1999
Coffee (*Coffea* spp.)	Coffee leaf scorch	De Lima et al., 1998
Citrus (*Citrus aurantium*)	Citrus variegated chlorosis	Chang et al., 1993; Hartung et al., 1994
Grape (*Vitis vinifera*)	Pierce's disease	Davis et al., 1978; Goheen et al., 1973; Hopkins et al., 1973

Xylella fastidiosa is a Gram-negative bacterium—it contains a unit membrane as the surface of the cell wall—and the only species within the genus (Wells et al., 1987). A high degree of DNA homology sequence identity (75%–

100%) exists between pathologically different strains of *Xf*, suggesting that the strains are indistinguishable at the species level (Kamper et al., 1985; Wells et al., 1987). Less than 5% DNA homology sequence identity was found between those strains and other strains representing different genera containing phytopathogenic bacteria and other Gram-negative bacteria. Phylogenetic analysis based on sequences of the 16S rRNA gene and the intergenic spacer region between the 16S and 23S rRNA genes indicates that—with the possible exception of one pear strain from Taiwan—*Xf* is a homogeneous species (Mehta and Rosata, 2001). Similarity and signature analysis of 16S rRNA sequences indicate that strains of *Xf* are most closely related to xanthomonads (Wells et al., 1987). Similar conclusions were drawn from phylogenetic analyses of DNA sequences (Mehta and Rosata, 2001).

Although strains of *Xf* that cause PD in grapevines can colonize members of at least 28 families of monocotyledonous plants, recognizable disease symptoms are produced in only a few of those plants (Freitag, 1951; Hopkins and Adlerz, 1988; Raju et al., 1980, 1983). But Hopkins (1989) speculates that the list of natural hosts of all strains of *Xf* probably is limited more by the effort spent looking for other hosts than by the host specificity of the bacterium.

Symptoms of PD in plants such as grape typically vary by season—most notably from spring to fall. Older leaves will exhibit non-uniform, often interveinal, chlorosis and then necrosis that usually starts at the leaf margins; the leaves turn yellow and then die. Fruit shrivels, and non-uniform wood maturity has been observed on grapevine canes. After winter dormancy in infected plants, delayed and stunted growth is exhibited in spring, as is erratic bud break, the emergence of smaller leaves, and chlorosis (American Vineyard, 2001).

The appearance and severity of PD also varies with geography and regional factors such as climate contribute to proliferation. In the southeastern United States, for example, the occurrence of PD among wine grapes (*Vitis vinifera*) was so great and widespread that it always has been impractical to grow this crop in states of the Gulf Coastal Plains. The disease therefore has not been studied in that region, and no serious epidemiologic analysis of PD has been carried out in those states (Hopkins and Purcell, 2002). In contrast, the Mid-Atlantic states are experiencing only limited problems with PD; certainly not to the extent as found in Florida or Southern California.

How, then, has the climate of the Gulf Plains states (particularly Florida) provided favorable conditions for PD? In Northern California and Virginia the disease has yet to proliferate. Evenings are cooler in Northern California and in Virginia than they are in Florida. More rain falls each year in Florida, and precipitation follows a different pattern in Florida than in California or Virginia. The Florida growing season is notably longer than is that of the other two states, so favorable conditions for *Xf* last longer and it more likely to that persistent infection will be established host plants. Hopkins and Purcell (2002) reported that "The only feasible control for PD in the southeastern United States … is genetically controlled plant resistance to *X. fastidiosa*." An alternative to *V. vinifera* in the southeast is the natural muscadine grape (*V.*

rotundifol Michx). Although not well suited for winemaking, muscadine grapes are highly resistant to PD, and therefore have been grown as a (table) fruit in the southeastern United States for some time (Loomis, 1958). Thus far, alternatives to host plant resistance—such as control of the insect vector for PD—have not been successful at stopping the spread of the disease in that region (Hewitt, 1970; Hopkins and Purcell, 2002).

Other states along the East Coast, including Virginia, are experiencing PD although not to the same extent as found in Southern California. The disease thus far, has been confirmed along the Eastern Shore of Virginia (in the Delmarva Peninsula and in Tidewater), but there is considerable uncertainty about the distribution of insect vectors throughout the state (Pfeiffer, 2002). Unlike the movement of PD in California, where the disease typically spreads from outside vegetation into vineyards (University of California, 2000), in the Southeast and the Mid-Atlantic, PD is more likely to spread by leafhoppers feeding *between* vines. Thus far, in the Eastern wine-producing states—such as Virginia—multifaceted approaches including integrated pest management (IPM), have been used to control the spread of PD and a variety of vectors, including leafhoppers (Pfeiffer, 2002).

Much attention has been given to the general absence of vine-to-vine transmission of PD in California vineyards, although a transmission has been demonstrated in the laboratory (Purcell and Finlay, 1979). Such variables as environmental conditions and exposure time (the amount of time an insect vector spends feeding on a PD-infected plant, or the length of the season) also influence whether a pathogen will become established and spread from vine to vine. Purcell and Saunders (1999) note that "most PD strains do not move systemically in most symptomless [*sic*] hosts."

GLASSY-WINGED SHARPSHOOTER

The glassy-winged sharpshooter (GWSS; *Homalodisca coagulata* [Say]) is a relatively new insect pest in California agriculture. It was introduced into the southern part of the state most likely through nursery plants transported from the southeastern United States (Cavanaugh, 1999). It is the primary vector of *Xf* in peach (it transmits phony peach disease; T.M.Perring et al., 2001) and grape in Georgia, Florida, and other southern states. A leafhopper (family Cicadellidae; sharpshooters are of the Cicadellinae subfamily), GWSS has been observed in high numbers in citrus along the of Southern California coast since the early 1990s. It is a close relative of the native smoke tree sharpshooter (*H. lacerta* [Fowler])—a pest also found in southern California. The leafhopper was identified as common to the southeastern states from Florida through eastern Texas, occurring as far north as Missouri. Early wine grape infestations of GWSS were noticed in 1996 in a chardonnay vineyard in Temecula Valley. The insect itself was discovered around 1989 on eucalyptus windbreaks in Ventura County and at a lemon grove near Santa Paula (Cavanaugh, 1999; Sorenson and Gill, 1996).

Over the past few years, GWSS has become locally abundant further inland in California, in Riverside and San Diego counties (Figure 1-1). Since the discovery of GWSS in the state, its abundance and distribution have increased. It can now can be found in Riverside County, and in areas of San Diego, Orange, San Bernardino, Los Angeles, Ventura, Santa Barbara, and Kern counties. Its range is continuing to spread northward, and recently it has been found in the San Joaquin Valley. In 1998 and 1999, high populations on citrus and adjacent vineyards were observed in southern Kern County. That county has been the site of a locally successful pilot program to control GWSS. GWSS is expected to spread north into the Central Valley citrus belt, and it could become a permanent part of various habitats throughout northern California.


Distribution of GWSS in California

California Department of
Food & Agriculture
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FIGURE 1-1 GWSS Distribution in California

Several biological and cultural factors influence the spread and the effects of GWSS in California. Although it is active throughout each season (Blua et al., 1999) and has two generations per year (Blua et al., 2001), cooler temperatures seem to keep populations down (Morgan and Brennan, 2002). GWSS is larger and flies farther than other sharpshooters—such as the native blue-green sharpshooter (BGSS; *graphocephala atropunctata [Signoret]*)—it presents a far greater threat to agricultural plants than do its relatives. The greater dispersal, longevity, and fecundity of GWSS relative to native sharpshooters are the primary causes of increased vectoring potential of PD. Moreover, it can fly as much as 4–5 m above the ground (Larsen, 2000a), so ground-based trapping is difficult. Unlike the native BGSS which feeds on young foliage, the larger GWSS can feed on basal, woody segments of stems, below the point at which annual pruning is done (Almeida and Purcell, 2003). This increases the probability that *Xf* infection will persist and spread systemically within the plant, rather than remaining peripheral where it might be pruned out or die out otherwise during winter. Late season (after May–June) infections introduced by GWSS are more likely to persist and become chronic than are those introduced by native sharpshooters. The ability of GWSS to feed on many different plant species also has important implications for *Xf* disease transmission. The CDFA Pierce's Disease Control Program web site (www.cdfa.ca.gov/phpps/pdcp) lists more than 200 genera on which GWSS feeds, and it, and can consume as much as 10 times its body weight for each hour of feeding on plant xylem fluids (University of California Riverside, 2003). Thus, GWSS has numerous opportunities and great capacity for obtaining and transmitting *Xf*.

Once insects begin to transmit the pathogen, the effects are progressive. Affected grapevines typically die within 1 or 2 years after infestation, and younger vines are especially susceptible. Purcell (1975) reported that the early-season distribution and infectivity of the BGSS sharpshooter in the Napa Valley coincided with the pattern of PD. Infection typically begins in April and May, when young shoots are susceptible (Adlerz and Hopkins, 1979). Left unchecked, *Xf* infestations carried by the BGSS typically spread at an annual rate of one-sixth of one percent of the total area of a vineyard. (Clarke, 2000). Adult sharpshooters that feed on plants infected by *Xf* transmit it to other plants, when the bacteria adhere to surfaces in their foreguts (Meadows, 2001). Chronic infections are likely to influence the epidemiology of PD in California, particularly by increasing the frequency of vine-to-vine spread of the disease by leafhoppers. Vine-to-vine spread is expected to result in an exponential—rather than linear—increase in the incidence of PD (Hashim, 2001).

COSTS OF PIERCE'S DISEASE

Relatively little in the literature discusses the economics of PD; only two reports have been published. The first is the work of Siebert (2001) on quantifying the economic effects of PD for wine grape growers; the second is a more specific study by Brown and colleagues (2002) on barrier crops for inhibiting GWSS movement. Drawing particularly on Siebert's work, this section presents information related to grape growers' costs attributable to PD, potential economic effects for citrus and almond production, and statewide costs of managing PD and GWSS.

Costs to Growers

Pierce's disease is expensive for grape growers, although the costs of production, income loss, and removal and replanting vary by location, grape variety, and vineyard age. Grower-added costs include removing and replanting parts of or entire vineyards; enhanced vineyard production management, including monitoring, replacement of diseased vines, and training new growth; vector management, including monitoring and application of vector controls such as pesticides; and GWSS host plant and riparian area management.

Siebert (2001) developed hypothetical estimates of income lost to PD for a wine grape vineyard over a 5-year period (Table 1-2). That scenario depicts a vineyard so infested with PD that it must be completely replanted. Of course, replacement of a vineyard involves more than just replanting; it also entails lost yield and revenue. As Siebert (2001) notes, the estimated income loss to grape growers also could affect other aspects of California's economy, such as employment and regional and state income, although those costs are not likely to have a large statewide effect.

Siebert's (2001) hypothetical example uses the costs for a Sonoma chardonnay vineyard (Table 1-2), and it assumes that the vineyard will suffer a 50 % loss in yield in the year before the vines are removed. Also assumed is a 7 ton/acre yield at the vineyard's maturity and a price of $1,060/ton. The establishment of a new vineyard—as shown in Table 1-2—would cost $13,369, amortized over 22 years; the annual cost would be $1,227.

Table 1-2 Hypothetical Cost and Revenue Scenario of Vineyard Replacement

	Year 0	Year 1	Year 2	Year 3	Year 4
Yield (tons/acre)	3.5	0	0	3	7
Revenue	$3,710	0	0	$3,180	$7,420
Revenue without PD	$7,420	$7,420	$7,420	$7,420	$7,420
Revenue difference	–$3,710	–$7,420	–$7,420	–$4,420	0
Replant cost		–$1,227	–$1,227	–$1,227	–$1,227

Source: Siebert, 2001

Table 1-3 estimates the cost of replanting a small percentage of the infected vines in a vineyard, by region and by grape variety (Siebert, 2001). The last two columns of the table present the cost of replanting a percentage of the

Table 1-3 Estimated Vineyard Establishment and Replanting Cost

Area, Variety	Variety	Established Cost/Acre	Cost/Vine	Amortized Cost/Acre	Vines/Acre	Replanting Cost	Vines Replanted
San Joaquin Valley	Wine	$4,105	$7.27	$621	565	$18	2%
Lodi	Cabernet	$5,949	$9.56	$381	622	$3	2%
Sierra Nevada	Zinfandel	$10,173	$17.22	$1,013	622	$105	5%
Sonoma	Chardonnay	$13,369	$14.72	$1,227	908	$103	4%
Lake	Sauvignon blanc	$8,640	$15.27	$834	566	$47	2%
Santa Maria	Chardonnay	$11,985	$11.01	$736	1,089	$256	5%
San Luis Obispo	Cabernet sauvignon	$9,526	$10.94	$585	871	$64	2%
San Joaquin Valley	Thompson seedless	$3,839	$7.40	$378	519	$22	5%

SOURCE: Siebert, 2001

vines in a vineyard; hence, for the San Joaquin Valley wine estimates, the cost is $18/acre to replant 2% of the vineyard. In this case, the cost reflects replanting 2% of 565 vines/acre, or approximately 11 vines/acre.

In addition to the costs that are directly attributable to PD, grape production costs can involve controlling GWSS as a vector. Pest monitoring must be implemented, and that could involve the placement of traps or sweeping the edges of a vineyard with a net to quantify GWSS infestations. Economic information on the density and number of traps to be used and on the labor costs of monitoring are not available.

Three pesticides generally are used in IPM programs for controlling sharpshooters. The formulations are chosen for their usefulness and efficacy on natural enemies. The first is imidacloprid (75% active ingredient [a.i.]), a foliar product that provides rapidly but short-term control (14 days). Imidacloprid is applied a rate of 0.75 oz/acre, but its use is limited to 2 oz/acre annually. The product costs $32 per ounce; so the cost per application is about $44/acre, assuming $20 to apply it. Another alternative is imidacloprid (21.4% a.i.) applied through an irrigation drip system at a rate of 16 oz/acre. The cost is $4.80/oz or $76.80/acre for one application. The third material is dimethoate, which is suggested for control of BGSS in coastal areas. Dimethoate is under a special-needs registration and no cost data are available (Siebert, 2001).

Aggregate estimates of grower costs attributable to PD will depend on the spread of the disease. So far, there has been little investment in identifying the full current or potential economic costs of the disease to California agriculture or the state's and economy. Although there are many host species that harbor GWSS, observations in Temecula, California, vineyards that are close to citrus groves show that vineyards are at greatest risk. Table 1-4 shows grape and citrus acreage by California county in 2001. The southern San Joaquin Valley has significant acreage in citrus in close proximity to vineyards. Vineyards in the rest of California would likely be likely to experience PD according to the presence of other habitats that harbor the vector, such as riparian areas.

Considerable uncertainty exists about the potential for PD to spread significantly more than it has in the past. For example it is not known whether GWSS can survive in the cooler Northern California vineyards

Potential Economic Effects on Almond and Citrus

According to information reported to the committee, almond leaf scorch (a disease caused by *Xf)* has been identified in almond orchards; although neither BGSS nor GWSS has been identified as the vector. A concern is that another, as-yet-unidentified vector is contributing to the spread of almond leaf scorch (Gleeson et al., 2004). Almond growers have observed the spread of PD and worry about its implications for their crops.

Management of almond leaf scorch consists of pruning the affected parts of the trees, and the economic consequences of the disease result from the increased pruning costs. Pruning a mature almond orchard currently costs about

Table 1-4 Grape Acreage by End Use, Citrus Acreage, Almond Acreage in California Counties, 2001

County	Raisins	Table Grapes	Wine Grapes	Citrus	Almond
Alameda	0	0	1,627	0	0
Amador	0	0	2,728	0	0
Butte	1	18	159	130	37,613
Calaveras	0	0	491	0	25
Colusa	0	0	1,350	0	22,138
Contra Costa	3	0	1,550	0	10
El Dorado	0	0	1,238	0	
Fresno	173,271	11,826	47,241	31,126	65,994
Glenn	0	0	1,748	570	29,390
Humboldt	0	0	10	0	0
Imperial	0	273	0	3,179	0
Kern	25,316	33,003	31,845	44,987	92,989
Kings	1,391	832	2,408	0	2,967
Lake	0	14	7,147	0	1
Los Angeles	0	0	75	0	0
Madera	44,248	3,017	47,787	4,745	51,153
Marin	0	0	87	0	0
Mariposa	0	0	57	0	0
Mendocino	0	2	16,008	0	0
Merced	1,339	149	13,962	0	85,734
Monterey	0	1	41,154	1,022	0
Napa	0	1	42,929	0	0
Nevada	0	1	350	0	0
Placer	0	1	91	0	40
Riverside	2,695	10,872	1,894	23,200	7
Sacramento	0	0	16,808	0	124
San Benito	0	0	3,440	0	1
San Bernardino	179	563	1,114	4,772	50

continues

Table 1-4 *(continued)*

San Diego	0	2	69	11,635	0
San Joaquin	54	1,827	66,583	0	33,818
San Luis Obispo	66	135	22,826	1,700	1,310
San Mateo	0	0	49	0	0
Santa Barbara	0	2	17,519	1,542	0
Santa Clara	0	0	1,500	0	3
Santa Cruz	0	2	276	0	0
Shasta	0	0	33	0	1
Solano	25	3	2,923	0	1,211
Sonoma	0	2	56,360	0	0
Stanislaus	583	39	13,972	0	81,119
Sutter	3	0	80	0	2,929
Tehama	1	8	129	0	7,413
Trinity	0	0	133	0	n/a
Tulare	29,323	26,767	13,182	100,356	11,600
Ventura	0	0	9	34,486	0
Yolo	0	12	8,394	110	5,465
Yuba	0	0	246	0	962
State Total	278,498	89,377	48,9579	254,595	53,4067

SOURCE: California Agricultural Statistics Service, California Grape Acreage Report, 2001.

$40/acre (University of California Cooperative Extension, 2001). Almond pruning is done to promote tree balance for wind tolerance, to stiffen main limbs, to manage light for increased productivity, and to limit alternate bearing—the tendency of some perennial crops, such as almonds, to exhibit intrinsic yield variability. California almond acreage is listed in Table 1-4.

The cost of GWSS infestation of citrus orchards has not been estimated. One possible expense is the cost of additional water necessitated by the presence of GWSS; however, estimates are unavailable. California citrus acreage is listed in Table 1-4. The data hint at the economic costs of PD, but they are insufficient to delineate the dimensions of the problem or inform the evaluation of solutions. That reality points to the immediate need for additional economics studies.

RESPONSE TO PIERCE'S DISEASE AND THE GLASSY-WINGED SHARPSHOOTER

During the summer of 1999, William J. Lyons Jr., who was secretary of CDFA, oversaw the creation of a task force to address the threat of GWSS. This culminated in the Pierce's Disease Advisory Task Force, which counsels the Pierce's Disease Control Program (CDFA, 2002a). In the spring of 2001, California Assembly member Patricia Wiggins (D-Santa Rosa) introduced legislation to raise $25 million for GWSS research. Her bill (Assembly Bill, or AB, 1394) proposed to secure $5 million annually for a period of 5 years. That funding would be obtained through an industry self-assessment on grapes grown for processing; producers would be charged a maximum of $3/$1,000 value of final purchase price. Moreover, AB 1394 would establish a PD/GWSS Board, which would collect the annual assessments. The bill also would allocate funds for research on IPM and other sustainable insect control practices. The law was to expire January 1, 2006, if not renewed. During the fall of 2001, the bill was signed into law by Governor Gray Davis, and it took effect immediately (State of California, 2001). An additional, $14 million was earmarked in the federal fiscal year 2002 agriculture appropriations bill for PD–GWSS research, to be divided between a U.S. Department of Agriculture–Agricultural Research Service (USDA–ARS) facility in Parlier, California; several state university research centers; and the USDA Animal and Plant Health Inspection Service (USDA–APHIS). The assessment on the grape growers' profits subsequently was lowered to $2/$1,000 value (CDFA, 2002c).

Diverse Community of Stakeholders

A sophisticated community of stakeholders is involved in scientific, policy, industry, and agricultural responses to the threat presented by PD in California: local growers, nongovernmental organizations (NGOs), CDFA administrators, research scientists from the University of California (UC) and CDFA, and USDA–ARS and USDA–APHIS investigators. The affected industries, however, are not homogeneous in their perspectives on and approaches to the various agricultural, environmental, and economic problems caused by PD. Given the nature of the recent GWSS-mediated outbreak of PD in California, a list of research needs has emerged from the exchange of information and data among local growers, county officials, state officials, and academic researchers. Research on PD is coordinated broadly through the Pierce's Disease Control Program [Figure 1-2]—an alliance consisting of CDFA, the agricultural commissioners of the various counties involved, researchers in the UC system and USDA, various state and local agencies, and several California agricultural organizations (CDFA, 2002a).

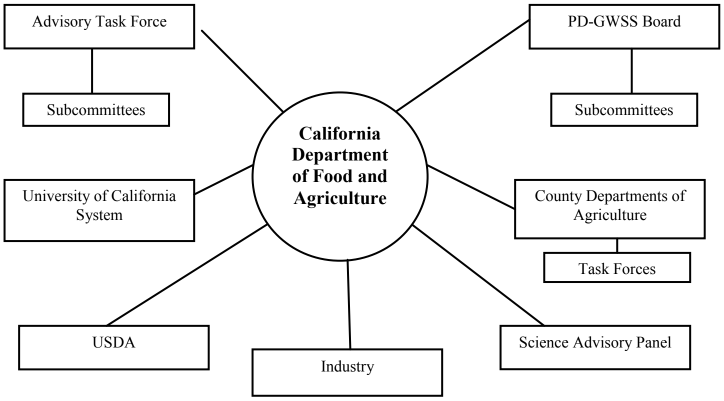

FIGURE 1-2 Research Coordination through the Pierce's Disease Control Program.
SOURCE: Adapted from CDFA, 2002a

California Department of Food and Agriculture

The California Department of Food and Agriculture coordinates research on PD. Its Advisory Task Force on Pierce's Disease and that task force's subcommittees assist in planning long-term research agendas and in identifying viable funding sources. The PD/GWSS Board and its subcommittees assist in the solicitation of new research projects, and in the scrutiny of funded projects. Members of the task force, the PD/GWSS Board, and their subcommittees serve as appointees; the California legislation (AB 1232 and AB 1394,[1] respectively) that established those entities does specify term lengths. A science advisory panel of six experts advises CDFA on technical matters, such as trapping and other techniques, for responding to PD–GWSS. Each year, the Pierce's Disease Control Program submits a report to the legislature that details the condition of the program and of the problem. The work of funded, continuing research projects for the Pierce's Disease Control Program culminates in an annual Pierce's Disease Program Research Symposium, where researchers and investigators present preliminary findings or data. Abstracts of that work are compiled and published in a set of proceedings that is available online to the public (CDFA, 2002b).

University of California System

Many researchers within the UC system are studying PD and GWSS. Because those investigators are familiar with the California agricultural landscape and because of their proximity to active PD–GWSS infestations and

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[1] AB 1394 was amended by AB 2890 in September 2002.

experimental sites and their access to the university system's resources and experts, the UC system has become very involved in the Pierce's Disease Control Program. But research on PD is by no means limited to the UC system. Many other researchers across the country (notably in the Southeast) are conducting high-quality, relevant work on the disease, its vectors, or other aspects of the problem that can be applied to the collective understanding of PD–GWSS. Some of those investigators receive support from the Pierce's Disease Control Program.

U.S. Department of Agriculture

The U.S. Department of Agriculture works with institutions, including the UC system, on the challenges created by PD–GWSS. Through ARS, USDA conducts investigations on PD–GWSS, using, for example, scientists, university researchers and other experts who work in the Cooperative Extension. ARS—the internal biological-research unit of USDA—is distributed among various facilities throughout the United States. Its San Joaquin Valley Agricultural Sciences facility in Parlier, California is considered USDA's headquarters for PD research. The Exotic and Invasive Diseases and Pests program was created at this facility and is overseen by a research leader. Updates and news concerning the facility are available from its Web site (USDA–ARS, 2002). USDA–APHIS also has been assessing the PD–GWSS problem in California, through surveys to assist CDFA in mapping GWSS movement throughout the state (USDA-APHIS, 2002).

County Departments of Agriculture

In light of the uneven distribution of PD and GWSS throughout California, the state relies heavily on county-administered programs to monitor and manage the problem. Given the dynamics of PD–GWSS infestation, county departments of agriculture implement programs and apply experimental techniques based on specific needs, many of which are determined by the production and flow of agricultural commodities within and across political boundaries. Thus, the counties are important stakeholders in coordinating responses to PD–GWSS. The counties also provide a central point of contact for government, university researchers, producers, and other counties. In Kern County, for example, Cooperative Extension specialists, CDFA, industry, and other associations of producers have converged to address GWSS management and control (University of California Cooperative Extension, 2003b). Kern and Tulare counties have created a Kern–Tulare GWSS Task Force.

Industry

Several California agricultural commodities are affected by PD–GWSS. Although the table grape and wine industries are most threatened they are by no means the only industries at risk. Almond, alfalfa, citrus, oleander, are among other plants affected by GWSS (see Table 1-1). Nor is there a single industry perspective on how to respond to the problem (see Box 1-1). There are many viewpoints about how the disease and its vector should be treated. Some perspectives are based on geography: Grape growers in Southern California—especially in areas affected most by PD, such as Temecula Valley—perceive the problem as being one of greater severity than do some growers in the north, where PD has not been established by GWSS. However, other growers from the north might perceive the appearance of PD in the south as an indication of an impending threat because of expansion of GWSS host range, thus calling for the application of resources and attention to managing what could be an eventual emergence of the disease in the north.

