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Managing Plant Virus/Mycoplasma Complexes in Maize/Bean Cropping Systems

July 1986-June 1990

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cc: BOSTON, CALIF

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Managing Plant Virus/Mycoplasma Complexes in Maize/Bean Cropping Systems

EXECUTIVE SUMMARY

A multidisciplinary team of scientists from Costa Rica, the United States, and England mounted a 3-year cooperative project to address the role polycultures and plant density play in the spread and severity of common insect-borne pathogens that cause debilitating diseases of maize and beans, and the effect such cropping systems have on the distribution and behavior of their insect vectors within a field. The principle goal of the project was to provide information that would lead to improved systems for managing virus and mycoplasma complexes associated with bean/maize cropping systems in Central America. Using a combination of experimental and simulation modelling approaches, this project revealed ways that crop structure influences vector movement and consequent insect-borne pathogenic epidemics.

Three diseases in maize were targeted, each vectored by the leafhopper, *Dalbulus maidis*. Modifying the behavior of this single species would therefore have a similar impact on the spread of all three diseases. Leafhoppers were found to be less less abundant in the whorls of more densely planted maize, and interplant movement could be decreased by planting in evenly spaced stands. Plant density influenced the spread of these leafhopper-vectored diseases more than the presence of bean in mixtures with the maize.

By contrast, the nonpersistent virus in bean can be vectored by over 25 species of aphids. Regardless of season, the majority of the aphids landing in bean during our experiments had the potential to transmit the virus. Because aphid behavior is not uniform across species, attempts to modify aphid landing rates and thus alter the spread of the virus required knowledge of the behavior, abundance, timing and identity of the prevalent species present during a particular growing season. This is a daunting challenge. Bicultures, however, tended to be less favored than monocultures to several prevalent aphid species and microclimatic conditions least favorable to aphid flight occurred in the high density bicultures.

Although maize yields were higher during the dry than the rainy season, while bean yields were higher during the dry season, total yields during any particular planting season were not significantly reduced in bicultures vs. monocultures. It appears that, overall, planting of bicultures benefits those farmers able to take advantage of the system.

This project fostered the training of two international students for their Ph.D.'s at US universities and a third is now pursing a Masters degree in Ohio. Costa Rican scientists profited from short-term training sessions with colleagues in US laboratories on aphid identification and in techniques of spiroplasma identification and culture. US scientists benefited from visits to Costa Rica to discuss details of the project and its progress and to form closer ties with fellow researchers. In addition to training, an IBM-XT microcomputer and state-of-the-art meteorological equipment purchases helped strengthen the research capabilities of the University of Costa Rica and now form a permanent part of that institution's inventory.

Sixteen scientific publications relating to this project are in preparation, including a general review article. One important work, intended for publication in Spanish, will be a set of illustrated keys to aid in the identification of trap-collected winged aphids to the species level. In addition, two Ph.D. dissertations have been completed and results of the project have been presented at professional meetings.

Computerized simulation models of viruses in bean and maize will be available for use on IBM-PC-compatible machines. They may be used for teaching at the University of Costa Rica, CATIE, or other Latin American institutions and will help advise in projects examining the impact and progress of insect-borne plant diseases. Furthermore, these models will allow extension specialists to advise growers of ways they can minimize the impact of such disease epidemics.

The bonds forged between researchers during this project are strong and will carry over into future projects and research. A workshop has been proposed on plant virus/mollicute epidemiology and control that will bring this group of researchers together once more to share their accumulated expertise with other scientists in the developing countries of Latin America.

managing plant virus/mycoplasma complexes
in maize/bean cropping systems

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universidad de costa rica
university of illinois at urbana-champaign

Final Report

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June 1990

INTRODUCTION

A multidisciplinary team of scientists from Costa Rica, the United States, and England mounted a 3-year cooperative project to address the role polycultures and plant density play in the spread and severity of common insect-borne pathogens that cause debilitating diseases of maize and beans, and the effect such cropping systems have on the distribution and behavior of their insect vectors within a field. The principle goal of the project was to provide information that would lead to improved systems for managing virus and mycoplasma complexes associated with bean/maize cropping systems in Central America. Cropping structure has been our main focus. Using a combination of experimental and simulation modelling approaches, this project has been successful in beginning to distill ways that crop structure influences vector movement and consequent insect-borne pathogenic epidemics.

Detailed observations of the pathogens, vectors, and crops for each cropping system were conducted, and simulation models of the dynamics of the plant disease systems have been constructed and evaluated. Ultimately, the empirical data and the models should be studied to develop crop management alternatives that can reduce the impact of insect-vectored plant diseases. Most of the field research was conducted at the Fabio Baudrit Experiment Station in Alajuela, Costa Rica, with the aid of laboratory facilities at the Cellular and Molecular Biology Research Center, University of Costa Rica, San José. The balance of the field work was accomplished at the Vegetable Crops Farm, University of Illinois at Urbana-Champaign.

The results of this project will be featured in over ten scientific papers (currently in preparation) that should provide valuable insights into the ecological principles underlying the management of pests in mixed cropping systems. These papers, in turn, should lead to a more scientific basis for cropping systems and cropping systems research, worldwide. We also presented our preliminary

findings to the IV International Plant Virus Epidemiology Workshop in Montpellier, France, 3-8 Sept. 1989. Computer models will be made available in the second half of 1990 for teaching purposes to the University of Costa Rica, and to CATIE and other Latin American institutions to help examine projects investigating the impact and progress of insect-borne plant diseases.

An outgrowth of this effort is a projected workshop to be held in San José, Costa Rica (additional funding is being sought to support this effort). The focus will be the virus problems of major crops in Latin America (Appendix A). In addition to lectures, the workshop will present an opportunity for scientists of developing countries to complete a series of hands-on field and laboratory exercises that will prepare them for leadership roles in developing team-oriented approaches to resolving plant virus problems throughout Latin America.

STRENGTHENING RESEARCH CAPACITY OF LDC INSTITUTIONS

Carlos Mario Rodríguez, University of Costa Rica, spent 15 days at the Illinois Natural History Survey, Champaign, Illinois. Working with Dr. David Voegtlin, Mr. Rodríguez developed expertise in aphid identification, and practiced on specimens trapped in the preliminary test plots in Alajuela. He also developed skills in the preparation of archival microscope slide mounts of aphids for voucher specimens as well as for the determination of specimens unable to be accurately identified from alcohol. He returned to Costa Rica with reference materials and a working key to aphid species found in that country, prepared by Dr. Voegtlin, to aid in his subsequent identifications. Mr. Rodríguez has been granted an AID fellowship to pursue his M.S. degree at The Ohio State University.

Mr. Harry Bottenberg, a graduate student at the University of Illinois, was sponsored by an AID research support grant. This research contributed greatly to the goals of the project. He joined the aphid identification and specimen preparation training sessions under Dr Voegtlin's direction. This prepared him for experiments he later conducted in Costa Rica and in Illinois for his Ph.D dissertation research. Dr. Bottenberg received his Ph.D in May 1990 and intends to pursue a career in international agriculture.

Ms. Carmen Rivera spent 10 days with Dr. Jacque Fletcher, Oklahoma State University, learning techniques of spiroplasma identification and culture. Using gel electrophoresis assays, they determined that strains of corn stunt spiroplasma from Florida, Mexico, and Costa Rica are different from one another. They also discovered that a simple serological assay, "dot-immunobinding," is effective for corn stunt. Ms. Rivera then visited Drs. Lowell Nault and Don Gordon, Ohio State University, Wooster, where she learned serological and cytological techniques associated with virus and mycoplasma identification.

Ms. Vilma Castro, Associate Professor, University of Costa Rica, will complete her Ph.D in 1990 under the direction of Dr. Scott Isard, Department of Geography, University of Illinois at Urbana-Champaign. The microclimatic studies included under this project formed the basis of her dissertation research.

In addition to training, an IBM XT microcomputer and state-of-the-art meteorological equipment purchases helped strengthen the research capabilities of the University of Costa Rica and now form a permanent part of that institution's inventory.

PROJECT PRODUCTS AND OUTPUTS

Primary Publications. The original series of primary publications envisioned for this project has been modified from those originally projected. The titles presented provide a reasonable assessment of the scientific productivity of this project. The scientists responsible for drafting (italics) and sharing authorship are listed, along with the current status of each paper.

Paper Title	Authors	Status
Microclimate of maize/bean cropping systems.	*V. Castro* and S. A. Isard.	*In preparation (submission 4th quarter 1990)*
Field experiments on bean common mosaic virus epidemiology in bean monocultures and bean/maize bicultures.	C. M. Rodríguez, *G. E. Kampmeier*, V. Castro, M. E. Irwin, and R. Gámez.	*In preparation*
A taxonomic key to identify the aphids occurring in Costa Rica.	*D. J. Voegtlin*, C. M. Rodríguez, and G. E. Kampmeier.	*In preparation (submission 2nd quarter 1991)*
The propensity for different aphid species to transmit bean common mosaic virus under field conditions.	*G. E. Kampmeier* and M. E. Irwin.	*In preparation (submission 4th quarter 1990)*
The influence of cropping background on the alighting behavior of aphids in Costa Rica and Illinois.	*G. E. Kampmeier*, M. E. Irwin, C. M. Rodríguez, D. J. Voegtlin, and H. Bottenberg.	*In preparation*
Windspeed influences residence time of *Uroleucon ambrosiae* (Thomas) alatae (Homoptera: Aphididae) on bean plants in bean monocultures and bean-maize bicultures.	*H. Bottenberg* and M. E. Irwin	*To be submitted to Environmental Entomology 3rd quarter 1990.*
Effect of mixed cropping of bean (*Phaseolus vulgaris* L.) and maize (*Zea mays* L.) on flight patterns of winged aphids.	*H. Bottenberg* and M. E. Irwin	*To be submitted to Economic Entomology 3rd quarter 1990.*
Crop architecture and aphid colony suppression in soybean-sorghum mixed cropping systems. I. Its impact on aphid landing rates.	*H. Bottenberg* and M. E. Irwin.	*To be submitted to Annals of Applied Biology 3rd quarter 1990*
Crop architecture and aphid colony suppression in soybean-sorghum mixed cropping systems. II. Its impact on soybean mosaic virus epidemics.	*H. Bottenberg* and M. E. Irwin.	*To be submitted to Annals of Applied Biology (3rd quarter 1990)*
A simulation model of bean common mosaic virus epidemiology and impact.	*W. G. Ruesink* and E. Brewer.	*In preparation*
A simulation model of maize rayado fino virus epidemiology and impact.	*W. G. Ruesink* and E. Brewer.	*In preparation*

Relationship between symptoms and identification by serology of three diseases in maize: maize rayado fino virus, corn stunt spiroplasma, and maize bushy stunt mycoplasma.	*C. Rivera*, J. Fletcher, L. R. Nault, and R. Gámez.	*Insufficient data to complete*
Host plant dispersion and disease transmission: the role of insect trivial movement.	*A. G. Power.*	*To be submitted to Ecological Entomology (3rd quarter 1990).*
Evaluation of two leafhopper sampling methods for predicting the incidence of a leafhopper-transmitted virus of maize.	*A. G. Power*, R. Gámez, and C. M. Rodríguez.	*To be submitted to Journal of Economic Entomology (3rd quarter 1990).*
The relationship of bioassay of leafhoppers for pathogens and disease incidence in the field.	*C. Rivera*, J. Fletcher, L. R. Nault and R. Gámez.	*Insufficient data to complete*
Effect of climate on disease development.	*V. Castro*, C. Rivera, C. M. Rodríguez, others?	*Insufficient data to complete*
Effect of climate on vectors of plant disease.	*V. Castro*, C. M. Rodríguez, others?	*In preparation (4th quarter 1990)*
Predicting plant virus epidemics in maize/bean cropping systems.	*W. G. Ruesink*, M. E. Irwin, R. Gámez, V. Castro, ...	*planned for 1991*

Review Articles. Currently a single article is planned for submission to *BioScience*:

Plant virus epidemiological studies in tropical mixed cropping systems: importance, approaches, and constraints. *J. M. Thresh*, R. Gámez, and M. E. Irwin.

Ph.D. Dissertations. Two Ph.D. dissertations have been completed through the University of Illinois at Urbana-Champaign.

Harry Bottenberg, 1990. Aphid movement and aphid-borne virus spread in mixed cropping systems of legumes and cereals.

