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CROP BIOTECHNOLOGY RESEARCH: THE CASE OF VIRUSES

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Summary

Viruses have been recognized as causal agents in the development of crop disease since the late 19th century. Virus infections are associated with a wide variety of disease symptoms which, if severe and widespread, lead to substantial crop damage and loss of potential production. Reliable and reproducible estimates of annual crop loss from virus diseases generally are not available, but benchmark figures were published by the United States Department of Agriculture during the 1940's and 1950's. In the absence of contradictory or trend information, a benchmark of 2 to 4 percent of crop production is assumed to represent a long term average loss for crops which are known virus hosts. The most important U.S. crop groups which are seriously affected by virus diseases include fruits, vegetables, wheat, and certain field crops, such as sugar beets, alfalfa, oats, and dry edible beans.

The most important principle of managing virus diseases in crops is avoidance of infection. The successful technologies for preventing infection are quarantine, virus-free seed and propagation stock, and breeding for resistance. Research using newly developed tools in molecular genetics and biochemistry is expected to enhance the development of disease resistance in susceptible crops.

Viruses are parasitic forms of genetic material which are endowed with the ability to cause plant hosts to replicate the virus genome. Plants which are hosts to viruses may be resistant by constitutive or induced means, and constitutive resistance may be controlled by one or more genes. Host plants lacking resistance are sensitive or tolerant depending on the severity of symptoms exhibited after infection. Symptoms are the manifestation of infection and the complex of symptoms is known as disease. The consequences of viral infection for the plant include altered metabolism, anatomical and morphological deviations, and plant death.

Viruses are classified according to their structure, form, host range, vector, and other factors such as serological affinity. Twenty-seven groups of plant viruses comprise nearly 420 viruses. Viruses are transmitted from host to host by vectors, mostly insects and other arthropods. Disease symptoms are classified by their apparent deviations from the normal plant state. The link between virus structure and host symptom is not fully known.

Biotechnology in plant protection is increasing the ability of researchers to study plant-virus resistance mechanisms. Advances with biotechnology are expected to require interdisciplinary efforts involving molecular geneticists, plant pathologists, and breeders in improving the scientific understanding of plant-virus resistance. Traditionally, advances in plant protection against viral diseases have proceeded through the literature of scientific phytovirology. Biotechnology is likely to contribute to the study of plant-virus resistance by testing the traditional models of plant-virus resistance.

Models of plant-virus resistance are developed and debated by phytovirologists in more than 100 scientific journals plus nonserial outlets such as books, symposia, and monographs. A group of five scientific review articles summarizing research on plant-virus resistance indicated the six most important journals in the field of phytovirology: <u>Phytopathology</u>, <u>Virology</u>, <u>Molecular Plant Pathology</u>, <u>The Journal of General Virology</u>, <u>Science</u>, and <u>Nature</u>. The countries leading research on plant-virus resistance are the United States,

United Kingdom, Japan, Israel, and the Netherlands. Although research on plant-virus resistance is established in the field's traditional core of scientific literature, biotechnology is expected to expand the field by generating scientific results in core and specialized noncore journals.

Research on plant-virus resistance using biotechnology, such as developing transgenic plants with genes isolated from Tobacco Mosaic Virus (TMV), has shown that transgenic plants exhibit delayed symptoms of mosaic disease. Although this research provided a degree of cross-protection against superinfection with related strains of TMV, it was not clear how the mechanism operated.

Biotechnology offers a set of techniques for testing traditional hypotheses from models of plant-virus resistance. As the technology becomes available, progress in understanding the resistance mechanism is expected to come from explaining virus host range, cross protection, hypersensitivity, and other phenomena of the plant-virus interaction.

The economic effects of preventing virus disease losses in U.S. crops include positive shifts in aggregate supply as yields increase, other factors unchanged. The assumptions of linear supply and demand schedules, a rightward parallel shift in supply, and no shift in demand for potatoes and tomatoes are used to model pre- and post-innovation market prices and quantities. Retail supply and demand characteristics for fresh-market and processed potatoes and tomatoes are combined with supply and demand characteristics of related commodities to arrive at post-innovation market equilibria. Economic surpluses are distributed among producers and consumers according to the supply and demand characteristics of each commodity.

The model suggests that a hypothetical reduction in potato and tomato losses from virus diseases, as expected, will reduce market-clearing prices and increase quantities. The inelastic demand for these commodities will cause consumer expenditures to decrease, with the rate of decrease in the processed market twice that in the fresh market. Consumers stand to gain relatively more, and producers relatively less, from a loss-preventing innovation in potatoes, compared to tomatoes. To the extent that a change in economic surplus indicates a change in social welfare, consumers are made better off by loss prevention technologies.

Progress in Crop Research: The Case of Viruses

John Love and Loren Tauer*

INTRODUCTION

Scientists have recognized viruses as agents of plant disease since Beijerinck's virus hypothesis was formed in 1898. Laboratory methods of screening fungi and bacteria at that time failed to filter the contagion of tobacco mosaic disease, and led scientists to look for the submicroscopic agent in contagium fluidum vivum (Corbett and Sisler). Since then, viruses have been implicated in many plant disease groups commonly known as mosaics, yellows, ringspots, streaks, flecks, and dwarfs. Crop diseases from viral infections, if severe and widespread, lead to substantial crop damage and loss of potential production. The magnitude and extent of crop damage from viruses are affected by factors in three broad classes: plant variety, virus strain, and ecology.

Crop farmers face problems in preventing virus damage because no chemical pesticides have been developed to directly control viruses. The traditional forms of plant protection against virus diseases are based upon crop breeding, vector control, and quarantine programs. Biotechnology in plant protection promises to radically change agriculture by augmenting or replacing the traditional means of preventing losses from diseases, weeds, and insects. Florkowski and Hill, for example, estimated from a sample of scientists that an even chance exists for biotechnologists developing virus-resistant potato varieties around the year 2000, and that this virus resistance could increase yields by 15 percent.

Molecular biologists, now with the means to transfer genetic material across previously insurmountable species barriers, are adding a new dimension to these traditional strategies. The potential for increasing plant resistance or tolerance to virus infection rests partly on developing recombinant DNA and cell fusion as tools to create "designer crops", engineered specifically to resist infectious viruses or suppress symptoms. Future advances in developing crops with increased virus resistance will come from continued collaboration among plant breeders, phytopathologists, entomologists, and others in the scientific community.

The major agricultural benefit from controlling virus infections is reducing losses from virus diseases. Understanding plant-virus interactions, though, offers more potential for agriculture than mitigating the loss problem. Plant viruses, parasites because they depend on the host plant for survival, are tiny bits of genetic material which lack the means of metabolism. This fact and their ability to replicate in plant cells render viruses a vector candidate in gene splicing technology. Plant breeders are attempting to use viruses to transmit genetic material across cell membranes and establish desirable traits in transformed crops. The use of virus technology to supplement breeding for improved crop productivity increases the potential payoff from research in plant virology.

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The objectives of this report are (1) to examine the factors affecting progress in plant virus research and (2) to show the potential economic benefits of agricultural research in plant virology. The purpose of this study is to give science policymakers a better understanding of the structure, conduct, and performance of plant virus research. The results also will provide research organizations with a framework for the examination of other scientific activity.

The report is divided into three sections. The first section summarizes a review of the literature on crop losses due to virus damage and the current control technologies available to farmers. The second section explores in more depth the fundamental nature of viruses and virus-crop interactions and examines the factors affecting scientific progress in plant virology and the prospects for a breakthrough in virus research. The final section reports the possible economic effects of a scientific breakthrough in crop protection against virus damage.

SECTION ONE

The Problem

Agricultural losses lower productivity of society's resources. How large is the problem? For total world agriculture, estimates are not available. For total world crop production, from planting to harvest, Cramer estimates that production is lowered by a third because of insect, disease, and weed pests. Cramer's estimates follow closely those of the U.S. Department of Agriculture surveys during the 1940's and 1950's. Agricultural research committees commonly cite these figures in policy statements as justification for increased funding and point to the social benefits of increasing the world food supply. This review of the literature on crop loss estimates will examine the relative importance of virus diseases among other causes. Because virus diseases are more important in preharvest losses, postharvest losses are not discussed.

The Concept of Agricultural Loss

A loss is defined as unrealized gain. Gain, in this definition, is synonymous with increased value; and unrealized means unaccomplished. The definition is necessary for understanding the problem of agricultural losses. The notion is vital to its measurement. Agricultural losses caused by many factors--among them virus diseases--result in lower productivity of agricultural land, labor, and capital.

An agricultural loss is measured commonly in units of potential production. Often, it is translated into other representative terms, such as monetary value or equivalent acreage or labor. The estimation of losses and their equivalent measures are predicated on the following condition: What would be the production, and its value, if the loss-causing agent had not acted? Therefore, under strict interpretation, loss estimates would not include the costs of controlling pests.

The production function approach to understanding agricultural losses involves general economic concepts which outline the problem. The production function represents the process by which a group of inputs are transformed into a group of outputs during a specified period. The total gain in production is the difference between the value of output and the cost of inputs. Potential production in one growing season is affected not only by the quantity of inputs applied, but also by the state of all constant factors. The shortrun constant factors of production will change over a longrun period. The state of technical knowledge, for example, is presumed to change during a period of years, not in one season. The incidence and virulence of viruses and their vector organisms will change over a period of years.

In the literature, agricultural losses are usually expressed as a percentage of maximum production and the percentage is applied to total output or some equivalent value. Frequently, motivations for reducing losses are the impending increased demand from future populations and minimizing average production costs. The usual policy questions are how many more people could be served by loss prevention and how much more is it costing society to produce food and fiber with the current losses in agriculture.[1]

Ordish writes that "... Mankind has never in its long history had sufficient to eat." And because of the inevitable growth in population, the problem of inadequate food "... presents an inescapable challenge to statesmen, economists and scientists." To meet this challenge, agricultural losses are often classified into groups. For example, the USDA (1954) classifies losses as

1. those that are unpreventable with present technological knowledge,

2. those that are presumably preventable but only through the use of control measures that are not economically feasible, and

3. those that are preventable with present technical knowledge and under current economic conditions.

This classification leads to the conclusion that USDA views potential output as a longrun variable. The USDA (1965) refers to two types of agricultural losses:

1. reduction in quantity or deterioration in quality during production, handling, and processing of farm and forest products, and

2. deterioration in land on farm and forests, affecting annual production immediately in some cases, and over a period of years in the future.

The Department is interested in quantifying "... current losses to agriculture from insects, diseases, fire, erosion, floods, etc., especially losses that might be controllable through more general application of methods already known or methods that might be worked out by additional research." By the nature of loss estimates, the USDA (1965) means "whether or not they arise from causes that are preventable with present technical knowledge."

Cramer's concept of crop loss is closely aligned with the U.S. Department of Agriculture. For example, "[USDA] data published in 1927, 1931, 1939, 1954, and 1965, ... together with the statistics for each of the Federal States in the USA presented in the journal 'Cooperative Economic Report' ... are among the most important sources of information" used by Cramer. Cramer supplemented his wide review of the literature on loss estimates with time series data from insurance records. Loss estimates based on insurance indemnities suggested "... there is no apparent tendency of a gradual reduction of the losses due to insect pests and diseases."