There are several industry perspectives concerning the breadth and quality of existing research programs on PD–GWSS. Some manifest themselves in the positions taken by agricultural associations (the Almond Board of California, the American Vineyard Foundation). In one respect, there is unity among industry representatives: Many of them acknowledge the significant improvement in basic and applied research over the past 5 years, noting that a concerted public- and private-sector research effort largely was missing until

BOX 1-1
Who Should Implement Control Strategies?

The diversity of California's agricultural landscape makes it difficult to place the perspectives of commodity producers into a single "industry" viewpoint. The agricultural threat created by PD–GWSS highlights the point. In its consultation with various representatives of industry, the committee learned of potentially growing frustrations among representatives of various industries, such as growers and nursery operators. The frustrations have emerged from questions about who should be held accountable and who should be responsible for implementing strategies for managing GWSS populations. Should individual nurseries bear prime responsibility for ensuring that their ornamental plants are GWSS- or pathogen-free? If so, how should the assortment of costs associated with implementing various strategies be shared? Should the responsibility of implementing management strategies be delegated more evenly throughout industry to lessen the tremendous burden placed on nursery owners who must serve as the first line of GWSS or pathogen screening? If so, how?

then (unpublished data submitted to committee, 2002). Industry representatives also must contend with the temporal element of responding to emerging pest problems. There is understandable frustration in the fact that the knowledge that is provided by research and that is needed for sustainable solutions lags behind the perceived need to solve the problem immediately. There is also a perception among some industry representatives that returns on their investments in research and management of PD–GWSS are marginal.

Another area of concern is related to the transparency of communication between researchers and the lay community. Industry is positioned to act on research recommendations for responding to PD–GWSS, so there is concern that the often highly technical nature of research projects will make it difficult to implement new management strategies. Another difficulty faced by industry is the call for widespread replanting of affected crops—an expense that growers want to avoid, given the time that it takes for plants to yield fruit. According to one industry representative, replanting is occurring at a fraction of the rate needed to replenish the acreage so far affected by PD. Mature vineyards are also popular among tourist attractions and tourism is a significant source of revenue for the wine industry.

Nongovernmental Organizations

The group of NGOs that has responded to the PD–GWSS threat is heterogeneous. Agricultural commodity groups, such as commodity boards, could be classified as NGOs, despite their affinity for industry objectives. Environmental watchdog groups also qualify as actors in the response to PD–GWSS, and many in those organizations are concerned about aerial spraying of pesticides. In 2000, the Northern California River Watch threatened to sue growers who used aerial sprays to control GWSS (CAWG, 2000), and in 2003, a coalition of NGOs filed suit in California Superior Court in defense of greater measures for protecting the environment and against the use of pesticides for managing GWSS (CATS, 2003).

OVERVIEW OF APPROACHES

The spread of PD–GWSS has elicited multifaceted responses. There is no exclusive, comprehensive means by which the spread of PD–GWSS can be inhibited. Some experts emphasize the need to focus on one element, the insect vector, the disease, the host plant; others would incorporate several techniques and strategies to respond to the problem (Meadows, 2001). Although long-term, advanced research on PD has given primacy to the development of grapevines that have improved disease resistance, several immediate management strategies are emerging or are being implemented. The use of the term "management," in contrast to "control" is deliberate. There are distinct philosophical and practical differences between the two concepts.

Quarantine

The state of California classifies GWSS as a Category B pest, so individual counties can implement controls or quarantine measures on agricultural products that are found to harbor the insect. (Category A pests must be eradicated wherever found; Category C pests do not warrant immediate action.) More than 10 counties in California have instituted the Blue Tag protocol, which requires the return of the entire shipment of plants (ornamentals, for example) to the place of origin if the plants are found to carry GWSS. It is permissible, however, to send shipments to counties that have not yet adopted the protocol (Cavanaugh, 2000). GWSS has settled into various settings, including farmland and urban areas. When GWSS egg masses are found on the rinds of citrus fruits, the fruits no longer are marketable. Consequently, some representatives of industry have expressed interest in seeing GWSS upgraded to Category A (Meadows, 2001).

Treatment at the Nursery

More than half of California's nurseries are in counties where GWSS infestations have been found, most commonly as egg masses on nursery stock (CDFA, 2002a). Because some nurseries ship their stock to counties that are not infested with GWSS, the importance of having nurseries monitor for and treat GWSS infestation is significant. Surveys entail setting traps at retail and wholesale nurseries and treatment commonly involves the application of ovicides or other chemical compounds to kill sharpshooter egg masses. Although chemical pesticides do not provide a comprehensive approach to treating sharpshooters that have infested nursery stock, it is suspected that older insects are more vulnerable to them (Akey et al., 2001). Current California law requires preshipment inspection of nursery stock that is to be shipped from an infested area to an uninfested one. Nurseries that receive stock must be notified to hold it for inspection (CDFA, 2002a).

Biological Control: Parasitoid Wasps

In September 2000, it was announced that a parasitoid wasp from Mexico (*Gonatocerus triguttatus* Girault) would be released in Fresno, Kings, and Tulare counties to control GWSS populations. This method of biological control (see Chapter 3) is being explored further with the parasitoid wasp *G. ashmeadi* Girault, which is lethal to sharpshooters that hatch during the summer. A wasp oviposition (egg laying) rate on the sharpshooters of about 90% effectiveness has been recorded. Unfortunately, the oviposition rates are much lower on sharpshooters that hatch during spring (Larsen, 2000a), the first generation of the season. The number of spring-hatching sharpshooters influences the number of sharpshooters in subsequent generations and thus their effects on vineyards and orchards.

Vegetation Management

Removing plants that serve as sharpshooter hosts outside of vineyards could help disrupt GWSS populations and thereby reduce the number of insects feeding on vines. However, when those plants are removed, many growers have replanted them, thereby introducing new host plants because many of those plants also are habitat for beneficial insect species and other wildlife. Border "trap crops" have been planted around vineyards to create protective buffers (University of California, 2000). It now is quite apparent that the distance between the insect vector and its host plant is crucial to managing the spread of PD. As Purcell and Saunders (1999) noted, along the California coast, PD generally is highest on the outskirts of vineyards "adjacent to riparian habitats that harbor overwintering vector populations". Because GWSS flies relatively low (typically below 15 ft. above the ground; Larsen, 2000a), some growers place barriers (mesh screens with sticky traps) between GWSS habitats such as orange groves and their feeding areas (vineyards). Nevertheless, without a better understanding of spatial relationships between vineyards and sharpshooter reproductive-breeding grounds, such as citrus groves, it will not be possible to prevent PD simply by adopting management practices "within a single vineyard" (T.M. Perring et al., 2001).

Other Pesticides and Insecticides

In addition to potential chemical treatments used against sharpshooter egg masses other pesticides and insecticides for managing GWSS populations are being tested or are in use (Akey et al., 2001; Extension Toxicology Network, 2003). However, no single pesticide or insecticide can solve the PD problem. For example, Provado kills the sharpshooter, but not quickly enough to prevent transmission of *Xf* to grapevines. The amount of time it takes an insecticide to inhibit the sharpshooter is pivotal to its effectiveness (the optimal situation would be one in which sharpshooters are killed before they can transmit *Xf*; USDA–ARS, 2001). Growers who apply pesticidal chemical formulations often look for products that offer long-term effectiveness, so as to increase the amount of time between chemical treatments and thereby to decrease the cost because fewer applications are required.

The use of pesticides does not constitute a comprehensive strategy for responding to the threat of PD–GWSS. Often, an area must be sprayed more than once, because the sprays do not kill sharpshooter egg masses. Spraying tends to offer local results, but not much widespread success (Larsen, 2000b). Spaying does not constitute a means of eradicating GWSS—and it is not known whether eradication can be achieved. Moreover, the acceptability of continual pesticide applications has social, environmental, and human health implications. If pesticide compounds are to be used in an environmentally safe way, they must be deployed within the context of IPM strategies (Akey et al., 2001).

Genetic and Genomic Strategies: Management Tools of the Future?

The genetic approach to controlling PD–GWSS will be a long-term endeavor. Muscadine grapes, which are native to the Southeastern United States are resistant to PD, but they are not well suited for winemaking. Scientists are exploring the possibility of transferring the genes that confer resistance in muscadine grapes to wine grapes. This is a goal of long-term research that targets PD (Cavanaugh, 1999). Some genetic studies of *Xf* have focused on the diverse strains of the bacterium with the goal of preventing the emergence of new *Xylella*-based diseases. As Chen and colleagues (2002) noted, inhibiting the development of new *Xylella*-based diseases calls for an understanding of how strains of the bacteria "select their hosts, and their ecological roles in the native vegetation." Those researchers point out that the strains of *Xf* that have been studied carefully are from "economically important hosts," but strains from less important hosts could become reserves for the onset of new diseases (Chen et al., 2002). Hence, the less well known strains merit greater attention.

Over the past few years, genomic analyses of *Xylella* strains have received a good deal of attention from the scientific community. The availability of completely sequenced genomes of more than one strain of *Xf* (Simpson et al., 2000; Van Sluys et al., 2003) and the development of microarrays (de Oliveira et al., 2002) provide the means to identify the genes involved in transmission, pathogenicity, and survival. In 2000, Simpson and colleagues reported the genome sequence of a citrus variegated chlorosis (CVC) strain of *Xf*. Recently, the completion of the genome sequencing of the Temecula PD strain of *Xf* was announced by Van Sluys and colleagues. (2003). Comparative analyses between the two *Xf* strains and among *Xf* and other sequenced plant-pathogenic bacteria reveal similarities and differences that could provide clues about the diverse biology of those bacteria (Bhattacharyya et al., 2002; da Silva et al., 2002; Van Sluys et al., 2003).

ACCEPTANCE OF MANAGEMENT STRATEGIES

It is important for all of the stakeholders involved in PD–GWSS research to consider several factors that will influence the acceptance and effectiveness of the research efforts and the management strategies that are developed for combating PD. Because of the diverse host range and dispersal abilities of GWSS, cooperation and coordination among grape, citrus, and nursery plant growers and their neighbors in rural, suburban, and urban areas will be essential for any successful strategy. Fortunately, because CDFA and the other research and regulatory entities are well aware of this need they have made considerable effort to promote cooperation. The discussion that follows highlights a few categories and a few examples of factors already identified as important.

Cultural Factors

Management strategies for PD–GWSS could influence crop production practices. Given the diversity and distribution of fruit, vegetable, tree nut, and grain production in California, any decision to pursue research that leads to new management strategies must account for those potential influences to ensure that practical management strategies result. For example, a PD–GWSS management strategy emerging from research that calls for chemical control of GWSS in citrus groves could conflict with current IPM practices for citrus, and citrus growers who are not involved in grape production might be reluctant to change their IPM practices for the sake of PD–GWSS management in grapes. Consequently, the likelihood of successful implementation of that strategy could be low unless incentives are provided or value is demonstrated to the citrus growers. One incentive for citrus growers would be the chance to reduce the amount of water used in citrus production because of the reduction in GWSS feeding. The committee was presented with evidence that GWSS infestations in citrus groves could significantly increase requirements for irrigation water and reduce the quality of fruit harvested. In view of the critical water use priorities in California, that could be a serious economic issue for citrus growers to consider.

Environmental Factors

PD–GWSS management strategies could have environmental implications that require careful consideration. A research priority that ultimately leads to areawide management of GWSS and other PD vectors by use of pesticides, for example, will likely affect IPM programs as well as the air, soil, and water where spraying takes place.

There are several formulations in evaluation that are not yet labeled for use on GWSS. Some—including most of the systemic neonicotinoids (see Chapter 3)—show considerable promise. Recent study results reported no residue of neonicotinoids in mammalian tissue, suggesting that it is safe for humans to consume grapes treated with those compounds (Tomizawa and Casida, 2003). The effect of those and other chemicals on exposed workers and in others who consume fruit or wine, and the unintended consequences relative to other plant diseases must still be determined. Grafton-Cardwell (2003) reported that applications of Surround (a finely divided inert kaolin clay) on citrus for GWSS control, also disrupted the parasitic wasps that control California red scale in citrus, resulting in an increase in scale infestation of the fruit. That finding is of particular concern because red scale infestations, left unchecked, can lead to the premature death of a citrus tree that might otherwise yield fruit for 40–80 years. Management strategies for BGSS, another PD vector, entail modification of riparian areas and other habitats where the adults reside. Such modifications include the removal of BGSS-preferred host plants. The environmental repercussions could be substantial, affecting many other species: fish, birds, mammals, and pollinating insects. Public concern about habitat modification is significant, and a legal challenge to the statewide CDFA vector management program has been brought by environmental groups (CALTOX v. CDFA, 2003). That litigation alone suggests that research-based PD management strategies must consider environmental issues and concerns.

Regulatory Factors

Because crop production practices can be influenced by PD management strategies, those that are consistent with a variety of research priorities research priorities considered in subsequent chapters of this report could require additional regulatory control. For example, orchard sanitation in citrus could be required to reduce GWSS populations to protect neighboring vineyards. In some cases, grower cooperation could meet that need, but new regulations could be required to overcome resistance from some sectors of the California agricultural community; those whose crops are not directly affected by PD but that contribute to the spread of the disease (see Box 1-1).

Several new regulations govern shipment of nursery stock and of citrus fruit from infected areas to noninfected areas in California. Those measures further limit the spread of PD. Thus, PD research priorities must admit the possibility of additional regulation.

Social Factors

Social factors are diverse and can reflect a broad set of concerns and perspectives, including some mentioned above. For example, environmental concern regarding pesticide use is greater in some communities than in others, and it can result in political pressure that leads to regulatory restrictions. The choice of chemical controls is likely to reflect human and environmental safety requirements and economic thresholds, such as the per-acre cost of pesticide application for growers. Public acceptance is never guaranteed for new formulations or procedures that can result in effects on neighboring areas through drifting sprays or movement of a compound through surface runoff or seepage into groundwater. Several studies have shown that conventional air-blast spraying and aircraft application of pesticides can result in measurable drift. The encroachment of urban development into agricultural areas means that exposure to drift often is not acceptable, and conflicts can arise between agricultural operators and their residential neighbors. That situation warrants the reduction of exposure, and it highlights the need to avoid the imposition of rules and regulations that reduce flexibility in controlling agricultural pests. It is clear that PD–GWSS research priorities must reflect awareness of the social milieu in which management strategies will be implemented.

Economic Factors

Pierce's disease is not new to California, but concern about it has increased since the introduction of GWSS (Office of the President, 1999). Clearly, the scale of the recent investment into PD–GWSS research indicates the potential economic consequences for California's agriculture and economy. Large-scale factors, such as the current supply of and demand for grapes and the resulting effects on prices, will influence the ability of the industry to respond to the threat. For individual growers and producers, options and approaches for PD–GWSS management will be influenced by perceived and actual costs, risks, and benefits. Recent trends in the market indicate an oversupply of California grapes, and that could influence the concern about yield loss attributable to PD, and dampen enthusiasm for PD–GWSS research (Murphy, 2003).

Economics is important in all aspects of the PD problem, from estimating current and future losses, to understanding how existing control strategies might be implemented most economically, to evaluating which management strategies still in development might realistically be adopted by growers and producers. One difficulty is that not much economic information has been collected on the PD problem.

2

Developing Priorities for Research

Over the past three years, nearly $20 million has been allocated to fund 125 completed and continuing research projects to address Pierce's disease (PD). Support for the projects has come from the California Department of Food and Agriculture (CDFA), the PD–GWSS [glassy-winged sharpshooter] Board, the University of California Pierce's Disease Research Grants Program, the United States Department of Agriculture–Animal and Plant Health Inspection Service (USDA–APHIS), the American Vineyard Foundation, the California Competitive Grant Program for Research in Viticulture and Enology, the California Citrus Nursery Advisory Board, the Almond Board of California, and the California Department of Transportation (Gleeson et al., 2004). The hope is that the research will produce tools and tactics for management of *Xylella fastidiosa (Xf*) and its insect vectors in the short term and to PD prevention and cure the long term (CFDA, 2004).

The research effort has yielded some progress. Successful management efforts include chemical control of GWSS populations; removal of PD-infected grapevines; and, to a lesser degree, the identification, manipulation, or removal of host plants for GWSS from the individual landscape. The research that focuses on prevention and cure has led to improved understanding of the genetics and biology of susceptible and resistant interactions between grapes (*Vitus vinifera L.*) and *Xf*.

Despite those accomplishments, however, there are numerous gaps in meeting the short- and long-term objectives. For example, it is not known whether management efforts are effective for maintaining the disease below economic thresholds, nor are there complete data on the effects of area wide management programs (Gleeson et al., 2004). The gaps in knowledge about prevention and cure are substantial. Given the short period of intense study, however, and the complexity of the challenges presented by PD, the insect vectors, the host plants, and the California agricultural landscape, those gaps are not unexpected.

Although most of projects funded over the past 3 years are only now beginning to yield results, current federal and state fiscal challenges are likely to reduce the amount of funding available for agricultural research, outreach, and management programs. That fiscal reality and the economic consequences of PD provide the context for the Committee on California Agricultural Research Priorities: Pierce's disease deliberations: the need to focus priorities for research on the biology and management of the PD–GWSS problem.

CURRENT RESEARCH

The California Department of Food and Agriculture has divided the current PD–GWSS program into nine areas of basic research (Gleeson et al., 2004):

- crop biology and ecology ($1.34 million)
- vector basic biology ($692,000)
- insect–plant interactions and vector population ecology ($1.09 million)
- genetics of *Xf* ($930,000)
- *Xf*—host plant–insect interactions ($3.2 million)
- *Xf* disease epidemiology ($1.26 million)
- vector monitoring and action thresholds ($1.38 million)
- *Xf* monitoring and action thresholds ($1.56 million)
- economics ($100,000)

The program also supports development of applied strategies for managing PD–GWSS:

- biological control of *Xf* and vector ($3.0 million)
- chemical control of *Xf* and vector ($3.68 million)
- cultural, physical, and behavioral control ($435,000)
- resistance to *Xf* diseases ($1.07 million)

Basic research accounts for just over half of the funding, with projects that examine interactions between the host, the insect vector, and the pathogen receiving the largest share. Most of the funding for applied research has been spent on studying chemical controls of the vector. Economics studies are noticeably under funded.

The collective of topics encompassed by the research program addresses the breadth of issues important in the exploration of the PD–GWSS problem. The program appears to be positioned to identify mechanisms for interfering with one or more of the interactions between the host, the vector, and the pathogen. Successful interference with any one of them could break the chain that culminates in plants succumbing to PD. By identifying particular mechanisms, researchers eventually can provide growers with tools and strategies to minimize risks or consequences of the disease in agricultural production. The concept of host–vector, vector–pathogen, and host–pathogen provided the committee with a logical way to group the research efforts. In subsequent Chapters 3, 4, and 5 of this report, the committee uses those groupings as the focus for evaluating the individual elements of the current program.

Although the PD–GWSS research agenda is broad, to most effectively address PD–GWSS, the program also should attempt to increase the odds of identifying interference mechanisms and consequent management strategies. It is important to recognize the varying pace at which information will flow from different projects and to assess the relative value and quality of information in leveraging progress from the whole of the program. Some subject areas or projects can be given more emphasis than others as the overall research progresses over time. It is also important to fund only those projects that meet the highest standards for scientific rigor. That strategic approach rests on the ability of the program to achieve significant coordination in the solicitation and selection of projects and to maintain the flexibility to shift priorities as research results provide new information.

For several reasons, including the relatively short life of the program, the research agenda seems to be the result of a loosely coordinated process. The committee had difficulty understanding the basis for or the process of priority setting. Communication among the various entities (see Figure 1-2) occurs through the overlapping of memberships of the various boards and panels. CDFA receives advice from the PD/GWSS Board about which projects to fund. That board relies on its research-screening subcommittee to solicit and evaluate new projects and to evaluate the projects already under way. The PD/GWSS Board seeks reviews and evaluates projects that are overseen by the CDFA, and there is board representation that overlaps with other entities that distribute research funds, such as the University of California Pierce’s Disease Research Grants Program and USDA–APHIS, or that are involved in PD–GWSS research, such as USDA–ARS. In addition, the Advisory Task Force on Pierce’s Disease is expected to assist CDFA in identifying viable funding sources and in planning long-term research agendas. A science advisory panel advises the Advisory Task Force on technical matters. Although coordination is attempted through the overlap of representation, interviews with experts and stakeholders familiar with the Pierces’ Disease Control Program reveal a lack of coordination among the various funding entities and the advisory groups. The result is a lack of clear communication between those bodies and CDFA, among the bodies themselves, and between the bodies and the scientists who receive research support.

The disparate priorities of stakeholders also affect strategic coordination of the program. For example, industry is searching for a solution to the commodity problem while much of the research community is still attempting to *understand* the basic biology and epidemiology of PD–GWSS. Although there are good reasons to pursue research on management options and on basic questions of biology, disjointed selection of projects could hinder opportunities to create synergies or hamper a logical progression of projects. The result could be a series of in individual, incremental successes that are inefficient from the perspective of the goals and the progress of the research enterprise as whole, particularly in the face of limited resources.

The greatest concern of the committee is that the scientific merit of the proposals is not receiving consistent scrutiny and attention. A strategic research program tries to ensure that consistently high scientific standards are applied in the review of proposals and in the evaluation of the research agenda so that the best work (and the best mix of projects) can move forward. Research proposals now are presented for consideration through multiple channels and follow different pathways to approval; there are even different methods of allocating funds once projects are approved. Depending on the pathway, proposals can receive different amounts of scrutiny and evaluation, and many proposals are reviewed more than once by the same peoples in the context of different committees associated with the program. Although that might eliminate the possibility that the same proposal would receive funding independently via different pathways, the redundancy still is inefficient and time-consuming.

So little information is available about the PD system that it makes sense to support a variety of projects, but ensuring the selection of the strongest scientific projects—those that are well conceived and that will generate reliable, useful data—is the best way to guarantee progress and the ability to intelligently focus resources on the most promising directions.

Recommendation 2.1. To ensure scientific rigor in, and enhance coordination of the PD–GWSS research program, participating research sponsors should consolidate the processes for proposal solicitation and review.

A consolidation would facilitate the identification of strategically critical projects and programmatic gaps (critical areas that are not receiving funding), avoid redundancy in the selection of research projects, eliminate overlapping processes, reduce costs, and distinguish projects for which teams or consortia should be established from those grants appropriate for one or two principal investigators. Consolidation adds uniformity and balance in determining the scientific merit of proposals. Box 2-1 explores some of the issues related to establishing high standards for proposal selection.

BOX 2-1
Ensuring High Scientific Standards in Proposal Selection

The National Institutes of Health (NIH), the National Science Foundation (NSF), and the USDA's National Research Initiative (USDA–NRI) are recognized for the rigorous processes they follow for evaluation of extramural projects and proposals. Their attention to scientific merit is considered to offer the best peer evaluation (NRC, 2003). The committee suggests the methods those groups follow as models for the PD–GWSS proposal review process.

Those agencies issue national (and sometimes international) requests for proposals, they set clear guidelines (program scope, grant length, funding, and evaluation criteria) that also clearly describe the funders' expectations for the progress required to receive continued support. Solicitations typically define and request individual and consortium (multi–investigator) types of projects based on the sponsors' visions of short-, medium-, and long-term program priorities.

To ensure the highest scientific standards, the grant programs require that those who oversee solicitation and review of proposals are distinguished scientists, free of conflicts of interest. That is, those persons are not themselves receiving support from the relevant grant program while they are involved in the review, or at a minimum, that they have no proposals under consideration in the current year. Those persons also must have experience in handling proposals, have the time to spend on the substantial work involved in proposal review, and be able to communicate effectively with principal investigators and agency sponsors. The people who oversee the review process come from the major areas of expertise relevant to the research in question. In the case of Pierce's disease, the disciplines would include entomology, ecology, economics, genetics, plant biology, plant pathology, microbiology, and molecular biology. Typically, membership in the oversight group rotates, using fixed term lengths to ensure stability and continuity and allow needed expertise and fresh perspectives to be incorporated.

Oversight groups for NIH, NSF, and USDA–NRI always recruit additional external peer reviewers, generally national and international experts, to help review the proposals. Based on the reviewers' assessments, individual proposals typically are ranked for scientific quality, cost effectiveness, and the degree to which they meet program criteria. The research sponsors (for example, different institutes within NIH) then decide which of those recommended will receive funding.

A similar process is used to determine eligibility for continued funding. Progress can be assessed through evidence of achievement of benchmarks established by a principal investigator at the beginning of the project, submission of annual reports, or publication of research reports in peer-reviewed journals—which constitutes an additional level of scrutiny. Presentations at scientific meetings can offer another means of assessing progress. The American Vineyard Foundation calculates a measure of efficiency for researchers in terms of how many results a researcher produces for each unit of resources invested. That kind of measure, however, might not consider the complexity of scientific endeavor, especially in the study of fundamental mechanisms that, once unlocked, lead to major breakthroughs in application.

EVALUATION FRAMEWORK

During the course of its work the committee established a framework that could assist CDFA in the development of its research agenda. Chapters 3, 4, and 5 use the framework to examine the current research program. If the PD program were to consolidate its processes, the proposed framework could be used as an evaluation and priority-setting tool. The framework flows from the principal that the problem of PD can and must be addressed by a range of approaches that are scientifically rigorous (regardless of whether the research is basic or applied), ecologically sound, and economically feasible and that provide sustainable solutions. The most effective response to PD is likely to emerge at the nexus of information contributed by different approaches. The framework consists of two independent evaluation criteria—feasibility and sustainability—and a system for grouping current and prospective research projects into categories that reflect differences in risk, cost, and relative effectiveness.