Vilma Castro, 1990. The microclimate of corn and bean cropping systems: Its relationship with *Dalbulus maidis*, some aphids and the diseases they transmit.

Computer Models. The plant disease models, developed by Dr. W. G. Ruesink, will be available for use on IBM-PC-compatible machines. They may be used for teaching at the University of Costa Rica, CATIE, or other Latin American institutions. They will also to help groups advise projects examining the impact and progress of insect-borne plant diseases. Furthermore, these models will allow extension specialists to advise growers of ways they can minimize the impact of such disease epidemics.

Presentation at Professional Meetings. To date, aspects of this project have been featured in a poster presented at an international meeting and in a graduate student paper competition at the national level.

Epidemiology of bean common mosaic virus in monocultures and in polycultures with maize in Costa Rica. *M. E. Irwin*, J. M. Thresh, C. M. Rodríguez, G. E. Kampmeier H. Bottenberg, and D. J. Voegtlin. *IVth International Plant Virus Epidemiolc Workshop, Montpellier, France.* 3-8 September 1989.

Crop architecture in mixed cropping systems: its impact on aphid movement and consequent virus spread. *Harry Bottenberg* and M. E. Irwin. Annual Meeting. Entomological Society of America, San Antonio, Texas, December 11, 1989.

Working Group Meetings. Two major and one minor meeting of the scientists involved in this project took place over the course of this project.

- Thirteen of the fifteen team members attended the meeting in March 1986 in Las Cruces, Costa Rica to organize the plan of work for this project. Many details of experimental design, microclimate studies, and needs of the conceptual models were discussed along with prospects for future directions and funding.
- Twelve of the fifteen team members attended the meeting in May 1988 in Costa Rica. Project progress and future plans were discussed and members had a chance to see experimental plots.
- Nine working group members met in Louisville, KY, Dec. 4, 1988 in conjunction with the annual national meeting of the Entomological Society of America. Discussion centered on results of experiments conducted from May-September 1988 in Costa Rica, Illinois and Ohio, the proposed workshop on Neotropical Plant Virus/Mollicute Epidemiology and Control, future prospects for a mixed cropping project, and possible spin-off projects.

RESEARCH CONDUCTED

Facilities, Resources and Personnel

The following is a brief summary of facilities, resources, and participating staff for each of the participating institutions:

University of Costa Rica, Cellular and Molecular Biology Research Center

The Cellular and Molecular Biology Research Center is a scientific, interdisciplinary research unit under the Vice-Presidency for Research, University of Costa Rica. It is dedicated to the study of biology, ecology, and evolution of plant and animal viruses in the tropics, particularly at the molecular and cellular levels. The Center promotes the training of promising young scientists from Latin America and supports graduate programs of the University. Included within the structure of the Center are three working groups, of which *plant and virus molecular biology* is one, and under

that group, the *ecology and evolution of plant pathogens* forms an important subgroup of concentration.

The Fabio Baudrit Experimental Station, located in Alajuela, provided the necessary equipment, land, and personnel to conduct the complex field experiments outlined in this project.

Rodrigo Gámez, Director. Co-Principal Investigator. Dr. Gámez is an expert in leafhopper-vectored plant pathogens. He coordinated all for aspects of the project conducted in Costa Rica.

Carmen Rivera, Associate Professor. Investigator. Ms. Rivera is a molecular virologist and was in charge of the laboratory aspects of this project and she performed serological and electron microscopic assays to detect the presence of pathogens in field-collected plant samples.

Carlos Mario Rodríguez, Researcher. Investigator. Mr. Rodríguez organized, managed and executed the field aspects of this project in Costa Rica. Furthermore, he identified the insects that were collected. His experiences during this project lead him to pursue a scholarship with USAID to attend The Ohio State University to obtain a Masters degree in entomology. He began his studies in January 1990. His thesis topic will involve the biodiversity of vectors in agricultural and natural landscapes.

University of Costa Rica, School of Physics

The School of Physics interacts strongly with the Cellular and Molecular Biology Research Center, particularly through its Meteorology and Climatology Programs. The School has a laboratory with electronic equipment for testing and calibrating meteorological instruments, microcomputers and software, vehicles to transports for heavy equipment, and a workshop for miscellaneous jobs.

Vilma Castro, Associate Professor. Investigator. Ms. Castro undertook a Ph.D. degree (expected December 1990) in the Department of Geography, University of Illinois, as an outgrowth of this project. Her dissertation topic is the micrometeorology of mixed cropping systems.

University of Illinois, Illinois Natural History Survey, and Illinois State Water Survey

The University of Illinois is one of the premier land-grant institutions of higher education in the United States. It has all of the support facilities befitting its stature: excellent library, computing services, consultation services for statistical analysis, experimental fields, and a host of others. The Illinois Natural History and State Water Surveys are physically on the campus of the University and enjoy the advantages of all of the available services. In addition, the Illinois Natural History Survey has an excellent insect collection and both Surveys have a network of personal computers linked with large campus and Survey mainframe computers.

Michael E. Irwin, Professor. Co-Principal Investigator. Dr. Irwin is an expert in vector movement and virus epidemics. He coordinated the project, making sure that reports were written and data were analyzed.

L. Keith Hendrie, Climatologist. Collaborator and Consultant. Mr. Hendrie worked with Ms. Castro on the meteorological aspects of the project. He selected and set up the appropriate state-of-the-art meteorological equipment in Costa Rica for use in this project.

Scott A. Isard, Associate Professor. Collaborator and Consultant. Dr. Isard is an expert in micrometeorology and has focused a portion of his research on the effects of meteorology on insect, particularly vector, movement. He was Ms. Castro's major professor.

David J. Voegtlin, Associate Taxonomist. Collaborator and Consultant. Dr. Voegtlin is an expert in the biology and systematics of aphids. He has a broad knowledge of the aphids of Central America. He served as a resource for the verification of aphid species trapped during the project and trained Carlos Mario Rodríguez to make the routine identifications.

William G. Ruesink, Professor. Collaborator and Consultant. Dr. Ruesink is an experienced modeler of plant disease epidemics. His soybean mosaic virus model was the starting point for developing simulative models of the diseases tracked during this project.

Gail E. Kampmeier, Associate Research Biologist. Investigator and Consultant. Ms Kampmeier served as the communicator for this project, helping to draft reports, consolidate and analyze data, and disseminate information.

Harry Bottenberg, graduate student. Investigator. Mr. Bottenberg completed his Ph.D. under Dr. Irwin with research conducted in Costa Rica and in Illinois relating to aphid movement and subsequent virus spread in single and mixed cropping systems.

Ohio State University

Lowell R. Nault, Professor. Collaborator and Consultant. Dr. Nault is renown for his work on virus-vector relationships, including the coevolution of viruses and their vectors. The team drew on his expertise with the maize pathogens and their vectors studied in this project.

Cornell University

Alison G. Power, Associate Professor. Investigator and Consultant. Dr. Power brought valuable experiences gained in studies in Nicaragua of the bioecology of leafhopper vectors of maize diseases and disease epidemiology.

Oklahoma State University

Jacqueline Fletcher, Associate Professor. Collaborator and Consultant. Dr. Fletcher has worked for several years on the identification and characteristics of mycoplasma-like organisms,

including spiroplasmas. She worked with Ms. Rivera, CMBRC, on the use of Dienes' stain and DAPI techniques to determine MLOs from plant tissue.

Natural Resources Institute, Overseas Development Administration

J. Michael Thresh, Senior Scientist. Collaborator and Consultant. Dr. Thresh is a world authority in plant virus epidemiology and movement of virus vectors. Author of numerous scientific articles, book chapters and books and extensive traveller to the tropics, Dr. Thresh brought a global perspective to our project.

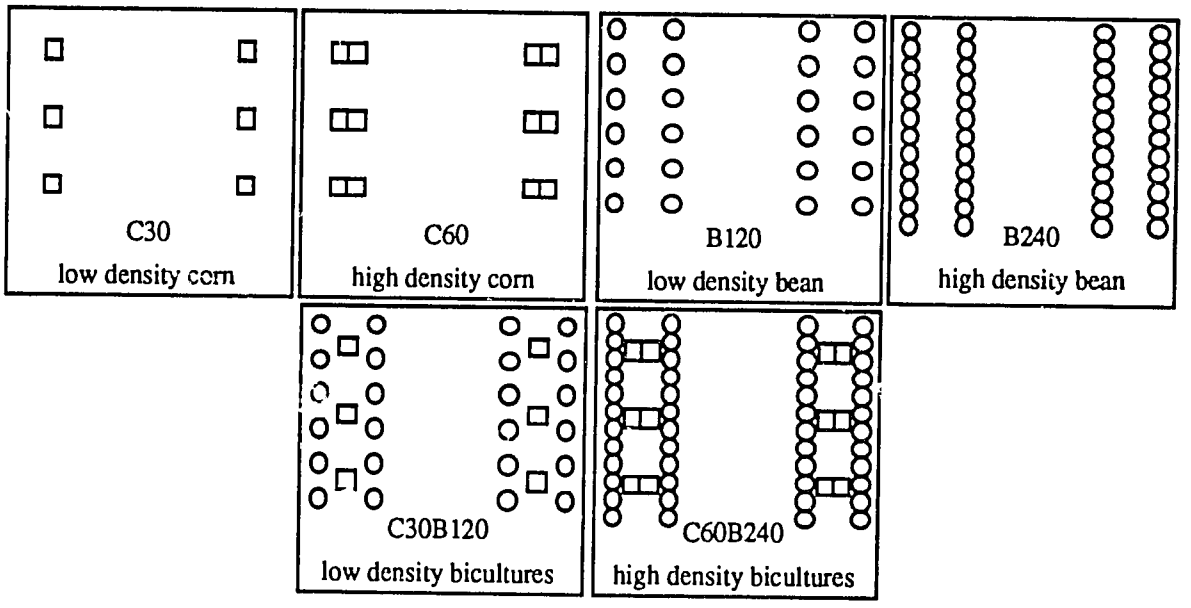
Organization for Tropical Studies

The Organization for Tropical Studies (OTS) is a consortium of 49 institutions in the United States and Costa Rica dedicated to understanding the ecology of tropical ecosystems. OTS has a strong central administrative unit at Duke University, North Carolina, and an equally strong administrative unit in San Jose, Costa Rica. Because the University of Costa Rica is a member institution, OTS is able to funnel funds from the United States into that institution. OTS also provides important infrastructural detail to our project by supporting our needs for vehicles and reservations in Costa Rica, by providing a conduit for communications between Costa Rica and the United States, by providing timely and well-documented ledgers of expenses incurred, and by granting us access to their biological stations in Costa Rica. OTS uses Duke University's overseas indirect cost rate of 26%, which provided increased usable funds for the project. This project subcontracted OTS to handle the costs to be incurred in Costa Rica, which proved to be an efficient means of getting funds to the researchers in Costa Rica. Partially as a result of our successful collaboration with OTS during this project, the University of Illinois made a commitment to rejoin OTS in 1990.

Experimental Methodology

Cropping systems comprised of maize and bean are part of the traditional polyculture system found not only in Central America but in other parts of the world as well. These crops therefore formed the foundation for the experiments, designated as Main Experiments #1-4, that were conducted at the Fabio Baudrit Experiment Station, Alajuela, Costa Rica (a complete list of experiments conducted appears in Appendix B). The first and third experiments were conducted from September to December in 1986 and 1987, respectively. The second was conducted from January to May 1987 and the fourth from June to August 1988. A fifth experiment, designated 'Plot Size,' ran from May to July 1987. All these experiments featured high (B240 = 240,000 plants/ha) and low (B120 = 120,000 plants/ha) density bean (*Phaseolus vulgaris* var. Huetar) plots, high (C60 = 60,000 plants/ha) and low (C30 = 30,000 plants/ha) density maize (*Zea mays* var. Across 7728) plots, and high (C60B240) and low (C30B120) density maize/bean bicultures.

The plots were designed according to the illustration below that shows a meter length of row.



Maize rows were 1 m apart, and double density meant two rather than one corn plants per hill. There were two bean rows per meter that were between 30 and 70 cm apart. Four replications were tested in the first two experiments and six in the latter two. Because of land limitations, the Plot Size Experiment was planted to determine the minimum plot size needed to carry out the main experiments. In that study, plot sizes of 25 m^2, 100 m^2, and 225 m^2 were tested. Although this experiment was unreplicated, where plot sizes were not significantly different, they were used as replicates to analyze differences between treatments.