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[1] Cook argues that because "crop loss" is an often-misused term, it should be replaced by yield constraint or production constraint. He prefers that "... the effects of pests and diseases... should be expressed by the greater yield possible when they are controlled rather than in terms of a yield 'decrease' if they are not controlled". Choosing actual rather than potential production as the basis for percentage yield constraints, though, only serves to increase the ratio. According to Cook, "... many estimates of the effects of disease on crop yield have been too conservative".

Measurement of Agricultural Losses

Assessing crop losses is not a simple or inexpensive matter. Given the area planted and the expected yield of a crop, one might say the difference in expected and actual output is lost or unrealized production. Establishing a reliable crop loss estimate, though, is difficult to do because production is variable--from year to year, region to region, farmer to farmer. Attributing the crop loss to a cause adds to the difficulty because crop damages are not always additive. Pests include viruses, bacteria, fungi, weeds, insects, and mammals such as deer or mice. Production is affected by drought, monsoons, high winds, hail, and other weather-related factors. Over 90 percent of U.S. Federal Crop Insurance Corporation indemnities are paid for weather-related crop losses (USDA, 1985). Final production is affected also by plant variety, soil fertility, and by farmer decisions such as what to plant, when to plant and harvest, how to store and market the crop, and by government policies based on land use and conservation. These factors affecting the difference between potential and actual production and the difficulties of measurement for the many crops, regions, and causative agents indicate the high costs of establishing reliable crop loss estimates.

The lower marginal value of increased production is commonly disregarded when estimating agricultural losses. Often, attaching dollar values to the individual estimates of agricultural losses is justified solely on the grounds of measuring comparable values among heterogeneous commodities--apples and wheat, for example, or losses in quality are more easily valued in dollar terms. Interpretations of these dollar amounts sometimes suggest their meaning in the concept of opportunity costs. The use of land or labor resources as equivalent terms to express agricultural losses is a particular expression of forgone alternative uses (Ordish).

Estimates of Agricultural Losses

The United States Department of Agriculture has the best tradition of agriculture loss assessment. This tradition extends back to specific assessments of crop and livestock damage from insects (1938 and 1942); animal diseases, parasites, and insects (1942 and 1952b); and plant diseases (1953). The most significant USDA effort was published in 1954, and represented a preliminary estimate of losses in agriculture during the 1942-1951 period. An updated report of losses during the 1951-1960 period was published in 1965. These latter two reports form the baseline for other efforts to estimate agricultural losses. The most notable research on world crop losses (Cramer) was based largely on U.S. estimates.

The USDA (1954) estimated losses in U.S. agriculture to be equivalent to about one-third of potential production value during the 1942-51 period. The total loss was attributed to:

1. diseases and insects affecting crops,

2. mechanical injuries, weeds, hail, and fire and brush damage to crops,

3. crop harvest inefficiencies and rodent and insect damage during storage,

4. crop marketing, processing, and distribution activities,

5. fire, wind damage, insects and diseases affecting forest growth and forest trees,

6. diseases, internal parasites, and insects affecting livestock,

7. erosion and other causes of deterioration of land, and damage to watersheds from floods.

In terms of forgone opportunities, USDA (1954) estimated "... if all these causes of loss had been eliminated ... some 123 million fewer acres of crop land ... would have [been required to produce the actual 1942-51 volume of production]".

By definition, maximum production requires the full utilization of producing capacity. In the context of agricultural loss assessments, the USDA (1952a) estimate of production capacity for the mid-1950's is complementary to their loss estimates for that period. Their reason for estimating agricultural production capacity was "to appraise production possibilities and resource needs of agriculture in the defense effort." This cooperative work between the Land-Grant Colleges and the USDA, was designed to not duplicate their agricultural loss research. The estimates were obtained from state-by-state appraisals of production potential in 1955. The Department estimated that total 1955 crop production could be increased by 20 percent over the 1950-51 average, with a concomitant 45 percent acreage increase and a 70 percent increase in nitrogen, potassium, and phorphorus fertilizers. The 20 percent of unutilized capacity could be realized under the following conditions: average weather, favorable economic incentives, sufficient input availability, and widespread use of available technology.

The USDA (1965) report on agricultural losses is a revision of the 1954 estimates of annual losses during 1942 to 1951. "The [1965] estimates ... are based on average prices for the period 1951 to 1960. Some of the estimates are based on surveys or actual records; most, however, represent the best judgment of Department specialists" (USDA, 1965). The total annual loss in value of agricultural production for the 1951-60 period was placed around $21 billion, higher than the 1942-51 estimate. The higher estimate resulted from higher prices for farm products, greater volume of production, and a larger number and better knowledge of losses compared to 1942 to 1951. Although, the USDA (1965) failed to report the total 1951-60 estimate in percentage terms, the one-third of total annual value reported for 1942 to 1951 is likely to be valid for the 1951-60 period.

Cramer estimated world crop losses using the available literature, crop insurance records, expert opinion, and rough guesses where necessary. The dearth of statistical information about USSR losses, for example, required Cramer to apply estimates from similar agriculture situations to Soviet production data. His estimate of total world crop losses is given for no specific period. Because it is based largely on USDA benchmarks, Cramer's 35 percent estimate for total world crop losses most likely applies to the 1940-60 period.

The distribution of disease losses by crop group is virtually the same for the 1951-60 period as in 1942 to 1951 (USDA, 1965). Field crops and alfalfa and other hays accounted for about 70 percent of the total because of the many acres planted in these crops (Table 1). Because high average values offset lower total acreage, fruit and nut crops and vegetables accounted for about half of the remaining 30 percent.

Table 1. Estimated distribution of total loss in value caused by plant diseases and air pollution to various groups of crops during production, 1951-60

Crop group	Distribution of Value
	--- percent ---
Field crops	53
Alfalfa and other hay plants	17
Forage seed crops	1
Pasture and range plants	5
Fruit and nut crops	6
Vegetable crops	8
Ornamental plants and shade trees	1
Other [a]	9
Total	100

SOURCE: United States Department of Agriculture (1965).

a/ Includes all crop losses from air pollution.

Cramer's calculations indicate that diseases are second behind insect pest damage in total world crop losses (Table 2). Diseases, which cause about one-third of all crop losses, are defined generally as physiological disorders, and in this context cause actual production to be less than potential production. Compared to insect pests, diseases are proportionately more important causes of loss in wheat, oats, barley, rye, potatoes, sugar beets, vegetables, fruits, coffee, cocoa, tea, tobacco, and soybeans.

Table 2. World Crops: Average annual loss of production from insect pests, diseases, and weeds

Crop	Cause			
	Insects	Diseases	Weeds	Total
	--- Percent ---			
Cereals	14.7	8.9	11.2	34.8
Potatoes	6.5	21.8	4.0	32.3
Sugar beets and cane	16.5	16.5	12.2	45.3
Vegetables	8.7	10.1	8.9	27.7
Fruits	5.8	16.4	5.8	28.8
Stimulants	11.4	14.9	10.5	36.8
Oil crops	11.5	10.2	10.8	32.5
Fiber crops and natural rubber	14.2	11.8	6.3	32.3
Total all causes including polyphagous pests	13.8	11.6	9.5	34.9

SOURCE: Cramer.

The evidence for substantial crop losses from diseases was established for the middle years of this century. How do these estimates apply to the later years? The comparison is made difficult by a lack of current evidence. Referring to virus diseases, for example, Matthews writes "Estimates of yield reduction for a particular crop and virus have no general validity. The extent to which yield is reduced in any particular year and locality will depend on many factors, including variety of host plant and strains of the virus present, the incidence and activity of any vectors, the time at which infection occurs, the nutritional state of the crop, the weather, and the presence of other parasites." The USDA estimates for the 1941-52 and 1951-60 periods, though, are averages taken from a variety of sources: actual records, experimental data, and perhaps most importantly consensus among experts. These averages mitigate the variation among particular years and localities, and generally suggest the magnitude of crop loss problems.

A one-third loss of crop production is being used currently to define the major problem for plant protection specialists. The National Science Foundation (NSF) writes "Factors such as weather can greatly influence the severity with which a disease affects a plant population. This makes it difficult to estimate accurately the annual losses in agriculture and forestry that result from plant disease. Nevertheless, it is estimated that plant diseases cause about a 30 percent loss in potential yield of major crops each year."

In recent years, total crop loss estimates which could be compared to the USDA series (1954, 1965), Ordish, or Cramer have not been published. Mulrooney's estimates of losses from diseases in soybean are calculated by methods similar to USDA (1954, 1965) but the survey is limited to 16 southern states and to the 1983 and 1984 crop years. They are solicited from "personnel of the Cooperative Extension Service and experiment stations...and are derived from IPM field monitoring programs; regional trials for seedling, nematode, and foliar disease control; field observations; laboratory diagnoses; grower demonstrations; and diagnostic clinic records." Mulrooney reported 19 and 15 percent losses from disease in soybean during 1983 and 1984, respectively. These two estimates correspond with the 14 percent loss from diseases reported for soybeans in 1951 to 1960 (USDA, 1965). Therefore, in the case of soybean disease losses in southern states, at least the current estimates are not seriously at odds with the USDA benchmark.

In summary, national estimates of agricultural losses and production potential in U.S. agriculture during the 1940's and 1950's indicate that actual output was substantially below the potential maximum by about 33 percent. The reasons for this difference include environmental and technical factors. Economic factors also may have affected which technologies were used by farmers. Since 1965, USDA has not published national estimates of agricultural losses in the 1942-51 and 1951-60 tradition. Therefore, these earlier estimates stand as benchmarks.

Virus Damage to Crops

Diseases are caused by various groups of organisms, and Cramer's world crop loss estimates do not detail the role of viruses in the total disease complex. The USDA (1954, 1965) estimates detail crop losses from virus diseases as distinct from other causes. For this reason, the following discussion about U.S.

crop losses from virus diseases is limited to a summary of USDA estimates and supplemented where possible with information from other sources. For the purposes of discussion, estimates of crop losses from diseases generally fall into two categories:

(1) those for which the loss is not attributable to a specific cause or which account for an insignificant proportion of the total, and

(2) those which account for a significant proportion of total losses and are attributable to particular causes.

The first group includes alfalfa and other hay products, forage seed crops, pasture and range plants, and ornamental plants and shade trees. The second group includes field crops, fruit and nut crops, and vegetables. Several important U.S. crops, including corn, are not significantly affected by virus diseases; therefore, they are excluded from the following discussion.

The USDA (1965) reports losses on alfalfa and all other hay plants are around 20 percent of total production. For alfalfa grown for hay, the losses are attributed to bacterial wilt (5 percent), crown and root rots (5 percent), virus diseases (5 percent), and foliar diseases including black stem (9 percent). Losses on all other hay plants are about 15 percent but are not attributed to specific causes. Virus diseases claimed about 5 percent of total red clover for hay production during 1951 to 1960, but the more important causes of loss are attributed to crown and root rots (23 percent) and leaf spots and rust (6.5 percent).

Production of alfalfa and clover for seeds is lowered by virus diseases (Appendix Table A.1). On average about 3 percent of potential production is lost to virus diseases; but about 12 percent is lost to other causes -- mostly fungal diseases. In the United States, alfalfa and red clover are planted on about 500,000 acres and losses from other diseases are about three times more serious than from viruses.

Pasture and rangeland plants are estimated to lose about 5 percent of potential production to diseases, but the losses are not distributed among causes (USDA, 1965). As of 1965, "... more than 75 fungi, bacteria and viruses have been identified as the causal agents of pasture grass and legume diseases".