The first evaluation criterion assesses the ability of projects to produce applications that will help solve the PD–GWSS problem.

1. **Feasibility:** Considering technical barriers and practical limits (including cost), what is the likelihood that the research will result in tools for effective management of PD–GWSS?
    - **a. Time**: What period is required for the research effort to deliver an effective strategy, approach, or tool?
    - **b. Effectiveness:** What is the likelihood that the research product will deliver a strategy that will improve the PD–GWSS situation? Because the degree to which a given strategy or product will change the situation will vary, it must be determined whether the degree of change is better or worse than that achieved by other management measures and whether the strategy or product is sufficiently effective to warrant funding.
    - **c. Cost**: What will it cost to accomplish the research objectives?
2. **Sustainability:** The second criterion addresses the important idea of long-term application of a strategy or product. Is the approach or product biologically adaptable and affordable? Will it remain useful for a long period? Efforts to manage disease or pest outbreaks in agriculture often promote research that results in effective short-term solutions, but because diseases and pests are dynamic and evolving, those control measures often are not sustainable.

With information on the first factors for any given project, the research can be classified into one of four categories:

- **Category 1:** The research option holds reasonable promise of generating successful tools for the management of PD–GWSS, either in the short term or in the long term.

- **Category 2:** The research approach looks promising, but either because of insufficient data or because of inconclusive results, it is difficult to predict whether it will lead to successful applications for management.
- **Category 3:** The research effort can produce data and results that are promising for successful management of PD–GWSS, but because of its complexity and the technology required, it would be prohibitively expensive for any one funding source to manage.
- **Category 4:** The research approach does not show promise even in the long term, for PD–GWSS management.

The assignment of projects to those categories provides a useful way to examine options for the program as a whole. In considering how projects might be selected from within any category, the committee returned to the criterion of sustainability, concluding that, because many short- and medium-term control options are unlikely to be sustainable, a mixture of projects should be considered.

It is important to recognize that several factors other than purely scientific considerations will affect decisions to pursue or implement particular management strategies. For example, the cultivation and maintenance of unique lineages of grapes that result in the production of distinctive varieties of wine, such as chardonnay or cabernet sauvignon, adds value to grape production, but it severely limits the opportunities for crop improvement strategies that focus on breeding for disease or insect resistance by the methods conventionally used in many other crops. Although the process of categorizing research options focused on the potential effectiveness, time, and cost of a particular approach, the report mentions those factors when applicable. In some cases they are directly related to the issue of sustainability.

Recommendation 2.2. Research priorities should be developed according to their ability to meet two criteria—the predicted ability of the approach to contribute to PD–GWSS management and its sustainability. The committee recommends a balance among short-, medium- and long-term research projects to ensure the development of sustainable management approaches.

Economics: An Overarching Research Need

At least some information is available about the scientific aspects of different research and management approaches, but the same cannot be said of economic data, as illustrated by the lack of information about the economic consequences of PD described in Chapter 1. But the cost of PD that drives research, and economic considerations provide the context for setting research priorities. Because it is not economically feasible to pursue all possible projects simultaneously, priorities for the advancement of PD management strategies must be examined relative to the costs incurred in their implementation. The objectives and costs are different for different stakeholders, including growers and the wine and table grape industries and for the general public. Economic costs (and benefits) are shaped by many factors, including environmental concerns, issues of sustainability, and the effects that PD can have on crops. Economic analyses should be implemented for short-, medium-, and long-term PD management strategies.

Chapter 3 discusses that issue as it obtains biological control and includes a more specific economic analysis of pesticide regimens. The attention given to the economics of pesticide-based control of GWSS should not be interpreted as suggesting that other management strategies should receive less attention from economists. Pesticide or chemical treatment is recommended for economic analysis because it is relatively easy to quantify and it lends itself to economic analysis. In fact, it is possible that other measures developed in the short run might be more useful for controlling PD, and those measures should also be evaluated from an economic perspective. For example, the use of barrier crops or nets along riparian area and vineyard interfaces are short-run measures that warrant economic analysis.

Thus far, however, economic analysis of PD has been confined to the studies by Siebert (2001) and Brown et al. (2002). No economic analysis of research-based management outcomes has been done. An economic analysis is needed to help determine which outcomes will be most satisfactory to growers.

Recommendation 2.3. An economic analysis, including a study of environmental impacts, should be conducted for *all* potential management strategies and outcomes (Category 1).

Economic analysis of management outcomes should focus on developing estimates of the economic consequences, including the implications for financial risk that are associated with management alternatives. That process would include estimating the cost, effectiveness, and reliability of management alternatives to identify the most attractive from a grower's financial perspective.

Economic Research Needed on Sustainable PD Management

The GWSS was introduced to California through human activities, and the species spread from its original location as a result of human activities. Some who are familiar with GWSS in California do not regard it as a unique or new PD vector. Remarks to the committee by the director of the American Vineyard Foundation (Gleeson, personal communication) indicate concern that GWSS is just one vector of PD; others eventually will emerge. Thus, GWSS is only the current focus of a more troubling long-term problem with PD.

The need to manage invasive species, such as GWSS and others that could emerge as PD vectors, could become even more significant in the years ahead than in has been in the past, for three important reasons: First, the trend toward reduced in barriers to trade will increase the volume of goods traded regionally and internationally and provide a concomitant increase in the accidental transport of potential PD vectors across regional and international boundaries. Second, the Internet is dramatically increasing the accessibility of biological commodities to buyers in all regions, and is thereby greatly adding to the difficulty faced by regulatory agencies in protecting regional and domestic environments. Third, there is a growing awareness of the biosecurity issues that attend domestic crop and livestock production (Wheelis et al., 2002). Because of potential multiplier in regional and statewide economic effects, high-value crops could be attractive targets in this regard.

The current concern about PD is the result of GWSS as introduced in California by human activities. In view of this, it is perhaps not surprising that changes in human behavior could be part of a more permanent solution to PD. Drawing parallels with public-health programming related to HIV. C.H. Perring and colleagues (2002) argue that, in general, the probability of both the establishment and the spread of invasive species depends on human behavior, and incentives and institutions are needed to help change behavior that is not in the public interest. They conclude that control of invasive species is a public good that cannot be provided by uncoordinated, individual efforts. Aside from current CDFA nursery regulatory, bulk grape, and bulk citrus programs, there could be an array of policy instruments and institutional structures that could reduce the probability of GWSS spread in California and avert the introduction and spread of other PD vector species. The relative cost of most policy alternatives is largely unknown, although efficiency studies are possible. Sharov and Liebhold (1998) focus on the general use of barrier crops to impede movement of invasive species. With specific reference to PD–GWSS, Brown and colleagues (2002) optimized barrier zone width in vineyards. More economic analyses along those lines are needed to promote efficiency gains in PD vector containment.

Private and commercial activities can disregard the risks imposed on the agricultural economy in California. Study of policy alternatives for internalizing those risks to lessen the probable consequences is lacking, as is the study of regional or multi/state institutions to deal efficiently with PD vector issues. Economic analysis is needed to inform cost-effective and equitable policy regulations, incentives, and institutions that will lessen the probability of PD vector introduction and movement. The current statewide inspection program reveals the crux of the problem. Significant costs are being borne by entities, such as nurseries, with little to gain. If effective and sustainable vector control is to occur, some mechanism for reward or compensation must be in place. The design of that mechanism must be based on analysis of costs and industry operations.

Recommendation 2.4. The long-term research agenda should include economic analyses of policy regulations, incentives, and institutions to limit introduction and movement of PD vectors (Category 2).

Although the introduction of GWSS as well as its spread and the costs that have followed for commercial agriculture must be dealt with in the present, it is also important to acknowledge that the future could hold additional PD vectors. The experience with GWSS could provide information about economic policy regulations, incentives, and institutions that could discourage introduction and movement of future PD vectors. We recommend that effort be carried out over 15–25 years because its intent is not to focus on developing incentives for growers to adopt given practices related to GWSS; rather it is designed to address a more general issue, of which GWSS is a current symptom. The experience with GWSS could facilitate learning that can be applied to new problems as they emerge.

In the remaining chapters of the report, the committee uses its framework to evaluate and categorize current and prospective research strategies for PD–GWSS and, ultimately, as the basis of its research recommendations.

3

Host–Vector Interaction

Insect–plant interactions can range from associations that are highly detrimental to herbivores to those in which herbivores overexploit their plant hosts. In this chapter, the Committee on California Agricultural Research Priorities: Pierces' Disease explores the naturally occurring mechanisms that control the outcome of insect–plant interactions that could be adapted to the management of the damage that attends pest–crop interactions. More specifically, the objective is to explore ways in which the links between the glassy-winged sharpshooter (GWSS), *Homalodisca coagulata* (Say), and its hosts, particularly its economically important crop hosts, can be eliminated, inhibited, or minimized; that is, to develop management strategies that reduce or impede this vector of the *Xylella fastidiosa* (*Xf*) bacterium. If management strategies are to be effective in sustainable pest management schemes they should include a cohesive, complementary, and coordinated set of tactics. Although discussions are provided on a variety of tactics, it is assumed that the overall approach to the resolution of the problem will involve implementation of an ecologically based pest management program.

Ecologically based pest management (EBPM) is "the release of living predatory, parasitic, pathogenic, or antagonistic organisms (biological control organisms), the deployment of biologically derived products, such as toxins or semiochemicals (biological control products), and the planting of resistant crop varieties (resistant plants)" (NRC, 1996). Thus, EBPM includes approaches that go beyond traditional biological control—the intentional use or manipulation of predators, parasitoids, pathogens, antagonists, or competitors (Van Driesche and Bellows 1996)—to control insects, weeds, or diseases. EBPM has been defined or described by a variety of names including biointensive integrated pest management (IPM) and biorational IPM. EBPM is an IPM scheme that considers all possible management options and tactics that are complementary, effective, and sustainable with regard to the management of a pest and the quality of the environment. To be effective, EBPM tactics or agents might require environmental conditions that do not exist in agroecosystems. Reestablishing those conditions could require specific inputs or modifications of management tactics. EBPM typically requires more intensive management and planning and a fundamental knowledge of interactions among crops, pests, natural enemies, and the environment—requiring more time and record keeping. Some EBPM practices (such as augmentation biological control) could require an infrastructure that facilitates rearing, storage, and distribution of natural enemies (Neuenschwander et al., 1989).

Unlike strategies that rely solely on the use of insecticides, most EBPM is either specific to a pest or nontoxic, so it is less likely to damage the environment. Although many natural enemies can be susceptible to insecticides used against target pests, the judicious use of selective or specific types of insecticides typically has been considered an important component of integrated or EBPM schemes. Because most EBPM practices do not result in toxicity or pathogenicity to mammals, particularly in comparison to the use of conventional pesticides, they are more acceptable in terms of public health and environmental safety. Furthermore, insect pests are less likely to develop resistance to biological agents or to ecologically based controls. If resistance does develop, it is likely to occur significantly more slowly than would be occasioned by the conventional use of pesticides. Nevertheless, EBPM could pose risks, as do most environmental manipulations.

TACTICS AND STRATEGIES FOR ECOLOGICALLY BASED PEST MANAGEMENT

Ecologically based pest management can involve the use of living natural enemies (biological-control organisms), resistant crop varieties, or any product derived from those and other organisms. The tactics are deployed in any fashion that enhances their effectiveness and sustainable use against pest species. Those tactics and management approaches include the following:

- host plant resistance (through conventional breeding or genetic modification)
- vegetation management (in- or off-crop field refuges, trap crops, alteration of refuge vegetation, plant barriers)
- traditional biological control (classical, augmentation, conservation)
- sterile male technique
- mass trapping using a compound derived from a living organism
- direct use of chemical agents (synthetic toxins, biorational insecticides, behavior-modifying chemicals, insect growth regulators)
- pheromone use and mating disruption

Although not all of those tactics are ready for implementation in the control of GWSS and Pierces disease, the tactics that could be used are reviewed below.

HOST PLANT RESISTANCE

Host plant resistance (HPR) is an important EBPM tool for minimizing crop damage caused by insect pests and diseases because it makes plants less suitable for or more tolerant of the pest. HPR has a long history of success in grape crops for management of phylloxera, grape leafhoppers, and various diseases (e.g., Granett et al., 1996; Jermini et al., 1996, Martinson and Dennehy, 1995; Walker, et al., 1994). HPR can be developed in three ways. Biosassays or direct observation in the field of apparent resistance or tolerance to a pest can be used to identify plant material for propagation. This has been the main approach to developing pest-resistant grapes because vegetative propagation is the norm, sexual reproduction delays the opportunity to perform crosses, and the value of the crop is directly related to its genetic pedigree (interspecific hybrids are not favored). Collecting and propagating resistant material can provide the quickest route to HPR, but the bases of resistance might not be known and resistance breakdown is common. HPR also can be developed from resistant or partially resistant plant material through standard breeding (crosses) if the plant's biology is compatible (early sexual reproduction, outcrossing, compatible genotypes, inheritance relatively simple). The third way to develop HPR is to modify plant traits using direct molecular manipulation. Genetically transformed or genetically modified (GM) plants express naturally occurring resistance traits, but to different degrees or in different combinations than found normally, or they might express entirely novel traits (the protein toxins of *Bacillus thuringiensis* are an example). There is considerable debate about the risks, costs, and benefits of such approaches, especially for application in food crops. Resistance phenotypes can sometimes be manipulated through cultivation practices, such as fertilization.

No matter how HPR to a given pest is developed, it is subject to periodic, repeated breakdown as a result of pest evolution or the introduction of new pest species or genotypes (e.g., Granett et al., 1996). HPR as a management tactic requires constant evaluation and modification for sustainability. Although constant searches for new plant material or germplasm could remain part of this process, common sense suggests that understanding the plant traits that do or can confer resistance would greatly accelerate HPR development. Successful HPR use in EBPM requires a detailed understanding of how the pest exploits the plant and how plant traits interfere with pests.

Plant-Herbivore Interactions and Host Plant Resistance

Insects have been consuming plants for 500 million years, and during that time diverse interactions between the two groups have evolved. As far as the committee knows, all plant species and all possible plant tissues are exploited as food, shelter, or reproductive sites by insects. Insect diets range from extremely narrow (limited to a particular tissue on a particular plant species) to very broad (feeding successfully on many plant species from several plant families). A striking feature of insects as herbivores is that relatively narrow diets (a single or a few plant species) are more common than are broader diets. Diet breadth is evolutionarily fixed; insects usually cannot broaden or narrow their diets during a lifetime, and often require significant genetic change (evolution) to switch or add host species to their diets. Identifying the proximate and ultimate factors that determine the structure of insect diets is an active area of in plant-herbivore research, and it is safe to say that a complex picture is emerging. Many factors can act as barriers to plant exploitation and thus are thought to influence the evolution and expression of insect host range.

Plant chemistry is a crucial barrier to plant use and is thought to be an important influence on insect's host ranges. Plants are generally suboptimal food either because they contain low concentrations of critical nutrients such as nitrogen or protein or because they produce chemicals (allelochemicals or secondary metabolites) that deter feeding, inhibit digestion, or are toxic to the insect. Insects have developed specific adaptations that permit specialization on hosts that have particular chemistries, Those adaptations include the ability to avoid toxic tissues and a variety of biochemical traits that counter the negative effects of plant chemistry.

Plant quality also can have indirect effects on herbivorous insects. Insect susceptibility to parasites, predators, disease, and insecticides has been shown to be influenced by the host plant (Wright and Verkerk, 1995). Nonlethal effects on fitness (those that reduce fecundity, for example) could influence insect population growth. It is likely that most aspects of insect performance are influenced by diet quality and that plant chemistry is a central factor in limiting consumption by insects.

Although research on the effects of plant chemistry on insect herbivores originally focused on constitutive traits (those that are present constantly and encountered by an insect when it first goes to the plant), studies over the past two decades have shown that changes in plant chemistry that are induced by the feeding insects are at least as important (Karban and Baldwin, 1997). All plants so far studied alter the concentrations or composition of allelochemicals when attacked, sometimes in an insect-specific fashion. Those changes can reduce diet quality or enhance toxicity or deterrence in a matter of minutes or hours. Related changes are elicited in plants by pathogen attack, and there is evidence that the suitability of plants for insects could be influenced by plant responses to pathogenic and symbiotic microbes (Bostock, 1999).

Most plants also emit volatile substances that attract the enemies of insect herbivores (parasitoids, predators) and could cue defense responses in nearby plants (Dicke and Bruin, 2001). Those indirect effects on insect herbivores could be more influential in protecting plants from insects than are the more direct constitutive or inducible defense traits (Karban and Baldwin, 1997). Volatile substances also could have a direct effect by repelling or poisoning sessile, sucking insects such as aphids (Birkett et al., 2000). Recent research indicates that plants also emit complex volatile mixtures when they are attacked by microbes (J. Huang et al., 2003); one study suggests that such pathogen-elicited emissions could have an effect on insect vectors of plant diseases (Eigenbrode et al., 2002).

Although the nutrient (protein, carbohydrate, fat, mineral) composition of plant tissues often is suboptimal for insect growth, it is assumed that all insects experience similar selection on their ability to extract sufficient nutrition from plants. Together with the need of plants to produce a minimal nutrient mix for their own functioning, the nutritional content of plants is rarely cited to explain evolution of insect host range. However, nutrition does shape insect adaptation and diet. It is true that even extremely nutrient-poor plant tissues are consumed by some insects, the insects that do so generally are limited to those tissues, presumably because adaptation comes at the cost of restricting the ability to use better tissues. The most germane example to the PD situation involves insects that feed on xylem, which generally is thought to contain extremely low concentrations of usable nutrients. Xylem also lacks or contains very low concentrations of allelochemicals (Rosenheim et al., 1996). Xylem-feeding insects usually consume large quantities to extract the limited nutrition (Brodbeck et al., 1993), and they generally cannot exploit other plant tissues, partly because of their specialized mouthparts, but also because they presumably are not adapted to the higher allelochemical concentrations found in more nutrient-rich portions of a plant.

There are fewer examples of insect adaptation to physical deterrents. Plant tissue toughness is a trait that some insects have overcome in ways that sometimes lead to restrictions in host use (e.g., Howard and Giblin Davis, 1997). Surface hairs and trichomes can combine to form to form a physical and chemical barrier, particularly to small insects. The physical structure of some plants can offer unique opportunities for insects to escape predators or parasites, although the degree to which this influences the evolution of diet is debatable (Mira and Bernays, 2002; Scheirs and De Bruyn, 2002; Zangerl et al., 2002). It is generally easier to understand insect adaptation to plants and the reasons for using particular plant species on the basis of chemistry than it is to explain the adaptation on the basis of adjustment to the physical traits of the host plant.

Insects do not always use the same plant species for food, shelter, and reproduction, so noncrop, alternative hosts might exert HPR-based effects on crop pests. There is long-standing controversy about the degree to which plant suitability for feeding adults is linked to suitability for offspring placed there (Wiklund, 1975). Plant traits that influence feeding might or might not be the same traits that influence oviposition or mating behaviors. When more than one plant species is exploited during the life cycle of an insect, each plant and its traits can make separate, significant contributions to the insect's success.

Insect herbivores can become agricultural pests when conditions permit them to consume or destroy an economically significant fraction of the agricultural product. There are several HPR-based causes of this outcome. One is the tendency to eliminate chemical (or physical) deterrents from food products, because they can be distasteful or toxic to human consumers as well. Another is to bring plant and insect species together for the first time. A lack of coevolutionary history could mean that the plant has no viable defenses against a newly encountered insect. Because insect adaptation to host plants is continuous, uniform populations of crop plants that express the same resistance traits favor the rapid evolution of insects to overcome those traits. For this reason, and because ecosystem complexity itself interferes with finding and exploiting host plants, the simplification inherent to modern agriculture also contributes to the development of insect pest problems.

Sharpshooters and Their Host Plants

Sharpshooters Are Xylem-Feeding Leafhoppers

Sharpshooters comprise a taxonomic subset of a family of insects (Cicadellidae) in the order Homoptera collectively called leafhoppers. All leafhoppers have piercing–sucking mouthparts, and they consume liquid from plants. Some species puncture individual cells or groups of cells, for example, the leaves; others penetrate xylem cells and consume the materials there. Sharpshooters are primarily xylem feeders, although some recent unpublished work suggests that they occasionally feed on cells that surround the xylem.

Sharpshooters and other xylem-feeding leafhoppers have powerful cibarial pumps for extracting xylem contents (which are under negative pressure), and they consume large quantities of fluid, presumably to compensate for the low nutrient concentrations in xylem. There is some uncertainty about where on an individual plant sharpshooters prefer to feed. It is clear that tissues surrounding the xylem, a site of lignification, can become too tough for leafhoppers to penetrate; young tissues would be suggested as preferred feeding sites.

Like many leafhoppers, sharpshooters, temporarily or permanently harbor microbes. They have a diverse assemblage of obligate symbiotic bacteria, the function of which is unknown (Moran et al., 2003). And of course, the plant-pathogenic bacteria they carry can be transmitted from plant to plant. There has been little work on host plant's influences on essential symbiotic microbes in insects or of plant responses to entomosymbionts.

Sharpshooters Have a Broad Host Range

All of the sharpshooter species involved in transmitting *Xf* appear at first to have large host ranges. They have been associated with many plant species—native and introduced—including many that grow adjacent to vineyards. This could be important because *Xf* can be acquired from other plant species and transmitted to grape or citrus and because the abundance and fitness of the insect vector could be influenced by the availability of suitable host plants. The insect's association with a plant species could mean that it feeds there, reproduces there, or both. There are examples of both types of association with various host plants, but the committee does not have a comprehensive picture of the associations between any of the *Xf*-transmitting sharpshooters and the host plant communities in their habitats. Indeed, the degree to which any of the sharpshooters actually feed, grow, or reproduce on the locally available plants has been established for relatively few plant species, and not always for plants found in or near California's vineyards (Brodbeck et al., 1995).

The literature evidences some confusion about which plants are suitable or preferred (Purcell, 1976, 1981; Purcell and Frazier, 1985), and the literature on host plant associations of insect herbivores is notoriously unreliable. An association is often assumed when an insect is found on a plant, although that says nothing about the insect's performance or preferences. The concept of preference should comprise a quantitative measure of active choice (among equally available alternatives), of choice and performance (growth, reproduction), or at least of abundance on a plant in relation to that plant's availability. None of those approaches appears to have been taken. Much of what is known about sharpshooters' use of hosts consists of singular, isolated observations, often of a single insect on a plant. Despite numerous studies in which sharpshooters have been trapped as they move among or within crops and other communities (e.g., Blua et al., 2001), the degree to which the sharpshooters prefer grape or find it suitable for growth or reproduction compared with surrounding vegetation lacks quantitative confirmation.

Factors Influencing Sharpshooter Plant Use

To employ HPR, it is necessary to know what plant traits determine the pest's use of a plant. Few if any of the usual factors thought to influence host plant use have been investigated as barriers to sharpshooter feeding or oviposition on any plant species. There has been little work of this kind on xylem feeders in general, probably because of the difficulty in acquiring and analyzing xylem contents. Studies tend to focus on nutritional chemistry and mostly ignore putative defenses (allelochemicals; Brodbeck et al., 1990,1993,1995,1999; Ponder et al., 2002). Published work links sharpshooter growth to amino acid content and balance in xylem of *Glycine max*, *Lagerstroemia indica* and *Euonymus japonica*, a *Vitis* hybrid, and *Catharanthus roseus* (Andersen et al., 1992; Brodbeck et al., 1990,1993,1995,1999). Growth and selection of host plants by another leafhopper, *Carneocephala floridana* (Ball), was influenced by plant fertilization (Rossi et al., 1996). Grafting on rootstocks that alter xylem amino acid content can influence sharpshooter feeding and growth (Gould et al., 1991) but recent unpublished work failed to show similar differences in *Vitis* grafts. Compensatory feeding can confuse interpretation of results in studies like these: Insects can appear to consume more of an unsuitable plant to compensate for its low quality nutrition. If *Xf* transmission by sharpshooters is linked to time spent feeding, low-quality plants (from the insect's point of view) could be more likely to become inoculated.

The assumption that sharpshooters can exploit many plant species makes evolutionary sense if the assertion that biochemical challenges (such as defenses) in xylem are few, because host specificity often is assumed to be a product of adaptation to plant exploitation barriers (for example., biochemical defenses, above). Xylem-feeding leafhoppers appear to have adapted to the low nutrient concentrations typical of most xylem, and if there are no other chemical influences, one plant's xylem thus could be as suitable as another's. Some xylem-feeding leafhoppers do exhibit relatively low activity of enzymatic detoxification systems and comparatively high susceptibility to chemical pesticides, an observation taken to indicate that they do not typically encounter substances that cause toxic reactions (Rosenheim et al., 1996). Despite the attractiveness of this logic, there are few studies of xylem chemistry or xylem-feeding leafhopper performance to support it. It could be that physical toughness, not chemistry, is the major barrier to leafhopper feeding (Brewer et al., 1986).

But the observations that sharpshooters apparently avoid or perform differently on various plant species (Brodbeck et al., 1992, 1995; Purcell and Frazier, 1985) and that various plant species exhibit genotypic resistance to xylem-feeding and other leafhoppers (Elden and Lambert, 1992; Kornegay et al., 1989; Martinson and Dennehy, 1995; Sanford et al., 1990; Tingey and Laubengayer, 1981) suggest that plant traits do influence sharpshooter attack. Leafhoppers must locate plants or suitable habitats from a distance, determine a plant's suitability, upon contact, penetrate tissues to get to the xylem, and grow and reproduce adequately as a result of feeding on the xylem. Plant odors, the taste and texture of tissues superficial to xylem, xylem toughness and xylem allelochemistry could produce the observed preferences and hence could be employed in HPR strategies. None of those possibilities has been investigated in any systematic way for *Xf*-transmitting sharpshooters, although trichomes have been found to constitute barriers to feeding by leafhoppers in several plant species (Elden and Lambert, 1992; Shockley and Backus, 2002; Tingey and Laubengayer, 1981) as has xylem lignification toughness (Brewer et al., 1986).