Four pathogens were tracked during these experiments. Bean common mosaic potyvirus (BCMV) is nonpersistently transmitted by many aphid species and is also seed transmitted. Seed transmission is an important mechanism by which the virus can cross geographical and temporal boundaries. Maize rayado fino virus (MRFV) is transmitted to maize in a persistent manner by the corn leafhopper, *Dalbulus maidis* Delong & Wolcott. This leafhopper is also the vector of two other pathogens of maize, corn stunt spiroplasma and maize bushy stunt mycoplasma. The incidence of these mycoplasma-like organisms (MLOs) were combined under the term mollicutes because subsequent experiments proved that symptom expression of these diseases was an unreliable indicator, as determined serologically, of these pathogens. In all main experiments, the inner 25 m^2 of each plot was examined for BCMV, or 300 and 600 plants respectively in low and high density beans. For the maize diseases, 675 plants were examined per plot in the low density maize and 1350 in the high density plantings. In the plot size experiment, all maize plants were examined in each plot size, i.e. 150, 600 and 1350 plants respectively.

Aphids and *D. maidis* were trapped in all cropping treatments. Aphid landing rates were measured daily from two water-filled mosaic green pan traps per plot. The traps were maintained at the bean canopy level in all treatments. The aphids were identified to species in Costa Rica and voucher specimens sent to Illinois for verification. Flight activity of *D. maidis* was measured

weekly from two yellow sticky cards (Olsen Products) per plot, oriented to face southeast (SE)/northwest (NW) and southwest (SW)/northeast (NE). These sticky traps were maintained at 1.5 m above the ground.

A meteorological tower was erected in the experimental site to monitor wind speed and direction. Keith Hendrie spent a week in Costa Rica during Main Expt. #1 with Vilma Castro calibrating and installing the meteorological equipment, which was designed to measure temperature, relative humidity, wind speed and direction, and solar radiation at three possible levels, above, at, and below the level of the plant canopy. The tower was moved from treatment to treatment during the season.

The primary objectives of the meteorological portions of the research were to 1) characterize, compare and contrast the microclimate of different cropping systems and 2) establish empirical relationships between microclimate and vector activity/pathogen spread. Secondary objectives were to establish 1) relationships between standard climatic data and micrometeorological data, and 2) guidelines for developing a weather-based strategy for insect/pathogen control.

Summary of Results by Experiment

Main Expt. #1 (September-December 1986)

- Low density bean plantings had significantly fewer infections of BCMV than did high density beans, although percentage incidence was significantly higher in the lower density bean plantings (Figs. 1-2).
- Although aphid numbers were very low, the behavior of *Aphis gossypii* landed significantly more frequently in the maize monocultures than in the bean monocultures or the bicultures (Fig. 3).
- Bean yield in numbers of bean pods per plant, seeds per plant, and grams of seed per plant when measured by date of BCMV infection was always significantly greater in the low density bean mono- and bicultures, suggesting that the higher bean density may have been agronomically too high.
- No significant difference was measured in yield per hectare between monocropped and intercropped beans, suggesting that at the densities we chose, a greater total yield could be obtained through intercropping..
- Leafhopper counts were lowest in the bean monocultures, and highest in the maize monocultures, while numbers caught in the bicultures were intermediate. All differences were significant at the 5% level (Fig. 4). Plant density did not appear to play a role in *D. maidis* flight activity measured by the yellow sticky traps.
- Orientation of the yellow sticky traps in maize monocultures and maize/bean bicultures was significant during this experiment, with cards facing northeast and northwest trapping more than those facing southwest, and the southeasterly faces collecting the fewest numbers (Fig. 5). This suggests that flight orientation was greatest from the north.

- MRFV incidence was significantly higher in the high density maize monoculture (Fig. 6) than in any other treatment. The majority of infections occurred by Nov. 12th, before large differences in height existed between maize and bean.
- Percent infection by MRFV was lowest in the high density maize biculture (Fig. 7).
- Incidence of mollicutes was not significantly different between cropping treatments, although percentage of plants infected was significantly higher in the low density maize monoculture than in other treatments (Figs. 8-9).

Main Expt. #2 (January-May 1987)

- BCMV symptoms were more easily recognized during the dry season because symptoms were more pronounced.
- Incidence of BCMV was low in all treatments. No significant differences were found in the incidence of the virus or percentage of plants infected among any cropping treatments (Figs. 1-2).
- Although the number of aphids trapped was slightly greater in this than Main Expt. #1, no significant differences were found in landing rates between treatments.
- Mean numbers of *D. maidis* collected on yellow sticky traps were much lower in the dry season. Significantly more leafhoppers were collected in low density maize than in the bean monocultures or low density biculture (Fig. 4).
- In this experiment, no significant differences occurred in numbers of leafhoppers collected by trap orientation.
- The incidence of MRFV was very low during this experiment, and no significant differences were found between treatments (Fig. 6).
- Mollicute incidence was significantly higher in the high density treatments, but no difference in the percentage incidence was found (Figs. 8-9), indicating either more movement or more immigration into those treatments by the leafhoppers.
- Maize yield was highest during this experiment, with mean ear weight doubling that of Main Expt. #3 (wet season). Although no significant differences (at 5% level) could be declared in mean ear weight between cropping treatments (Fig. 10), higher density maize plots yielded significantly more per hectare.
- Temperatures ranged from 18-30°C. Early in the season, the maximum temperature was reached by 15 h, while later in the season it was reached by noon. Temperature readings taken at three levels (above, at, and below canopy level) were similar, increasing with height at night and decreasing with height during the day (Fig. 13). Shelter box temperature was similar to field temperature at night but was much higher during the day.
- Vegetation temperature was usually lower than air temperature at night but extremely high canopy temperatures were recorded during the day because sensors were exposed to the sun.

- Relative humidity was similar at all three levels, although it was slightly higher closer to the canopy which appeared to act as a humidity source during the day (Fig. 13).
- Maximum wind speeds were recorded between 12-16 h and velocities increased with height. The afternoon average maximum windspeed was 9 m/s while overnight speeds dropped to 3 m/s. Wind speed measured at the meteorological station and in the field appear to be highly correlated.
- Solar radiation levels are very high during the dry season, with a high percentage of UV radiation in the solar spectrum.

Plot Size Expt. (May-August 1987)

- Aphid populations peaked in May-June, reaching numbers that for a single week were much higher than those of the entire previous plantings. Significantly more aphids landed in the bean monocultures than any other treatment. This was due in large part to the preference by *Aphis spiraecola* for beans in monoculture. *Aphis helianthae*, although not present in great numbers, showed a similar preference (Fig. 11).
- BCMV-infected plants were correspondingly numerous and disease progress rapid. The greatest percentage of plants infected was in the low density monoculture beans, followed by the high density monoculture (Fig. 2). BCMV incidence in these two cropping treatments were not significantly different from one another, but were significantly greater than the high and low density bicultures (Fig. 1).
- Leafhopper collections were extremely low, the lowest numbers of all experiments conducted during the project (Fig. 4). No significant differences were found among cropping treatments or between sticky card orientation, probably because so few *D. maidis* were captured.
- Although numbers of plants infected with MRFV were greater than in Main Expt. #2, neither incidence nor percentage of infected plants showed significant differences among treatments (Figs. 6-7).
- Plot size was highly significant, however, when incidence of MRFV was examined. It is not surprising, however, that the largest plot size had significantly greater incidence of MRFV, because the possible number of maize plants examined in the 25 m^2 plots was 150 plants, the 100 m^2 had 600 plants and the 225 m^2 had 1350.
- Low numbers of mollicute-infected plants, the lowest of any experiment conducted during this project, showed no differences among cropping treatments (Figs. 8-9).

Main Expt. #3 (September-December 1987)

- Numbers of aphids were very low during this experiment; thus no significant differences in landing rates were found between cropping treatments.

- BCMV incidence was also low, due in part to the fact that plants were not mechanically inoculated to initiate sources within the field. No treatment ended the season with more than 3.1% of the plants infected, resulting in no significant differences in percentages of plants infected among cropping treatments (Fig. 2). Incidence, although low, was still significantly greater in the high density than in the low density bean monoculture (Fig. 1).
- As in Main Expt. #1, the lowest number of *D. maidis* were found in the bean monocultures, the greatest number in the maize monocultures, with the numbers trapped in the bicultures intermediate. All were significant at the 5% level (Fig. 4).
- Leafhoppers were caught in significantly greater numbers on north facing cards (Fig. 12), as in Main Expt. #1.
- The highest incidence of MRFV was recorded in this main experiment, with high density maize mono- and bicultures significantly greater than lower density treatments (Fig. 6).
- Percentage of plants infected with MRFV was significantly greater in the lower density treatments (Fig. 7) than in the higher density treatments.
- The greatest number of mollicute infections occurred during this experiment, coupled with significantly greater incidence in the high density plots (Fig. 8).
- The percentage of plants infected with mollicutes was significantly greater in the low density cropping treatments (Fig. 9).

Main Expt. #4 (June-August 1988)

- Significant differences in the percentage of mechanically inoculated source bean plants that showed symptoms were found between replications. Therefore, only three of the six replicates were used to analyze the results of BCMV infection in this experiment.
- The percentage incidence of BCMV was minimal during this experiment, exhibiting no significant differences among cropping treatments (Fig. 2).
- Incidence of BCMV infection was significantly lower in the low density biculture than in the high density biculture (Fig. 1).
- A total of 414 aphids were trapped over the season, predominantly *Aphis spircecola, Aphis gossypii, Rhopalosiphum maidis,* and *Tetraneura spp.* No significant differences were found between aphids landing in different treatments; however, when examined by species, *Aphis gossypii* landed in significantly greater numbers in the maize monocultures than in the high density bean treatments.
- *Dalbulus maidis* numbers were generally low, averaging less than 200 per plot over the season. Maize monocultures had fewer *D. maidis* than did other treatments (Fig. 4), a fact countered by the trend in Main Experiments 1-3 and the Plot Size Experiment.

- The spread of MRFV was also minimal, and no significant differences were found between cropping treatments, either by incidence of infected plants or by percentage within plots (Figs 6-7).
- The weather during this experiment was characterized by high rainfall and unusually low wind speeds.
- Vilma Castro used soap bubbles to follow air parcel movement in the canopy. On calm days, no discernable wind pattern could be detected within the canopy, but on windier days, soap bubbles rose out of the canopy. Bubbles penetrated more deeply into sparser canopies. Wind speed was usually below the sensitivity threshold (ca. 0.2 m/s) of the cup anemometer inside canopies.
- The height above or below the crop canopy level was key to differences in wind speed, temperature and humidity (Fig. 13). The actual cropping composition was less important than crop density for wind profiles. At night, humidity always reached 100% in the canopy. Even after 5-7 days without rain, water was always present in maize whorls.
- Because of high temperatures at canopy level, thermal convection could play a role in the dynamics of aphid landing.

Discussion

Effect on Bean and Maize Growth and Yield Components

- Maize yields were higher during the dry than rainy season (Fig. 10), while bean yields were higher during the rainy than the dry season. The growth habit of beans may in part account for this yield difference, being vine-like during the rainy season and bushy during the dry season.
- The earlier the infection by an insect-borne pathogen, the greater the yield reduction to the respective bean or maize crops.
- Beans in monoculture were more susceptible to root diseases, especially *Fusarium*, than were those intercropped with maize.
- Numbers of bean pods per plant, seeds per plant, and grams of seed per plant when measured by date of infection by BCMV, were always significantly greater in the low density bean mono- and bicultures, while bean yields per hectare were not affected by density, suggesting that the higher bean density may have been agronomically too high.
- On a per hectare basis, intercropping maize with beans did not significantly decrease yields of either crop at similar densities, suggesting that at the densities we chose, a greater total yield could be obtained through intercropping.
- Although mean ear weight of maize tended to be higher in lower density plots (Fig. 10), higher density maize, when planted in monoculture or intercropped with bean, yielded significantly more per hectare than did comparable low density plots.