Diseases are important causes of production losses in ornamental plants and shade trees, but reliable estimates for this group are not available. Although viruses are known to cause significant losses in particular floral crops, it should be noted that viruses are cultivated into some flowers for their desirable chimeric effects on color.

Viruses are not the most important cause of disease losses in field crops; fungi cause the majority of the average 14 percent reduction. The annual losses from virus diseases range from 1.4 percent (tobacco) to 10 percent (hops). Appendix Table A.2 presents a list of field crops and disease loss esimtates. Viruses cause reductions of about 5 percent in barley production from stripe mosaic and yellow dwarf diseases, and about 3 percent in dry bean production from bean yellow mosaic, common bean mosaic, and curly top. In wheat production, disease losses come in epidemics, usually caused by the rust fungi, but occasionally by the wheat streak mosaic virus--about one percent annually during 1951 to 1960. The overall importance of field crops in total loss estimates arises from the acreage planted in this group. In three crops alone--wheat, barley, and oats--60 million to 80 million acres are planted in the United States.

Fruits and vegetables are highly susceptible to virus infections; especially the solanaceous crops (peppers, potatoes, and tomatoes), bramble-berries (blackberry and raspberry), and noncitrus tree fruits (pear and cherry). Appendix Tables A.3 and A.4 illustrate the wide range of damage caused by virus and other diseases in fruits and vegetables. On average, annual disease losses in fruits and vegetables total about one-sixth of potential production, and about one-fifth of that is due to virus damage.

Walkey lists crop losses from virus diseases for the United States and other countries. A close examination of the post-1970, U.S. reports, though, reveals that the estimates are based either on pre-1950 reports or on experimental plots where one of the scientific objectives is to encourage disease.

Mulrooney (1985, 1986) estimates that 15 percent to 19 percent of soybean production was lost to diseases during 1983 and 1984, and that virus diseases were insignificant to the total loss in both years (Table 3). In both years, North Carolina, Louisiana, and Virginia reported greater problems with virus diseases than other States.

Table 3. Estimated loss of soybean yields to disease in 16 Southern States, 1983 and 1984

	Disease cause		
	Viruses	Other	All
	-----	Percent	-----
1983	0.2	18.4	18.6
1984	0.14	14.71	14.85

Source: Mulrooney (1985, 1986).

Bos is concerned with the lack of quantitative estimates for virus disease effects in crops. The apparent lag in developing quantitative assessments and predictions of economic losses leaves "farmers and government... faced with the questions of how damaging viruses actually are, which ones are the most damaging, how yield reductions can be assessed on a farm, in a district, a country or region of the world, and how such losses can be predicted. Answers to these questions are essential to determine economic thresholds for control measures and to enable administrators to assign research priorities." Bos provides more general information about methods in crop loss assessment than about the extent and magnitude of actual crop yield reductions from virus diseases.

The USDA (1954, 1965) estimates of average annual losses generally do not provide national-level information about yield variability caused by virus diseases. Anecdotal evidence for yield losses in single crop and virus combinations are cited where the disease has been severe or pervasive. However, the interactions among climate, crop, and virus apparently are too numerous to allow for long term estimates in yield variability.

The paucity of current information about actual crop losses from virus diseases is evident in Walkey's recently published book and in Bos' emphasis on method development. Corbett and Sisler's listing of nearly 60 reports of crop yield reductions published during 1924 to 1963 illustrates the fragmented state of loss assessment. Corbett and Sisler's introduction concludes "From these few cases it becomes evident that viruses extract an annual loss from most commercial crops." Wiese asks for better crop loss assessments as a basis for arranging research priorities and improving crop production systems. Nyvall, in the same vein, believes that reliable disease loss estimates must be published in the scientific literature.

Virus Control Practices

Agriculture's most important principle of managing virus diseases in crops is avoidance. Because chemical methods of disease eradication are not available with current technology, farmers must prevent virus infection to avoid disease development. To effectively manage virus diseases, farmers must begin by obtaining virus-free seed or stock material. The methods of producing virus-free seed or stock include propagation in virus-free areas, heat treatment, and meristem culture. High heat can damage plant tissue, so heat therapy incorporates alternating high and normal temperatures for prolonged periods. Meristem culture, raising whole plants from small amounts of tissue, has produced virus-free clones of previously infected plants. The mechanism for this is not known, but the result has been related to the location of virus-free cells in infected plants and to properties of artificial media used in tissue culture techniques (Walkey).

Once virus-free material is obtained, the farmer must be vigilant in avoiding contamination from mechanical and natural vectors. Viruses are transmitted by a variety of vectors which include farm machinery and workers, and natural vectors such as insects, nematodes, fungi, and weeds. Avoidance measures fall into two general categories:

1. temporal -- altering planting and harvesting dates and rotation schedules to avoid contact with vectors, and

2. spatial -- erecting barriers to entry by cleaning tools and clothing, removing virus reservoirs such as weeds and other hosts, deterring insect vectors with hedges, eradicating vectors with chemical controls, and roguing infected plants.

Virus disease management is difficult to accomplish because it requires cooperation among the levels of production and marketing. For example, insect vectors easily cross boundaries between production areas, and seed trade between countries must be monitored. Consumer purchases of virus-susceptible products are sometimes quarantined before allowing their entry into high-risk areas. Government programs, therefore, including quarantine, seed certification, eradication, and information management play important roles in agricultural efforts to reduce disease losses from crop viruses.

Crop breeding for resistance to virus infection has been more important to agriculture than any other single measure of avoidance. Furthermore, crop breeding holds the most promise for future advances in reducing crop losses from virus disease. The National Science Foundation believes that "... growing disease-resistant varieties is easier, less expensive, and often more effective than other methods of control". Their 1980's outlook for plant protection possibilities included more multiline seed planting to reduce the risk of severe disease outbreaks, increasing the durability of resistance by breeding for multigene traits, cloning, and recombinant DNA technology.

The guiding principle in designing disease management strategies is likely to remain the integration of diverse tactics. No one method of control is successful against biological pests for long periods if it is employed in a single-handed fashion. This axiom of plant protection is especially relevant in the management of plant diseases where the goal is improving resource productivity.

Conclusions

The USDA (1954, 1965) estimates of annual crop losses from diseases average about 15 percent of potential production for the 1940-1960 period. When viruses are part of the crop disease complex, they can account for about 20 percent of the disease loss. The post-1960 scientific literature offers no indications of a trend in crop losses from virus disease. Virus control methods which include mainly avoidance and crop breeding for resistance remain the most important components of an integrated approach and total losses from new virus epidemics have not been documented recently. For these reasons and because of the lack of trend data, the USDA (1954, 1965) estimates of 2 to 4 percent loss from virus diseases in crop production are likely to remain the accepted figure.

A comprehensive program of crop loss assessments similar to USDA's surveys (1954, 1965) is not in place in the United States. Furthermore, Chiarappa, et al. point to "the weakness of the surveys...that...rely too heavily on the subjective estimates of individual observers with their bias and inevitable variability." The United Nations Food and Agriculture Organization publishes a manual of crop loss assessment methods but no current regional or world estimates. "For studying actual losses inflicted by plant viruses over whole areas or countries, surveys have to be made and... [standard methods] for loss appraisal need [to be developed]" (Bos 1982). In a recent statement of the need to quantify the effects of pests on agricultural production, Walker indicated that changes in population, climate, cropping patterns, and pest and disease pressures have increased the importance of reliable loss estimates. Until a program with more objective and uniform standards is put into place, subjective estimates of the actual losses in agriculture will remain the best alternative for placing priorities on pest problems.

SECTION TWO

The Science

The peculiar nature of viruses, with their mysterious ability to infect, spread, and cause diseases in plants, explains part of why understanding their mode of action is important to scientists. Three important subjects for phytovirology are virus biochemistry, molecular genetics, and variable interactions with different hosts. A major problem for phytovirologists has been developing tools with which to identify and characterize these extremely small pests in their vectors and in normal plant cell material. Viruses have been associated with plant diseases since the late 19th Century, but how viruses cause crop losses is not completely understood.

The many combinations of plants and viral pathogens display a wide range of biochemical and genetic behavior (Fraser, 1982 and 1986). A plant is either immune to a virus, in which case it is referred to as a non-host, or it is infectible (Cooper and Jones). A host plant is either susceptible to disease or resistant. Symptoms of infection are severe in a sensitive host and mild in a tolerant host. Resistance is classified as either constitutive or induced, depending on the source of resistance (Fraser 1986). Induced resistance comes from factors initially outside the host, for example, other viruses. Constitutive resistance owing to one or a few genes is known also as vertical resistance. Horizontal resistance is controlled by many genes.

A significant portion of the total scientific activity devoted to plant viruses has focused on their identification, classification, and association with disease symptoms. Viruses, which lack metabolic faculties, are not considered members of the animal or plant kingdoms. The association between virus characteristics and disease symptoms has led the scientific community to recognize certain typical viruses as representatives of various virus groups. Therefore, scientific nomenclature for viruses has developed explicit reference to host range and disease symptoms rather than the classical binomial terminology.

The objective of this section is to provide a brief overview of virus structure, classification, and disease symptoms. The main purpose of this overview is to present information which can be useful in judging prospective virus control technologies. With a background of information to understand the problem of plant-virus pathology, science policymakers will be helped in making informed decisions about the potential of this research to increase crop productivity.

What is a Virus?

In the Atlas of Plant Viruses, Francki, Milne, and Hatta develop "...our current concept that virus particles consist of a nucleic acid genome surrounded by protein; the function of the protein being, at least in the simplest cases, to protect the nucleic acid from the hazards of nucleolytic enzymes when the virus is outside the host cells."[2] The ordinary use of genome refers to the sum of all

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[2] The information under this heading is drawn mostly from Francki, et al., Walkey, Corbett and Sisler, and various standard scientific reference materials.

chromosomal genes in a haploid cell (including prokaryotes) or the haploid set of chromosomes in an eukaryotic cell. A haploidal cell has a single set of unpaired chromosomes. Although viruses are considered neither prokaryotes nor eukaryotes, viral nucleic acids function as carriers of genetic information.

A nucleic acid is a sequence of nucleotide molecules bonded with amino groups and linked by phosphoric acids. Two important nucleic acids are characterized by their carbohydrate moieties: ribonucleic acid (RNA) and deoxyyribonucleic acid (DNA). The virus genome encodes the necessary genetic information for self-reproduction, but viruses are dependent upon the host cell to transcribe and translate that information into new virus particles.

The coat protein, so-called because it normally covers a portion of the genome, consists predominantly of amino acids linked in sequence by peptide bonds. Lengthy combinations of about 20 common amino acids are the normal components of proteins. Viruses shed their coat protein once inside the cell in order to free the nucleic acid genome and allow for replication. Following replication, the new genome triggers the manufacture of new coat protein subunits.

Virus Classification

Twenty-seven distinct groups have been created by the International Committee on Taxonomy of Viruses (Table 4) to classify nearly 420 different plant viruses (Francki, et al.). The distinguishing group characteristics include nucleic acid content, morphology, host range, vectors, and other identifiers such as serological affinities. Caulimoviruses and geminiviruses are the only two plant-virus groups containing DNA genomes, the other 24 groups contain RNA viruses. The nucleic acids are commonly arranged as single-strands, with the exceptions being Reoviridae (double-stranded RNA) and Caulimovirus (double-stranded DNA). Common shapes in viruses are the isometric and the rod-shaped morphologies.