Plant xylem can include allelochemicals and can express enzyme activity that could influence sharpshooters and provide bases for HPR in grapes. In other plants, alkaloids and other allelochemicals that are toxic to leafhoppers (Sanford et al., 1996) and synthesized in roots are translocated to shoots and leaves in xylem, often in response to aboveground insect attack (Baldwin et al., 1994). Phytoalexins have been found in xylem of several plant species (Kragh et al., 1995; Resende et al., 1996). Xylem of some plants contains phenolics and oxidative enzymes (e.g., Kpemoua et al., 1996; Young et al., 1995). Many authors assume that the presence of those compounds is related to xylem lignification (Kpemoua et al., 1996), but phenolics can be toxic; inhibit enzymes (including digestive enzymes); and could bind to cations, proteins, and amino acids, especially when activated by peroxidases or other enzymes (Appel, 1993; Morales and Ros-Barcelo, 1997). Phenolic production and activities of oxidizing enzymes can be induced by insect signals (Kruzmane et al., 2002) and could be elevated during pathogen infection in xylem (Kpemoua et al., 1996; Young et al., 1995). Peroxidase activity and phenolic accumulation have been associated with the stylets of feeding insects as they penetrate the plant (Crews et al., 1998) and oxidized allelochemicals form a basis of resistance to leafhoppers in corn (Dowd and Vega, 1996). The discovery of proteases in the saliva of other xylem feeders (Foissac et al., 2002) and unpublished work finding the same in sharpshooters suggests that digestive activity (not just uptake) could occur and could be inhibited by xylem chemistry. Recent work in grapes suggests that rootstock identity—which one might expect to influence xylem chemistry—has little or no effect on aboveground sharpshooter feeding. The xylem chemistry arising from various grafts in *Vitis* has not been examined.

A promising form of HPR that is consistent with EBPM and IPM is the emission of volatile compounds that attract pest-consuming predators and parasites. There are no studies of grape plant (or other host plant) volatile substances on sharpshooters or their parasitoids, despite the indication that grape leaves produce ample volatile signals when they are wounded by insects (Loughrin et al., 1996, 1997) and that some leafhoppers are responsive to leaf volatiles in other plant species (Saxena and Basit, 1982; Shockley and Backus, 2002; Todd et al., 1990). Recent studies suggest that plants infected by insect-vectored pathogens emit volatile substances that attract the insect vectors (Eigenbrode et al., 2002). There are no studies of the effect of *Xf* (or other pathogens) on sharpshooter host plant use, or vice versa.

HPR has been developed against several pests in wine grapes, largely by trial and error, by locating apparently resistant material in the field. Vines that are apparently resistant to *Xf* or sharpshooters and also compatible with producing high-quality wine have not yet been identified by this method. Identifying resistant plants and useful HPR traits would be accelerated and enhanced by understanding how plant and pest interact. A library of phenotypic and genetic resistance traits is needed for effective use of HPR, but few resistance traits have been identified because too little is known about how the insects and plants interact.

Although each of the *Xf*-transmitting sharpshooter species can be found on and could feed on a large number of plant species, the insects' preferences for those plants and the suitability of various plants and plant tissues for insect performance have not been determined. It is evident that transmission of *Xf* to grapevines is linked to insect and disease presence in surrounding vegetation, so it is important to identify with confidence the relative importance of individual plant species in the system.

All plants express heritable, phenotypically plastic "defense" traits thought or known to influence their susceptibility to insects. Sharpshooters and their hosts should be no exception, and the fact that some plants clearly seem unacceptable to them supports this view. Comparisons of plant species' suitability can provide rough clues about important resistance traits, but similar comparisons must be made within plant species, because intraspecific variation in resistance provides the raw material for developing resistant plants. And there is informal evidence that such variation exists in *Vitis vinifera*. But because the basic studies of factors that could influence plant suitability have not been done for sharpshooters, it is difficult if not impossible to guess what sort of plant traits might be useful in developing resistant cultivars or grafts, or in instituting cultivation practices to maximize plant resistance.

Recommendation 3.1. Studies that provide more information about sharpshooter feeding, host-finding behavior, host plant preferences, and the factors that influence reproductive success and natural-enemy-caused mortality are needed. The potential effects of *Xf* infection on sharpshooter behavior and performance should be included in those studies. Those factors must be examined with statistical rigor so that the results are reliable (Category 1).

Recommendation 3.2. All the modern chemical, molecular, ecological, and statistical tools available to scientists should be used to identify the mechanistic bases of grapevine resistance to xylem-feeding leafhoppers. Studies should be done in the ecosystem context and consider multitrophic interactions among plants, insect pests, and natural enemies (predators and parasites), and they should include insect- and *Xf*-induced changes in plant quality (Category 2).

Recommendation 3.3. Host plant resistance should be emphasized as a component of ecologically based insect management strategies in the grapevine–sharpshooter–*Xf* system. Methods for manipulating grapevine resistance should be developed for experimental use to identify key resistance traits and with an eye toward eventual deployment. The methods should allow work with genetically transformed plant material, use of chemical or other elicitors, and cultivation practices (Category 2).

MANAGEMENT OF VEGETATION

Research on plant resistance to insect feeding is complementary to studies of how crop and noncrop components of an agricultural landscape influence the population dynamics and movement of herbivorous insects that attack crops (Gurr et al., 2003) and, if the insects are vectors of plant pathogens, to studies of the epidemiology of those pathogens (A.G. Power, 1990). Vegetation management can be an important element in a comprehensive pest management system and has been effective for the control of insect-transmitted plant pathogens (Wisler and Duffus, 2000). Insects and pathogens respond to vegetation structure and diversity both inside the agroecosystem itself and in the surrounding landscape.

Vegetation Management within the Cropping System

Although the response of individual herbivores to particular cropping patterns varies, crop diversification within an agroecosystem often leads to reductions in herbivorous insect populations (for reviews, see Andow, 1991; Tonhasca and Byrne, 1994; Hooks and Johnson, 2003) and in the pathogens that they transmit to plants (A.G. Power, 1990). The effect of increasing diversity can result either from "bottom up" effects (the effects of the host plants themselves on herbivore population dynamics and behavior) or from "topdown" effects (enhancement of natural enemy populations or behavior). That range of processes which might explain lower herbivore abundance in diverse systems, was first described by R. B. Root (1973) when he posed the resource concentration hypothesis and the enemies hypothesis. The first predicts that herbivores, particularly specialists, in pure, dense host plant stands will be more likely to find their hosts and more likely to survive and reproduce. In contrast, herbivores in less dense or more host-plant-diverse stands should be less likely to find their hosts and more likely to lose them.

Although the details of herbivore–host interactions vary considerably, subsequent experimental tests of this hypothesis generally have supported it with respect to the effects of diversity, especially for specialist herbivores. Host-finding behavior and insect colonization and emigration appear to be important in the response of herbivorous insects to agroecosystems. Densities of specialists could be lower in diverse systems because they have difficulty locating hosts, because of interference with olfactory or visual cues; or because they leave hosts more often because of lower plant quality and then have difficulty relocating the hosts. Those behaviors are significantly affected by the chemical, nutritional, and structural diversity that accompanies crop diversity.

Although the predicted effects of plant diversity on insect herbivores with narrow host ranges are reasonably straightforward, predictions for herbivores with broad host ranges are less clear. The determining factors for insect response are the distribution of host and nonhost plants in the system and the preferences of the herbivore. The expectation of lower abundance in diverse systems attributable to effects on host finding and "host losing" (Kareiva, 1985) is predicated on the existence of nonhost or nonpreferred plants in the system.

The enemies hypothesis predicts that the diverse systems will have higher densities of herbivore natural enemies (predators and parasites) because they provide more resources for those natural enemies, such as alternative prey or hosts, nectar, pollen, and refuge. The hypothesis also has largely been supported in experimental studies, particularly for parasitoids (Andow 1991; Russell, 1989). Compared with monocultures, diverse systems are likely to have higher rates of predation, higher rates of parasitism, and higher ratios of natural enemies to herbivores, all of which can contribute to lower pest densities of specialist and generalist herbivores.

Vegetation Management of Leafhoppers

Leafhopper abundance in crops can be significantly lower in mixtures of host and nonhost species than in monocultures of the preferred host. Those effects have been demonstrated for specialist herbivores—such as the corn leafhopper, *Dalbulus maidis* (DeLong and Wolcott)*,* whose densities on maize in Central America are significantly reduced in maize and bean polycultures and in weedy maize fields as compared to maize monocultures (A. G. Power, 1987), —and for polyphagous leafhoppers. For example, intercropping with beans reduces colonization of maize by the leafhoppers *Cicadulina mbila* Naude and *C. storeyi* China in Africa (Page et al., 1999). Studies in natural grasslands also suggest that leafhoppers are less abundant in diverse plant communities than they are in low-diversity communities (Koricheva et al., 2000).

The most extensive research on controlling leafhoppers with intercropping has been done with the potato leafhopper, *Empoasca fabae* (Harris), a highly mobile, polyphagous herbivore with an extremely broad host range that can be a serious pest of alfalfa, common bean, soybean and potato. Potato leafhopper populations are significantly reduced when hosts and nonhosts are intercropped. Leafhopper colonization to alfalfa can substantially be reduced by intercropping with oats (Lamp and Zhao, 1993) or with forage grasses (Roda et al., 1997). Compared with bean monocultures, intercropping with tomatoes reduced leafhopper densities on snap beans by 75% (Roltsch and Gage, 1990). Leafhopper populations also were lower on beans in weedy plots than in weed-free plots (Andow, 1992). Populations of potato leafhopper on soybean are reduced when soybean is intercropped with maize (Tonhasca, 1994) or wheat (Hammonds and Jeffers, 1990; Miklasiewicz and Hammond, 2001). Several species of *Empoasca* are found in lower abundance on squash in polycultures than they are in monocultures (Letourneau, 1990). The use of cover crops or ground covers in orchards and vineyards can help reduce leafhopper populations (Costello and Daane, 2003; Daane and Costello, 1998; Hanna et al., 2003; Roltsch et al., 1998). Surveys and field experiments in raisin grape vineyards in the San Joaquin Valley have shown consistently lower leafhopper populations in vineyards planted with ground covers (Costello and Daane, 2003; Daane and Costello, 1998), although the reasons for the reduction in grape leafhoppers could have more to do with reduction in vine vigor because of competition with cover crops than with such factors as enhanced predation or parasitism. This might point to the need for integration of pest management into viticulture practices.

In many systems, crop colonization by vectors can be reduced by continuous ground cover. In some cases, such decreased leafhopper populations could result from the expansion of predators and parasitoids into the system, although the evidence for it is largely correlative. For example, Roltsch and colleagues (1998) reported greater abundance of predatory spiders and lower abundance of the leafhopper pest *Erythroneura variabilis (*Beamer) in vineyards with ground cover. Subsequent open-vine exclusion experiments indicated that leafhopper populations were 35% higher when spiders were excluded (Hanna et al., 2003), although an accompanying spider addition experiment did not show a significant effect of ground cover on leafhopper populations, possibly because of low overall leafhopper numbers (Hanna et al., 2003).

Although no ground cover studies have been done with GWSS, the effects of ground cover on other leafhopper pests of grapes suggest that it would be worth investigating ground covers as one part of an EBPM program to reduce sharpshooter colonization of grape hosts. It will be important to select ground cover species that are not hosts of *Xf*.

Recommendation 3.4. Detailed, quantitative studies should examine leafhopper performance (survivorship, fecundity, development time) on and preference for a broad range of potential ground cover crops (Category 2).

Recommendation 3.5. The feasibility of using carefully selected cover crops in vineyards to reduce sharpshooter colonization to grape should be investigated (Category 2).

Vegetation Management of Leafhopper-Transmitted Pathogens

Mixtures of host and nonhost species that lead to reductions in leafhopper abundance also can lead to lower prevalence of leafhopper-transmitted pathogens. For example, lower densities of the corn leafhopper in maize and bean polycultures or in weedy maize fields leads to reduced prevalence of the corn stunt spiroplasm in mixtures than is found in maize monocultures (A. G. Power, 1987). Similarly, maize streak virus transmitted by *Cicadulina* leafhoppers can sometimes be reduced in intercrops of maize with beans or finger millet, although results have not always been consistent (Page et al., 1999). The black-faced leafhopper, *Graminella nigrifrons* (Forbes), which also transmits the corn stunt spiroplasm to maize, exhibited higher populations in weedy maize fields than in weed-free fields, but the prevalence of the pathogen was lower (Pitre and Boyd, 1970). Feeding preference tests indicated that the leafhopper preferred to feed on some of the weed species, so pathogen transmission to maize was low despite greater vector abundance in weedy systems (Boyd and Pitre, 1969). This example illustrates the complexity of transmission patterns in vector-transmitted pathogens and emphasizes the need to investigate vector behavior in addition to population dynamics in order to elucidate epidemiology.

The transmission of *Xf* in vineyards could to be influenced by the presence of ground covers, but inadequate information on host relations and plant-to-plant movement of GWSS prevents clear recommendations. To select appropriate candidate species for ground covers, leafhopper performance on, and preference for, a range of crops should be investigated. Candidate species would be examined for water-use requirements (an important consideration in California). Those potential cover crops also must be screened for the capacity to develop epidemiologically significant populations of *Xf*.

Recommendation 3.6. Potential ground cover crops should be screened for the capacity to develop epidemiologically significant populations of *Xf* (Category 2).

Vegetation Management outside the Cropping System

The natural vegetation in an agricultural landscape also can have important effects on the population dynamics and movement of herbivorous insects that attack crops. Noncrop plant species can be alternative hosts of insects and pathogens, thereby serving as important reservoirs. Field borders of noncrop plants can increase the populations of natural enemies that visit adjacent crops (Dyer and Landis, 1997; Hickman and Wratten, 1996). Natural areas adjacent to agricultural systems can provide habitat for pollinators and natural enemies of pests (Dennis and Fry, 1992; Landis et al., 2000). For example, Thies and Tscharntke, (1999) demonstrated that rates of parasitism of pest insects and yield losses in oilseed rape were strongly affected by the complexity of European landscapes. In general, parasitism and plant damage were highly correlated with the amount of uncultivated areas, including field margins, fallow fields, grasslands, and forests. Parasitism of the rape pollen beetle by parasitoid wasps in rape fields went from zero in landscapes with little or no uncultivated area to an average of 40% in landscapes with 50% or more uncultivated area. This example demonstrates the potential for natural pest control through modifications in landscape structure.

Vegetation Management of Leafhoppers

There are a few examples of the use of vegetation management at the landscape scale for controlling leafhoppers. The best known is the eradication of Russian thistle to control the beet leafhopper, *Circulifer tenellus* (Baker), which transmits beet curly top virus to sugarbeets and other vegetables (Wisler and Duffus, 2000). In northern California, the removal of host plants of the blue-green sharpshooter in riparian vegetation bordering vineyards can reduce leafhopper populations (A. H. Purcell, unpublished data).

Vegetation management in the landscape surrounding vineyards could have significant effects on GWSS populations. Studies in Southern California indicate that GWSS is more likely to move into vineyards from citrus groves than from riparian vegetation or nonriparian coastal sage scrub vegetation, particularly in the winter months (Blua and Morgan, 2003). The management of GWSS in citrus groves near vineyards raises difficult issues (see Box 1-1 in Chapter 1), but cooperation between the two agricultural sectors is essential and quantitative and qualitative studies can draw firm conclusions about the role of citrus in the PD problem.

Vegetation Management of Leafhopper-Transmitted Pathogens

The successful control of beet curly top virus was accomplished through the eradication of Russian thistle, a highly suitable host of the virus and its vector, the beet leafhopper, (Wisler and Duffus, 2000). Overgrazing in many western states had allowed native perennial grasses and shrubs to be replaced by the leafhopper's preferred host plants, including Russian thistle, mustard, and plantain. In Idaho, replacement of the preferred hosts with a nonhost species, crested wheatgrass (*Agropyron cristatum*), substantially reduced the abundance of beet leafhoppers and virtually eliminated beet curly top as a significant threat to sugarbeet and vegetable production in the 1960s (Wisler and Duffus, 2000). Although current control of the beet leafhopper in California relies heavily on pesticides, good land management practices by livestock farmers to maintain native grass and shrub cover can dramatically reduce leafhopper populations, leading to significant reductions in the prevalence of beet curly top virus (Wisler and Duffus, 2000).

Epidemiologic models suggest that other leafhopper-transmitted pathogens also could similarly be limited by effective vegetation management at the landscape scale. Zhou and colleagues (2002) show that the arrangement of susceptible and nonsusceptible crops in the landscape can significantly influence the epidemiology of the aster yellows phytoplasm transmitted by the highly polyphagous aster leafhopper, *Macrosteles quadrilineatus* (Forbes). Using a similar modeling approach, Holt and Chancellor (1997) showed that the spatiotemporal pattern of host availability in the landscape can influence the epidemiology of the leafhopper-transmitted rice tungro virus.

The success in reducing abundance of highly mobile, polyphagous leafhoppers through the management of host and nonhost plants suggests that the densities of sharpshooters can also be affected by vegetation management. However, it is essential to understand which hosts serve as feeding hosts and which are reproductive hosts, and it is important to identify the preferences of sharpshooters for those potential hosts. Highly preferred alternative hosts can be sometimes be used as trap crops to attract herbivores away from less preferred crops. This is especially effective for pathogen control where the preferred leafhopper host plant is not a host for the pathogen (Al-Musa, 1982; Farrell, 1976; Toba et al., 1977).

Many riparian plants are hosts of grape strains of *Xf* in Northern California (Purcell and Saunders, 1999), and some of those species also are feeding and reproductive hosts of the blue-green sharpshooter (Hill and Purcell, 1995; Wistrom and Purcell, 2002). There is also accumulating database on noncrop hosts of *Xf* in Southern California (Cooksey and Costa, 2003). However, largely because of logistical difficulties, few studies have demonstrated that the pathogen can be acquired from those alternative hosts and transmitted to grape. Cooksey and Costa (2003) indicate that the pathogen can be transmitted from grape to other hosts, such as Spanish broom and wild mustard, but the transmission from those hosts to grape has not been tested. As Wistrom and Purcell (2002) point out, for a plant to be an epidemiologically important source of *Xf*, it must be an attractive food plant for sharpshooters and support populations of *Xf* above 10,000 cfu/g plant tissue, the threshold for acquisition by sharpshooters, after inoculation by an infectious sharpshooter. Many plant species can support some bacterial growth, but relatively few have the characteristics that make them epidemiologically important in the spread of PD. Before undertaking significant weed management programs to control PD, it is essential to collect basic information about the vector's feeding preferences, bacterial growth potential in alternative hosts, and effective transmission rates from such hosts to grape (Freitag, 1951).

Recommendation 3.7. Detailed, quantitative studies should examine leafhopper preference for potential host plants in the context of natural assemblages of hosts in the field. Studies of leafhopper performance on a broad range of potential host plants are essential to elucidate host ranges (Category 2).

Recommendation 3.8. The plant-to-plant movement of GWSS at multiple scales should be examined throughout the year to identify long-range seasonal and trivial movements that lead to disease spread (Category 2).

Recommendation 3.9. Sharpshooter host plants should be screened for their capacity to develop epidemiologically significant populations of *Xf* and examined for effective transmission rates from hosts to grape (Category 2).

Recommendation 3.10. After the epidemiologically important noncrop host plants of the vectors are identified, the ecological and socioeconomic barriers to removal of those plants from areas that influence disease prevalence in grapes should be explored (Category 2).

BIOLOGICAL CONTROL

Among the most important tactics and approaches in EBPM are those of traditional biological control. Often, the results of using biological control within an EBPM approach are not as dramatic or as rapid as those produced by pesticide use. There are three primary approaches to the use of predators, parasites, and diseases to manage pests. Classical biological control (importation) involves the collection of natural enemies of the target pest in the country or area from which an introduced pest originated. Introduced natural enemies could establish viable populations (as is typical of classical biological-control introductions) or could require augmentation if pest reduction is inadequate. Augmentation aims to increase the population of a natural enemy (either introduced or native) known to attack a target pest. Typically, this is accomplished by mass rearing one or more natural enemies for field release. Augmentation biological control often relies on continual releases to control. In some cases, augmentation can be more expensive than are other types of biological control, usually because of rearing, storage, and delivery costs (Obrycki et al., 1997; Tauber et al., 2000), and it can be less cost-effective than are pesticides. However, there have been few if any economic feasibility analyses of augmentative biological-control efforts (Parrella et al. 1992; van Lenteren et al., 1997).

The third approach is the conservation of natural enemies; it involves identifying and then eliminating any factors that limit the survival and effectiveness of natural enemies. For example, native natural enemies that occur in affected areas might not provide necessary control because of the lack of food or shelter for natural enemies. Thus, conservation could be used to enhance biodiversity, and provide food and shelter, thus promoting natural-enemy effectiveness. The economic feasibility of conservation or augmentation biological control is likely to depend on the development of economical, efficient, and effective augmentation strategies or conservation tactics. Leafhopper abundance is regulated by a variety of natural enemies (J. M. Fry 1989). Leafhoppers have a variety of generalist vertebrate predators (birds, lizards) and invertebrate predators (spiders, mirid bugs, wasps, robber flies) (J. M. Fry 1989; Hanna et al., 2003). Leafhoppers also are attacked by various parasitic insects as nymphs or adults (dryinid wasps, epipyropid moths, pipunculid flies, strepsipterans), and as eggs (mymarid, trichogrammatid, aphilinid, and eulophid wasps, although there are only a handful of records of parasitism by species in the latter two families) (Freytag 1985; Heinrichs 1979; Turner and Pollard 1959). Because they feed on plant sap, leafhoppers are usually not susceptible to infection by viral, bacterial, or protozoan entomopathogens. Because entomopathogenic fungi need not be ingested to infect insects, they are the most important pathogens of leafhoppers (Soper, 1985).

The list of important leafhopper pests includes, but is not limited to the grape leafhopper (*Erythroneura comes* [Say]), the three-banded leafhopper (*E. tricincta* [Fitch]), the potato leafhopper, beet leafhopper, and the white apple leafhopper (*Typhlocyba pomaria* McAtee). However, only a few of their natural enemies have been used as biological controls and only with limited or mixed results. Other leafhoppers—*Macrosteles phytoplasma*, *Empoasca vitis* Goethe, *Scaphoideus titanus* Ball, and *Scaphytopius magdalensis* Provancher—are disease vectors and thus add other dimensions and complexities to biological control. The most commonly used biological-control agents for leafhoppers have been egg parasitoids in the genera *Anagrus*, *Gonatocerus*, and *Polynema* (Flaherty et al. 1985, Freytag 1985, J. M. Fry 1989). However, using Clausen's (1978) review, Stiling (1994) concluded that establishment of parasitoid species was successful in only 38% of the worldwide biological-control efforts using parasitoids against *Auchenorrhyncha*. In only 7.7% of the biological-control projects was some degree of control achieved. Reviews of biological-control efforts since 1978 indicate that importations of natural enemies have been done for beet leafhopper, potato leafhopper, and *Edwardsiana crataegi* (Douglas), (Coulson 1988, 1992, 1994) and success of parasitoid establishment was inconsistent (Cameron et al., 1989; Clausen 1978, Waterhouse and Sands, 2001). No predators or pathogens have been introduced against leafhopper pests.

CURRENT TACTICS AND STRATEGIES IN BIOLOGICAL CONTROL

Most attempts to manage GWSS using biological control have involved egg parasitoids, most notably those in the Mymaridae and Trichogrammatidae (Triapitsyn, 2003; Triapitsyn and Phillips 2000; Triapitsyn et al., 2002a, b). Exploration for parasitoids has started in Florida, Texas, and Louisiana in the United States and in Argentina, Chile, and Mexico (Triapitsyn and Phillips, 2000; Triapitsyn et al. 2002b; Triapitsyn 2003). Those selected for evaluation as biological-control agents include species reared from GWSS and from other U.S. leafhoppers (*Oncometopia nigricans* [Walker] and *Homalodisca insolita* [Walker]) and from exotic species (a South American sharpshooter, *Tapajosa rubrimarginata*) (Triapitsyn, 2003; Triapitsyn et al., 2002a). More than a dozen egg parasitoid species have been collected.

Most current efforts focus on native and introduced species of egg parasitoids in the genus *Gonatocerus*, parasitic wasps. Species that have been or are being targeted for importation into California include the mymarids *Gonatocerus fasciatus* Girault, *G. triguttatus* Girault, *G. morrilli* (Howard), *G. novifasciatus* Girault, *G. incomptus* Huber, *G. atriclavus* Girault, and *Acmopolynema sema* Schauff and the trichogrammatid *Ufens spiritus*. Most of them have not been propagated successfully; some have been reared in limited numbers. One native species, the egg parasitoid *G. ashmeadi* Girault, is abundant in California and attacks several leafhoppers including *lacerta (*Fowler) (smoke-tree sharpshooter), but it is effective primarily during the summer. *G. ashmeadi* usually causes relatively low parasitism (30-60%) of the spring GWSS egg population (Triapitsyn and Phillips, 2000). Summertime GWSS egg parasitism by *G. ashmeadi* is higher, often exceeding 95%. The introduced parasitoid *triguttatus* is receiving a great deal of attention for that application.