Canopy and Microclimatic Characteristics in Single and Double Density Crops

- The rainy season is from June-Sept. and the dry season from Dec.-April. May, October and November are transitional months.
- Canopy roughness, as measured by sparse and irregular spatial distribution of foliage, was greatest in low density maize plots, followed by high density maize and low density bean plots. The smoothest or most uniform canopies were obtained in the high density bicultures, followed by high density bean monocultures and low density bicultures.
- Percentage ground cover is inversely proportional to canopy roughness. The bicultures both attained closed canopies, while the high density bean achieved 95% canopy closure. Low density maize attained the least percentage ground cover, followed by high density maize and low density beans.
- Microclimatic differences between crops tend to be small when the parameters are averaged over 7 day periods. Differences become more apparent when data are examined on a daily basis and under specific circumstances, e.g. clear vs. overcast days, calm vs. windy days, dry vs. rainy days.
- When wind speeds were low (about 1 m/s measured 0.75 m above the crop canopy), wind speed within the canopy was similar in all cropping systems, regardless of contrasts in canopy height or plant density.
- At higher wind speeds (>4 m/s measured at 0.75 m above the canopy), winds above high density plots were as much as 1 m/s greater than those over low density plots for the range of wind speeds measured during the experiment; however these differences were not statistically significant, except in the mixed cropping plots. Similarly, wind profiles, although steeper over the high density than low density crops, were not significantly different from one another. This was possibly an artifact of small plot sizes that did not allow the air flow to fully equilibrate with the underlying canopy characteristics.
- Daily average temperature fluctuates only about 5°C between the rainy and dry seasons, but the daily temperature amplitude is much higher during the dry season.
- Overall temperature gradients above each cropping system did not differ significantly. However, when individual days were considered, larger temperature gradients occurred near noon over C60B240 and B240 plots (up to 1.5°C in 4 m), than within C30B120 and C60 plots (up to 1°C in 4 m), or above B120 crops (less than 0.5°C in 4 m). Large temperature gradients are related to upward air movement that may affect light flying objects. During the night, temperature profiles approach isothermal conditions.
- Solar radiation is higher during the dry season.
- Inside the crop canopy, bare ground rather than the foliage was usually the most effective radiation absorption surface. Air temperature increased during the day and decreased during the night from the top to the bottom of the foliage. In high density mixed plots and high density beans whose canopies were well developed, temperature profiles were isothermal (unchanging)

during the night and inverted during the day, with temperatures decreasing by as much as 2°C from the top of the bean canopy to the ground.

- During the day, air humidity is consistently as much as 20% lower during the dry season.
- Although relative humidity was approximately 10% higher in the denser plots (C60B240, C30B120, B240) than in the sparser ones (C60, C30, B120), hourly measurements of leaf wetness duration on bean leaves was similar among cropping systems. To detect differences in leaf wetness among crops, we would have had to read the sensors at least every fifteen minutes. Visual observations revealed that water droplets remained on the maize leaves many hours after the bean leaves had dried. Water invariably occurred within the maize whorl, even during the dry season. Unfurled leaves of both bean and maize remain wet for most of the day during the rainy season, and almost always dry during the dry season.

Relationships between Microclimate, Vector Activity and Pathogen Spread

- Wind speed is much higher during the day and during the dry season.
- Wind speed was the only environmental variable that appeared to influence the number of aphid landings over the diel period. Air temperature, relative humidity, atmospheric pressure, rainfall, solar radiation, and wind direction did not show any relationship with the daily fluctuations of aphid landings. Daily landing rates usually decreased when mean daytime wind speeds increased, no matter the magnitude of the wind speed. Similarly, landing rates usually increased when mean daytime wind speeds decreased.
- Throughout the year, the largest number of aphid landings occurred during the five week period following the start of the rainy season. Large numbers did not occur at any other time of the year, even when wind speeds were low. Southwesterly winds become more persistent than those from the northeast as the rainy season progressed from northward in Costa Rica. It is suspected that aphids may be carried relatively long distances from the south by these winds, from areas where the rainy season is well established to areas where rain is just beginning.
- Because crop density did not have an impact on aphid landing rates during these experiments (Figs. 3 and 10), either microclimatic differences were not large enough to influence aphid landings or other factors such as crop species or species mixture overrode such influences. The mosaic green traps do not differentiate between inter- and intrafield movement of aphids. The preferences shown by *Aphis gossypii* for landing in maize monocultures and by *A. spiraecola* and *A. helianthae* for alighting in bean monocultures were unlikely to be related to microclimate, as such differences between crops were undetected during these experiments.
- Microclimatic conditions unconducive to aphid flight (high wind speeds, turbulence, low air humidity) occurred most frequently over high density biculture plots. Although aphid landing rates in these plots were not generally statistically different from other treatments, they were always among the lowest recorded.

- Wind speed at the experimental site can change substantially from one day to the next and wind direction switches direction almost 180° twice a day. Because the yellow sticky traps were monitored only once a week, it was impossible to establish a clear relationship between *Dalbulus maidis* and wind direction. Because more insects were usually caught in the northward than on the southward facing traps, wind probably influenced the horizontal movement of *D. maidis* (Figs. 5 & 12).
- Throughout the life cycle of the maize crop, the relative number of *D. maidis* trapped reflected the developmental stage of maize plants to a greater extent than weather. Leafhoppers trapped were bimodal over the season, with a first peak 30 to 40 days after planting (immigrants) and a second 45 to 60 days after planting, probably indicating movement of next generation specimens. Rainfall is crucial to population size: few *D. maidis* were trapped during the dry season, but numbers increased as the rainy season progressed.
- The preference of *D. maidis* for maize in monocultures rather than in mixture with beans (Fig. 4) cannot be explained by microclimate because differences in microclimatic factors tended to be larger between crops planted at different densities than between crops.

Relationship between Standard Climatological Data and Micrometeorological Data

- Because temperature and relative humidity at similar heights above the ground were equivalent measured in either meteorological screens or at the crop canopy, weather screens can be used to approximate temperatures and humidities above crops. However, under high irradiance circumstances, the standard meteorological screens usually produce higher temperatures and thus lower relative humidities than the well-ventilated sensors mounted above the crops.
- Because physical characteristics of the terrain have a strong impact on correlations of wind speed and direction, it is important where possible to minimize the distance differences between an experimental site and a meteorological station. At Alajuela, a good linear relationship was found between the wind speed and direction of the two sites only when wind speeds were high and wind direction persistent.
- Wind speed, measured at 10 m above ground level, as is customary for climatological purposes at standard meteorological stations, cannot be extrapolated to the ground surface by using a logarithmic relationship at a site where there are large vertical obstacles upwind because such obstacles tend to reduce wind speed near the ground. For this reason, it is important to understand the characteristics of vegetation and topography in the surrounding area and their influence on wind speed and direction before one extrapolates wind speed measurements from meteorological stations to lower levels and to experimental sites in neighboring fields.

Disease Incidence and Spread

- When aphids landing show distinct preferences for beans in monoculture (Fig. 11), both plant density and the presence of maize in the cropping system can influence the spread of BCMV

(Figs. 1-2, Plot Size Expt.). However, when aphids show no preference for landing in beans in sole or mixed crops, the density of bean planting has a greater influence on the spread of BCMV than does the influence of maize in the cropping system.

- Dense bean plantings reduce the percentage incidence of BCMV.
- BCMV infections were greatest when large numbers of aphids were collected in a given crop, but spread also occurred when aphid numbers were low and during any season of the year.
- Symptom expression of BCMV was less obvious during the rainy season.
- The density of maize planting has a greater influence on the spread of MRFV, CSS and MBSM than does the influence of beans in the cropping system (Figs. 6-9), even though leafhopper movement is more influenced by plant types in the cropping system (Fig. 4).
- Lower density plantings of maize had generally a higher incidence and thus greater percentage of MRFV, CSS and MBSM than did the higher density maize plots.
- The percentage of MRFV, CSS and MBSM-infected plants was usually more closely related to the number of *D. maidis* collected. However, in one experiment conducted just after the start of the rainy season (Main Expt #4, June-August 1988), although a considerable number of *D. maidis* were trapped, the spread of MRFV was low. One possibility is that the leafhoppers were moving into the field from healthy host plants.
- MRFV, CSS and MBSM are all more common during the rainy season.
- The percentage of plants with BCMV, CSS and MBSM was usually larger in the single than in the double density plots, but differences were not always statistically significant (Figs. 2 &9). The percentage of plants with MRFV was larger in the single density than in the double density crops in only one of the experiments (Fig. 7).
- In the plot size experiment, incidence of BCMV and mollicutes was generally greater in the 25 m^2 plots than in the 100 or 225 m^2 plots. This did not hold true for MRFV, where no clear trend was established. Incidence of CSS was negligible.

Vector Activity

- When wind speed is high, aphids tend to disperse by walking rather than flying.
- Some aphid species exhibit differential landing characteristics on bean and maize. *Aphis gossypii* has a distinct preference for landing in maize, but landing rates in polycultures are similar to those found in bean monocultures. *Aphis spiraecola,* on the other hand, preferred to land on beans. Polycultures reduced landing rates of *A. spiraecola* to the level of those found in maize. Several species showed no distinct preference for one plot over another, and plant density did not appear to influence landing rates significantly.
- Fewer than 300 aphids were trapped in each main experiment (#1-3), but nearly 1700 aphids were collected in the plot size experiment, which took place at the end of the long dry season (May-July 1987).

- *Dalbulus maidis* was over ten times more numerous during the wet season (Sept.-Dec.) than during the dry or beginning of the rainy season (Jan.-April; May-July).
- Plant density appears to have no effect on numbers of leafhoppers trapped on yellow sticky cards, although on examining the plants, more leafhoppers are found in the double density maize crops.
- Leafhoppers are more likely to move along than across rows.
- Whenever there is free water on maize leaves, *D. maidis* prefers to remain on the plant.
- Significant differences in trap catches were found based on wind direction, traps oriented to the northeast and northwest catching higher numbers than those facing southeast and southwest.

Propensity of Aphids to Transmit BCMV

A propensity study was performed once at the Alajuela Experiment Station, Costa Rica, in April-June of 1986, but was unsuccessful due to a lack of aphids, so it was conducted at the Vegetable Crops Farm, at the University of Illinois from 15 July-24 August 1987. A 15.4 m x 15.4 m plot was planted in bean cv. Stringless Greenpod in late June and the beans, thinned to one plant per 0.3 m, were mechanically inoculated with BCMV (strain NY-15 from Gaylord Mink, Washington) at the primary leaf stage in early July. Two vertical nets 2 x 5 m were placed in the center of the plot forming a cross, and as aphids alighted, they were picked from the net and caged on healthy bean seedlings (Halbert et al., 1981). The aphids were recovered and identified after being caged for at least one hour. Aphids were trapped 5 days each week, mainly in the morning, but occasionally in the evening. Data collected in these experiments have been incorporated into the BCMV model.

- Nearly 900 aphids were trapped in Illinois, but fewer than 3% of the test plants became infected.
- Twelve species of aphids transmitted the virus, seven of which had never been reported as vectors (*Aphis maidiradicis* complex, *Tetraneura* sp., *Brachycaudus cardui, Anoecia oenotherae, Aphis nerii, Rhopalosiphum rufiabdominalis,* and *Rhopalosiphum maidis*). Twenty-two species of aphids have been reported to be vectors of BCMV in the literature (Appendix C).
- From our studies and from reports in the literature, potential vector species comprised 86% of the aphids trapped in Illinois. In Costa Rica, potential vector species comprised 71% of the catch in Main Expt. #1, 66% in Main Expt. #2, 82% in Main Expt. #3, 89% in the Plot Size Expt., and 76% in Main Expt. #4.
- Aphids landed on the net that caught the prevailing wind.
- When no wind blew, no aphids were seen flying or landing on the nets, yet when the wind picked up, aphids appeared again on the nets.
- On clear days with high wind speeds few aphids were caught, although during sudden gusts from an upcoming storm, aphids were collected from the net.