The tobamovirus group, for example, is characterized by rigid tubes with dimensions of 18 by 300 nanometers, built from multiple copies of a single species of protein subunit, and arranged in a helix. A tobamovirus contains one molecule of single-stranded RNA, and is easily transmitted by mechanical means but has no efficient natural vectors. Tobamoviruses parasitize solanaceous plants (tobaccos, tomatoes, potatoes), cucurbits (squashes), legumes, orchids, cacti, and crucifers.

Virus Vectors

Virus vectors are carriers of the pathogen and can be classified into mechanical and natural (Walkey). Mechanical vectors include cultural tools such as pruning and cultivating equipment. Natural vectors include insects and other arthropods, nematodes, and fungi. Insects are the most important natural vector of viruses (Walkey). The aphids, leaf- and treehoppers, and white flies are the most important insect vectors. Natural mechanical means are rare but can be mentioned as plant-to-plant contact when, for example, leaves brush together in windy conditions.

Table 4. Plant Viruses: Group names, type members and acronyms

Group Name	Type Member (Acronym)
Caulimovirus	Cauliflower Mosaic Virus (CaMV)
Geminivirus	Maize Streak Virus (MSV)
Reoviridae	Wound Tumor Virus (WTV)
	Fiji Disease Virus (FDV)
Rhabdoviridae	Lettuce Necrotic Yellows Virus (LNYV)
	Potato Yellow Dwarf Virus (PYDV)
Tomato Spotted Wilt Virus	Tomato Spotted Wilt Virus (TSWV)
Maize Chlorotic Dwarf Virus	Maize Chlorotic Dwarf Virus (MCDV)
Tymovirus	Turnip Yellow Mosaic Virus (TYMV)
Luteovirus	Barley Yellow Dwarf Virus (BYDV)
Sobemovirus	Southern Bean Mosaic Virus (SBMV)
Tobacco Necrotic Virus	Tobaco Necrotic Virus (TNV)
Tombusvirus	Tobacco Bushy Stunt Virus (TBSV)
Comovirus	Cowpea Mosaic Virus (CPMV)
Nepovirus	Tobacco Ringspot Virus (TRSV)
Pea Enation Mosaic Virus	Pea Enation Mosaic Virus (PEMV)
Dianthovirus	Carnation Ringspot Virus (CRSV)
Cucumovirus	Cucumber Mosaic Virus (CMV)
Bromovirus	Brome Mosaic Virus (BMV)
Ilarvirus	Tobacco Streak Virus (TMV)
Alfalfa Mosaic Virus	Alfalfa Mosaic Virus (AMV)
Tobamovirus	Tobacco Mosaic Virus (TMV)
Potexvirus	Potato Virus X Virus (PVX)
Carlavirus	Carnation Latent Virus (CLV)
Potyvirus	Potato Virus Y Virus (PYV)
Closterovirus	Beet Yellows Virus (BYV)
Tobravirus	Tobacco Rattle Virus (TRV)
Hordeivirus	Barley Strip Mosaic Virus (BSMV)
Velvet Tobaco Mottle	Velvet Tobacco Mottle (VtMoV)

SOURCE: Franki, R.I.B., et al. and Walkey.

The primary mode of infection through insect vectors is passage via sucking mouthparts. As the insect punctures the plant and inserts its proboscis to withdraw plant fluids, the host is vulnerable to infection with the virus which may be present in the proboscis or in other insect organs connected to its digestive tract. The same principles apply to soil-borne vectors such as nematodes and fungi--particular differences exist in various virus, vector, and host combinations.

Viral Diseases

Disease is a notoriously difficult concept to define precisely and phytopathologists occasionally differ in their interpretations of disease. Bos concludes "that there is no sharp limit between normal and abnormal or between 'sick' and 'healthy' in plant growth because of the natural variation in normal development". In plant-viral diseases, symptoms are considered the result of infection and the "whole cycle of symptoms is called disease." Infection of the host occurs by passive entry through a wound or opening to the cell. Symptoms usually develop locally, followed by virus spreading in some cases or by continued local development. The results of disease range across the spectrum of altered metabolism to reduced plant vigor to tissue or plant death.

Viral pathogenecity is a series of genetic events in which the viral genome contributes genetic information to the metabolic processes of the host plant (Bos, 1978). Physiological and biochemical disturbances in the host cell lead to anatomical deviations and, in cases of visual symptoms, macroscopic deviations. An important anatomical deviation includes abnormal growth rates in cells of plant phloem and xylem tissues which are necessary for nutrient transport. Macroscopic deviations include abnormally shaped organs such as fruit and leaves, changes in pigments such as chlorophyll, and necrotic lesions resulting from local tissue death.

Symptom classification is an important tool for phytopathologists to identify and associate virus properties with host disease characteristics. Dwarfing and stunting in plants refer to growth reduction from luteoviruses, for example. Streaks, yellows, mottles, and mosaics refer to virus-induced color changes in leaves and can be distinguished according to size, shape, distinctness of boundary, and number of patches (Bos,1978). Streaking and striping are also virus-induced color changes and are associated with the parallel vein pattern in grasses, as in maize streak caused by a geminivirus. Wilting refers to water deficiencies which may lead eventually to loss of plant turgidity and eventual death.

Leaves showing the mosaic disease sometimes show areas of dark green tissue in which the virus is detected at reduced levels. These observations form the "green island" effect, and have led to the hypothesis that plants have the ability to restrict disease in these areas (Ponz and Bruening). A plant's reaction to infection may involve tissue death which, in turn, reduces the chances of virus spread. These restrictions are known as "hypersensitive" responses. Thus, hypersensitivity is considered as another form of restriction against disease. Cross-protection and acquired immunity are various degrees of a phenomena in which initial infection by one virus leads to restricted "superinfection" or "challenge infection" by related viruses or pathogens. The mechanism of cross protection is not known, but may be related to virus competition for host sites or direct interference with the super-infecting pathogen.

The links between infection, symptom manifestation, causal agent, and mechanism of disease are not fully known for plant viruses. Bos states "Thus, from purely physiological and biochemical studies of the infected hosts, the nature of changes in metabolism of virus-diseased plants has not yet been clarified. Various abnormalities point to a non-specific but comprehensive derangement of normal host metabolism. How this is brought about is unknown."

Biotechnology in Plant-Virus Resistance Research

Interdisciplinary research to improve plant protection and classical crop breeding methods through biotechnology involves molecular geneticists, plant pathologists, and breeders in explaining a range of plant-virus interactions in a biochemical and genetic framework. Biotechnology has the potential to provide new insights into related phenomena such as pathogen-derived host resistance, cross protection, the "green island" effect, and hypersensitivity. The potential of this new understanding for plant-virus resistance is "... more efficient and responsible exploitation of available genetic resources...if the basic genetic mechanisms are known. Furthermore, decisions about the strategies of resistance gene deployment, and predictions of the likely future patterns of interaction with the evolving genetic system of the pathogen, can only be based on sound genetic knowledge" (Fraser, 1986).

The transfer of laboratory-based biotechnology to the development of virus-resistant crops is likely to take the traditional path of discovering resistance genes followed by testing in greenhouses, controlled field environments, and limited commercial settings before new varieties are available to farmers. By analogy, this scheme of varietal development suggests a path from developing laboratory biotechnologies to understanding plant-virus resistance. Scientific progress requires the development of hypotheses which meet traditional standards of explaining the mechanisms of plant-virus resistance. Plant pathologists test and debate these hypotheses in the scientific literature. Therefore, biotechnology can contribute to progress in phytovirology by developing and testing hypotheses to explain these traditional problems.

The objective of this discussion is to assess the contribution of biotechnology to progress in plant-virus resistance research by examining the relationships among five review articles representing the core literature on plant-virus resistance. Following a description of the core literature on plant-virus resistance, two research reports on the biotechnology of plant-virus resistance are compared to the core literature. The comparison is followed by a discussion of the role of biotechnology in plant-virus resistance research. This approach accounts for a substantial portion of the journals, scientific reports, and principal scientists performing research on this subject. The results of this approach will be useful in assessing the future potential of biotechnology in preventing crop losses from viral diseases.

The Core Literature

Five scientific review articles published between 1982 and 1986, which present a comprehensive picture of the various scientific approaches to understanding plant-virus resistance, are used to describe the literature of research on plant-virus resistance: Fraser (1982, 1986), Hepburn, et al., Ponz and Bruening, and Van Loon. Fraser (1986) presents the "negative" and "positive" models of gene-based plant resistance. The negative model hypothesizes that resistant plants lack the genes necessary to produce substances vital to virus survival. The positive model hypothesizes that resistant plants possess the genetic ability to produce virus-interfering substances. Fraser's positive model suggests five targets for interference: virus transmission, establishment, local spread, systemic spread, and symptom formation. Both models produce hypotheses about inheretability and durability of resistance.

The hypotheses in Fraser's (1986) genetic models of virus disease resistance are summarized in a series of questions:

-- Is resistance based on simply one or a few genes clustered together, or many genes in different chromosomal locations?

-- Does resistance share common genetic features among different plant species?

-- What is the genetic basis of virulence?

-- How does gene evolution affect resistance durability and changes in virulence?

Generally, Fraser (1986) favors the model containing mono- or oligogenic resistance factors because the "... majority of [known] virus resistance mechanisms in plants are genetically very simple...More complex, and probably more durable resistances, can be more difficult to establish and certainly more difficult for which to breed." The positive model suggests that genes promoting resistance could be isolated and transferred to susceptible hosts, while the negative model suggests that genes could be deleted to reduce a pathogen's virulence.

Fraser (1982) prescribes a methodology of developing a biochemical model of resistance. In this methodology, identification and purification of the resistance gene products should be followed by isolation of the production intermediaries and use of the intermediaries as probes for locating the resistance gene. Fraser (1982) believes a biochemical model which locates a resistance gene product has the greatest potential for designing resistant crops.

Ponz and Bruening, noting the correlation between the spread of viruses and the development of symptoms, defines a systemic infection as the reference point to discuss the mechanisms of restriction. Restriction mechanisms are viewed as single-virus or multi-agent phenomena where multi-agent mechanisms explain cross-protection and acquired resistance. The hypothesis of single-virus mechanisms is designed to explain limited systemic infection and hypersensitivity. Van Loon emphasizes the role of inhibitory factors such as pathogenesis-related proteins, cell permeability, and enzyme reactions in explaining the expression of resistance. Hepburn, et al. calls for alternatives to reliance on major gene resistance in designing technical approaches to resistance gene exploitation. One alternative switches emphasis in breeding to "more general or horizontal resistance", the other "seeks to make greater use of the available genetic resources, whether single gene or oligogenic, with the use of artificial mutation, somaclonal variation and use of haploids...to expose existing variation, increase it, or offer fresh combinations of resistance with other characteristics."

Ponz and Bruening, Hepburn, and Van Loon generally subscribe to Fraser's philosophy that progress in developing virus-resistent crops is more likely to come through biotechnology if genes for interference can be located. Similarly, the mechanism by which viruses interfere with super-infection (cross-protect) is viewed as a promising approach to enhancing resistance to disease. A single model, though, which isolates a particular interferring substance for one or more viruses is not clearly defined in the scientific literature.