Biological Control and Pest Abundance

A major constraint on EBPM of GWSS is its function as a vector of PD. The use of biological control of any pest species with parasitoids, predators, pathogens, or another EBPM tactic, is more problematic when the targeted pest being is a vector (Mahr and Ridgway, 1993). The difficulty arises from the relationship between the size of vector populations and disease spread. Biological control attempts is unlikely to prevent either the initiation of disease in uninfested areas or the spread of the disease in areas where it is established because generally only a few individuals are required to initiate the spread of disease. Nevertheless, the release of biological-control agents or the conservation of indigenous natural enemies (if they are effective in substantially decreasing vector population) can slow the spread of the disease. Whether biological-control agents do slow the spread of PD should be confirmed with appropriate research. The ability to reduce disease spread, of course, depends on the relationship between the number of effectively transmitting vectors and the efficiency with which disease spreads from plant to plant, within the context of the economic threshold for the particular crop. Those factors are not known for GWSS, PD, and affected crops, or at best they are only now being investigated. Thus, an initial, important question should be asked: Can natural enemies (whether parasitoids or predators) reduce the GWSS abundance?

Biological-control agents generally are assumed to be most effective when they depend on density; that is, if the effectiveness of released biological-control agents increases as pest density increases. Clearly, that assumes that density dependence is necessary for biological control (but see Hanski et al. 1993; Morrison and Barbosa, 1987). Cronin and Strong (1994) reported that in only 25% of the studies they examined was there evidence of density-dependent response in the Auchenorrhyncha. However, they also reported that egg parasitoids were more responsive to host density than were other types of parasitoids. Clearly, any recommendation for the use of biological control as a means of controlling pest populations or even reducing pest populations requires further research into interactions between GWSS and its natural enemies.

Recommendation 3.11. Basic and applied research should establish protocols for the effective selection of natural enemies, develop strategies to increase the success of inoculative releases of parasitoids, and rigorously evaluate the effectiveness of released natural enemies (Category 2).

Basic and Applied Research on Rearing and Release of Natural Enemies

The release of native and introduced parasitoid species is being considered as a component of EBPM for GWSS. The use of introduced parasitoids such as *G. triguttatus* will likely require the development of rearing, storage, and release technologies. Mass-rearing (which could differ from basic rearing techniques) will be required to augment the population of natural enemies. There are two basic options available for rearing parasitoids or predators: Natural enemies can be reared using GWSS or they can be reared using an alternative host–prey (another alternate leafhopper host for parasitoids or any alternative prey for generalists predators). For either option the host–prey must be reared either on a synthetic diet or on living plants. Although some success has been achieved with live plants, mass rearing GWSS could be problematic. Preliminary data suggest negative consequences for GWSS survival and development when reared at high densities (Lauziere et al., 2002).

One approach to the rearing of GWSS (or another leafhopper) involves the development of a synthetic leafhopper diet and an effective means of providing the diet to feeding insects. The artificial diet presents more problems for leafhoppers than it would for mandibulate insects because leafhoppers have piercing–sucking mouthparts. So, feeding could require the development of some specialized means of delivering the diet to insects (through membranes, for example, or by sandwich packing of a fluid diet). Some diets have been developed for other leafhoppers (Hou and Brooks, 1975; Hou and Lin, 1979; Wei and Brooks, 1979) but the development of a synthetic leafhopper diet that is appropriate for successful mass rearing is difficult (Mitsuhashi, 1979). There are preliminary efforts to develop such a diet, and any diet that is developed must be relatively inexpensive, considering the number of insects likely to be needed.

Glassy-winged sharpshooters, like other leafhoppers, can be reared on living plants. However there is some doubt about whether a large enough number of herbivores can be produced efficiently that way, and appropriate economic analyses have not been done. Significant improvements in any of the approaches will be needed to produce sufficient numbers of one or more parasitoid species to implement effective, large-scale field releases over the extensive acreage affected by the PD–GWSS. The efforts required to undertake the needed basic research and to implement a mass-rearing program that will produce vigorous and competitive natural enemies are likely to take many years and substantial funding (Neuenschwander et al., 1989).

Recommendation 3.12. Support for classical biological control (inoculative releases) is preferred over augmentation if inoculative releases result in self-sustaining populations and can be shown to be less costly than augmentation (Category 2).

Economic Feasibility of Biological Control

The determination of whether control exerted by natural enemies is sufficient and economically feasible should be made within the context of economic thresholds. There are, of course, several to consider depending on the crop and the type of pest. Economic thresholds are the levels at which control measures are implemented to prevent a pest population from reaching the density called the economic injury level—the lowest population density that will cause economic damage. Another important threshold is the economic damage threshold—the amount of damage level that justifies the cost of implemented controls (Dent, 1991). Thresholds can be used to determine whether single tactics, such as biological control, or a set of EBPM tactics should be incorporated into an EBPM scheme (Reichelderfer, 1981). The establishment of a threshold for a vector species is a daunting task. There currently is no established economic threshold for GWSS, and if such a threshold were to be determined or estimated, it would likely amount to a relatively few individuals. Small numbers of GWSS can transmit enough *Xf* to cause economically important disease. Development of thresholds is complex and subject to some debate, and even when thresholds are developed they can differ among crops or they can differ depending on the intended use of a crop (wine grapes vs. raisin grapes).

Given what is known about the biological control of vectors, the use of predators and parasitoids to control vector populations is not likely to provide a broadly applicable, effective resolution to the PD problem (Harpaz, 1982). However, only rigorous threshold data will provide an absolute determination of the likely usefulness of biological control. Biological control of GWSS should be viewed as one of many tactics to force abundance of populations to fall below economic thresholds. This presumes that all tactics, in the aggregate, will yield economically important pest reductions.

Determining the economic competitiveness of alternative EBPM tactics is complex and often can be daunting because it could force reliance on assumptions made because of gaps in available data. Determining cost–benefit ratios in circumstances in which partial control is achieved, is perhaps even more difficult. It could be difficult to assign an economic value to the effect of tactics such as biological control, particularly when its use "merely" reduces pest abundance rather than bringing populations below the economic injury level. Many economic assessments of biological-control programs have focused on the value of the crop yield salvaged. In contrast, assessments could determine the economic value of biological control compared with other tactics or strategies (Andres, 1977; Harris, 1979; Hussey, 1985; Zeddies et al., 2001).

"The economic feasibility of any given biological control strategy is unique, and depends on and will vary with the independent and interactive effects of the ecological and economic characteristics of the crop-pest system considered" (Reichelderfer, 1981). No single estimate is representative or indicative of the overall economic feasibility of a biological-control strategy (Reichelderfer, 1981). In general, economic analyses, even when rigorous, can involve assumptions (Headley, 1985) that influence determinations of cost–benefit ratios. They include the amount of control achieved by biological control relative to the use of insecticides (Reichelderfer, 1979), the rate of spread of a pest (Ervin et al., 1983), or the value assigned to environmental quality. Assessments might disregard farmer economic inputs, market dynamics, and other externalities (Reichelderfer, 1981). The factors considered in economic evaluations might differ depending on who the evaluator is (Hussey, 1985). Thus cost–benefit ratios developed for growers, consumers, producers of biological-control agents, or governments could differ in part because each "end user" might choose to include only certain variables or assign different economic value to each factor (Carlson, 1988). End users might include the costs of acquiring a biological-control agent (the costs of foreign exploration, quarantine, production, quality control, storage, transport, release technology) or the costs of alternative tactics, such as the development of insecticides used to control the pest, or the costs of the implementation of alternative tactics. Similarly, the value of improvements in environmental quality, environmental risks and their consequences, or market demand for the crop also varies in different assessments.

There are no economic thresholds to assist managers in PD-affected crops, although methods for their development are available (D.C. Hall, 1988;

Liu et al., 1999; Moffitt, 1986; 1988; Osteen et al., 1988;). All of this points to the need for economic research.

Recommendation 3.13. Research should assess the economic feasibility of biological-control tactics and strategies (Category 2).

Recommendation 3.14. Biological-control tactics within EBPM schemes should be evaluated within the context of working economic thresholds (Category 2).

Compatibility of Management Tactics and Maximizing Effectiveness

There are several constraints on the use of EBPM. In many agroecosystems, even the implementation of IPM currently consists of little more than the application of a variety of insecticides (Ehler and Bottrell, 2000), few of which are benign to the target species' natural enemies. To achieve the best probability of success, it is necessary to establish conditions that optimize the survival and effectiveness of natural enemies. These conditions would include the reduction of insecticidal drift, and the use of insecticides that selectively target the pest species and are nontoxic to natural enemies (Hull and Beers, 1985). The more accurate the timing of sprays, the more likely that exposure of natural enemies to insecticides will be minimized. Ensuring that these "favorable conditions" for natural enemies persist will likely increase the effectiveness of biological control.

Recommendation 3.15. Research on the use of biological-control agents (predators and parasitoids) should be a priority in commercial vineyards where there is a minimal use of insecticides in vineyards where selective insecticides that are nontoxic to natural enemies are used, or in where the timing of insecticide use is such that mortality to natural enemies is minimal. Similarly, research should be supported that advances the use of biological-control agents in areas or habitats where insecticide use can be severely restricted or eliminated. Areas for study could include riparian habitats, watershed areas, wetlands, and urban and suburban green areas (Category 2).

The committee's recommendations assume that the objective of biological control is not to prevent the GWSS from vectoring PD but to reduce the GWSS reservoir persisting in nonagricultural areas on noncrop hosts.

Some of the constraints on the use of biological control are the limitations of the organisms themselves or of the environments in which they must exist. Introduced species, if successful, will establish viable populations but could fail to do so at the densities needed for effective pest management. Thus, it might be necessary to augment (when economically feasible) or conserve populations of introduced species or native natural enemies. Because native parasitoids are species that occur in affected areas but have not provided the necessary amount of control, enhancing their effectiveness is likely to depend on the development of conservation strategies that improve their habitat and provide missing or limited requisites. The habitats to which they are introduced might not be optimal for the natural enemies' survival and effectiveness and thus, where possible, those conditions should be altered or manipulated to conserve natural enemies, through provision of sugar or nectar sources for adult natural enemies, introduction of alternate hosts or prey, or maintenance of a toxin-free habitat, for example. Similarly, any manipulation, including alterations in viticulture practices, that enhances overwintering survival of natural enemies can be important, particularly because mortality imposed by parasitoids in the spring generation of the GWSS appears to be lower than in summer. Nevertheless, the rigorous experimental confirmation of the importance of such manipulations in agroecosytems has only recently been undertaken, and if manipulations are found to be practical for that agroecosystem, they too should be evaluated experimentally.

Environmental Impact of Biological Control

Many of the consequences of EBPM are unknown. The use of introduced natural enemies, sterile insects, microbial pesticides, and pheromones has sometimes directly or indirectly affected not only the targeted pest species but nontarget plants or other insects. The release of biological-control agents raises ecological concerns, particularly when natural enemies have relatively broad host ranges, as do many of the parasitoids being considered for the use against the GWSS (Triaptisyn et al., 2003). Because many of the parasitoids will parasitize the eggs of other leafhoppers (in the tribes Proconiini, Athysaniini, and others), the effect on leafhopper biodiversity is a valid area of concern that merits investigation. However, important risks also are associated with the failure to control the pests. Thus, concern about the consequences of releasing natural enemies must be balanced against the effect of outbreak levels of GWSS on leafhopper biodiversity or in biodiversity in general. A pest species such as GWSS, which, in California, is a nonindigenous disease vector with a broad hostplant range, can significantly alter unmanaged native ecosystems. The use of introduced biological-control agents has provided significant benefits and fewer risks than have most other control tactics and approaches, although the environmental consequences of biological control are still the subject of considerable debate (Howarth, 1991; Wajnberg et al., 2001).

Human exposure to agents or products used in EBPM can occur at many stages of the production and release of natural enemies. Employees of the facilities in which natural enemies are reared can be exposed to the organisms or to materials used in their rearing. Farm personnel and residents of nearby communities also risk exposure. Although perhaps unlikely, consumers might unknowingly consume microbial pesticides or fragments of arthropod natural enemies in foods. Despite that, few human health effects—with the exception of allergic reactions—or risks attributable to EBPM agents or products have been reported in the literature. Health concerns arise more often from the use of microbial pesticides.

OTHER OPTIONS

The recommended incorporation of some tactics and approaches into an EBPM scheme does not mean that other tactics will not be shown to be effective as more research is done. However, available information on leafhoppers in general and on GWSS and its host plants in particular, suggests that the potential of some approaches to the management of the PD–GWSS is highly questionable. In some cases, the absence of data makes an approach impossible to evaluate.

Insect Growth Regulators

Formulations of chitin inhibitors that affect an insect's ability to develop from one instart to the next have been evaluated. Buprofezin, diflubenzuron and benzoylphenyl were evaluated by Akey and colleagues (2002), and Toscano and colleagues (2002) have studied buprofezin and pyriproxyfen. The chitin inhibitors are applied using standard air blast field sprayers. Akey and colleagues reported that buprofezin controlled eggs and nymphs at a rate of 90–100%, and produced 70% control of adults. Diflubenzuron was nearly as effective, and benzoylphenyl was less effective than the other two inhibitors. Toscano and colleagues reported that buprofezin was effective against first-instar GWSS but that higher doses were required to control third and fourth instars. Pyriproxyfen was effective against GWSS eggs but not against nymphs (Toscano et al., 2003). The effects of chitin inhibitors on beneficial insects were not reported.

One or two formulations that restrain development of chitin have been reported to be effective in preventing nymphs from advancing to the adult stage. Because the nymphs tend to reside on the underside of leaves to avoid predators some new application technology would be required to deposit the spray on those surfaces. Charging fine spray particles can enhance such deposition. However, there are still questions to answer about the amounts of inhibitors required for field control and about the means of application.

Biorational Insecticides

Sugar esters, insecticidal soap and neem oil derivatives constitute a new class of insecticides that is being evaluated by organic growers for GWSS control. In one study, sucrose octoanate, sorbitol octoanate, and insecticidal soap were applied with a hand gun sprayer. Several neem derivatives were applied by air blast sprayer. Those materials are being investigated as a means for GWSS control that circumvents conventional chemical insecticides. Depending on the rate of application, the sucrose materials produced about 98% adult mortality; the insecticidal soap produced 97% mortality rates (Paterka, 2001). The neem derivatives resulted in 33–48% mortality of eggs, 62–78% in nymphs, and 16–50% in adults (Akey, et al., 2002). All of those biorational insecticides are nontoxic to humans and believed to be environmentally neutral.

Research results for biotrational insecticides indicate acceptable control provided by sugar esters and possibly by insecticidal soaps. This is a recent area of research and additional studies would be useful to more clearly develop the application process for such materials. Important questions must be answered: What amounts of these materials should be applied? Do any of them harm beneficial insects?

Biological-Control Agents other than Parasitoids

Biological-control agents of equal or greater effectiveness, such as entomopathogenic fungi, predators, and parasites, could still be developed. The use of entomopathogens such as *Hirsutella*, a fungus that is known in the southeastern United States to affect sharpshooters, is being explored. However, abiotic constraints, including the need for high humidity, can hamper the use of fungi in many agroecosystems (Soper, 1985). Other options will require considerable basic and applied level research. For example, many of the potentially useful GWSS predators are generalists, and although some of those species have been identified, not all are known. The species that actively feed on GWSS would need to be identified, but more important, their influence on the survival and numerical increase of GWSS would need to be determined. Although many management innovations have resulted from similar research and thus should be encouraged and funded, generalist natural enemies could dramatically affect other indigenous species so it will be important also to study their ecological consequences.

Mating Disruption

It is not currently practical to use pheromones to cause GWSS mating disruption as part of an EBPM strategy. Although sex pheromones have been used to manage other pests, there is no empirical evidence of pheromone-mediated sexual communication in leafhoppers. Available evidence suggests that mating in most leafhoppers, including species that vector plant pathogens (Claridge, 1985) is mediated by substrate-borne vibrations (R. E. Hunt et al., 1992; R. H. Hunt and Morton, 2001).

Behavior-Modifying Chemicals

Relatively little is known about the host plant chemical compounds that influence the way pest insects find them, begin to feed on them, or initiate other behaviors. The use of behavior-modifying chemicals as attractant lures or repellant sprays is unlikely to result in the effective control of PD–GWSS. As plant and other influences on GWSS host preferences are uncovered, compounds might be identified that could make it practical to use synthesized or natural compounds.

Sterile Male Technique

The sterile male technique has been used to manage pest insects; such as medflies, tsetse flies, and screwworms. Factory-reared flies that have been sterilized, usually by exposure to gamma radiation, are released into a natural population. The males are expected to mate with feral females, thus inhibiting the females' ability to reproduce. The approach works only if the females mate once, if the released males are competitive with feral males, and if the number of released males at least matches that of feral males. The use of the sterile male technique has been applied against few pest species, in part because of the technique's biological and ecological requirements. Substantial financial and infrastructure resources also are required to rear and sterilize the millions of individuals generally required. To achieve control, the total pest population in a region must be targeted. Reinfestation of individuals from adjacent areas often interferes with the technique and thus must be prevented with quarantines, insecticidal sprays, or continued releases of sterile males to create a barrier zone that is wider than the flight range of the insect pest. Research has been insufficient, but at present the sterile male technique does not seem to be a useful approach for GWSS management.

Mass Trapping

The use of mass trapping generally involves traps that are baited with an attractant chemical derived from a living organism. Traps must be distributed over a large area, in a specific pattern. The traps and chemicals are expensive, however, and the need for formulations that are more attractive than are compounds that occur in the ecosystem and the difficulty with the deployment of traps limit the usefulness of the approach. Because there are not data on the use of this approach to control GWSS, the method is not recommended.

INSECTICIDES

Although studies of EPBM techniques could eventually lead to control of PD, it is probable that several years of study with field verification will be required before they are accepted commercially. Until then, grape growers are faced with an expanding infestation that portends serious economic consequences. Research that addresses the use of chemical or biological pesticides offers the most near-term solution to controlling and possibly eliminating the GWSS population in California vineyards and orchards.

Many pesticides can be effective against GWSS eggs, nymphs, and adults (Akey et al., 2002; Toscano and Castle, 2002). GWSS eggs, nymphs, and adults prefer different plants at different stages (Daane and Johnson, 2002). Citrus and grape are highly preferred for egg masses. Oleander and grape are preferred by the nymphs and adults, and adults also favor *Agapanthus* (African lily). Two peak periods of GWSS egg density on citrus have been identified, one in March and April and the other in July and August (Coviella and Luck, 2003). Coviella and Luck (2003) reported a single peak of nymph activity in May and June and an adult activity in June and July. T. M. Perring and Gispert (2002) reported a peak in adult activity on grape and citrus in June and July. Knowing the preferred locations of eggs, nymphs, and adults and the time of their peak presence can help inform the choice of a control strategy. Several pesticides have been studied for their effectiveness against GWSS at different stages of development. They are discussed by class in the following sections.

Systemic Formulations

Systemic pesticides act through a plant's vascular system. Neonicotinoids, for example, are introduced into the plant either through the root system or through the leaf cuticle. The pesticides kill the GWSS nymph or adult as it feeds on the xylem fluids. When applied through drip irrigation, the pesticide is taken up by the root tips and transported through the xylem tissue throughout the plant. It takes about 10 days for the compound to reach all parts of a grapevines and about 6 weeks for a citrus tree to become infused (Toscano and Castle, 2002). When applied as a foliar spray, the pesticide diffuses through cell walls and is ingested by GWSS during feeding. There is some evidence that systemics applied to leaves can be diluted by sprinkler irrigation, so that there is incomplete penetration or diffusion (Grafton-Cardwell, 2002).

Applying systemics through drip irrigation systems is an efficient way to treat the whole plant. There would be some loss in the root zone, but worker exposure and drift are minimized. Mortality of 99% of small and large nymphs and 74–79% of adults can be achieved by this method (Akey et al., 2002). Pesticide retention is significant, and data indicate that imidacloprid remains effective in a plant for 1 year (Toscano and Castle, 2002).

Foliar application of systemics can be done by aircraft, by air blast sprayers or by hydraulic sprayers. Aircraft spraying is quick, but it results in significant drift. Air blast sprayers require a large amount of power, are very inefficient, and produce drift—as much as 256 m after spraying through a canopy in a calm wind (Derksen et al., 2000; Fox et al., 1993). Foliar application of neonicotinoids (where they are translaminar) is effective for a shorter period—3–4 weeks—than is application by drip irrigation, which remains effective for 8–11 weeks (Grafton-Cardwell, 2002). Research comparing the use of air blast spraying with air-assisted electrostatic charging of a fungicide indicated that the dislodgeable foliar residue from grapevines was 68% less with the air blast sprayer, even though the application rate for the electrostatic sprayer was a tenth that of the air blast sprayer (Welsh et al., 2000). This suggests that research should be done to determine whether some of the problems accompanying foliar application of the neonicotinoids can be reduced with a more efficient application technology.

Systemic application is better than foliar application because it requires a smaller amount of the substance to achieve the same plant protection—although that needs verification—because worker exposure and drift are minimized. Research on efficient spray application technologies could lead to reduction in drift for spray applications with ground equipment.

Several questions about the use of the compounds themselves remain, including the quantification of the efficiency of transport into the plant root system and its persistence in the soil after drip irrigation. There also have been reports that repeated use of neonicotinoids, in this case, Assail causes flare-ups of infestatation by spider mites (Michigan State University, 2002).

More serious questions concern the presence of systemic compounds in harvested grapes and their possible consequences for human health. Where systemic pesticides are applied to the surfaces of leaves, what is the role of absorption and adsorption through the cuticle? Their apparently longer term effectiveness warrants intensification of research into the mechanisms of their uptake and movement through the xylem of the plant. More information is needed about their residual presence in the xylem and any effect that might have on grape quality and safety for consumption. Finally, there is some evidence that sprinkler irrigation can dilute or wash out or off systemic formulations. Does this pose a hazard to vineyard workers? When applied by aircraft or air blast sprayers is there a chance that the material will drift into adjacent areas and affect human or animal health? Animal studies have shown neonictinoids are likely to be moderately toxic to humans. They can be highly toxic to birds and bees, although studies show that birds can learn to avoid seeds treated with neonictioids (EXTOXNET, 2004).

Nonsystemic Insecticides

Pyrethroids, organophosphates, and carbamates generally are effective but for a shorter period than systemic compounds—3–4 weeks compared with almost 3 months after application (Grafton-Cardwell, 2002). Nonsystemic insecticides are commonly applied by air blast sprayers. Where they are used to kill GWSS eggs or nymphs it is desirable to place the compound on the underside of the leaves, where the eggs and nymphs reside to avoid predators. Charging small droplets can significantly increase deposition on lower leaf surfaces (Splinter 1968a, b, c). Manufacturers of air-assisted electrostatic sprayers usually recommend application at one-half the rate of active ingredient. There are no reports of spray application equipment used by any of the researchers funded by the PD program other than the air blast sprayers in the sponsored research program reports. Pyrethroids, organophosphates, and carbamates provide close to nearly 100% kill rates for eggs and nymphs and 70%–80% kill rates for adult GWSS (Akey et al., 2002). The are reported to last 2–3 weeks for adults but less than 2 weeks for eggs. Several nonsystemic chemical insecticides have been shown control nymph and adult GWSS, but their effectiveness generally lasts only a few days. In contrast, the systemics show persistence over a growing season. The most effective use of nonsystemic insecticides therefore would be as a rapid response to an invasion of GWSS from adjacent host plants.

Most of those chemicals have exposure limits for field workers and dissipation times before human consumption. There is evidence that carabaryl (Sevin) residue can be dissipated with repeated sprinkler irrigation (Grafton-Cardwell, 2002). Some compounds in the organophosphates group are highly toxic; and chlorpyrifos and dimethoate have been found to be moderately toxic to humans (EXTOXNET, 2004) so there is concern about drift into adjacent residential areas, pasture, or croplands. Organophosphates are readily absorbed by humans and can affect the nervous system through the inhibition of acetylcholinesterase (IOM, 2003; Michigan DNR, 2004).

In addition to determining the toxic effects of those compounds, research should be done to find ways to reduce the amount applied and minimize drift from the point of application. As with any pesticide, efficient application is essential to minimizing the amount of material applied. Conventional application technology—which used air blast sprayers or aircraft—poses inherent problems with the unintentional drift of toxic substances. Commercial application equipment (Law, 1978) is available that effectively charges fine spray particles. The question of whether the amount of pesticide can be reduced through more efficient application methods—while retaining the desired GWSS control level—could be worth investigating.

Inert Materials

Finely divided kaolin, marketed as Surround, has been found to repel GWSS nymphs and adults to the extent that they refuse to remain on the plant or to feed (Paterka, 2002; Paterka and Reinke, 2003). A fine coating of this material deters GWSS from settling on treated plants and therefore from oviposition. The material is applied biweekly using air blast sprayers. Kaolin clay has no adverse effects from contact or ingestion.

However, Grafton-Cardwell and Reagan (2003) found that the kaolin coating also repelled the parasitic wasps *Aphystus melinus* and *Comperiella bifasciata* and prevented them from attacking California red scale, an unintended consequence to the use of kaolin in citrus. California red scale is not a problem for grapes. The white coating on the leaves, although harmless, raises esthetic concerns that the clay on the grapes could be visually disconcerting to tourists—a major source of revenue for the vineyards—and could taint wine produced from them.