Taxonomic Keys to Identify Aphid Species Occurring in Costa Rica

Aphids transmit nearly 60% of plant viruses for which the vectors are known (Easton 1977). However the role of each aphid species in virus spread varies in importance. Because of this, it is insufficient to know how many aphids are trapped in a field; each aphid must be identified to the species level. Although the number of species known from the tropics is fewer than from temperate zones, few aids exist to help the tropical epidemiologist. Most traditional keys require knowledge of the host plant with which the aphid is associated; however, the keys being prepared for publication by Dr. Voegtlin are designed for use in the many projects involving the identification of trap-collected winged aphids. The paper will be divided into two parts, 1) a key to aphids as they appear in alcohol when viewed through a dissecting microscope of reasonable quality, and 2) a key to aphids mounted on microscope slides, as seen under a compound light microscope. Each key serves an essential function in scientific research. Because of the need for rapid and accurate identification of the large numbers of specimens often collected in traps, determination of aphids in alcohol to the species level without going through the laborious process of mounting each onto a microscope slide is desirable. However, because the differentiation of several aphid species can only be resolved to the genus or species complex level in alcohol, more detailed keys requiring higher magnification are also imperative. In addition, examples of the many species collected during a project must be preserved in a permanent collection that can be verified by a trained taxonomist.

These keys will be thoroughly illustrated with black and white photographs and possibly line drawings to illustrate diagnostic characteristics. Photographs are particularly critical to the key to aphids in alcohol as the "gestalt" or total appearance of the specimen is often as useful to its identification as are particular, detailed characteristics.

Much of the key to aphids mounted on microscope slides has been written. Photography will be done in the last half of 1990. This publication is to be translated into Spanish by C. M. Rodríguez and intentions are to have it published in Costa Rica. Although the title of this paper restricts it to species occurring in Costa Rica, realistically, these keys will aid workers in most of Central America.

Aphid Movement and Dispersal with the Aid of Fluorescent Dyes

Harry Bottenberg spent two cropping periods in Costa Rica looking at aphid movement and dispersal with the aid of fluorescent dyes. In October-December 1986 he attempted to determine the weed hosts of aphids outside of Main Experiment # 1, mark the aphids with fluorescent dyes, and recapture them in mosaic green water traps placed in a grid network in the field, thereby characterizing dispersal distances and patterns. He also observed the population dynamics of the aphids on their weed hosts, especially noting the timing of alate production.

- Few aphid colonies were discovered on weed hosts, therefore marking proved infeasible.

- The 50 water traps distributed in a 600 m x 600 m area within the field gave consistently low catches, and no distinct pattern in landing rates of different species over time and space was noted.
- This leads us to postulate that many distinct and separate sources of aphids were present both inside and outside of the area surveyed.

Aphid movement within the maize-bean polycultures was monitored using mark-release-recapture techniques of wild colonies transported to the field (February-April 1987). Mr. Bottenberg marked wild cultures with fluorescent dyes of the only species found in abundance, *Uroleucon ambrosiae*. He released them from a central bean plant within the field and attempted to recapture them using a combination of water and sticky traps. Insufficient numbers of aphids were recaptured, suggesting that when this species takes flight, it may disperse longer distances. Visual inspection of plants for the presence of marked alates was attempted but time limited this activity to short distances.

The Impact of Windspeed and Canopy Bridging on Residence Time on Alate Aphids on Bean Plants in Bean Monocultures and Bean-maize Bicultures

To study the effect of wind speed and canopy bridging in crop mixtures on the flight behavior of winged aphids, alatae of *Uroleucon ambrosiae* (Thomas) were released in batches of one to 30 on three to six bean plants in sparse and dense bean monocultures and bean-maize bicultures in Alajuela, Costa Rica. The numbers of alatae remaining on a plant at discrete time intervals after release were fit to a regression model to estimate the "mean residence time" i.e., the amount of time required to reduce the initial density of alatae on the plant by 50 percent.

- Mean residence time was shorter in mixed cultures than in bean monocultures and was negatively correlated with lower wind speed at bean canopy level in mixed cultures (Fig. 18).
- No relationship between mean residence time and the number of interplant leaf bridges was found, except in two experiments involving sparse plantings, where mean residence time was weakly and negatively correlated with leaf bridging.

Effect of Cropping Bean with Maize on Flight Patterns of Winged Aphids

The vertical distribution of winged aphids flying through crop canopies in bean monocultures and bean-sparse maize and bean-dense maize bicultures was studied with vertical translucent sticky traps.

- *Rhopalosiphum maidis* (Fitch) alatae, comprising 47% of total catch, flew more abundantly at bean canopy level than at higher trap levels whereas *R. padi*, *Tetraneura sp* (Hartig) and alatae of all other aphid species combined flew more abundantly at higher trap levels than at bean canopy level, indicating that various species of aphids may behave differently within the same

habitat. *Hyadaphis foeniculi* (Passerini), the second most numerous species caught, showed no distinct vertical gradient.

- Densely planted maize rows in maize-bean bicultures interfered with dispersal more than sparse maize rows, which may be related to alterations in wind flow patterns. At bean canopy level, all aphid species or groups tested were more numerous in bean monocultures than in bicultures.

The Impact of Crop Architecture and Aphid Colonization on Aphid Landing Rates in Soybean-Sorghum Bicultures.

Aphid landing rates were monitored with horizontal green mosaic pan traps in monocultures and bicultures of soybean and dwarf and tall isolines of sorghum in central Illinois to evaluate the potential of mixed cropping to limit aphid dispersal and virus spread in legumes. Aphidicide spot applications controlled colony development and alate production of the aphid, *R. maidis*, in sorghum whorls.

- Colony suppression significantly reduced the densities of *R. maidis* apterae and alatae in sorghum whorls (Fig. 19) but did not affect landing rates of *R. maidis* alatae on sorghum or soybean (Fig. 20), indicating that the majority of the *R. maidis* alatae caught in pan traps above sorghum and soybean canopies were mainly immigrants to the plots.
- Landing rates of eight major aphid species, including the most frequently caught species, *R. maidis*, were generally higher in monocultures than in bicultures, but the difference between the dwarf and tall sorghum mixed crops was not significant.
- The percentage ground area covered with vegetation was generally less in monocultures than in bicultures (Fig. 21). After removing variability due to time, culture, insecticide and plant effect, ground cover was found to be more important than crop height or sorghum row porosity (Fig. 22) in affecting landing rates of *R. maidis, Aphis maidiradicis* Forbes and *Aphis nerii* Boyer de Fonscolombe.

The Impact of Crop Architecture and Aphid Colonization on Soybean Mosaic Virus Epidemics in Soybean-Sorghum Bicultures

The spread of aphid-borne soybean mosaic potyvirus (SMV) from a centralized inoculum source was studied in monocultures and bicultures of soybean and sorghum to evaluate the potential of mixed cropping to suppress nonpersistently transmitted, aphid-borne legume virus epidemics. Dwarf and tall sorghum isolines were used to determine how canopy structure affects virus spread (Fig. 23). Aphidicide spot applications in sorghum whorls controlled colony development and alate production of *Rhopalosiphum maidis* (Fitch), a common vector of SMV, in sorghum whorls.

- Colony suppression significantly reduced the densities of *R. maidis* apterae and alatae in sorghum whorls but did not affect within-plot virus incidence, rate of disease spread, or percentage SMV-induced seed mottling (Fig. 24) in soybean-sorghum bicultures.
- Dwarf (cv. G522DR) and tall (cv. 102F) sorghum inhibited virus spread equally. Lower virus incidences in mixed cultures correlated well with lower landing rates of transient aphids (Fig. 25), which may have been less attracted because of the higher percentage canopy cover in these mixed habitats.

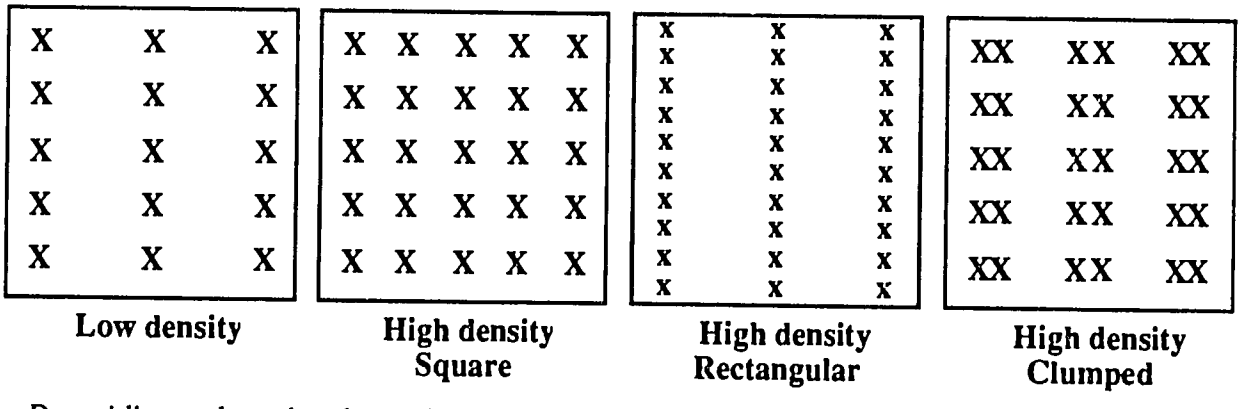
Evaluation of Two Leafhopper Sampling Methods for Predicting Incidence of Maize Rayado Fino Virus in Maize

Two sampling methods for estimating the abundance of *D. maidis* were evaluated with respect to their utility for predicting the incidence of MRFV, a virus transmitted to maize in a persistent manner by *D. maidis*. Leafhoppers were sampled weekly using both on-plant counts and yellow sticky traps in maize twice during that period.

- There were fewer leafhoppers per plant (Fig. 26) and a lower incidence of MRFV (Fig. 27) in maize planted at a higher density, but there were no differences in the number of leafhoppers caught per trap (Fig. 26).
- The number of leafhoppers per plant was a highly reliable predictor of disease incidence, but no relationship between trap catch and disease incidence could be detected by multiple regression analysis.

Intrafield Movement of D. maidis *and Consequent Disease Spread*

The plant-to-plant movement of *D. maidis* and the spread of MRFV were investigated in four patterns of maize dispersion.



- *D. maidis* was less abundant (Fig. 28) and the spread of the virus was slower (Fig. 29) in dense stands of maize than in sparse stands.

- When plant density was held constant, leafhoppers were more abundant in stands with relatively equidistant spacing than in stands more rectangular or clumped dispersion patterns (Fig. 28), but there was no difference in virus incidence among these dispersion patterns.

Percentage of *D. maidis* that had emigrated from the field, dispersed to other nearby plants, or remained on the release plant after 24 h in the mark-release experiment. Within each column, values followed by different letters are significantly different at $p<0.05$ according to Tukey's method.

Treatment	% disappeared	% dispersed	% remaining
Low density : control	37.6 ab	33.9 ab	28.5 a
High density: rows	54.0 a	25.4 b	20.6 ab
High density: plants	51.6 ab	32.8 ab	15.6 b
High density: hills	32.0 b	46.8 a	21.2 ab

- Plant-to-plant movement of leafhoppers was slower in evenly spaced stands than in either rectangular or clumped plant dispersion patterns. This result may explain the lack of higher virus incidence in evenly spaced stands, despite higher leafhopper abundance.

Modeling

The conceptual models for these diseases consist of verbal statements and rough graphs that describe all of the logical and cause-effect relationships that were later included in the simulation models. As BCMV is epidemiologically similar to soybean mosaic virus, for which we had a working model (Ruesink and Irwin, 1986), developing the conceptual model of BCMV was relatively straight forward. The maize diseases differ in that they are vectored in a persistent rather than a nonpersistent fashion. Thus the logic for calculating the daily rate of new infections in maize differs greatly. The maize model differs from the bean model in assuming that a) there is no secondary spread of the virus; and b) adults are very poor vectors (<2%) if the virus is acquired by the adult leafhopper. Leafhopper vector intensity was calculated using weekly catches from yellow sticky traps and an estimate of the propensity of *D. maidis* to vector the virus (Fig. 14). Cumulative observations of maize plants infected with MRFV (+) did not agree well with the model's predicted disease progress (Fig. 15). This discrepancy could be attributed to the fact that yellow sticky trap catches do not, in fact, correlate well with MRFV incidence.

Models for both MRFV and BCMV are complete. Unfortunately, due to low vector activity and minimal virus spread in Main Experiment #4, Dr. Ruesink was unable to test the hypotheses and simulations based on earlier experiments.

For BCMV, the model for crop yield assumes that plant age at infection is the primary determinant of yield reduction for a given virus strain and bean cultivar. The model for seed transmission makes the same assumption. Data from field plots in Costa Rica is used to establish the quantitative relationships for these functions.