The scientific basis for these five articles are the 650 references used in citing the relevant evidence (Table 5). Fraser's two reviews of the biochemistry and genetics of plant-virus resistance share 25 references, of which six also appear in Ponz and Bruening and nine in Van Loon. Ponz and Bruening and Van Loon share 43 references, of which eight appear in Fraser (1986), and 13 in Fraser (1982). Hepburn, et al. shares 11 references with Fraser (1986). The large number of references covered by these five review articles and their explicit links are assumed to accurately reflect the core literature.

Table 5. Number of own- and cross-references in 5 scientific reviews of plant-virus resistance research

	Fraser (1982)	Fraser (1986)	Ponz and Bruening	Van Loon	Hepburn, et al.
Fraser (1982)	84	25	15	34	0
Fraser (1986)		243	19	20	11
Ponz and Bruening			151	43	0
Van Loon				203	0
Hepburn, et al.					105

Although the core literature comprises research spanning half a century, about two-thirds of the references appeared during 1977 to 1986. The core literature is published in over 114 different journals (excluding books, proceedings, dissertations, experiment station bulletins, and other non-serial outlets). Out of 650 references published since 1931, 42 percent are published in six major journals: Phytopathology, Virology, Molecular Plant Pathology, The Journal of General Virology, Science and Nature (Table 6). Eleven percent of the total core references are published in non-serial outlets, mostly since 1977.

Table 6. Core literature of plant-virus resistance research: Distribution by publication source and date of publication

Journal	Date of Publication		
	1931-1976	1977-1986	1931-1986
		Percent	
Phytopathology	26	6	13
Virology	22	8	13
Molecular Plant Pathology	3	8	6
Journal of General Virology	3	7	5
Science and *Nature*	2	5	3
Plant Disease	1	2	2
Books and other non-serial outlets	6	14	11
Other serial publications	37	50	47

SOURCES: Fraser (1982, 1986), Hepburn, et al., Ponz and Bruening, and Van Loon.

Non-serial publications and journals other than the major six accounted for a one-third larger share of the post-1976 references. Principal investigators, as represented by the number of different senior authors, totalled 431 scientists. The leading countries associated with these authors are the United States, Japan, Israel, the Netherlands, and the United Kingdom.

The core literature of phytovirology resembles a brief sketch of all phytopathology literature drawn for the American Phytopathological Society in 1972 (Table 7). Garfield indicated that the prominent position of Virology in the list of most important phytopathology journals suggests the high value placed on applied plant-virus research. In tracing the information flow to genetics journals, Balog chose five of that field's leading journals to map citation patterns over the 1975 to 1980 period. Among her conclusions were that multidisciplinary journals (for example, Science and Nature) serve as intermediaries between basic biochemistry and its applications in genetics. Small and Greenlee hypothesized that clusters of cocitations shift emphasis as a field alternately expands with innovation and contracts with consolidation. Although previous research on the field of plant-virus resistance is unavailable, preliminary indications suggest that it has a stable core of journals related to the discipline of phytopathology and that it is likely to expand with the increased use of biotechnology.

Table 7. Most frequently cited phytopathology journals, October to December, 1969

Journal	Citations
Phytopathology	3,288
Plant Disease Reporter	476
Virology	320
Canadian Journal of Botany	240
Plant Physiology	204
American Journal of Botany	188
Nature	184
Annuals of Applied Biology	164
Annual Review of Phytopathology	164
Phytopatholgia Z.	148
Journal of Agricultural Research	144
Science	120
Journal of Bacteriology	88
Journal of Biological Chemistry	88
Mycologia	80
All Others	5,424

SOURCE: Garfield (1972).

Biotechnology and the Core Literature

Abel, et al. and Beachy, et al. represent two related examples of biotechnology in plant-virus resistant research. In both, viral genes for producing capsid protein were transferred from tobacco mosaic virus strains to tomato plants via the Ti-plasmid system. Gene expression was marked by delayed symptoms of disease.

Abel, et al., in discussing the experimental results, makes a single reference to the core literature followed by the conclusion "Whether or not the delay in symptom development in the transgenic plants is the result of a mechanism similar to that of classical cross-protection remains to be determined." And, the statement "... the methods described here provide a way of producing virus-resistant plants that should complement those used in classical plant breeding" suggests that a major objective in this biotechnology research is the development of new techniques to increase plant-virus resistance.

Beachy, et al. explains the construction of chimeric genes in tobacco mosaic virus which are suspected of producing three factors: (1) viral replicase, (2) a 30 Kd factor necessary for cell-to-cell virus spread, and (3) the viral coat protein. Transgenic expression of viral coat protein and the 30 Kd gene indicated that the transformation was successful, but the results did not ascertain that "... this level of coat protein is sufficient to confer cross protection, if indeed protein is involved in [the cross protection] phenomenon." Beachy et al. concludes from experiments using chimeric gene technologies that "... we have not yet determined if either the viral coat protein or 30 Kd protein is involved in conferring cross protection to transformed plants."

Beachy, et al. speculates that anti-sense viral RNA cannot be produced in sufficient quantities to block translation or replication of viral RNA with current biotechnologies. However, Beachy, et al. recognizes the potential of biotechnology to develop more effective gene promoters that would lead hosts to hybrid-arrest the translation of viral mRNA responsible for producing viral replicase, the 30 Kd gene, and coat protein. Beachy, et al. also discusses the possibilities of hybrid-arresting replication of viral RNA by binding antisense RNA with the replicative intermediate. Ongoing research "results of these experiments are as of [Beachy, et al.] either not known or are preliminary."

Beachy, et al. describes the potential of using the anti-sense viral RNA approach as depending on technological factors, such as production levels and stability in different cell environments. This approach also depends on "...details about most viral replicase enzymes and sites to which they bind on their templates [which] are not fully elucidated, and the hypothesis relating to cytoplasmic amplification of RNA [which] remains to be tested."

Beachy, et al. concludes the assessment of biotechnology for plant-virus resistance research with words of cautious optimism. Although its potential is apparently great, biotechnological approaches have yet to determine "... whether the sequences and protein products will serve to protect plants from super-infection or to induce a state of systemic immunity against other pathogens."

Discussion

Abel, et al. appeared as a research article in <u>Science</u> after Beachy, et al. was published in a book of symposia articles. The emphasis in Abel, et al. differs only slightly from Beachy, et al., and both articles exemplify the classical approach to scientific reporting.

In the classical approach to science, a set of related factual observations are posed as problems to be explained with competing hypotheses. The successful hypotheses are integrated into a comprehensive model which explains a broader range of observations. For example, a genetic and biochemical model of plant-virus infection, multiplication, and symptom development is expected to explain cross protection, the green-island effect, and other facts about plant-virus interactions.

Abel, et al. and Beachy, et al. demonstrate a strong link to the core literature in developing factual observations and competing hypotheses (Table 8). Both papers, though, derive their techniques from the specialized literature of biotechnology. The discussions of results are only weakly linked to the core literature.

Table 8. Distribution of citations in the texts of Abel, et al. and Beachy, et al. by relationship to core literature and article position

Article Position	Abel, et al. Core	Abel, et al. Noncore	Beachy, et al. Core	Beachy, et al. Noncore
		Percent		
Observations	100		67	33
Hypotheses	100		100	
Experimental Methods and Results	11	89	14	86
Discussion or Conclusions	20	80	no citations	

A possible explanation for the relationships among citation patterns between the core literature and the two biotechnology research papers is that the latter are designed to demonstrate primarily the success of new laboratory techniques. Biotechnology is a set of new tools whose research implications are not completely known by the scientific community. Therefore the arguments in Abel, et al. and Beachy, et al. are directed to demonstrating the feasibility of creating transgenic plants, rather than the meaning of their results in a comprehensive model of plant-virus resistance.

Conclusions

Biotechnology in plant-virus resistance research is expanding the possible set of experimental outcomes available to research scientists who are seeking to discover resistance genes. The questions which are asked by scientists using biotechnology to enhance virus resistance arise from observations in the core literature. The answers which follow from experimentation with chimeric genes, anti-sense RNA, and transgenic protection are related more often to laboratory technologies than to traditional problems in developing models of plant-virus resistance.

Plant-virus resistance research is acquiring new approaches through improved biotechnology and these improvements are reported in disciplinary and specialized journals, books, and monographs as well as interdisciplinary intermediaries such as Science and Nature. Plant-virus resistance research is likely to expand the core literature rapidly with new laboratory technology in the leading countries of the United Kingdom, United States, Japan, Israel, and the Netherlands.

Biotechnology in plant-virus resistance research is in a pre-application stage of development. Biotechnology is likely to contribute virus-resistance genes to new crop varieties as the technologies emerge from "basic science" and are applied to field conditions and with economically important crops. The experimental prototype hosts are currently solanaceous crops such as tomatoes and potatoes, but virus diseases are important also in cucurbits, citrus crops, and leafy vegetables.

Similarly, biotechnology is likely to contribute to progress in plant-virus resistance research as new approaches are applied to the traditional explanations of the resistance mechanism. The nature of biotechnology in plant-virus resistance research does not lead to clearly quantitative measures of progress in this area. However, biotechnology comprises new tools for researchers to experiment with genetic factors affecting resistance (Beachy). Before field tests are completed, forecasts of advances in crop productivity are mostly speculative and problems of commercially adopting "designer crops" are largely not mentioned. Development of biotechnology's potential for plant-virus resistance will likely involve plant breeders, geneticists, and molecular biologists working together in the field, the laboratory, and through the scientific literature.

SECTION THREE

The Economics

Scientific institutions which seek through research and development to reduce agricultural losses are motivated, in part, by the prospect of lowering society's cost of food production. The obvious goal of increasing agricultural productivity by improving technology is linked ostensibly to increasing the sum of consumers' and producers' economic surplus. A measure of economic surplus is central to most studies of agricultural research benefits; and when taken with measures of research costs, ex post comparisons among benefit-cost relationships typically show extraordinary rates of return from public investment in agricultural science (Evenson, Waggoner, and Ruttan).

Ex post benefit-cost studies of agricultural research usually lead to recommendations for increased financial support in public research but without significant information about the differences among crops. Ex ante studies, on the other hand, typically focus on science agencies' and administrators' methods of setting research priorities; but these studies are rarely comparable, thus ranking different strategies is difficult (Norton and Davis).

Norton and Davis, in distinguishing between ex post and ex ante analyses of the benefits of agricultural research, places the Pinstrup-Anderson, Londono, and Hoover (PLH) method in the former category. More appropriately, because PLH models the distributional result of a hypothetical supply increase, that analysis belongs in the ex ante category. For crop biotechnology, economic analyses are necessarily ex ante because of the preliminary status of this type of research and development.

The objective of this section, following the PLH framework, is to present ex ante estimates of economic effects from hypothetical biotechnologies which reduce crop losses from virus disease. The central question asks what would be society's benefit from agricultural research on crop viruses. The answer is based on general characteristics of commodity supply shifts and their relationship to biotechnologies in crop science.