Applying a coating of finely divided kaolin clay has been found to effectively repel both GWSS nymphs and adults. However, the mechanism for this response is poorly understood and the indirect effects (e.g., the impacts on beneficial insects) are also unknown.

ECONOMIC CONTROL STRATEGY

In the short-term, the management of PD is likely to focus on the control of GWSS by pesticides, despite their hazards. The economic sustainability and effectiveness of pesticide use is closely tied to how, when, and where pesticides are applied in the field. For acceptable economic control of GWSS, and to minimize workers' exposure to the pesticides a precise amount must be applied at the best time, in the correct locations, and for the lowest cost. The factors involved in understanding how pesticides can be used most cost efficiently represent a good case study for the economic analyses needed for all prospective management tools.

Amout of Pesticide Applied

Pesticides are chemical formulations that are intended to kill insects or plant pathogens. Their toxicity to humans is always a concern; even sulfur, which has had a long history of use used to control mildew is being challenged because of its possible allergenicity. And there is always the potential for unintended consequences, as is classically illustrated by the effect of dichlorodiphenyl-trichloroethane (DDT) on the eggshells of birds. Even the inert clay kaolin has met resistance because it whitens grape leaves and because of the concern that it could alter wine flavors. All pesticides carry costs of application, and they all have costs of acquisition.

Therefore fewer applications are better, but the challenge is to determine the minimum amount that will provide acceptable control. The 2002 volume of the *Proceedings of the Pierce's Disease Research Symposium* (CDFA, 2002*b*) contains reports of several studies that evaluate lethal doses for GWSS in a spectrum of pesticides. The work of Blua and Walker (2002), for example, who investigated sublethal doses of neonicotinoids, provides an excellent regression of dose to mortality. That type of study should lead to a rational basis for setting acceptable rates of application.

Timeliness of Application

The best time to control GWSS is before it reaches the adult stage, when it becomes more mobile and can spread the PD as it feeds. Daane and Johnson (2002) reported significant differences in the locations of eggs, nymphs, and adults on host plants. Citrus, gardenia, grape, and hibiscus were preferred for egg laying; oleander and grape were preferred sites for nymphs. Grape and citrus were the primary host plants for adults.

T.M. Perring and Gispert (2002) reported a peak in adult GWSS trap catches in July. If GWSS primarily overwinters as adults, and there appears to be a small population peak in February and March, it would be efficient to schedule a control application with the emergence of the adults at the location of first egg laying on neighboring host plants, such as gardenia and citrus. Grape will be dormant at this time. After the eggs hatch, another application on oleander, hibiscus, and euonymus would target nymphs. Adults should then be targeted in citrus. A second control sequence before the peak in June and July would be indicated, and grapes should be included at this point. Discussions with the research scientists who provided background information to the committee indicate that feeding by GWSS on grapevines after July can infect plants, but that the effect is minimal because the infected stems are pruned. This is reinforced by studies by Coviella and Luck (2003), who reported peaks in egg densities in citrus in March and in August; a peak in the nymph population in citrus was found in June and a peak in the adult population was found in August. They observed high egg mortality during the August in egg density.

Location of Pesticide Application

Conventional application of pesticides has been found to be only 1%–2% efficient for delivering the active material to the effective site (F.R. Hall, 1985; Pimental and Levitan, 1986). This clearly is an area for improvement.

Egg masses generally occur on the bottom surfaces of the host plant leaves. Nymphs also hide on lower leaf surfaces. Mature GWSS evidently feed on larger stems than do smaller leafhoppers. This information should dictate the target area for control.

Toscano and colleagues (2002) reported on simple and effective means of GWSS control that used systemic application of imidacloprid (Admire) through the root system of grapes and citrus. Nymphs and adults were controlled with a single application per season for areawide management programs. The best control was achieved with the application of the pesticide at a rate of 32 oz/acre. The researchers also tested rates of 20 oz and 16 oz/acre. The pesticide moved through the vascular system in 10 days but required about 6 weeks for citrus. Because imidacloprid can be applied through drip irrigation, it has major advantages as a potential control method.

Systemic pesticides can also be applied by aerial or conventional ground rig spraying equipment, requiring only that the active ingredient be applied to the leaf surface where it can be absorbed. This allows the formulation to be introduced more quickly into the vascular system where GWSS feeds, but one would expect drift losses because vineyards and orchards have large cross-sectional areas that are not occupied by fruit crops.

Many pesticides are applied by air blast sprayers, at 80–100 gal/acre at velocities up to 60 mph. Drift can be measured as far as 100 yd away after spraying through a tree canopy in relatively calm wind (Derksen et al., 2000 Fox et al., 1994). The air blast system uses a large amount of energy, requires the transport of large amounts of solution, and presents obvious concern about drift.

Welsh and colleagues (2000) compared the results from an application of fungicide to grape by air blast sprayer at a rate of 80–100 gal/acre with results from application by electrostatic-spray-charging nozzles at 8–10 gal/acre. They measured dislodgeable foliar residue because they were interested in determining exposure of workers to fungicide. They reported that, at an application of 4 oz/acre a.i., leaf deposition for the air blast sprayer was 68% of that provided by the electrostatic sprayer, as indicated by dislodgeable foliar residue, even though the electrostatic application was one-tenth the volume.

Economic Research

Several current research projects are addressing the effectiveness of a spectrum of GWSS control strategies. The commonly accepted method for pesticide application—the air blast spray system—is inefficient, uses an excessive amount of energy, and creates problems with drift. Newer methods—such as drip irrigation application of systemic pesticides—offer several advantages. The use of air-assisted electrostatic sprayers should be evaluated for application efficiency and drift. Development of that technology for citrus orchards would be appropriate because citrus hosts all GWSS stages. There have been no engineering studies to evaluate the potential for reduction in pesticide application rates or for reduction in drift. Minimizing application rates produces concomitant reductions in cost. Reducing drift addresses a sensitive issue, especially in residential areas. Research is needed to assess the feasibility and effectiveness of methods other than air blast or aircraft spraying, including recirculating tunnel sprays and the charging of fine sprays—as means for improving deposition efficiency and decreasing pesticide drift.

Any new pesticide offers the potential for undesirable or unanticipated consequences. Therefore the potential risk to agricultural workers, to wildlife, to the environment, and to crop quality must be determined as soon as a new control technology is identified. The committee, therefore, makes the following recommendations:

Recommendation 3.16. Control strategies should be pursued that limit the use of insecticides to narrow-spectrum, sustainable formulations that are minimally incompatible with ecologically based approaches to pest

management. A premium should be set on minimizing the negative consequences of pesticide use for human health and environmental quality.

Recommendation 3.17. Research should assess the economic feasibility of specific chemical control strategies and develop decision and cost models to guide growers in setting up chemical control methods for GWSS (Category 1).

4

Plant–Pathogen Interaction

A study published by the National Academy of Sciences (NAS 1968) described six general principles for plant disease control: avoidance, exclusion, eradication, protection, disease resistance, and therapy. In practice, the most widely used and effective measures for controlling xylem-localized plant pathogenic bacteria are exclusion, (as in the use of uninfected propagative materials for control of the bacterial wilt pathogen *Ralstonia solanacearum*, or host plant disease resistance conferred, for example, by the use of major genes for resistance to control bacterial blight of rice caused by *Xanthomonas oryzae* pv. *oryzae*. That limited repertoire does not preclude the development of effective control approaches that use other principles, but the development of novel strategies or the rational application of existing disease management strategies does require understanding how, when, and where disease develops and spreads. In the case of Pierce's disease (PD), this also requires and understanding of the basic biology of the three partners involved, *Xf* (*Xylella fastidiosa*) grape, and insect vectors. This chapter details the current understanding of how *Xf* and grape plants interact to result in PD, and it identifies the information needed to develop effective management strategies to interfere with that interaction. Several comprehensive reviews are available that provide more in-depth discussions of the disease interaction (Hopkins, 1989; Hopkins and Purcell, 2002).

ANALYZING VIRULENCE

The disease cycle of *Xf,* the bacterial pathogen that causes PD, involves intriguing interactions with plant and insect hosts. The bacterium persists and multiplies in both types of hosts. In plants, colonization is limited to the xylem. Several species of xylem-feeding insects, predominantly leafhoppers (Almeida and Purcell, 2003; Hewitt et al., 1942; Purcell, 1979) but also spittlebugs (Severin, 1950), can transmit *Xf* while feeding on host plants. Juvenile insects can transmit the pathogen until they molt (Purcell and Finlay, 1979) and adult insects transmit *Xf* throughout their lifespans (Severin, 1949). After entering the plant, the pathogen multiplies, forming microcolonies at the inoculation site (Hopkins, 1985; Tyson et al., 1985). The bacteria then efficiently and systemically colonize the plant by moving within and between xylem vessels (Newman et al., 2003). Movement of the pathogen between vessels is correlated with the expression of pathogen genes encoding degradative enzymes that are predicted to facilitate movement by degrading the pit membranes between vessels (Scarpari et al., 2003). Although the pathogen spreads through the plant and is detected in low numbers in many vessels, symptoms do not appear unless vessels contain high populations of bacteria (S.M. Fry and Miholland, 1990; Newman et al., 2003). *Xf* is not observed outside of the plant's vascular system. Recent genome sequence data and comparative analyses with sequences of other bacterial pathogens show that *Xf* colonizes insect and plant hosts and induces disease in the plant host using genes that are expressed from a relatively small (2.5 Mb) genome (Simpson et al., 2000).

The complete genome sequence of *Xf* (including sequences for two strains and draft sequences for another two) and the microarrays based on the sequence are facilitating the identification of genes that could lead to effective management strategies. In fact, many genes have been implicated or eliminated from consideration based on comparison of the *Xf* genome sequences with other pathogenic bacteria (Van Sluys et al., 2002). For example, genes encoding the type III secretion system, which are common to and essential for virulence in many mammalian and plant pathogenic bacteria, are not found in *Xf.*

Several genes similar to those encoding putative virulence factors were identified in *Xf.* The presence of sequences related to virulence genes found in other organisms can inform the process of creating hypotheses; it does not prove that the genes are involved in pathogenicity. To determine gene function, in this case in the induction of disease, requires systematic analysis of mutagenesis and complementation, gene expression, physiologic and biochemical activity, and pathogen–host plant interactions. Several hypotheses that describe putative roles of particular genes in disease have been built from comparisons of genome sequences. Targeting genes for functional analysis will allow critical questions related to disease to be addressed. Some of those questions are presented below.

Cell Attachment

Is attachment to cells in the insect vector or host plant critical for transmission and induction of disease? Genomic analyses indicate that *Xf* strains have genes related to those that encode hemagglutinins, adhesions, sticking pili, and fimbriae that could mediate different attachment strategies in the insect gut and plant xylem vessels. Attachment of bacteria to host tissues is important for colonization and pathogenicity for several pathogenic bacteria (Hultgren et al., 1993; Ojanen-Reuhs et al., 1997). *Xf* exhibits polar attachment to the insect cells (Brlansky et al., 1983; Purcell et al., 1979) and, although not polar, attachment to plant cells (Huang, 1986; Mollenhauer and Hopkins, 1974). Two genes, *fimA* and *fimF*, that encode major fimbrial proteins related to the Type I fimbriae of *E. coli* (Peek et al., 2001) have been found in *Xf*. Site-directed mutants of the *Xf fimA* and *fimF* genes were developed to study their requirement for attachment in the development of virulence and disease (Feil et al., 2003). When they were grown in culture, the mutants, produced in two *Xf* strains from grapevines, were deficient in the two major fimbrial proteins and they exhibited reduced fimbriae size and number, cell aggregation, and cell size, compared with the parent strains. Both mutants remained pathogenic to grapevines, although their populations were slightly smaller than those of the wild-type strains. There is insufficient evidence to determine whether the mutations affect the insect transmission of *Xf* or whether they are important in attachment to the insect.

Targeted experiments guided by genome comparisons have led to the identification of genes that are essential to vector colonization. *Xf* contains a homologue of the *Xanthomonas campestris* pv. *campestris rpfF* gene, which is required for synthesis of a diffusible signaling factor (DSF) that regulates virulence (Barber et al., 1997; Slater et al., 2000). Mutational analysis of the *Xf rpfF* gene revealed that the gene also is required for production of DSF (Newman et al., 2004). Although the *Xf rpfF* mutant was not transmissible by insects, the mutants that were mechanically inoculated to plants were more virulent than were the wild-type *Xf*. Colonization of the insect foregut by the mutants was severely impaired, and it was associated with an inability of the bacterium to form biofilms in the insect. However, the mutant formed biofilms in the plant xylem. Why the *rpfF* mutants are more virulent to grapevine is not understood.

Motility and Disease

Is motility of *Xf* critical for disease? It is not clear whether *Xf* is motile within xylem and, if so, what significance motility would have for pathogenicity. The *Xf* genome does not contain sequences related to flagellar genes, and there is no evidence for flagellar motility. However, the genome sequence does contain sequences related to fimbrial and pili genes; there are at least three Type 4 fimbriae gene clusters in *Xf*–CVC and *Xf*–PD. Some of the genes associated with Type 4 pili, such as *fimT*-, *pilZ*-, and *pilA*-like genes, are present in more than one copy. Type 4 pili are involved in a sum of bacterial processes as adherence to surfaces, cell–cell interaction, twitching motility, and biofilm formation. Other Type 4 pili serve as receptors for bacteriophage and are required by some bacteria for natural transformation (Kang et al., 2002). Type 4 fimbriae also are involved in adhesion, surface translocation (twitching motility), and phase variation (Gerlach et al., 1989). It is not known whether products of those genes are involved in movement or adhesion of *Xf* within plant xylem vessels or the insect foregut

Virulence Regulation

How are virulence genes regulated? The virulence genes of bacterial pathogens are frequently regulated by host signals, such as wound compounds or particular nutrient conditions, or through bacterial cell–cell signal molecules, such as those involved in quorum sensing (Morris and Monier, 2003; Parsek and Greenberg, 2000; Parsek and Singh, 2003). *Xf* contains genes that could be involved in quorum sensing and that could be important in sensing population size for activation of virulence genes. Gene array- and proteome-based studies demonstrate that activation of different gene networks is associated with different experimental growth conditions of *Xf*–CVC strain 9a5c (de Souza et al., 2003; Nunes et al., 2003; Smolka et al., 2003).

Symptom Expression

What genes are involved in host symptom expression? Genome analyses have identified many genes that are similar to those that encode pathogenicity factors in other bacterial pathogens. Genes related to those for secreted toxins in other pathogenic microbes have been found in the *Xf* genome. The role of those genes in the scorch phenotype characteristic can now be explored. Other genes are similar to those that encode enzymes that produce xanthan gums, which could be involved in biofilm formation and vascular plugging, or that cause degradation of plant cell walls, allowing movement of bacteria between and within vessels. In addition to gum production and structural genes for fimbriae and pili, genome sequencing uncovered in *Xf* the presence of genes that encode large proteins similar to hemagglutinins (FhaB) from *Bordetella pertussis* and *Neisseria meningiditis*. FhaB protein is associated with *Neisseria* species that induce disease (Klee et al., 2000) and in *Bordetella*, FhaB protein has been implicated in adhesion and tissue invasiveness (Ishibashi et al., 1994). In another plant pathogen, *Erwinia chrysanthemi*, an FhaB homologue (HecA) contributes to the early stages of bacterial infection and epidermal cell death on the plant host (Rojas et al., 2002). Like *Xf* strains, the plant pathogen *Ralstonia solanacearum* also carries multiple copies of FhaB homologues (Salanoubat et al., 2002), however, none is as long as are those of *Xf*. The genes that encode those proteins in *Xf* could be as long as 10,000 bp, which is 10 times larger than the usual size of a bacterium gene. It is not known whether *Xf* FhaB homologue are responsible for disease symptoms.

The availability of the genome sequence for several *Xf* strains and for other bacterial pathogens and the development of techniques that permit mutation and complementation analyses of target genes in *Xf* (Guilhabert et al., 2001; Guilhabert et al., 2003), provide opportunities to systematically assess the roles of genes in pathogenicity. Studies are already identifying genes essential to pathogenicity that are potential targets for management strategies. To develop novel management strategies based on interference with bacterial pathogenicity, the committee makes the following recommendation:

Recommendation 4.1. A systematic analysis of *Xf* pathogenicity should be accomplished with a combination of biochemical, genetic, and genomic analyses. Such research lends itself to a collaborative approach (Category 2).

TOWARD HOST PLANT RESISTANCE

It is not well understood how the *Xf*–plant interaction results in disease symptoms, but in general, pathogens that target the xylem induce water stress in the host plant by increasing resistance to water flow (Tyree and Sperry, 1989; Zimmermann, 1983). In fact several physiologic changes occur in grapevines infected with *Xf* that are also observed commonly in hosts infected with the pathogens that cause nonflaccid wilts, such as the verticillium wilts of hops, sunflower, and sycamore (Goodwin et al., 1988a, b; Robb et al., 1982; Talboys, 1968). In PD and nonflaccid wilts, the hosts develop marginal and interveinal chlorosis and necrosis with little or no wilting. The changes observed—chlorosis, stomatal closure, membrane damage, lipid peroxidation, and increased superoxide anion accumulation—are associated with plant senescence and resemble nondisease-induced water stress (Goodwin et al., 1988a, b; McElrone et al., 2001).

The xylem dysfunction caused by *Xf* has been attributed to the accumulation of bacterial polysaccharides or bacterial cell masses (colonies) that clog the elements (Hopkins, 1981; Tyson et al., 1985) or to host responses, such as the production of gels, gums, and tyloses (Esau 1948; Mollenhauer and Hopkins 1976. The major effect of infection of *Xf* in Virginia creeper (*Parthenocissus quinquefolia (L.)* Planch) is reduced water flow that is caused by clogged vessels; *not* increased cavitation and embolism of xylem elements (McElrone et al., 2001). Reduced water flow also occurs in citrus plants affected with CVC (Machado et al., 1994). The blockage likely occurs as a result of the formation of large colonies of bacteria in the vessels, and it could be exacerbated by the formation of gels or gums (Hopkins, 1981; Newman et al., 2003). The plugging of vessels interferes with water flow through the leaf petioles to produce classic symptoms of water stress. The reduction of water flow by *Xf* inhibits plants' overnight recovery from daily transpirational water losses. Failure of the leaves to rehydrate makes the leaves more susceptible to damage from photoinhibition and high leaf temperatures. Prolonged water stress in diseased leaves, even if mild, can induce leaf senescence. Eventually the leaf dies and abscises. Symptom onset is accelerated in *Xf*-infected plants exposed to drought, because the stresses are additive.

Plant defense responses to wilt pathogens are common to defenses observed for other types of diseases. Those induced responses involve biosynthesis of structural barriers (including cell wall, callose, and lignin biosynthesis or modification), production of soluble inhibitory intermediates or compounds (such as active oxygen species or phytoalexins), and induced expression of genes for enzymes that degrade or otherwise affect the pathogen. Of importance to vascular diseases, those cellular precursors or products are transported into vessels, where they can alter the pathogen's environment. In response to many fungal vascular pathogens, callose materials are synthesized and secreted through the plasmalemma for final deposition onto the pits of the paravascular parenchyma cells at sites of attempted penetration and then onto the entire walls of infected vessels (Beckman, 1987). Lignin precursors then polymerize onto the callose, producing a highly resistant barrier to degradation and penetration by pathogens. Inside the vessel lumen, other putative defense responses include the accumulation of phytoalexins; increased concentrations of phenolic compounds; and accumulation of enzymes, such as peroxidases, polyphenoloxidases, chitinases, and polygalacturonases (Beckman, 1987). Collectively, those barriers and compounds can prevent or impede movement or growth across the vessel end walls, perforation plates, pit pairs between adjacent vessels, or the pits between vessels and xylem parenchyma. The barriers also can reduce pathogen-induced movement of nutrients from the xylem parenchyma cells into the vessel.

The formation of gums and tyloses in response to diseases caused by *Xf* was first reported by Esau (1942), who observed that the formation of gums was among the first visible changes attributable to disease development. Excessive quantities of tyloses were found in the wood of vines with PD. Esau also noted the absence of a cork cambium and excessive accumulation of nonfunctional phloem in green patches on diseased canes. In contrast, normal cork cambium on healthy canes produced brown bark. Excess accumulation of gums and tyloses also was observed in *Xf*-infected peach with phony disease. However, only excessive gum accumulation occurred in *Xf*-infected alfalfa exhibiting symptoms of dwarf disease.

Differences between types of grapevines are apparent. Mollenhauer and Hopkins (1976) reported that the frequency of gums and tyloses is 7 or 8 times greater in tolerant muscadine (*Vitis rotundifolia* Mich) and wild grapevines than in those in susceptible bunch grapevines. They also observed gums and tyloses encapsulating the pathogen and speculated that the gums and tyloses imparted tolerance to PD in some grapevines. P.Y. Huang and colleagues (1986) observed the more extensive encapsulation of *Xf* cells in muscadine vines than in more susceptible bunch grapes and concluded from histochemical tests that the encapsulating materials were predominantly pectic substances of plant origin.

Changes in the topography of the *Xf* cell wall from rippled to smooth were more prevalent in muscadine grapevines.

Although defense mechanisms are commonly observed in wilt diseases and have been observed in *Xf*–plant interactions, how they are activated, which processes are most effective in inhibiting pathogen spread, and what aspects can be manipulated to enhance resistance are currently unknown. The plant's responses are complex, and dissecting the relevance of each component in the process would be tedious and not necessarily revealing. Total genome expression profiling and other high-throughput technologies that allow analysis of complex interactions are being used to explain how those processes interact in disease and resistance for model plants whose genomes have been sequenced, such as *Arabidopsis* and rice. Because the genome sequence for grapevine is not available, application of information from model systems will allow development of hypotheses to explain disease and resistance in the *Xf*–grapevine interactions. However, the extent to which those model systems will apply is not clear.

A genome approach to analysis of grapevine is in its infancy, partially because the genome is so large (483 Mb over 38–40 chromosomes) and complexity (only 4% of the genome is transcribed) (Vivier and Pretorius, 2002). A multinational consortium recently announced an effort to sequence the complete *Vitis* genome (University of British Columbia, 2004). Efforts have been in place in several countries to develop molecular markers for grapevine and to construct and sequence cDNA libraries from various grapevine tissues in different stages of development or subjected to different stresses (Sefc et al., 2001; Thomas and Scott, 1993). There also is an effort to sequence cDNA libraries constructed from tissues of *X* –infected and uninfected grape genotypes that represent the susceptible *V. vinifera* (L.) and resistant and tolerant *Vitis* species (D. Cook, personal communication). A convenient, searchable database that includes the grape expressed sequence tags is available from the International Grape Genome Program (http://www.vitaceae.org).

Host Plant Resistance

The use of resistant varieties is an environmentally acceptable and effective means of managing crop plant diseases if satisfactory, durable resistance can be incorporated into culturally desirable plants (Maloy, 1993). Resistant varieties are particularly useful for protection against vascular pathogens that often cannot be adequately or reasonably controlled by other means. For example, the use of resistant varieties has stabilized rice production in areas where bacterial blight, caused by the vascular bacterial pathogen *Xanthomonas oryzae* pv. *oryzae,* is endemic (Mew, 1987).

Two kinds of resistance are recognized. *Qualitative* resistance, which confers specific resistance against some pathogen races, is easiest to incorporate into breeding programs because it is controlled by one or a few genes. However, qualitative resistance often is not durable because of changes in virulence within the pathogen population. *Quantitative* resistance, which is controlled by many genes, usually with small but additive effects, is considered more stable. However, quantitative traits for resistance have not been widely exploited for breeding programs because of the difficulty in accumulating multiple genes into plant varieties.

Quantitative and qualitative disease resistances have been described for grapevines. Qualitative resistance to *Plasmopara viticola*, the downy mildew pathogen, is controlled by a single dominant resistance gene that confers hypersensitivity at the point of infection. Multigenic quantitative resistance restricts the growth of mycelia beyond the site of penetration (Boubals, 1959). Similarly, grapevines demonstrate both types of resistance to the powdery mildew pathogen (*Uncinula necator*) a qualitative type involving necrosis of the appressoria inside the epidermal cells and a quantitative type involving necrosis of host cells after the development of the fungal haustoria (Boubals, 1961; Bouquet, 1986).

Genetic variation for resistance to *Xf* is available in several wild species of *Vitis* and in the genus *Muscadina* (Mullins et al., 1992). Early studies identified three sources where inheritance of PD resistance was dominant (qualitative) and controlled by as many as three loci (Mortensen et al., 1978). The sources of resistance were three species of *Vitis* native to Florida; *simpsoni, smalliana* and *shuttleworthi.* Genetic sources of resistance vary greatly in the phenotypic expression of resistance, that is, in their ability to either resist or tolerate *Xf.* Tolerant vines grow well in the presence of the pest but permit pest build-up; resistant vines grow well in the presence of the pest but greatly limit pest populations (Mullins et al., 1992). For example, some *Vitis* species, such as *V. rotundifolia, V.*shuttleworthi, and some selections of *V. simpsonii* Munson, restrict movement of *Xf* in the xylem; others, including *V. aestivalis* Michx and *V. californica* Benth., allow increased bacterial movement in the xylem.