The daily number of new infections is computed from the number of inoculations by adjusting for redundancy using equations that take into account the number of susceptible plants in the plot versus those plants already infected. Two different equations were evaluated: one assumed a random distribution of inoculations whereas the other assumed that, either due to clumping or preference, infected plants receive more than their share of inoculations. The best agreement with field data was consistently obtained using the equation based on the assumption of randomness.

For BCMV, the number of inoculations occurring each day was therefore calculated from, and is proportional to, the number of aphids alighting in the plot and the amount of virus source material present. The equation for vector intensity (Fig. 16) also accounts for differences in transmission capability among vector species, using data obtained in the propensity experiment described above. It was also assumed in the model that aphids did not bring the virus with them from outside of the field. An improved equation was developed over that used in the SMV model to account for percent canopy closure, for the possibility of transmission to multiple plants following a single acquisition feeding and for the percentage of canopy occupied by a potential host of the virus.

In the example of model output for disease progress of BCMV (Fig. 17), the + marks indicating the observed infected plants do not conform well with the model's predicted curve of cumulative infections. During this experiment, plants were not mechanically inoculated with the virus and thus virus sources had to originate from seed transmission or from outside of the field. In this instance, the lack of fit of the model could be attributed to greater virus spread from infective aphids arriving from outside of the field.

The two models, one for BCMV, the other for MRFV, have been combined into one FORTRAN computer program. This code has been compiled in IBM-PC-compatible form and is currently being prepared for distribution to potential users in Central America. All that remains to be done is to write the instructions for use and to select appropriate examples for people who are learning how to use the models. We anticipate that distribution will begin in third quarter 1990.

CONCLUSIONS

Despite the fact that there were three insect vectored diseases in maize, only one vector was involved in spreading these diseases from plant to plant, and modifying its behavior would likely have a similar impact on the spread of all three diseases. The maize diseases (MRFV, CSS, and MBSM) were all more common during the rainy season, correlating well with overall greater numbers of their vector, *D. maidis*, and with lower yields. However, plant density tended to influence disease spread more than the presence of bean in mixtures with maize, while leafhopper flight activity, as measured by sticky trap catches, was more influenced by the presence or absence of bean in the cropping system. Companion studies performed in addition to the main experiments later showed that sticky trap catches were less reliable than on-plant counts of leafhopper vectors as predictors of the incidence of these persistently transmitted plant pathogens. However, while on-

plant counts may be more reliable, leafhopper abundance does not provide the entire story, as movement between plants can be influenced by plant spacing. Despite greater leafhopper abundance in evenly spaced high density stands of maize, *D. maidis* moved from plant to plant more slowly than in irregularly spaced (rectangular or clumped) patterns, leading to a lower than expected virus incidence in evenly spaced stands.

Many common aphid species landing in a crop on a nonpersistent virus source have some potential ability to transmit that virus. However, because the propensity to transmit these viruses varies greatly among species, it is important to know the behavior, abundance, timing, and identity of the active species during the critical period when yield and seed transmission are most likely to be affected. During the experiments conducted in this project, some species of aphids were present in sufficient numbers to discern patterns of behavior.

The majority of *R. maidis* alatae from colonies building on sorghum in mixed cropping with soybean tended to emigrate from the habitat and did not disperse locally. By contrast, the activity of transient alatae, monitored with horizontal green pan traps, correlated well with the spread of a nonpersistent virus in soybean.

Some aphid species exhibited preferential landing rates in crops grown in monoculture. Mixed cultures often reduced landing rates to the level of the unpreferred host. The behavior of vector species attracted to a crop with a nonpersistent virus may therefore be altered by planting that crop in mixtures with an unpreferred host and thus reduce the spread of nonpersistent viruses.

Mixed cultures provide a varied habitat to potential vectors. A vertical barrier imposed by tall intercrops (e.g., sorghum or maize) had little effect on nonpersistent virus spread in shorter intercrops (e.g., bean or soybean) but the increased percentage canopy cover by a non-host of the virus did lower rates of virus epidemics, by lowering the landing rate of transient aphid species.

Wind speed was the only environmental variable that appeared to influence the number of aphid landings over the diel period. The microclimatic conditions least favorable to aphid flight (high wind speeds, turbulence) occurred most frequently over the high density biculture plots and aphid landing rates in these plots were always among the lowest recorded. Larger scale plantings may well accentuate microclimatic differences among cropping systems and thus may influence the number of aphid landings and hence the spread of nonpersistent viruses.

Dispersal by flight may be more common than crawling from plant-to-plant via leaf bridges for aphids on non-hosts. Furthermore, in mixed crops, maize rows form barriers that reduce wind speed at bean canopy level, allowing aphids to take flight more readily from bean plants in bean-maize mixtures than alatae in bean monocultures. Under the windy conditions that are common during the dry season, such flight behavior may result in more plant-to-plant movements per unit time, which, in turn, may increase the spread of nonpersistently transmitted aphid-borne viruses. However, this effect appears to be nullified by overall reduced landing rates in bicultures and/or an increased ability for aphids to escape from the habitat once airborne, as there was no apparent increase in nonpersistent virus spread in bicultures over the monocultures.

Because peak aphid flights occurred during the five week period following the start of the rainy season and large numbers did not occur at any other time of the year, even when wind speeds were low, we suspect that aphids may be carried relatively long distances from the south by southwesterly winds, from areas where the rainy season is well established to areas where rain is just beginning. Such long distance transport of aphids from their hosts increases the number of possible species and the difficulty of identifying specimens collected in traps. The keys being developed for publication as an outgrowth of this project will aid researchers and IPM specialists in the species level determination of aphids trapped.

Because maize yields were higher during the dry than rainy season, while bean yields were higher during the rainy than the dry season, there appears to be no "perfect" time to plant such intercrops. However, because total yields during any particular planting season were not significantly reduced in mixed vs. single cropping, and vector movement can often be reduced in such systems, the planting of mixed crops appears benefit farmers who are able to manage the logistics of systems.

Models developed during this project should be very helpful to agricultural planners and research scientists. For the first time, they will have a tool that permits them to separate the role of factors such as planting date, cultivar, row spacing, plant density, and intercropping from the poorly understood impact of vector abundance and behavior.

This grant brought together a team of scientists from three countries and several disciplines in an ambitious project to discern how crop structure influences vector movement and spread of insect-borne pathogens. The bonds forged between researchers during this project are strong and will carry over into future research. Two international students have earned Ph.D's at US universities under this grant and a third is now pursuing a Masters degree in Ohio. The proposed workshop on plant virus/mollicute epidemiology and control will bring this group of researchers together once more to share their accumulated expertise with other scientists in the developing countries of Latin America.

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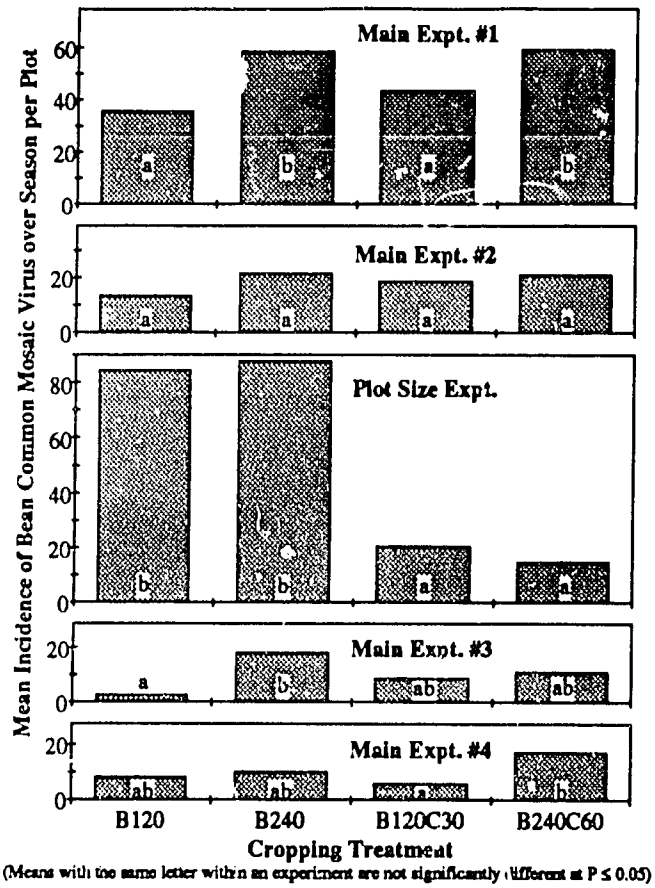
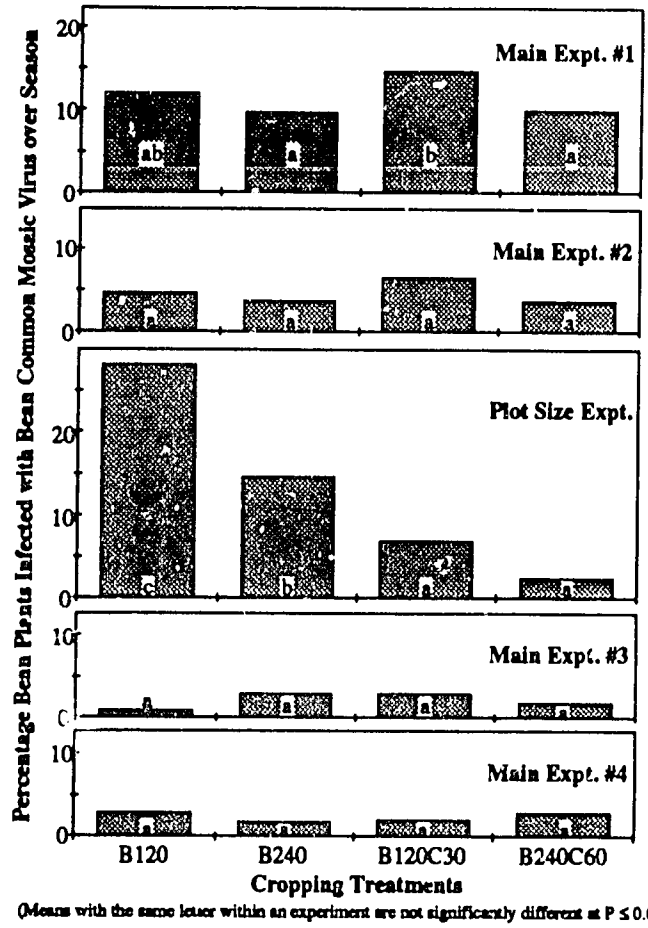


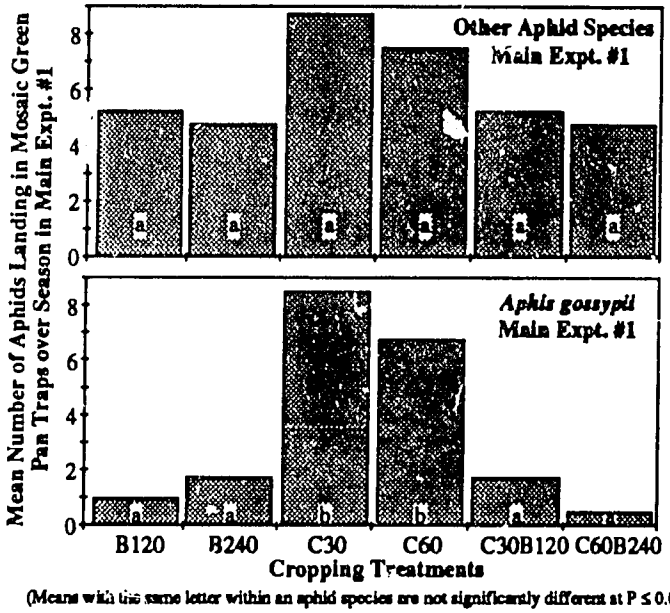
(Means with the same letter within an experiment are not significantly different at $P \leq 0.05$)

Figure 1. Incidence of bean common mosaic virus in low (B120) and high (B240) density bean monocultures and bean/maize bicultures.