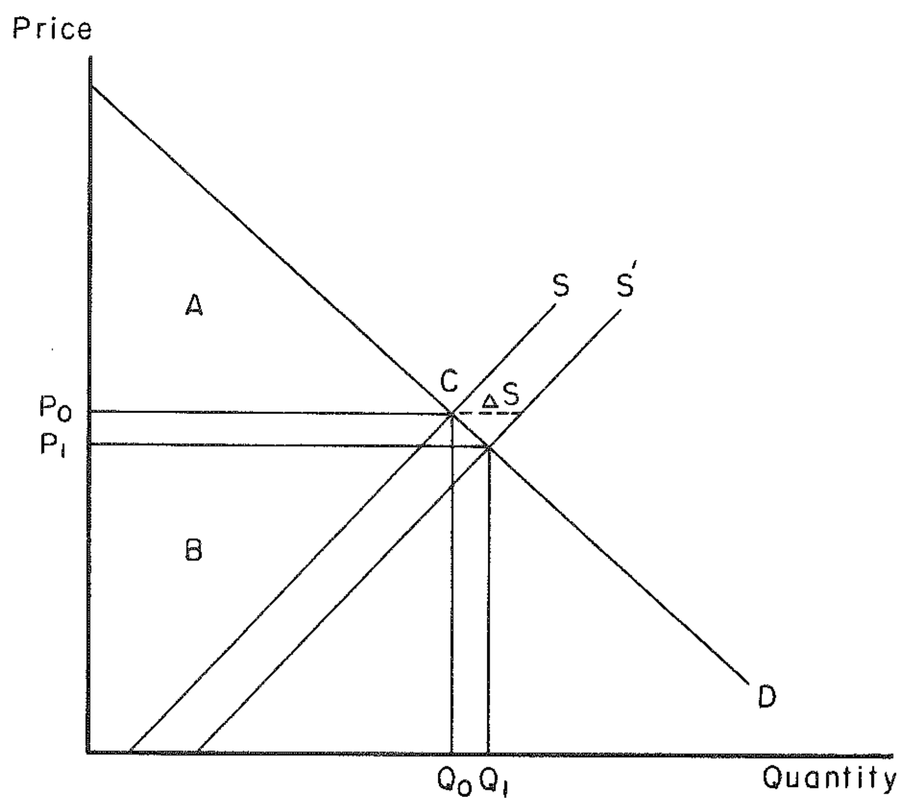
The analysis is prospective rather than predictive, per se, because future developments in crop science are unknown. This study intends to illustrate a simple economic model of static equilibrium theory in which market-clearing prices and quantities are obtained following a supply increase from the hypothetical innovation. The model is designed to demonstrate the importance of commodity supply and demand characteristics for assessing the possible economic outcomes from improved agricultural technology.

Economic Surplus

The technique of measuring social benefits from increased supply through agricultural research follows a comparative static equilibrium approach (Hertford and Schmitz). Under the assumptions of linear supply and demand schedules, a parallel shift in supply, and no shift in demand for a commodity, the gains in economic surplus to consumers and producers, respectively, are calculated in a model using equations (6) through (11) of Pinstrup-Anderson, Londono, and Hoover (Appendix C contains PLH equations (6) through (11)). These equations incorporate own- and cross-price elasticities of demand among commodities in the solution of post-innovation equilibrium conditions. A post-innovation supply schedule is estimated from the parallel shift. To estimate the change in economic surplus resulting from the loss-preventing technology, pre- and post-innovation surplus measures are compared. Biotechnological change is assumed to shift the supply schedule in a parrallel fashion, but the results would be different if biotechnology leads to convergent or divergent shifts (Lindner and Jarrett, Rose).

Economic surplus is a measure of benefits derived by consumers (producers) who pay (receive) actual prices lower (higher) than they are willing and able to otherwise pay (receive). The illustration in Figure 1 represents static market equilibrium in which a combination of market-clearing price, P_o, and quantity, Q_o, obtain for all participants. The area, A, below the market demand curve, D, and above the price line, P_oC, represents consumers' surplus. The area, B, above the market supply curve, S, and below the price line, P_oC, likewise represents producers' surplus (or as some prefer, producers' economic rent). The combined area, A + B, represents the total economic surplus obtained at initial equilibrium. This measure of economic surplus is calculated at the retail level by transforming the farm-level supply elasticity (see Appendix B).

FIGURE 1. SHIFT IN SUPPLY AND RESULTING EQUILIBRIUM



The hypothetical shift (ΔS) in market supply moves S parallel and to the right to S', under the present set of assumptions. The post-innovation equilibrium allows calculation of a new price (P_1) and quantity (Q_1) combination. The new result under this scenario always leads to an increase in consumers' surplus, but the change in producers' surplus depends on the market's supply and demand characteristics.

The Model Using Potatoes and Tomatoes

Potatoes and tomatoes are chosen as an example to illustrate the model results. Virus diseases cause significant losses in potato and tomato production (Table 9). Although U.S. estimates of virus disease losses in these crops pertain to the 1950's, no empirical evidence exists for recent trends toward increasing or decreasing losses. Therefore, it is presumed that virus diseases cause an average loss of about 5 percent in potatoes and tomatoes.

Table 9. Potatoes and Tomatoes: U.S. annual loss of production from disease a/

	Disease		
	Virus b/	Other c/	Total
Potato	5	14	19
Tomato			
fresh-market	6	15	21
greenhouse	8	12	20
processing	4	18	22

Source: United States Department of Agriculture, 1965.

a/Estimated for the 1951-1960 period.

b/Includes for potatoes: leaf roll, latent mosaic, mild mosaic;
for tomatoes: curly top, tobacco mosaic, tobacco streak

c/Includes for potatoes: late blight, Verticillium wilt, scab, early blight, Rhizoctonia black scurf, rugose mosaic, Fusarium wilt, black leg, ring rot, spindle tuber, bacterial brown rot. Includes for tomatoes: gray leaf spot, Verticillium wilt, bacterial spot, blossom end rot, early blight, Fusarium wilt, bacterial wilt, late blight, leaf mold, Septoria leaf spot, anthracnose.

Molecular biologists and plant pathologists are seeking biotechnological solutions to problems of virus disease in potatoes and tomatoes. Both crops are hosts to common viruses, for example Tobacco Mosaic Virus (TMV) which was the first plant-virus to be discovered and since has been characterized thoroughly with respect to host range, mode of infection, symptoms, and genetic structure. One of the first scientific reports of cross protection in transgenic plants used TMV and tomato plants to show that disease symptoms could be delayed in plants which were genetically engineered to manufacture viral protein (Abel, et al.).

The supply and demand characteristics of potatoes and tomatoes are known sufficiently to apply the model (Table 10). Both potato and tomato are solanaceous crops with shared botanical traits, and each exhibits both common and distinct horticultural and market characteristics. Commercial potato production yields the edible root-like storage organ for consumption (a) as a fresh-market product immediately or after months of storage, or (b) as frozen, dehydrated, chipped, and other forms of processed potatoes. Commercial tomato production yields the edible fruit for consumption (a) almost immediately, due to the perishable nature of the fresh-market product, or (b) as juiced, canned whole, sliced, sauced, pureed, or similar concentrated products.

Growth in U.S. production of potatoes and tomatoes centered in the western United States during the 1970's, following the combination of improved processing technologies and increased consumer demand for convenience in both commodities (Tables 11 and 12). During this period, per capita use of processed potato and tomato products rose 1 to 2 percent annually. Washington, Oregon, and Idaho supply nearly half of the U.S. potato crop. California alone supplies the bulk of commercial tomato demand, except during winter months when Florida and Mexico supply most of the U.S. fresh tomato market.

Table 10. Potatoes and tomatoes: Demand, supply, price and utilization characteristics

Item	Elasticity		Price		
	Demand	Supply a/	Farm	Retail	Utilization b/
			Dollars per pound		Pounds per capita
Potatoes					
Fresh-market	-.37	.64	.05	.22	49
Processed	-.21	4.3	.05	.64	25
Tomatoes					
Fresh-market	-.56	.57	.23	.77	12
Processed	-.38	9.3	.03	.53	18

Source: Demand elasticities, Huang; supply elasticities (adjusted for marketing costs), Taylor and Shonkwiler (potatoes, fresh), Estes, et al. (potatoes, processed), Nerlove and Addison (tomatoes, fresh), Brandt and French (tomatoes, processed); prices and utilization, USDA (1986).

a/ See Appendix B for a discussion of elasticity calculation.

b/Retail-weight equivalent. Processed potatoes includes canned, frozen, chips and shoestrings, and dehydrated. Processed tomatoes includes juice, whole, and other concentrated products.

Table 11. Potatoes: U.S. acreage and production, and share in Idaho, Oregon, and Washington, 1964 and 1982.

State	Acreage 1964	Acreage 1982	Production a/ 1964	Production a/ 1982
	---- percent ----			
Idaho, Oregon and Washington	26	38	26	47
Other	74	62	74	53
	1,000 Acres		Million hundredweight	
U.S.	1,174	1,268	221.9	344.6

SOURCE: U.S. Department of Commerce (1964, 1982).

a/Includes fresh-market and processing.

Table 12. Tomatoes: U.S. acreage and production, and share in California, 1964 and 1982

State	Acreage 1964	Acreage 1982	Production a/ 1964	Production a/ 1982
	---- percent ----			
California	41	63	59	75
Other	59	37	41	25
	1,000 Acres		Million hundredweight	
U.S.	388.5	403.5	112.2	172.7

SOURCE: Acreage, U.S. Department of Commerce (1964, 1982); production, U.S. Department of Agriculture

a/Includes fresh-market and processing.

The United States' international trade in potatoes and tomatoes is a minor part of total U.S. supplies. The exceptions have been during winter months, when U.S. imports of Mexican fresh-market tomatoes sometimes equal Florida production, and in the early 1980's, when total U.S. imports of processed tomatoes rose to about 10 percent of domestic processed supplies. U.S. potato trade, mainly with Canada, is significant in local areas for some years, but the U.S. advantage in production is great relative to Canada. Overall, trade in both crops accounts for less than 10 percent of total U.S. supplies.

The demand for tomatoes is more elastic than for potatoes, probably owing to differences in consumer uses. These relationships are represented by own- and cross-prices elasticities from Huang. Fresh-market tomatoes are considered a vegetable along with other salad items such as cabbage, carrots, celery, lettuce, and onions. Processed tomatoes are used increasingly in prepared foods with meat, cheese, bread or pasta, and spices. Fresh-market potatoes, on the other hand, are commonly grouped with staples such as rice, bread, and milk. Frozen french fried potatoes, the principle processed form, are served with convenience foods such as sandwiches.

Supply characteristics of potatoes and tomatoes differ, in part, because of their different biological requirements in production and marketing, contracting agreements, and alternative land uses in western and northwestern States. Potatoes, are mainly a dual usage crop: fresh-market and processed uses can be derived from the same variety. Tomato varieties, though, are bred for one or the other use. Processing tomato varieties are bred for compatibility with mechanical harvesters and high solids content. Fresh-market breeding programs focus on appearance, shelf-life, and taste. Tomato breeding programs, whose goals include improved yields of processing varieties, have helped to increase per acre output at a greater rate than potatoes during the 1950's to 1980's (Table 13).

Table 13. Potatoes and tomatoes: U.S. average yields, 1954, 1964, 1974, and 1984

Year	Potatoes	Tomatoes Fresh-market	Tomatoes Processing
	--- Hundredwieght per acre ---		Tons per acre
1954	155	84	10.3
1964	189	132	16.8
1974	246	162	20.8
1984	278	229	26.3

SOURCE: U.S. Department of Agriculture. Agricultural Statistics.