Once a source of resistance is identified, it can be introgressed into agronomic varieties of a crop species through recurrent selection. However, the introduction of traits into grapevines, particularly wine grapes, is complicated by several factors (Mullins et al., 1992). Excellent grape cultivars contain highly subtle combinations of many genes with small effects that can be disrupted by the sexual process. Good wine quality is traditionally associated with a few cultivars within *V. vinifera;* conservative consumers, producers, and sellers resist alteration of the genetic nature of those vines. Moreover, the wine business worldwide is built on the traditional wines of the classic European wine regions and the grape varieties historically associated with those regions. Wine is identified and marketed by those names; merlot, chardonnay, cabernet sauvignon, pinot grigio. Switching to a new variety with a new name, even if the variety does represent the solution to a production problem, is simply not a realistic answer for California wine, because the variety name is an integral part of the product identity. Clonal selection, which exploits genetic variation within traditional cultivars, has been used widely to improve grape cultivars. However, introduction of pest and disease resistance through intraspecific hybridization (crosses between genotypes of *V. vinifera*) has been used to improve table grapes and, in a few cases, wine grapes (Alleweldt and Possingham, 1988). Thus, development of hybrid wine grapes that are resistant to disease and pests is an important and feasible approach; however, hybridization with *Vitis* species other than *V. vinifera* is unacceptable in the global wine market because of the historical stigma attached to interspecific hybrid wine grapes and their subsequent prohibition in Europe.

Because the wine industry relies on a few select and very old cultivars for commercial production, classical breeding programs have not developed many new varieties that are commercially successful, and thus have not had a significant effect on grapevine improvement. However, those programs have significantly influenced the development of rootstock varieties that provide resistance to soil-borne pests and pathogens and to some abiotic problems (Mullins et al., 1992). Rootstocks can contribute to PD management (Gould et al., 1991; Pierce, 1905), and one advantage of their use for improving resistance is that a single new rootstock cultivar could be used with many wine grape varieties or clonal variants. Furthermore, breeding for traits in grape rootstocks, which are based on *Vitis* species other *than V. vinifera*, is much faster than is scion breeding because it can employ sources of resistance from those other species without requiring generations of recurrent selection to recover fruit quality. Those advantages have encouraged scientists to evaluate the effects of rootstock variety on PD symptoms and to consider the possibility that a rootstock could be developed that would produce mobile compounds that inhibit *Xf* or discourage GWSS feeding.

Novel Approaches to Controlling *Xylella fastidiosa*

The hypersensitive response (HR) is a defense that can contribute to inhibition of infection by vascular bacterial pathogens. Typically, the response occurs in one or a few cells at the site of pathogen invasion and can restrict pathogen growth in plant tissues (for review, Goodman and Novacky, 1994; Heath, 2000). The hypersensitive response is under genetic control and shares characteristics of programmed cell death (PCD) in animals (Gilchrist, 1998; Greenberg, 1997; Leach, 2001). Although it has not been described to occur in grapevine resistance to *Xf*, it does occur in defense responses to vascular pathogens of other crop species (Goodman et al., 1986; Hilaire, et al., 2001; Horino, 1976, 1981; Horino and Kaku, 1989; Sequeira et al., 1977). In those cases, it is the xylem parenchyma, the living cells adjacent to the xylem, that exhibit the response. Control of leaf cell death and defense are linked in some cases. For example, the *Arabidopsis lsd1* mutant and other lesion-mimic mutants show spontaneous cell death and broad-spectrum resistance (Alvarez et al., 1998; Jakubowski et al., 2003; Schulze-Lefert and Vogel, 2000). Identification of the controls of PCD, therefore, could lead to novel strategies for disease control. Expression of the genes that inhibit PCD reveals that it is important for disease and for resistance, depending on the host–pathogen interaction. Expression of PCD inhibitors allows accessibility to a biotrophic fungal pathogen of barley (Huckelhoven et al., 2003) and yet reduces disease symptoms caused by necrotrophic pathogens (Dickman et al., 2001). Thus, altering PCD in plants is not a short-term strategy for disease control in any plant–pathogen system. Significant research is needed to identify plant pathways to PCD and to determine the repercussions of manipulating that essential cellular response.

Transgenic Approaches to Resistance

Transgenic technology for introducing traits for resistance to pathogens and pests shows promise because it could bypass the many complications and time constraints that attend the induction of resistance through breeding. If only one or a few genes are introduced, the use of transgenic technology could alleviate concerns about significant genetic changes in the grape variety but still allow for improvement of disease and pest resistance, productivity, and wine quality.

Efficient transformation systems that are applicable to a wide range of cultivars are key to the successful application of transgenic technologies. One major barrier has been the inability to regenerate plants from transformed tissues. With the use of embryonic cell lines as target tissues for transformation, many laboratories are now efficiently transforming (using biolistic or *Agrobacterium*-mediated technologies) and regenerating grapevine plants (e.g., Colova-Tsolova et al., 2001; Franks et al., 1988; Iocco et al., 2001; Martinelli and Gribaudo, 2001; Mauro et al., 1995; Mozsar and Viczian, 1996; Perl and Eshdat 1998; Perl et al., 1996; Torregrosa, 1998). The next limitation is that there are not many genes with known function that could be introduced to target desired effects. However, progress is being made (Vivier and Pretorius, 2002). Of relevance to PD, antimicrobial peptides (such as lytic peptide, Shiva-I, defensins, and polygalacturonase-inhibiting proteins) are being introduced into the major wine grape cultivars of *V. vinifera,* and those transgenic lines should be tested for improved resistance to *Xf* (C. Meredith, personal communication; Mourgues et al., 1998; Reisch et al., 2003).

Even with the tremendous advances that transgenic technologies have made in the potential for grapevine improvement, there are huge hurdles that are unrelated to the science of transgenics that must be overcome before technology can help solve the PD–GWSS problem. Vivier and Pretorius (2002) discuss several areas that remain beyond the science, including legal and regulatory issues, intellectual property and patenting, political and economic barriers, problems with marketing, traditional and cultural objections, and public perception. Public perception is particularly relevant to California's current sociological landscape, which is not receptive to the use of genetically modified plants. Although not insurmountable, the successful commercialization of grapevine varieties improved through transgenic technologies will depend on the resolution of those areas of difficulty.

The assumption of introducing useful genes and minimizing disruption of desirable complex trait combinations currently is reasonable but can only be predicted, not assured. Thousands of transgenic plants are likely to be discarded before one is developed that has the right combination of traits. Nevertheless, the information gained in the process of using powerful transformation tools can provide valuable insights to the basis of plant resistance.

Recommendation 4.2. As with the pathogen, systematic and global approaches to address host plant responses (disease or defense) to pathogen invasion are essential to identify important plant defense factors. However, until the sequence of the grape genome is available and until other tools, such as grapevine mutants for the dissection of defense responses, are available, that approach should be viewed as a long-term, expensive effort (Category 3).

Recommendation 4.3. Host plant resistance to *Xf*, whether quantitative or qualitative, is important to long-term management of the disease. Immediate emphasis should be placed on identification and characterization of the genetic basis for resistance to *Xf* host plants. Characterization of the genetic loci and biochemical mechanisms responsible for resistance will facilitate classical approaches (which use molecular markers) and transgenic breeding to create *Xf*-resistant plants (Category 2).

Recommendation 4.4. Improvements in tissue transformation systems and in the ability to regenerate plants from transformed tissue have made transgenic technology increasingly feasible, although the availability of genes of known function that could be introduced to target desired effects is limited. In the long term, however, transgenic technology could hold promise for improving resistance to *Xf* (Category 2).

Although scientifically appealing, for transgenic grape varieties to be viable solutions to PD, numerous barriers, including legal and regulatory hurdles, and public resistance to the release of genetically modified organisms, must be overcome.

CHEMICAL CONTROL

The discovery in 1973 that PD is caused by a bacterium and not a virus (Goheen et al., 1973; Hopkins and Mollenhauer, 1973) was supported in part by evidence showing the remission of PD symptoms in grapevines treated with tetracycline antibiotics or with heat. The antibiotics were applied by drenching, and the treatments resulted in symptom remission but not cure (Hopkins and Mortensen, 1971). Similarly, injection of almonds with Terramycin at 5–7 g/tree resulted in remission of almond leaf scorch symptoms. Lower doses were not effective and higher doses were phytotoxic (Mircetich et al., 1976a). Tetracycline antibiotics also caused remission of bacterial leaf scorches caused by *Xf* in landscape trees (Sherald, 2002). However, antibiotic treatments are not effective with some leaf scorches and are impractical in other situations, such as treatment of elm leaf scorch at the National Mall in Washington, D.C. (Hartman, 2000).

Current research on management of PD through chemotherapy involves the following steps:

(1) Tests the efficacy of plant micronutrients, such as zinc, copper, manganese and iron, and antibiotics for controlling the disease in grapevines.
(2) Develop methods to introduce those materials into grapevine xylem tissues.
(3) Determining whether bacteriocides can be used prophylactically to prevent infection of healthy grapevines.

Some compounds, such as a terpene called AC-2, are highly inhibitory to *Xf* in culture (Chang and Franklin, 2002), but preliminary field studies using those and other chemical applications for therapeutic protection against PD have not been promising (B. C. Kirpatrick, University of California, personal communication, 2003). However, preliminary results suggest that treating diseased grapevines with zinc or streptomycin might reduce disease (Darjean et al. 2000; B. C. Kirkpatrick, personal communication, 2003). The economics of such treatments have not been evaluated.

Systemic acquired resistance (SAR) acts nonspecifically throughout a plant and reduces the severity of diseases caused by all classes of pathogens (Heil, 2002; Metraux et al., 2002; Sticher et al., 1997). SAR can be induced by application of synthetic chemicals derivatives of isonicotinic acid and benzothiazoles. Those compounds have no direct antimicrobial activity but they activate defense responses systemically in the host plant. Current studies testing several of these and other putative resistance-inducing compounds in vineyards infested with PD suggest that the compounds might not offer significant protective effects in grapevine (B. C. Kirkpatrick, personal communication, 2003).

Existing chemical control methods or compounds have not provided effective control of *Xf* or any other vascular bacterial pathogen. Thus, with existing chemistries and approaches, chemical control is not promising for short-term disease management, and the committee views them as Category 4 approaches. However, the identification of novel targets in the bacteria for which highly specific chemicals could be developed has not been explored.

Recommendation 4.5. Long-term projects should focus on identification of pathogen targets for existing or novel chemical control approaches or for the means to stimulate or alter host defense response pathways (Category 2).

CULTURAL METHODS TO REDUCE BACTERIAL INOCULUM

Several cultural methods provide effective options to manage PD, particularly if they can be integrated with other control measures. The methods reduce the amount of pathogen inoculum by eliminating alternative hosts, by physically or temporally distancing the crop species from alternative hosts, or by creating conditions that are unfavorable to the pathogen. The use of vegetation management as a strategy for disease management was described in Chapter 3. One question for which the committee could find no answer was whether there are cultural practices, such as different vineyard training systems, that might help reduce transmission or survivorship of the pathogen over the winter.

Manipulation of Alternative Hosts

Many pathogens infect large numbers of hosts and, in some situations, those alternative hosts are important sources of inoculum for the crop species. The host plant range of *Xf* is broad, including plants from at least 28 families (for review, see Hopkins and Purcell, 2002). Hosts include monocots and dicots, annuals and perennials, woody and nonwoody species, weeds and crop plants. Hopkins and Purcell (2002) noted that the number of natural or potential hosts reported is limited only by the number of plants that have been tested; the actual number of is probably much higher. One study of 116 plant species reported that 91 were hosts of PD strains, based on vector transmission studies (Freitag, 1951). That raises the concern that alternative species, such as weeds or other crops surrounding vineyards, might be sources of inoculum for the grape. Raju and coworkers (Raju et al., 1980; Raju et al., 1983) detected the PD bacterium in seven of 52 alternate host plant species that were sampled in areas adjacent to vineyards. Those strains caused PD symptoms after inoculation of the grapevines. Epidemiologic studies describing the spatial patterns of PD show evidence of vector transmission of *Xf* from surrounding vegetation to vineyards (Hewitt et al., 1942; Purcell, 1974).

The epidemiologic importance of alternative hosts varies considerably (Hill and Purcell, 1995) and limits the ability to recommend avoidance and eradication strategies. The host plants that pose the highest risk are considered to be those that develop large populations of *Xf*, allow systemic movement of *Xf*, and are preferred for vector feeding. Host plants can exhibit several kinds of interaction with *Xf*. Although many plants support some amount of *Xf* multiplication after artificial inoculation, few support large populations of bacteria, and systemic spread after infection is limited. Where the pathogen infects and multiplies but does not move within a host, disease symptoms do not appear, and the epidemiologic risks are relatively low (Hill and Purcell, 1995; Purcell and Saunders, 1999). When the bacterium multiplies to high numbers and moves throughout the plant, as in blackberry, the epidemiologic risks are high, particularly if the plant is a host for an insect vector (Hill and Purcell, 1995).

Knowledge of host specificities and pathogen preferences in intensive agricultural settings can guide management strategies. Although *Xf* has a broad host range, there are *Xf* strains that exhibit considerable host species specificity. Strains that cause oleander leaf scorch will not cause disease on grapevines, and strains that cause PD will not cause disease on oleander (Purcell et al., 1999). However, strains from alfalfa that cause alfalfa dwarf disease can cause PD in grapevines (Hewitt and Houston, 1941; Hewitt et al., 1946) and almond leaf scorch (ALS) in almond trees (Mircetich et al., 1976a). In fact, alfalfa is considered an important source of inoculum for vineyards or orchards adjacent to alfalfa fields (Hewitt and Houston, 1941).

Potential for Change in Host Specificity

The evidence gathered from years of research suggests that although *Xf* strains exhibit host species specificity, strains do evolve to cause disease on new hosts. Combinations of tools were used to assess the relationships of *Xf* strains that cause disease in many plant species. They included plant inoculation tests, serologic tests (Davis et al., 1983; Hartung et al., 1994), and genome comparisons using molecular markers (Chen et al., 2002; Coletta-Filho and Machado, 2002; Coletta-Filho et al., 2001; da Costa et al., 2000; Harakava and Gabriel, 2003; Hendson et al., 2001; Meinhardt et al., 2003; Minsavage et al., 1994; Wichman and Hopkins, 2002) or whole genome sequences (Van Sluys et al., 2003). Molecular methods were used to group strains into 3 clusters: the first consisted of strains from citrus and coffee; the second was grapevine, mulberry, oleander and some almond strains; and the third was strains from elm, oak, plum, periwinkle, and some other almond strains (combined results from Chen et al., 2002; Van Sluys et al., 2003). Those clusters suggest evolutionary relationships, and they suggest that the CVC and PD groups evolved recently (Chen et al., 2002). In fact, CVC strains in Brazil are believed to have evolved from coffee strains after coffee plantations were replaced with citrus orchards (Chen et al., 2002; Li et al., 2001).

The ability of *Xf* strains to shift host range is a source of some alarm in areas such as California and Florida, where citrus orchards flank grape vineyards. In fact, CVC and PD strains have been demonstrated to cross-infect (Hopkins, 1982; Hopkins et al., 1978; Li et al., 2003). In a recent report, CVC strains of *Xf* were demonstrated to infect and induce PD symptoms after mechanical inoculation in the greenhouse of seven commercial *V. vinifera* varieties (Li et al., 2003). Hopkins (1982) reported the development of symptoms resembling those of citrus blight in citrus inoculated with PD strains. The relevance of that particular finding to United States grape and citrus growers is not clear because CVC strains do not occur in the United States, and because PD strains have not been reported to cause CVC symptoms in citrus. CVC strains have not been detected in vineyards in Brazil (Li et al., 2003).

Recommendation 4.6. Research should determine the efficacy and the economic and environmental feasibility of manipulating alternative hosts for PD management (Category 2).

Cultural practices such as those described above are currently being systematically investigated for efficacy in management of PD. However there are major gaps in our knowledge about the complex interactions of the environment, pathogen, vector, host, and alternative host plants. They include the need for research to identify the importance of various alternative hosts to epidemic potential, the genetic potential for the pathogen to adapt to other hosts, the abilities of the new vector—the glassy-winged sharpshooter—to transfer the pathogen between and among various hosts, and the environmental consequences of manipulating particular alternative hosts.

BIOLOGICAL CONTROL

Biological control of bacterial pathogens that cause vascular diseases has had limited success and has focused mainly on diseases of annual crops as opposed to long-lived perennial hosts, such as grapevine. In some cases, avirulent or attenuated variants of the pathogen itself are used as the control agent. Mutants of the soil-borne pathogen *Ralstonia (Pseudomonas) solanacearum* that are unable to induce wilting after root inoculation (HrcV mutants) have been investigated as potential biological-control agents to control tomato bacterial wilt (Frey et al., 1994). Those mutants colonize and multiply in xylem vessels of tomato roots and lower stems, but their final numbers are several orders of magnitude lower than are those produced by the pathogenic strain (Frey et al., 1994). Co-inoculation of the wild-type strain and HrcV mutant resulted in reduced colonization of the plant by the wild-type *R. solanacearum* strains. The mechanism for that protective ability is probably competition for space in xylem vessels, because no direct antibiosis has been measured between the HrcV strains and the wild-type strains, and microscopic examination revealed that invasion of the competitors always occurred in separate xylem vessels. The greater the number of vessels colonized by the HrcV strain, the greater the prevention of establishment of the pathogenic strain (Etchebar et al., 1998).

Agrobacterium vitis is a bacterial pathogen that causes crown gall in grapevines. Crown gall is not a wilt disease and the pathogen is not exclusively located in the xylem, but systemic movement of the pathogen depends on invasion of the xylem vessels (reviewed in Burr and Otten, 1999). Several potential biological-control strains—strains of *A. vitis* that do not cause disease and either that exhibit antibiosis to virulent *A. vitis* strains or inhibit tumorigenesis when co-inoculated with virulent strains—are being studied. Even if the strains exhibit antibiosis in culture, the mechanisms for inhibition of disease in plants seem to be a competition for attachment sites on grape cells (Burr et al., 1997).

The use of avirulent and hypovirulent strains of the pathogen might be theoretically promising, but the committee knew of no successes in controlling a bacterial vascular pathogen such as *Xf*. Only a few attempts to use hypovirulent strains of *Xf* to control the diseases caused by *Xf* have been made (Hopkins, 1994). Those tests were limited, and although a decade has elapsed, follow-up studies to evaluate their effectiveness in the field have not been reported. Theoretically, hypovirulent strains, and not avirulent strains, are marginally capable of systemic invasion of grapevines and could prevent colonization of plants by more virulent strains by occupying the xylem first. However, there seems to be a negative correlation between virulence and the ability to colonize the plant systemically. The correlation holds true in host range studies as well. Thus, there appears to be a delicate balance between virulence and colonization that might be difficult to maintain for effective management of PD. It follows that there might also be a direct correlation between the ability of a hypovirulent strain to survive in grapevine for extended periods. Hypovirulent strains could be relatively more virulent on grapevine cultivars that are more susceptible to PD.

Evaluations of nonpathogenic, naturally occurring bacterial endophytes of grapevine to control PD are in progress. Because *Xf* develops small colonies even in unplugged vessels and can spread to newly formed xylem tissues over different growing seasons, a biological-control agent would need to establish a long-term endophytic relationship with the host and continuously colonize the newly formed vessels to curtail establishment of pathogenic strains of *Xf*. Some endophytes seem to offer many of these advantages; they are natural colonizers of plant xylem vessels that will move into and colonize newly developed vessels as the plant grows. It has been speculated that those organisms might control PD either through competition with *Xf* for space or binding sites in the xylem or that they could be naturally or engineered to be antagonistic to *Xf*. Preliminary, unpublished reports indicate that an endophyte inoculated into grapevine did not prevent infection by *Xf* after sharpshooter inoculation. However, a significant reduction in PD severity was observed in four of nine plants in a greenhouse trial. Based on those results, field experiments are being planned (B. C. Kirkpatrick, University of California, personal communication, 2003).

Genetic modifications of endophytes to be inhibitory toward *Xf* could enhance their potential for biological-control. Although that approach has not been used to control plant pathogens, the endophytic bacterium *Clavibacter xyli* subsp. *cynodontis* expressing the cry-IA(c) insecticidal protein gene of *Bacillus thuringiensis* was shown to control the European corn borer (*Ostrinia nubilalis [Hubner]*) in field corn (Tomasino et al., 1995). Corn borer damage was reduced; but grain yields were not improved over the nonprotected controls, possibly because the endophyte was weakly pathogenic to corn.

There are major reservations with the use of genetically engineered or altered endophytic bacteria for biological control that will need to be addressed experimentally before such organisms are released. First, transfer of genetic material between the engineered endophyte and *Xf* or other microbes could occur. Genome-sequencing projects have revealed strong evidence for lateral transfer of genes to *Xf*. Examples include the tryptophan operon (Xie et al., 2003), 19 genes common to *X. axonopodis* pv. *citri* (da Silva et al., 2002), and a type II restriction–modification system similar to *Nostoc* (Van Sluys et al., 2003). A second problem concerns the inability to confine an altered organism once it is released into the environment. Finally, use of the approach could produce unintended effects on other microbes, particularly beneficial microbes or naturally occurring endophytic populations in nontarget insects and plants.

Because projects that have examined biological control of bacterial vascular pathogens, particularly of perennial crops, generally have shown limited success, the committee views them as Category 4 studies. Naturally occurring endophytes or attenuated strains of *Xf* have not been effective to date in control of PD in the field. However, better information about the *Xf* and endophyte genes required for colonization, establishment, and virulence or antagonism that could come from genome analysis could be used to identify target genes and allow development of effective biological-control agents. No biological-control organism, particularly one that is genetically modified, must ever be introduced to the environment without thorough evaluation of consequences. The current public concern over release of non-native or engineered organisms into the environment is significant, particularly in California.

SUMMARY

Of the six general principles for disease control listed in the beginning of this chapter the most feasible for management of *Xf* are avoidance and disease resistance. The best prospects for research that will lead to management through interference with *Xf*–grapevine interactions, either in the short or in the long term, are projects that identify vulnerable points in the *Xf* life cycle or in its interactions with grapevines (attachment); those that evidence host plant resistance, either through identification and manipulation of genetic traits for resistance or through introduction of novel resistance through transgenic technologies; and those that promote avoidance of disease through cultural practices (vegetation management).

5

Vector–Pathogen Interaction

The relationship between pathogens and their vectors can range from highly specific associations, in which the pathogen depends on a single species of vector for transmission, to more general associations, in which the pathogen can be transmitted by a wide range of vector taxa. But transmission often requires highly specific pathogen transport mechanisms in the vector (Gray and Banerjee, 1999; van den Heuvel et al., 1999). In the case of the interaction between *Xylella fastidiosa* (*Xf*) and its vectors, relatively little is known about the mechanism of transmission. The pathogen can be transmitted by most sharpshooter leafhoppers and spittlebugs, and probably by most xylem-feeding homopterans, but the efficiency of transmission varies among vectors and plant hosts. Thirty-nine species of sharpshooter in the subfamily Cicadellinae have been demonstrated to transmit *Xf,* as have 4 species of spittlebug and 1 cicada (Redak et al., 2004). However, many species, particularly those found only in the tropics, have not been tested for the ability to transmit, and it is highly likely that more vectors could be identified (Redak et al., 2003). Data suggest that members of the sharpshooter tribe Cicadellini transmit more efficiently than do members of the Proconiini tribe (Almeida and Purcell, 2003; Krugner et al., 1998; Redak et al., 2003). In California, the blue-green sharpshooter (BGSS), *Graphocephala atropunctata (*Signovet*),* is in the Cicadellini; the glassy-winged sharpshooter (GWSS) *Homalodisca coagulata* (Say) is a Proconiine sharpshooter.

STRATEGIES OF INTERFERENCE

Several approaches to interfering with the interaction between the vector and the pathogen have been proposed for controlling the spread of Pierce's disease (PD). In theory, interference could be targeted at one or more of three stages: at the acquisition of the bacteria by the vector, during attachment and replication of the bacteria in the vector, or during the inoculation of the bacteria to a healthy host. Most of those approaches are experimental, and their effectiveness has not been demonstrated for other insect-vectored disease systems. However, several strategies are worth considering in the context of long-term management of PD: feeding disruption, inhibition by other bacteria of *Xf* attachment in the vector, and inhibition of transmission of PD strains of *Xf* by other strains by paratransgenesis.

PATHOGEN TRANSMISSION

The characteristics of *Xf* transmission by GWSS are similar to those of other known leafhopper vectors of *Xf*, although GWSS is a less efficient vector than is BGSS, a primary vector in Northern California. Leafhopper vectors acquire *Xf* through feeding on the xylem of host plants, and the bacteria replicate in the mouthparts (Purcell et al., 1979). Although *Xf* can be acquired by adults and nymphs, it is lost during the molting process—a fact that suggests that the bacteria attach to the foregut, because the foregut lining is shed in molting. Scanning-electron microscopy of leafhopper vectors shows bacteria attached to the cibarial pump and the lining of the esophagus in the foregut (Purcell et al., 1979). Adults that acquire the bacteria can continue to transmit throughout their lifetime (Severin, 1979). Although there is currently no strong evidence of gender differences in transmission (Redak et al., 2003), differences have been shown for other leafhopper-transmitted pathogens and could have significant effects on epidemiology (Beanland et al., 1999).

Adult GWSS can acquire *Xf* from infected plants and inoculate healthy plants in less than an hour of access time on a plant. There is no evidence for latent period between acquisition of the bacteria and the ability to transmit it (Almeida and Purcell, 2003). The rate of successful inoculation increases with increased time on the plant, but acquisition efficiency does not increase after 6 hours. Nymphs and newly molted adults transmit more efficiently than older adults do. Almeida and Purcell (2003) reported, in their experiments, that a maximum of 20% of individual leafhoppers acquired and transmitted *Xf*. In contrast, experiments with BGSS indicated an average transmission efficiency of 90% (Purcell and Finlay, 1979). More work demonstrated 68% efficiency of *Xf* acquisition from infected grape and 56–99% inoculation efficiency to grape, depending on the number of days post acquisition (Hill and Purcell, 1995). One striking difference between the two major vectors is that GWSS feeds on woody tissues throughout the year and can transmit *Xf* to stems that are more than 2 years old, but BGSS transmits only to green shoots (Almeida and Purcell, 2003).