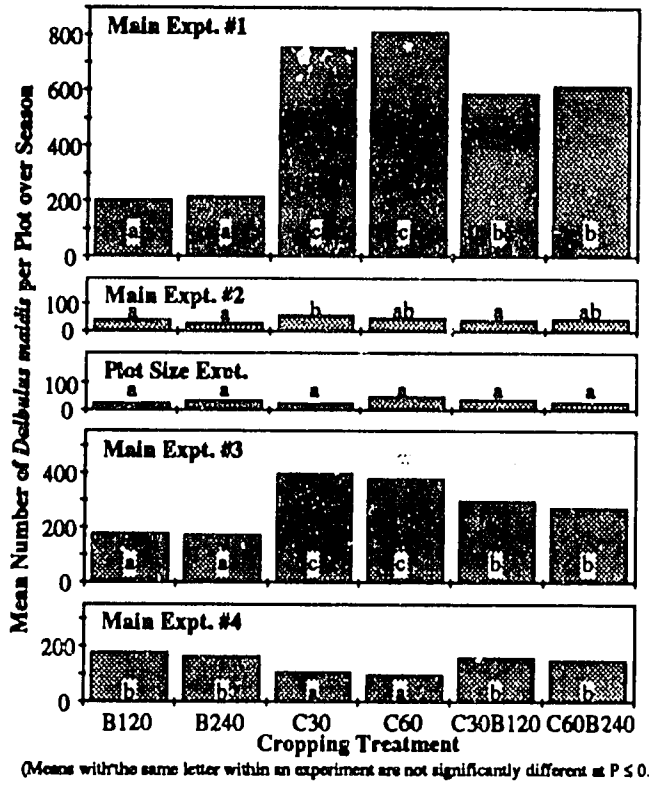
(Means with the same letter within an experiment are not significantly different at $P \leq 0.05$)

Figure 2. Percentage incidence of bean common mosaic virus in low (B120) and high (B240) density bean monocultures and bean/maize bicultures.



(Means with the same letter within an aphid species are not significantly different at $P \leq 0.05$)

Figure 3. Mean numbers of aphids landing in mosaic green pan traps during Main Expt. #1 (Sept.-Dec. 1986) in low (B120) and high (B240) density bean and in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.



(Means with the same letter within an experiment are not significantly different at $P \leq 0.05$)

Figure 4. *Dalbulus maidis* collected weekly from yellow sticky traps in low (B120) and high (B240) density bean and in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.

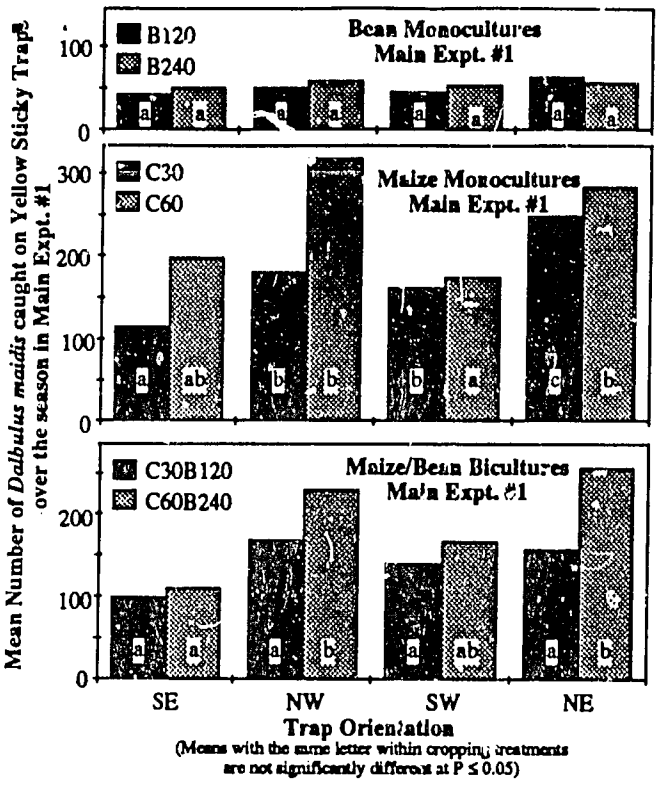


Figure 5. *Dalbulus maidis* collected weekly during Main Expt. #1 (Sept.-Dec. 1986) from yellow sticky traps oriented by compass directions in low (B120) and high (B240) density bean and in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.

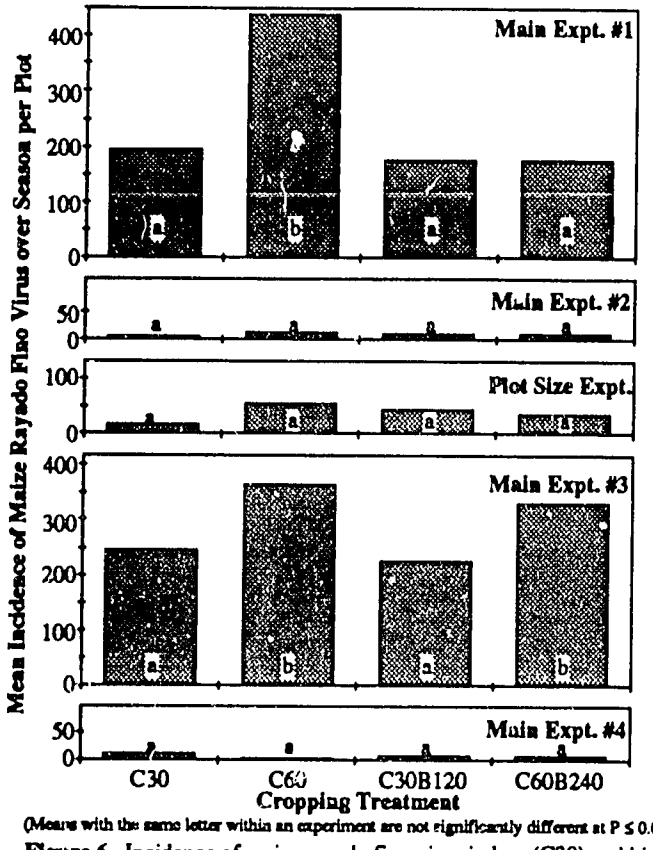


Figure 6. Incidence of maize rayado fino virus in low (C30) and high (C60) density maize monocultures and bean/maize bicultures.

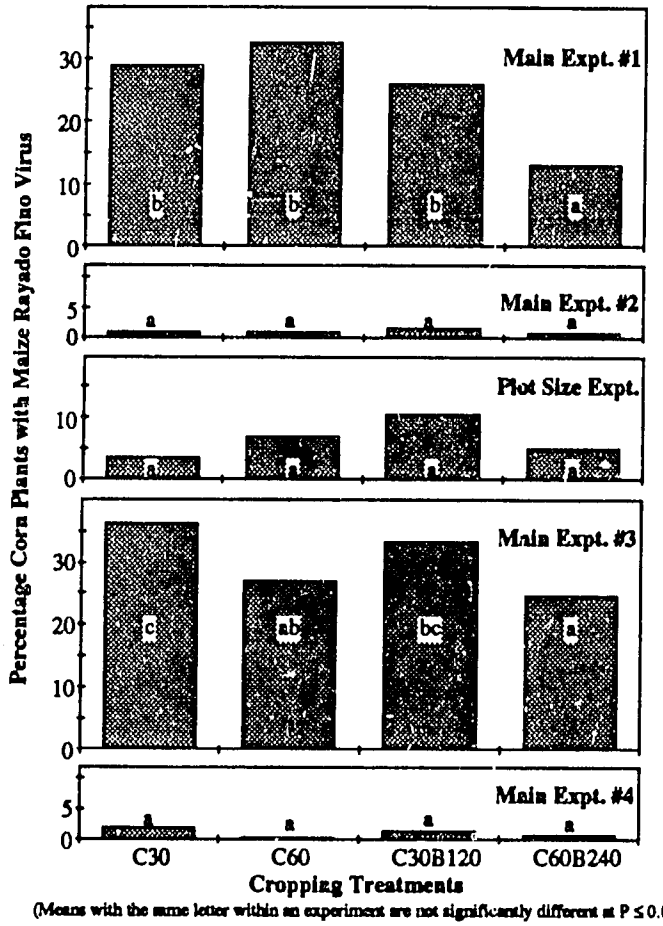


Figure 7. Percentage incidence of maize rayado fino virus in low (C30) and high (C60) density maize monocultures and bean/maize bicultures.

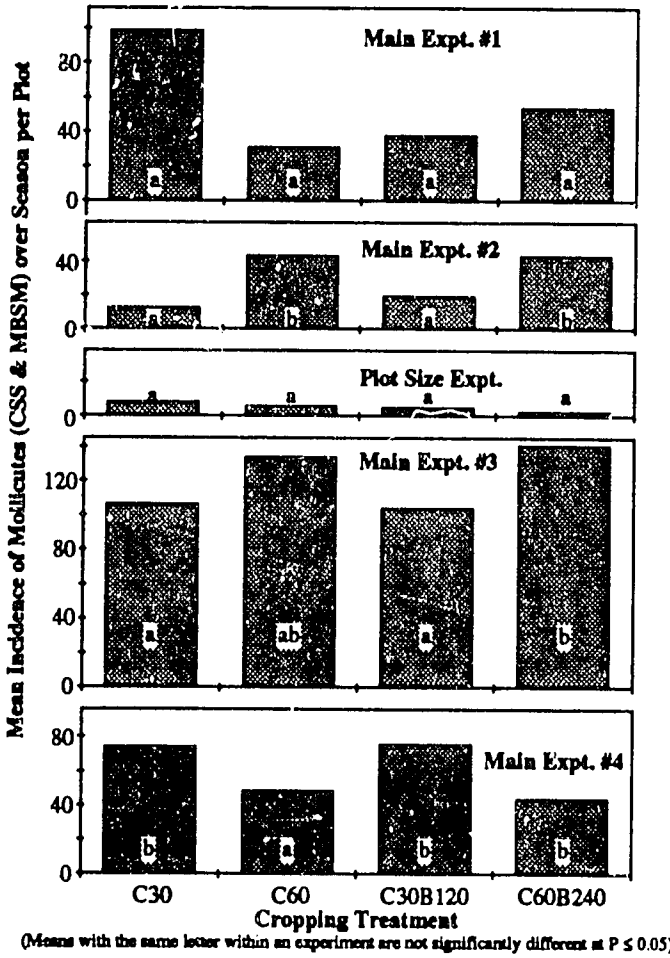
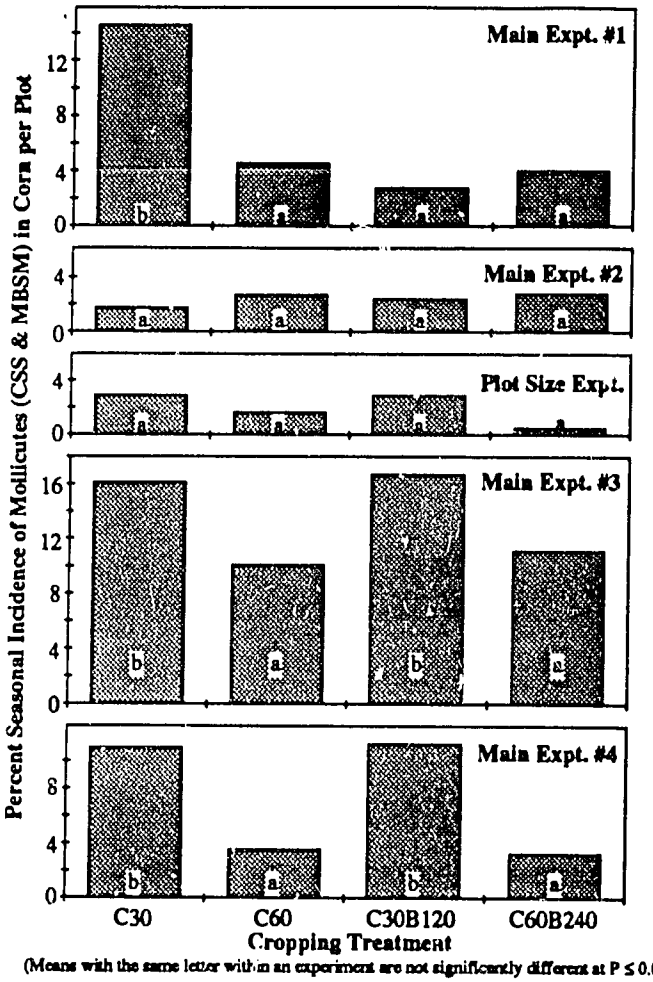
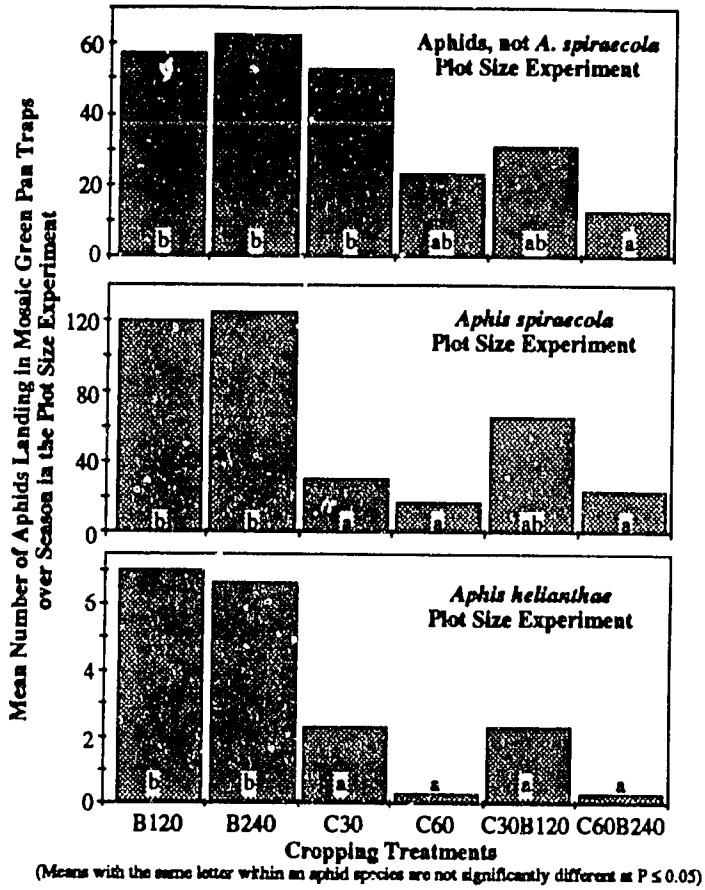