Results and Discussion

The model tests the effects of a 5 percent increase in potato and tomato yields from reducing virus disease losses. While the 5 percent increase in yields is not completely arbitrary (Table 9), there is no scientific basis for expecting that virus-disease protection technologies will lead to a 5 percent reduction in potato and tomato production losses. Nevertheless, as expected, the results of the model test are reduced market-clearing prices and increased quantities (Table 14). Total economic surplus increased from 2.6 to 5.0 percent as a result of shifting the supply schedule to the right by 5 percent. Adams, et al. recently reported similar results for hypothetical reductions in ozone damage to U.S. agriculture. For example, Adams, et al. reported a 2.0 percent increase in annual total benefits triggered by a 2.5 percent increase in crop yields. The similar results are likely due to common demand and supply characteristics of agricultural products.

Table 14. Potatoes and tomatoes: Changes in retail prices, quantities, and economic surplus from a 5-percent increase in yields

	Market Changes			Economic Surplus Changes		
	Quantity	Price	Expenditure	Consumer	Producer	Total
	--- Percent ---			--- Percent ---		
Potatoes						
Fresh	1.8	-14	-12.1	6.9 (1.01)a/	-5.8 (-.43)	2.6 (0.58)
Processed	0.2	-24	-23.8	5.2 (2.01)	0.5 (0.009)	5.0 (2.02)
Tomatoes						
Fresh	2.4	-9.0	-6.8	7.6 (0.63)	-2.6 (-0.17)	3.1 (0.46)
Processed	0.2	-13	-12.9	5.2 (0.65)	0.4 (0.002)	5.0 (0.65)

a/Numbers in parentheses are dollars per capita U.S. surplus changes.

The inelastic demand for potatoes and tomatoes will cause consumer expenditures to decrease, with the rate of decrease in the processed market twice that in the fresh market. Retail supplies of the processed products are more elastic than fresh-market supplies because of higher marketing costs; therefore total economic surplus in the processed market would increase at a greater rate than in the fresh market. Finally, consumers stand to gain relatively more, and producers relatively less, from a loss-preventing innovation in potatoes, compared to tomatoes.

The meaning and use of economic surplus remain controversial in the economics literature; but after a thorough review of its concepts, Currie, Murphy, and Schmitz conclude "While it is easy to raise objections to the use of the concept of economic surplus for providing answers for policy formulation, it is difficult to find any workable alternative." Therefore to the extent that a change in economic surplus is an indication of a change in social welfare, consumers are regularly made better off by technological improvements in agriculture -- loss prevention technologies being no exception. Therefore policies that seek to increase food supplies will affect the distribution of welfare gains. In the case of reducing virus-disease losses in potato or tomato production, scientific advances for either crop are likely to spillover to the other. The same spillover potential is likely also to hold for fresh-market and processing varieties.

The prospects for a yield-enhancing breakthrough in plant-virus resistance research generally can not be quantified; but the phytovirology literature suggests several important scientific puzzles for solution by biotechnological means. An examination of the scientific literature in Section Two has suggested that biotechnology is expanding the core literature of phytovirology and that this could lead to progress in crop protection. Hypotheses about virus action are especially amenable to the techniques of genetic engineering, and public and private sources are investing in this research hoping to reduce virus disease losses.

The results of the analysis indicate the economic impacts of yield-enhancing technologies on consumers and producers of potatoes and tomatoes. The framework of analysis, though, can be used for other crops to obtain comparable results because of similar price elasticities of demand and supply. The demand for agricultural products generally is price inelastic, and because of common production constraints, the supply elasticity of many crops is relatively low. For these reasons and because of public agricultural research, the benefits of new U.S. production technologies pass rapidly from producers to consumers.

REFERENCES

Abel, P.P., R.S. Nelson, B. De, M. Hoffman, S.G. Rogers, R.T. Fraley, and R.N. Beachy. "Delay of Disease Development in Transgenic Plants that Express the Tobacco Mosaic Virus Coat Protein Gene." Science (1986):232:738-743.

Adams, R.M., S.A. Hamilton, and B.A. McCarl. "The Benefits of Pollution Control: The Case of Ozone and U.S. Agriculture." Amer. J. Agr. Econ. 68(1986):886-893.

Balog, C. "Information Flow to Genetics Journals." Scientometrics 9(1986):51-57.

Bos, L. Crop losses caused by viruses. Crop Protection 1(1982), 263-282.

Bos, L. Symptoms of Virus Diseases in Plants. Centre for Agricultural Publishing and Documentation. Wageningen. 1978.

Brandt, Jon A. and Ben C. French. An Analysis of Economic Relationships and Projected Adjustments in the U.S. Processing Tomato Industry. Giannini Foundation Research Report, Number 331. 1981.

Beachy, R.N. Genetic Cross Protection in Transgenic Plants. Presentation to Boyce Thompsom Institute in Distinguished Lecture Series, January 28, 1987, Ithaca, New York. 1987.

Beachy, R.N., P. Abel, M. Oliver, B. De, R.T. Fraley, S.G. Rogers, and R.B. Horsch. Potential for Applying Genetic Transformation to Studies of Viral Pathogenesis and Cross Protection. In Biotechnology in Plant Science. Zaitlin, M. and P. Day, Eds. Academic Press, New York. 1985.

Chiarappa, Luigi, Huai C. Chiang, and Ray F. Smith. Plant pests and diseases: Assessment of crop losses. Science 176(1972):769-73.

Cook, R.J. "Use of the Term 'Crop Loss'." Plant Disease 69(1985):95.

Cooper, J.I. and A.T. Jones. "Responses of Plants to Viruses: Proposals for the Use of Terms." Phytopathology 73(1983)2:127.

Corbett, M. K. and H. D. Sisler. Plant Virology. University of Florida Press. Gainesville. 1964.

Cramer, H. H. Plant Protection and World Crop Production. Pflanzenschutz Nachrichten "Bayer" 20(1967):1-599.

Dahlgren, Roger A. A Synthesis of Microeconomic Duality Theory and Distributed Lag Modeling with Implications for the U.S. Dairy Policy. Northcentral J. of Agr. Econ. 7(1985):132-149.

Estes, Edmund, Leroy Blakesless, and Ron C. Mittlehammer. Regional and National Impacts of Expanded Pacific Northwest Potato Production. Western J. of Agr. Econ.. 7(1982):239-252.

Evenson, R., P.E. Waggoner, and V.W. Ruttan. Economic Benefit From Research: An Example from Agriculture. Science. 105(1979):101-107.

Florkowski, W.J. and L.D. Hill. Expected Commercial Application of Biotechnology in Crop Production: Results of the Survey. University of Illinois, Department of Agricultural Economics. AE-4605. December 1985.

Franki, R.I.B., R.G. Milne, and T. Hatta. Atlas of Plant Viruses. Volumes I and II. CRS Press. 1985.

Fraser, R. S.S. Biochemical Aspects of Plant Resistance to Virus Disease. A Review. Acta Horticulturae. 127(1982):101-116.

Fraser, R.S.S. Genes for Resistance to Plant Viruses. In Critical Reviews in Plant Sciences. 3(1986):257-294.

Garfield, E. "Most Frequently Cited Phytopathology Journals." Phytopathology News, 6(1982):4.

George, P.S. and G.A. King. Consumer Demand for Food Commodities in the United States With Projections for 1980. Giannini Foundation Monograph Number 26 (March 1971).

Grant, W.R., J.W. Richardson, B.W. Brorsen, and M.E. Rister. "Economic Impacts of Increased Price Variability: A Case Study with Rice." Agri. Econ. Res. 36(1984):17-27.

Hepburn, A.G., M. Wade, and R.S.S. Fraser. Present and Future Prospects for Exploitation of Resistance in Crop Protection by Novel Means. In Mechanisms of Resistance to Plant Disease. R.S.S. Fraser, Ed. Martinus Nijhoff/Dr. W. Junk, Publishers. 1985.

Hertford, R. and A. Schmitz. "Measuring Economic Returns to Agricultural Research." Resource Allocation and Productivity in National and International Agricultural Research, T.M. Arndt, D.G. Dalrymple, and V.W. Rutan (Eds). Minneapolis: University of Minnesota Press, 1977.

Huang, Kuo S. U.S. Demand for Food: A Complete System of Price and Income Effects. Economic Research Service, USDA, Technical Bulletin Number 174. 1985.

Lindner, R.K. and F.G. Jarrett. "Supply Shifts and the Size of Research Benefits." Amer. J. of Agr. Econ. 60(1978):48-58.

Mulrooney, Robert P. Soybean disease loss estimates for southern United States in 1984. Plant Disease 70(1986):893.

___________________. Soybean disease loss estimates for southern United States in 1983. Plant Disease 69(1985):92.

National Science Foundation. 5-year Outlook on Science and Technology. United States Government Printing Office. 1981.

Norton, George W. and Jeffrey S. Davis. "Evaluating Returns to Agricultural Research: A Review." Amer. J. of Agr. Econ. 63(1981):685-699.

Nyvall, Robert F. The reporting of estimated plant disease losses. Plant Disease 67(1983):1303.

Ordish, R. G. Untaken Harvest: Man's Loss of Crops from Pest, Weed, and Disease. Constable Co., Ltd. London. 1951.

Pinstrup-Anderson, P., N. Ruiz de Londono, and E. Hoover. The Impact of Increasing Food Supply on Human Nutrition: Implications for Commodity Priorities in Agricultural Research and Policy. Amer. J. of Agr. Econ. 58(1976):131-142.

Ponz, F. and G. Bruening. Mechanisms of Resistance to Plant Viruses. Annual Review of Phytopathology. 24(1986):355-381.

Rose, Roger N. Supply Shifts and Research Benefits: Comment. Amer. J. of Agr. Econ. 62(1980):834-837.

Salathe, Larry and Souchada Langley. An Empirical Analysis of Alternative Export Subsidy Programs for U.S. Wheat. Agr. Econ. Res. 38(1986):1-18.

Taylor, Timothy G. and J. Scott Shonkwiler. Interdependent Supply Functions and Revisional Price Expectations. Can. J. of Agr. Econ. 33(1985):285-298.

United States Department of Agriculture. Food Consumption, Prices, and Expenditures, 1965-1985. Economic Research Service. Statistical Bulletin Number 736. 1986.

______________________. Agricultural Statistics, 1985. U.S. Government Printing Office. Washington, DC. 1986.

______________________. Losses in Agriculture. Agricultural Research Service, Agricultural Handbook No. 291. 1965.

____________________. Losses in Agriculture: A Preliminary Appraisal. Agricultural Research Service, Agricultural Information Bulletin No. 1. 1954.

____________________. Agricultural Statistics. United States Government Printing Office. 1985.

____________________. Plant Diseases. Yearbook of Agriculture. United States Government Printing Office. 1953.

____________________. Agriculture's Capacity to Produce. Agricultural Research Service, Agricultural Information Bulletin No. 88. 1952a.

____________________. Insects. Yearbook of Agriculture. United States Government Printing Office. 1952b.

______________________. Keeping Livestock Healthy. Yearbook of Agriculture. United States Government Printing Office. 1942.

United States Department of Commerce. Bureau of the Census. 1964 Census of Agriculture.

______________________. Bureau of the Census. Census of Agriculture. Volume 51. 1982.

Van Loon, L.C. 1983. Mechanisms of Resistance in Virus-Infected Plants. In The Dynamics of Host Defense. J.A. Bailey and J.B. Deverall, Eds. Academic Press, Australia.

Walker, P. T. 1983. The need to quantify the effects of pests, diseases and weeds on agricultural production. Agriculture, Ecosystems, and Environments (9):119-158.