For GWSS there is no significant difference in transmission to woody stems or to green shoots, and transmission to dormant vines also is apparent. That pattern has important implications for virus epidemiology: it shows a polycyclic pattern of disease spread that contrasts with the general pattern of monocyclic spread of PD in California (see Chapter 1).

Therefore, to develop ecologically based management strategies that rely on economic thresholds and to arrive at an understanding of pathogen epidemiology, the committee recommends the following:

Recommendation 5.1. Research should be done on the transmission biology of the disease system, including acquisition from and inoculation to alternative hosts and acquisition from and inoculation to dormant grapevines (Category 2).

Transmission efficiency is influenced also by the population of *Xf* in host plants. In experiments by Hill and Purcell (1997), higher bacterial densities in source plants led to greater rates of transmission. Despite the evidence that the number of bacteria acquired by the vector can dictate subsequent transmission, the relationship between number of bacteria in vector heads and transmission efficiency is not well understood. Efficient transmission of *Xf* requires less than 100 cultivable bacteria for the BGSS (Hill and Purcell, 1995), and no clear relationship between cultivable bacteria in the head and transmission has been identified for GWSS at a detection threshold of about 265 colony-forming units per head *(*Almeida and Purcell, 2003). Those findings, and the rapidity with which vectors can transmit the bacteria, suggest that the threshold density of bacteria necessary for transmission is very low. Unfortunately, this implies that not strategy that involves feeding disruption is likely to be successful in preventing transmission. Similarly, rapid transmission makes it difficult to use insecticides effectively to control disease spread.

Attachment and Replication in Vectors

The precise mechanism by which *Xf* attaches to the sharpshooter mouthparts is not well understood. Processes that have been identified as important in attachment and replication in plants and in media include attachment to cell walls by ionic bonds (Leite et al., 2002), production of a polysaccharide gum (Silva et al., 2001), and formation of biofilm (Marques et al., 2002). The pH and nutrient content of the substrate could also influence bacteria replication (S.M. Fry et al., 1994), so xylem chemistry could be important for replication in the vector. Attachment in the vector can pose challenges for the bacteria; the rate of sap uptake by sharpshooters GWSS is extremely high. Average midstream velocities within the food canal of the vectors' mouthparts have been reported to be nearly 10 cm/s for BGSS (Purcell et al., 1979) and at least 50 cm/s for GWSS (Andersen et al., 1992). Polysaccharide fibers produced by bacteria are thought to function in attachment in other turbulent habitats, such as streams with rapid flow and animal guts (Costerston and Irwin, 1981).

Identification of the mechanisms of attachment and replication in the vector could lead to strategies that decrease the probability of attachment or that reduce the replication rate. A reduction in bacterial population in the vector's foregut should lead to a lower efficiency of transmission. Although the number of bacteria needed for successful transmission is quite low, presumably there is a threshold below which no transmission takes place. Research to determine that threshold-using methods more sensitive than culturing, such as polymerase chain reaction–based methods, would be useful *(*Almeida and Purcell, 2003). Therefore, the committee makes the following recommendation:

Recommendation 5.2. Research should be done on the determinants of transmission efficiency, including attachment and reproduction of *Xf* in GWSS (Category 2).

Inhibition of *Xylella* Transmission by Other Bacteria

There has been speculation that the transmission of *Xf* could be reduced by the presence of other microbes within the vector. Almeida and Purcell (2003) cultured several microbes, mostly bacteria, from the head capsules of GWSS and suggested that those microbes could compete with *Xf* for attachment sites in vectors' mouthparts. Preliminary identification of common bacteria in the foregut and midgut of GWSS also has been done by Peloquin et al., (2002), but no one has addressed the competitive relationships between those bacteria and *Xf*. That will be a necessary step toward evaluating the potential for biological control of PD through interfering with the attachment and replication of *Xf* in the vector. Obviously, because attachment occurs in the foregut, it would be most useful to target bacteria there, rather in than the midgut. Bextine and colleagues (2004) have begun developing a plant-based delivery system to introduce endosymbiotic bacteria into GWSS. Such a system would be useful if an appropriate biological-control agent were available.

It is useful to consider the possibility of interference between two strains of *Xf* within the vector. That strategy is similar to the cross-protection that has been used successfully for some viral diseases, but it focuses on interference within the vector rather than within the host plant. Work with virus transmission by insect vectors has shown that the acquisition of one strain of a virus can reduce acquisition or the transmission of a second strain. For instance, acquisition of the MAV strain of the barley yellow dwarf virus by aphid vectors markedly reduces the transmission of the PAV strain by those insects (Gildow and Rochow, 1980). Similarly, there is some evidence that the acquisition of a spiroplasma (a plant-pathogenic mollicute) by a leafhopper vector interferes with the replication and transmission of another mollicute (Maramorosch, 1958). The mechanism interference is not well understood, but the process can be reliable.

Preliminary results by Costa and Cooksey (Proposal to CDFA, March 2003) suggest that there may be some degree of inhibition between the PD and oleander leaf scorch strains of *Xf* within GWSS, but the effect appears to be small. It would be interesting to pursue that idea using other strains of *Xf*, including nonpathogenic ones, as well as other species of bacteria. Although the research is interesting from a biological perspective, the committee concluded that biological control of bacterial vascular pathogens, particularly of perennial crops, has generally shown little success in the field. Thus the committee views this as Category 4 research.

Transgenic Interference of Transmission

There are two potential transgenic approaches to interfering with interactions between vector and pathogen to reduce successful transmission. The first is genetic manipulation of vectors to reduce transmission competence. That approach requires the development of efficient transformation of the targeted vector species, the identification of pathogen-specific molecules that impair competence, and the development of a mechanism to drive the competence-reducing molecules through the vector population (Beatty, 2000). Proposed mechanisms include transposable elements, densoviruses, and bacterial symbionts of the vectors such as *Wolbachia*.

Research on genetic modification of vectors has focused on vectors of human pathogens, particularly mosquito vectors of malaria, and mosquitoes have been transformed to express antiparasitic genes that make them inefficient vectors (Ito et al., 2002), although genetic modification often reduces fitness (Catteruccia et al., 2003). Driving the competence-reducing molecules through the vector population is likely to take decades, during which time some of the vectors remain competent. Consequently, in the case of malaria control, the ecological hurdles could well exceed the technical hurdles to success (Spielman et al., 2001). It is likely that the barriers to genetic transformation of PD vectors as a means of disease control would be equally daunting.

The second transgenic approach focuses on genetic engineering of bacterial symbionts of vectors to express and release transgene products that damage the pathogen. That process has been called "paratransgenesis." In the Chagas disease system, researchers have engineered the bacterial symbiont *Rhodococcus rhodnii* to express and release transgene products into insect tissues that are damaging to the disease agent (Durvasula et al., 1997). The most promising drive mechanism in this system is the coprophagic behavior of the insect vector which should promote the dispersal of the recombinant symbiont (Durvasula et al., 1999). However, as in the case of malaria, effective disease control is mainly in the future.

Using paratransgenesis to manage PD clearly would be a long-term strategy, and one in which the likelihood of success is limited. Although some progress toward transformation of GWSS endosymbionts has been made (Lampe and Miller, 2002), the committee views this as Category 4 research. In addition to its scientific uncertainty, there are ecological and regulatory barriers to success that are at least as significant as any technical barriers.

PATHOGENS AND VECTOR FITNESS

Many studies have shown that plant pathogens transmitted by insects can significantly affect vector fitness (for review, see A. G. Power, 1992). Those effects can be direct or indirect, mediated by changes in host plant nutrition induced by virus infection of the host (Box 5-1). Indirect effects can result because virus infection often increases the amino acid content of the phloem (Matthews, 1981), thereby improving the nutritional value of plans for phloem-feeding insects. However, differences in nitrogen mobilization in different host species in response to virus infection can lead to enhanced or diminished vector fitness (Blua et al., 1994; A. G. Power, 1992). Aphids have received the most attention; fewer studies have examined the responses of leafhoppers or whiteflies to plant infection status. However, no studies have isolated unambiguously the direct effects of a pathogen on vector fitness from the indirect effects mediated through the host.

BOX 5-1
Pathogen Effects on Vector Survivorship and Reproduction

There have been no studies of the effects of *Xf* on GWSS survivorship, but some work has demonstrated the effects of viruses on leafhopper survivorship on infected plants. For example, R. E. Hunt and Nault (1990) reported increased survivorship of the leafhopper *Graminella nigrifrons* (Forbes) on plants infected with maize chlorotic dwarf virus. However, the longevity of the green rice leafhopper *Nephotettix virescens* (Distant) was reduced on rice plants infected with tungro viruses (Khan and Saxena, 1985). Tungro-infected plants had higher concentrations of free sugars, but lower concentrations of soluble amino acids, but the effects on vectors, whether positive or negative, could be limited to those that feed on phloem. It is not clear whether virus-induced changes in xylem would similarly influence vector survivorship.

Host plant infection with plant pathogenic mollicutes (phytoplasmas and spiroplasmas) also can lead to greater survival of leafhoppers (Beanland et al., 2000; Madden and Nault, 1983; Madden et al., 1984; Maramorosch, 1960; Purcell, 1988), despite the fact that the pathogens typically propagate in vector as well and host plant alike. In the case of the corn stunt spiroplasma and the maize bushy stunt phytoplasma, fitness of the primary, most efficient vector is improved by acquisition of the pathogen, whereas the fitness of occasional vectors or those with low efficiency is impeded (Madden and Nault, 1983; Madden et al., 1984). Corn leafhoppers (*Dalbulus maidis;* DeLong and Walcott) survive better at cool temperatures when they are infected either with corn stunt

continues

Box 5-1 *continued*

spiroplasma (Ebbert and Nault, 1994) or with maize bushy stunt phytoplasma (Moya-Raygoza and Nault, 1998). Thus the effects of plant pathogens on leafhopper survival can be complex and environment dependent.

Most research on aphid vectors shows higher reproductive rates on plants infected with viruses than healthy plants, although some studies have shown negative effects of plant infection on fecundity (reviewed in A. G. Power, 1992). These conflicting results are probably attributable to differences among host plants in nitrogen mobilization in response to plant infection with a diversity of viruses (A. G. Power, 1992; Blua et al., 1994). Studies of whiteflies that are vectors also have shown higher fecundity on virus-infected hosts (Mayer et al., 2002; McKenzie, 2002), although Costa and colleagues (1991) reported differing effects of virus infection on whiteflies in different hosts and detected no correlation for amino acid concentration and whitefly reproductive rate. In one study of leafhoppers, the fecundity and population growth of the green rice leafhopper were lowered when the leafhoppers fed on rice plants infected with tungro viruses than they were when the insects ate healthy rice plants (Khan and Saxena, 1985). As noted above, the work so far has involved phloem-feeding vectors, and the effect of virus infection on xylem-feeders is not documented.

Recommendation 5.3. A subset of studies of the vector should explore the effects of *Xf* on vector survivorship, fecundity, and population growth rates (Category 2).

INFECTION AND VECTOR BEHAVIOR

Like the effects of pathogens on vector fitness, effects on vector behavior can be either direct or indirect, the latter mediated by changes in host plant nutrition or morphology induced by virus infection of the host. The evidence for direct effects of insect-transmitted pathogens on vectors is limited, but several studies have documented indirect effects in which vector behavior was influenced by the infection status of the host plant. Most of those studies have been done with aphids (Box 5-2).

The preference of sharpshooters for plants infected with *Xf* is not known, but a few studies of leafhoppers have shown vector preference for plants infected with viruses or phytoplasmas (Box 5-3). Bennett (1967) reported that beet leafhoppers preferentially colonized, and performed better on, beet plants infected with beet curly top virus than they did on healthy beets. Similarly, aster leafhoppers prefer carrot plants infected with the aster yellows phytoplasma over

BOX 5-2
Vector Attraction to Infected Plants

Aphids are likely to show greater preference for infected plants than for healthy plants (e.g., P. B. Baker, 1960; Castle et al., 1998; Eckel and Lampert, 1996; Eigenbrode et al., 2002; Fereres et al., 1999; Macias and Mink, 1969), although that pattern is not completely consistent (A. G. Power, 1992). Beetle vectors also have been reported to prefer virus-infected host plants (Musser et al., 2003). In many cases, the preference appears to be driven by a visual attraction to yellowing, senescent plants, and many viruses cause symptoms similar to those of senescence. The "leaf scorch" symptoms of PD can also appear similar to senescence in some grape varieties, suggesting that vectors could be attracted to infected vines.

In one interesting study, Castle and colleagues (1998) compared the preference of aphids for virus-free potatoes and those infected with potato leafroll virus (PLRV), potato virus X, and potato virus Y. Earlier studies had shown that aphid population growth rates were higher on potatoes infected with PLRV, which depends on aphids for transmission, than they were on virus-free plants or on plants infected with the other viruses, that are not obligately transmitted by aphids (Castle and Berger, 1993). Augmenting the earlier study, Castle and colleagues (1998) demonstrated that significantly more aphids settled on hosts infected with the obligately aphid-transmitted PLRV than on either virus-free plants or on plants infected with the other viruses. Recent studies by Eigenbrode and colleagues (2002) indicate that volatile compounds from PLRV-infected potatoes are involved in the attraction and arrestment of aphid vectors of the virus, and that those compounds could similarly influence the behavioral responses of other vectors to infected hosts.

healthy plants (Peterson, 1973) and have better fitness on infected carrot and aster plants than they exhibit on healthy plants (Beanland et al., 2000; Peterson, 1973).

Recommendation 5.4. A subset of studies of the vector should explore the effects of *Xf* on vector behavior, including movement and attraction to infected hosts (Category 2).

BOX 5-3
Implications for Epidemiology

Epidemiologic models can be useful for evaluating the potential of various management strategies to control the spread of plant pathogens (Jeger and Chan, 1995). In the case of insect-transmitted pathogens, such models suggest that effects on vector fitness that lead to higher rates of population growth on infected plants could significantly affect rates of pathogen spread (Holt et al., 1997; Zhange et al., 2000). One model of the whitefly-transmitted African cassava mosaic virus is based on substantial field data (Holt et al., 1997) which showed that the rate of spread was sensitive both to vector population dynamics (abundance, birth rate, mortality) and to virus transmission rates (inoculation and acquisition). When virus infection of hosts leads to increased vector fecundity, spatial aggregation of vectors is promoted (Zhang et al., 2000). Models predict that vector aggregation should have a dual effect. Within the infected crop, it should reduce the effective contact rate between vector and host and thus lead to lower disease incidence than would be predicted without aggregation. On the other hand, it could cause increased emigration rates of infective vectors to other hosts in the area (Zhang et al., 2000).

Most of the models described here are based on systems in which the vector insect reproduces within the crop. However, when the incidence of disease depends primarily on the immigration of vectors from alternative hosts that act as reservoirs of pathogens and of vectors, other models show that disease incidence is largely insensitive to vector mortality unless the vector population is extremely small, and therefore insecticide treatment is ineffective (Holt et al., 1999). To evaluate the potential of targeting various aspects of the interaction between *Xf* and its vectors for control, it is essential to understand the population dynamics of vectors inside and outside of the vineyard.

Epidemiologic models have predicted that vector preference behavior will have a significant influence on the rate of pathogen spread, and conventional wisdom postulated that vector preference for infected hosts over healthy ones would promote the spread of disease (e.g., Irwin and Thresh, 1990; Matthews, 1991). However, the results of several recent epidemiologic models suggest that often the reverse is true (McElhany et al., 1995; Real et al., 1992). That is, a preference for healthy plants often leads to greater rates of pathogen spread, because an infective vector is less likely to “waste” a visit to a plant that is already infected. However, the effect of vector preference depends on the frequency of infected plants in the population and on whether the transmission system is persistent, nonpersistent, or semipersistent. Models predict that pathogens with even moderate persistence are likely to have higher rates of spread by vectors that prefer healthy plants at most disease frequencies (McElhany et al., 1995). Given the persistence of *Xf* in adult sharpshooters, vector preference for healthy grape plants could lead to faster spread of PD.

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Appendix A

Committee Biographies

Jan E. Leach (Chair), University Distinguished Professor of Plant Pathology, Kansas State University, is recognized for her expertise in molecular plant-microbe interactions. Dr. Leach studies the molecular and physiologic mechanisms for induction and manifestation of resistance in plants, using rice and the bacterial blight pathogen *Xanthomas oryzae* pv. *oryzae* as a model host-pathogen interaction system for her research. She is a member of the American Phytopathological Society, the American Society of Plant Physiologists, and former President of the International Society for Molecular Plant-Microbe Interactions. This past year Dr. Leach was selected as a Fellow of the American Association for the Advancement of Science. She also is a current member of the Advisory Board for the US Rice Genome Sequencing Project. Dr. Leach has published numerous peer-reviewed articles and book chapters on the population biology, genetic diversity, and movement of *Xanthomas oryzae* pv. *oryzae*, in addition to several other related research topics. She earned B.S. and M.S. degrees in microbiology from the University of Nebraska, and received a Ph.D. in plant pathology from the University of Wisconsin, Madison.

Pedro Barbosa, Professor of Entomology, University of Maryland College Park, is an expert in theoretical and applied ecology of the natural enemies of insects and trophic level interactions. Dr. Barbosa's research has helped to demonstrate the multifaceted and essential role of plants in insect herbivore ecology, and it has helped to bring an entomological perspective into the discipline of ecology. Much of his work has focused on the question of whether insects are significant regulators of plant population abundance and distribution. He has published an extensive array of peer-reviewed articles, books, and book chapters on tri-trophic level interactions, in addition to numerous Cooperative Extension Service documents. Dr. Barbosa earned a Ph.D. from the University of Massachusetts Department of Entomology.

Michael J. Davis, Professor, University of Florida Tropical Research and Education Center, has made significant contributions to our understanding of diseases that affect tropical/subtropical fruit and crops. He has performed a substantial amount of research on plant diseases caused by fastidious prokaryotes. Dr. Davis was the first individual to isolate in pure culture a number of significant fastidious, xylem-inhabiting bacterial plant pathogens, including *Xylella fastidiosa*. He also was one of the first scientists to clone DNA for diagnostic probes for plant pathogenic phytoplasmas. Dr. Davis's current research is focused largely on the development of transgenic papaya and sugarcane for disease control. He earned a Ph.D. in Plant Pathology from the University of California, Berkeley.

David G. Hoel, Distinguished University Professor, Medical University of South Carolina, and Clinical Professor, Department of Radiology, University of South Carolina School of Medicine, is recognized for his contributions to epidemiology and environmental medicine. Dr. Hoel also brings special expertise in biostatistics/biometrics, and in general mathematical applications to biology and medicine. He has authored or co-authored numerous peer-reviewed articles and editorials concerning biometrics, toxicology, and environmental medicine. Dr. Hoel is a past director of the National Institute of Environmental Health Sciences, and the National Toxicology Program, Research Triangle Park, North Carolina. In 1988 he was elected to the Institute of Medicine, and in 1997 he received the National Institutes of Health Director's Award. Dr. Hoel received a Ph.D. in statistics from the University of North Carolina, Chapel Hill.

L. Joe Moffitt, Professor, and Outreach Coordinator, Department of Resource Economics, University of Massachusetts, Amherst, is an expert in the applications of economics to biology-based crop protection for production agriculture. A significant amount of his 20 years of research has been on the economics of crop protection, with special emphasis on new technology and biosecurity. Dr. Moffitt also is interested in the applications of biology-based quantitative methods to economics and econometrics. His research and extension/outreach publications address topics such as the economics of pest control, integrated pest management, and international priorities in agricultural extension. Dr. Moffitt earned a Ph.D. from the University of California, Berkeley.

Alison G. Power, Professor, Department of Ecology and Evolutionary Biology, and Department of Science and Technology Studies, Cornell University, is recognized for her expertise in agroecology. Dr. Power's research focuses on insect-borne plant pathogens, interactions between agricultural and natural ecosystems, biodiversity in managed ecosystems, and tropical ecology. She has worked extensively on the ecology and epidemiology of disease systems such as leafhopper-borne pathogens of maize in Central America, the leafhopper-borne rice tungro virus in Thailand, and the aphid-borne barley yellow dwarf virus in grain crops and wild grass hosts in the U.S. Currently, her research focuses on the role of agricultural practices on the spread of plant diseases in natural ecosystems and in production agricultural systems. Dr. Power currently is Dean of the Graduate School at Cornell University. She also served on the National Research Council Committee on Agricultural Sustainability and the Environment in the Humid Tropics. Dr. Power received a Ph.D. in Zoology from the University of Washington, Seattle.

Terry L. Root, Senior Fellow, Center for Environmental Science and Policy, Institute for International Studies, Stanford University, is recognized for her work on large-scale ecologic questions. Among her research interests are geographic variation in the population biology and community ecology of species across landscapes, the influence of environmental factors and physiologic demands in shaping the distribution and abundance patterns of species, and the mitigation of detrimental anthropogenic disturbances, by enhancing communications between scientists, policymakers, and the general public. Dr. Root has studied both small- and large-scale ecologic factors such as climate change in shaping the range and distribution of animals. She served on the National Research Council Committee to Evaluate Indicators for Monitoring Aquatic and Terrestrial Environments. Dr. Root earned a Ph.D. in biology from Princeton University.

Jack Schultz, Professor, Department of Entomology, The Pennsylvania State University, is an expert in chemical ecology, natural products chemistry, and tri-trophic interactions. Working at The Pennsylvania State University and the Pesticide Research Laboratory of the Department of Entomology, Dr. Schultz studies chemically mediated interactions among plants, insects, microbes, and vertebrate predators, as well as the importance of dynamic plant responses to environmental stimuli. His research encompasses systems including agronomic crops, desert shrubs, and temperate shrubs and trees. In addition to numerous peer-reviewed publications concerning chemical, population, and molecular ecology, Dr. Schultz has made many contributions to GenBank, the major repository of genetic sequences in the U.S. He earned a Ph.D. from the University of Washington.

William E. Splinter, Professor Emeritus, biological systems engineering, University of Nebraska, is recognized for his expertise in biological engineering. Dr. Splinter invented and developed safer aerial spray systems and improved harvesting systems that have contributed to the strengthening of agriculture. His research interests include computer modeling of the growth rate and development of plants as affected by environmental variables such as light intensity and soil water potential. Dr. Splinter oversaw a project that developed instrumentation to measure plant growth rate within a three-minute period of time. He also is interested in the use of ionized field charging of agricultural pesticidal dusts and sprays to reduce the dosage required to control plant diseases and insect pests. Dr. Splinter has taught courses in agriculture and bioresources, biological engineering (plant and animal processes), and ergonomics/human factors. He has authored over 100 technical papers and holds five patents. Currently, Dr. Splinter is serving as Interim Director of the Nebraska State Museum. He was elected to the National Academy of Engineering in 1984.

Brian J. Staskawicz, Professor, Department of Plant and Microbial Biology, University of California, Berkeley, is an expert in the molecular mechanisms underlying plant resistance to disease pathogens. Dr. Staskawicz is recognized for his use of molecular biologic techniques to clone the genes responsible for plant-pathogen interactions. His laboratory presently is using various model systems—including the interaction of *Arabidopsis thaliana*, tomato, and pepper—with several phytopathogenic bacteria in the genera *Pseudomonas* and *Xanthomonas*. Dr. Staskawicz currently is employing multiples genetic approaches to identify plant genes that control disease resistance to phytopathogenic bacteria. He earned a Ph.D. from the University of California, Berkeley, and was elected to the National Academy of Sciences in 1998.

Marie-Ann Van Sluys, Associate Professor, Department of Botany, University of São Paulo, Brazil, is recognized for her expertise in the genomic analysis of plant-associated bacteria. Dr. Van Sluys is the co-director of the research team that presented the full genomic sequence of a Pierce's disease strain of the bacterium *Xylella fastidiosa*. She also was among a group of scientists that recently provided a genomic comparison of two *Xanthomonas* pathogens with different host specificities. Dr. Van Sluys has authored or co-authored numerous peer-reviewed and extension publications addressing topics such as transposable elements and gene expression in *Arabidopsis thaliana*, genomic organization, and plasmid constructs. She is a member of several scientific professional societies, including the Brazilian Society of Geneticists, the International Society for Plant Molecular Biology, and the American Society of Plant Physiologists. Dr. Van Sluys earned a Ph.D. in Molecular Biology from the University of Paris.

T. Ulf Westblom, Professor of Internal Medicine and Infectious Diseases at Texas A&M System Health Sciences Center, and Chief of Medicine, Central Texas Veterans Health Care System, is known for his expertise in microbial pathogenesis and bacterial growth characteristics. Dr. Westblom has conducted field research in the attempt to identify genetic traits that confer resistance to Pierce's Disease, while focusing on the microbiology and epidemiology of *Xylella fastidiosa*. In his laboratory, Dr. Westblom has been investigating the growth characteristics of *Xyllela fastiodiosa* and potential ways to eradicate it. His research on the improvement of isolation techniques for *Helicobacter pylori* have allowed him to incorporate his work into studying the control of *Xylella fastidiosa*. Dr. Westblom also is a winemaker and small winery owner in Texas, where he is actively cultivating Pierce's Disease-resistant grape varieties. He holds a M.D. from the Karolinska Institute (Stockholm, Sweden).

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