Walkey, D. G. A. 1985. Applied Plant Virology. John Wiley and Sons. New York.

Wiese, M. V. 1983. Loss assessment: A requisite for crop research and production. Plant Disease 67:839.

APPENDIX A

Annual Loss of Crop Production from Diseases

Appendix Table A.1. Agricultural Seeds: U.S. annual loss of production from diseases, 1951-60

Crop	Diseases: Virus	Other	Total
	--- Percent ---		
Alfalfa	3.0	6.0	9.0
Clover, crimson	2.5	9.5	12.0
Clover, red	5.5	24.5	32.0
Clover, white	13.0	11.0	24.0
Lupines	25.0	27.0	52.0

Source: United States Department of Agriculture, 1965.

Appendix Table A.2. Field Crops: U.S. annual loss of production from diseases, 1951-60

Crop	Diseases: Virus a/	Other	Total
	--- Percent ---		
Barley	4.8	9.2	14.0
Bean, dry	3.0	14.0	17.0
Flax	2.0	8.0	10.0
Hop	10.0	3.0	13.0
Oat	4.3	16.7	21.0
Pea, field	2,5	11.5	14.0
Sugar beet	6.0	10.0	16.0
Tobacco	1.4	9.6	11.0
Wheat	2.0	12.0	14.0

SOURCE: United States Department of Agriculture, 1965.

a/ Includes curly top, bean mosaic, aster yellows, yellows, tobacco mosaic, yellow dwarf, stripe mosaic, bean yellow mosaic, crinkle, soilborne mosaic, ratoon stunting, and mosaic.

Appendix Table A.3. Tree nuts and fruits: U.S. annual loss of production from diseases, 1951-60

Crop	Diseases: Virus a/	Diseases: Other	Total
	--- Percent ---		
Almond	0.5	8.5	9.0
Apple	0.2	7.8	8.0
Apricot	1.0	6.0	7.0
Blueberry	1.0	13.0	14.0
Brambleberry			
Blackberry	9.4	24.6	34.0
Raspberry	12.4	25.6	38.0
Cherry	10.7	13.3	24.0
Citrus			
Grapefruit	0.1	1.9	2.0
Lemon			25.0
Orange	1.9	10.1	12.0
Grape			27.0
Peach	1.2	12.8	14.0
Pear	12.2	4.8	17.0
Strawberry	5.0	21.0	26.0

Source: United States Department of Agriculture, 1965.

a/ Includes ring spot, tristeza, phony peach mosaic, pear decline.

Appendix Table A.4. Vegetables: U.S. annual loss of production from diseases, 1951-60

Crop	Diseases		
	Virus a/	Other	Total
	--- Percent ---		
Artichoke	1.0	2.0	3.0
Bean, snap	4.0	16.0	20.0
Cantaloupe	3.5	12.5	16.0
Carrot	2.0	6.0	8.0
Cauliflower	1.0	7.0	8.0
Celery	5.0	12.0	17.0
Cucumber			
fresh-market	4.0	14.0	18.0
greenhouse	1.0	7.0	8.0
pickling	4.5	6.5	11.0
Eggplant	0.5	11.5	12.0
Escarole	1.0	5.0	6.0
Lettuce	5.0	7.0	12.0
Melon	4.0	10.0	14.0
Pea, green	6.0	17.0	23.0
Pepper, green	2.5	11.5	14.0
Potato	5.0	14.0	19.0
Shallot	4.0	17.0	21.0
Spinach	3.5	16.5	20.0
Tomato			
fresh-market	6.0	15.0	21.0
greenhouse	8.0	12.0	20.0
processing	4.0	18.0	22.0
Watermelon	1.5	8.5	10.0

Source: United States Department of Agriculture, 1965.

a/ Includes curlytop, bean mosaic, aster yellows, cucumber mosaic, western aster yellows, tobacco ringspot, watermelon mosaic, yellows, lettuce mosaic, curcurbit latent, potato virus y, potato leaf roll, yellow dwarf, malva yellows, mosaic, tobacco streak.

APPENDIX B

Potatoes and Tomatoes:
Demand, supply and price data

Demand elasticities

Price elasticities of demand are available for 40 foods and 1 non-food item based on annual per capita utilization and retail prices during 1953 to 1983 (Huang). The matrix of own-price and cross-price elasticities of demand for potatoes, tomatoes, and their related commodities are given in the following tables.

Appendix Table B.1. Own-price and cross-price elasticities of demand for potatoes, fluid milk, flour, and rice.

	Potatoes	Fluid milk	Flour	Rice
Potatoes	-.3688	-.1946	-.0207	-.0216
Milk, fluid	-.0230	-.2588	-.0565	.0387
Flour	-.0019	-.0567	-.1092	.0503
Rice	.0187	.2638	.3512	-.1467

SOURCE: Huang.

Appendix Table B.2. Own-price and cross-price elasticities of demand for fresh-market vegetables

	Cabbage	Carrots	Celery	Lettuce	Onions	Tomatoes
Cabbage	-.0385	-.0537	.0967	.2594	.0235	.3931
Carrots	-.0479	-.0388	-.0173	.3610	-.0467	.0818
Celery	.0879	-.0179	-.2516	.1708	.0021	-.0094
Lettuce	.0563	.0881	.0409	-.1317	-.0230	.0148
Onions	.0144	-.0327	.0015	-.0655	.1964	-.0411
Tomatoes	.0950	.0220	-.0026	.0161	-.0163	-.5584

SOURCE: Huang.

Supply elasticities

Price elasticities of supply are available in the agricultural economics literature, but because they are not estimated in a system similar to that for demand elasticities, cross-price elasticities of supply are assumed negligible in this analysis. Related problems of noncomparable supply elasticities arise from the variety of estimation techniques, length of period, and region or country used by different researchers. Therefore, the published estimates provide generally appropriate values to be used in calculations of total supply response. A survey of published supply elasticities for vegetables and the staple commodities is given in the following table.

Appendix Table B.3. Own-price elasticities of supply for staples and vegetables

Commodity	Supply elasticity[1]	Source
Staples		
Milk	.12	Dahlgren
Potatoes	.18	Taylor and Shonkwiler
Wheat	.22	Salathe and Langley
Rice	.35	Grant, et. al.
Vegetables		
Fresh-market		
Cabbage	.36	Nerlove and Addison
Carrots	.14	Nerlove and Addison
Celery	.14	Nerlove and Addison
Lettuce	.03	Nerlove and Addison
Onions	.34	Nerlove and Addison
Tomatoes	.16	Nerlove and Addison
Processing		
Potatoes	.3	Estes, et. al.
Tomatoes	.65	Brandt and French

[1] With respect to farm price.

Prices and utilization

Average annual U.S. farm and retail prices and per capita utilization are available from the Economic Research Service, USDA. Annual prices and quantities were averaged over the 1981-85 period and presented in the following table.

Appendix Table B.4. Average U.S. retail prices and utilization of selected staples and vegetables, 1981-1984

Commodity	Farm share of retail price	Retail price	Utilization
	Percent	Dollars per pound	Pounds per person
Staples			
Flour, white	11	.22	111
Milk, fluid, whole	49	.28	131
Potatoes, white, fresh	28	.22	49
Rice, white, uncooked	11	.50	10
Vegetables			
Fresh-market	28		
Cabbage		.29	8
Carrots		.37	7
Celery		.45	7
Lettuce		.53	23
Onions		.34	10
Tomatoes		.77	12
Processed[1]	7		
Potatoes		.64	18
Tomatoes		.53	18

SOURCE: Food, Prices, Consumption, and Expenditures. Economic Research Service, USDA

[1]Retail price includes frozen french fried potatoes or canned whole tomatoes only.

APPENDIX C

Comparative static equilibrium model, PLH equations (6) though (11), and discussion of economic surplus calculations

Comparative static equilibrium model

The model of comparative static equilibrium is represented by equations (6) through (11) of Pinstrup-Anderson, Londona, and Hoover. These six equations are reproduced below with numbers corresponding to their original description. The model solves the problem of obtaining new equilibrium prices and quantities by utilizing measures of elasticity to account for the relationships between a commodity's supply and demand characteristics and the relationship among similar commodities. The new equilibrium solution is obtained interatively with not more than three iterations.

In equations (6) through (11), the elasticities are defined as changes in quantity demanded with respect to changes in price. The shift, B, in the supply schedule is calculated as a percentage change from the original equilibrium position. Equilibrium is approached iteratively as price, P, changes from its level at K-1 to the new level at K and quantity demanded, Q, responds to the change in price. Cross-price elasticities are used to account for changes in related commodities' demand.

(6) $$P_i^K = P_i^{K-1} \{1 - [B/(e_{si} - e_{ii})]\}$$

(7) $$Q_i^K = Q_i^{K-1} \{1 + B/[1-(e_{si}/e_{ii})]\}$$

(8) $$Q_j^K = Q_j^{K-1} \{(1 + p_i e_{ji})[1-(1-e_{sj}/e_{jj})^{-1}]\}$$

(9) $$P_j^K = P_j^{K-1} (1 + p_i e_{ji}) / (e_{sj} - e_{jj})$$

(10) $$Q_i^K = Q_i^{K-1} \{1 + \sum_{j=1}^{n} p_j e_{ij} [1-(1-e_{si}/e_{ii})^{-1}]\}$$

(11) $$P_i^K = P_i^{K-1} [1 + \sum_{j=1}^{n} (p_j e_{ij} / e_{si} - e_{ii})]$$

where K = time period

P = price

Q = quantity

B = ΔS expressed as percent change w.r.t. Q^{K-1}

p = $(P^K - P^{K-1}) / P^{K-1}$

e = elasticity

i,j = designates commodities $(i,j = 1,i,\ldots j,n)$, $i \neq j$

e_{si} = own-price elasticity of supply for commodity i

e_{ii} = own-price elasticity of demand

e_{ij} = cross-price elasticity of demand for commodity i w.r.t. price of commodity j

Economic surplus

Straight-line supply and demand schedules are projected from initial equilibrium using slopes derived from elasticities and equilibrium prices and quantities. Price-axis and quantity-axis intercepts are necessary for calculating the area which lies below the demand schedule and above the supply schedule in the quadrant of positive prices and quantities.

Lindner and Jarret argue that a negative supply price is "clearly illogical as it implies that producers are prepared to supply positive quantities at zero price in the long run." It can be shown that any straight-line supply schedule with an elasticity less than one will intercept the price axis at negative values. Let $P = a + bQ$ represent a supply schedule with constant, positive slope $b = \partial P/\partial Q$ and intercept a. The elasticity of supply with respect to price, e_s, is $\partial Q/\partial P\ (P/Q)$. Because $a = P - (\partial P/\partial Q)(Q)$, multiplying the second term by P/P and factoring out P gives $a = P\ (1 - 1/e_s)$. Therefore if $e_s < 1$, then $a < 0$.

Rose shows that Lindner and Jarret overestimated the sensitivity of economic surplus measures by miscalculating producer rents and argues that "it is unlikely that any knowledge of the shape of the supply curve...will be available. The only realistic strategy is to assume that the supply shift is parrallel."

This compromise results in the necessary subtraction of area below the price axis when the price intercept is negative.

No attempt was made to distribute producer surplus among the various levels of production. Instead, farm-level supply elasticities were adjusted to represent the retail market. Therefore, producer surplus at the retail level represents a seller's surplus which incorporates farmer's, wholesaler's, and retailer's benefits.