Figure 8. Incidence of mollicutes in low (C30) and high (C60) density maize monocultures and bean/maize bicultures.



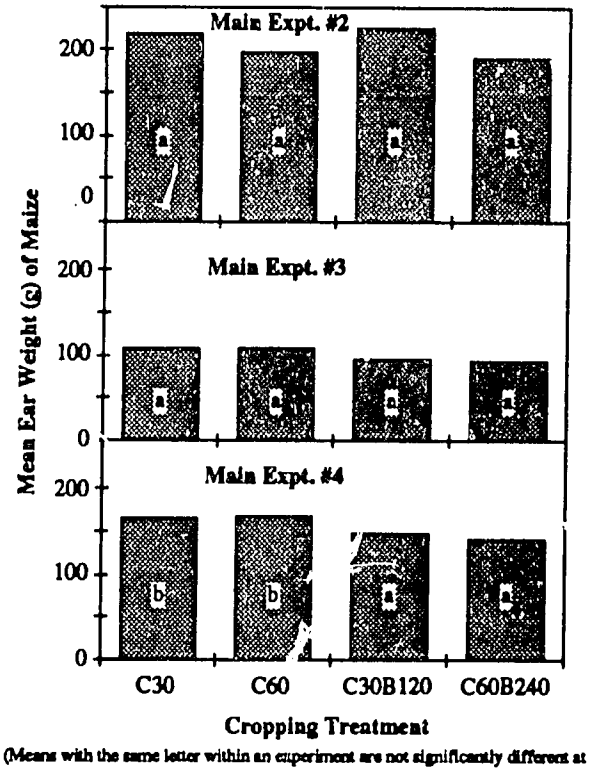
(Means with the same letter within an experiment are not significantly different at P ≤ 0.05)

Figure 9. Percentage incidence of mollicutes in low (C30) and high (C60) density maize monocultures and bean/maize bicultures.



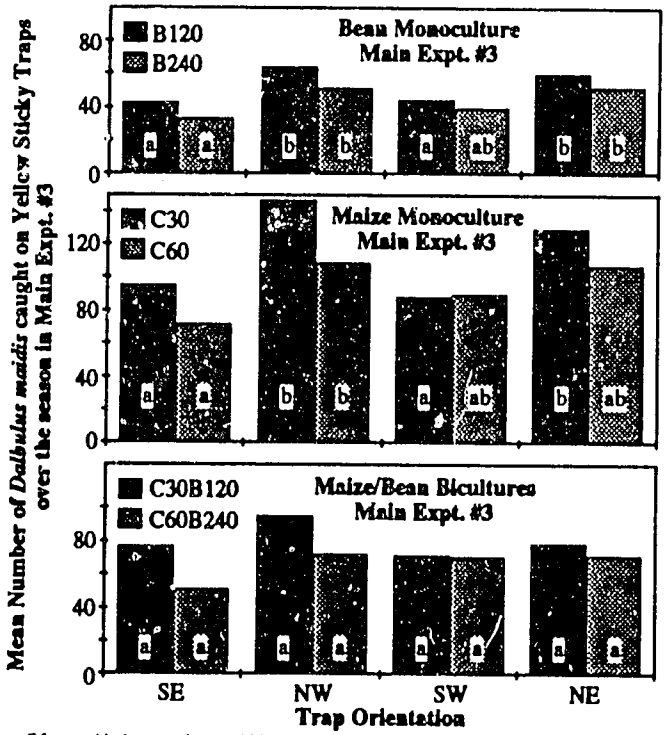
(Means with the same letter within an aphid species are not significantly different at P ≤ 0.05)

Figure 11. Mean numbers of aphids landing in mosaic green pan traps during the Plot Size Expt. (May-August 1987) in low (B120) and high (B240) density bean and in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.



(Means with the same letter within an experiment are not significantly different at P≤ 0.05)

Figure 10. Mean maize ear weight (grams) in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.



(Means with the same letter within cropping treatments are not significantly different at P ≤ 0.05)

Figure 12. *Dalbulus maidis* collected weekly during Main Expt. #3 (Sept.-Dec. 1987) from yellow sticky traps oriented by compass directions in low (B120) and high (B240) density bean and in low (C30) and high (C60) density maize monocultures and maize/bean bicultures.

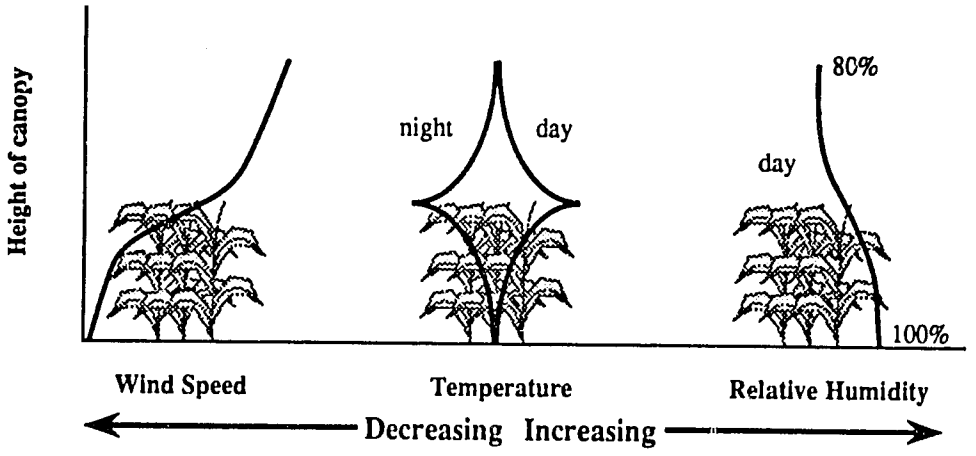


Figure 13. The key to differences in wind speed, temperature, and relative humidity is height above or below the plant canopy.

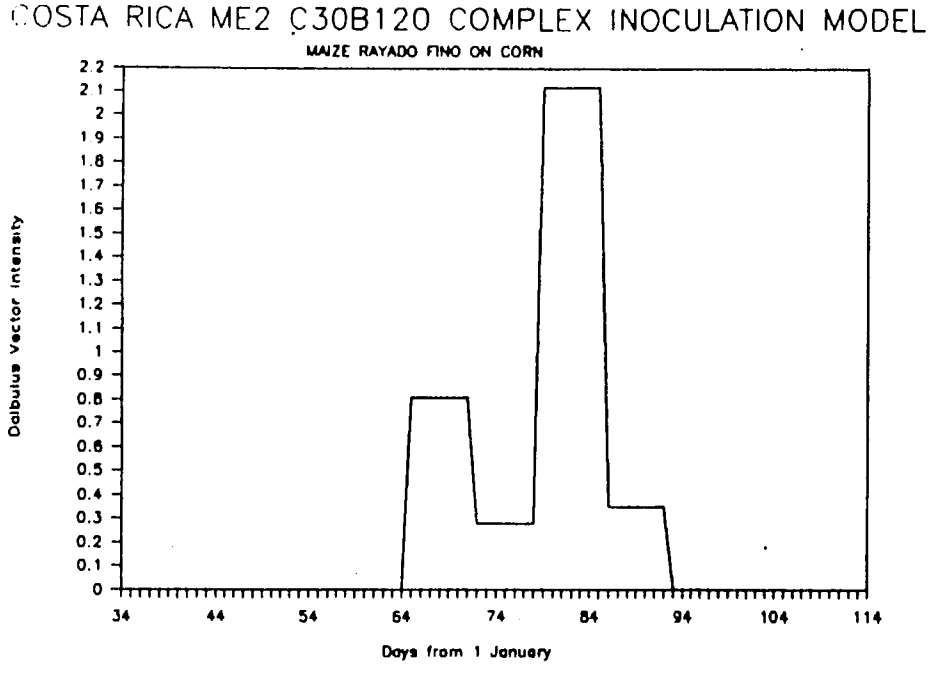


Figure 14. Plot of the vector intensity averaged weekly for *Dabulus maidis* in the low density maize/bean biculture during Main Expt. #2 during the dry season of 1987 in Alajuela, Costa Rica.

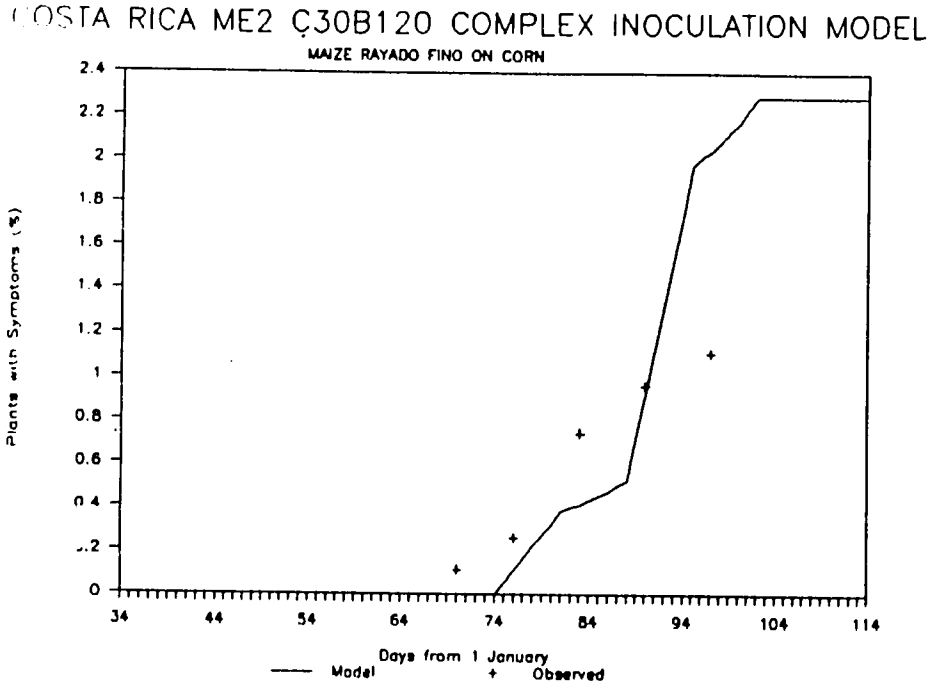


Figure 15. Observed and expected cumulative incidence of MRFV in the maize/bean low density biculture during the dry season 1987, Alajuela, Costa Rica.

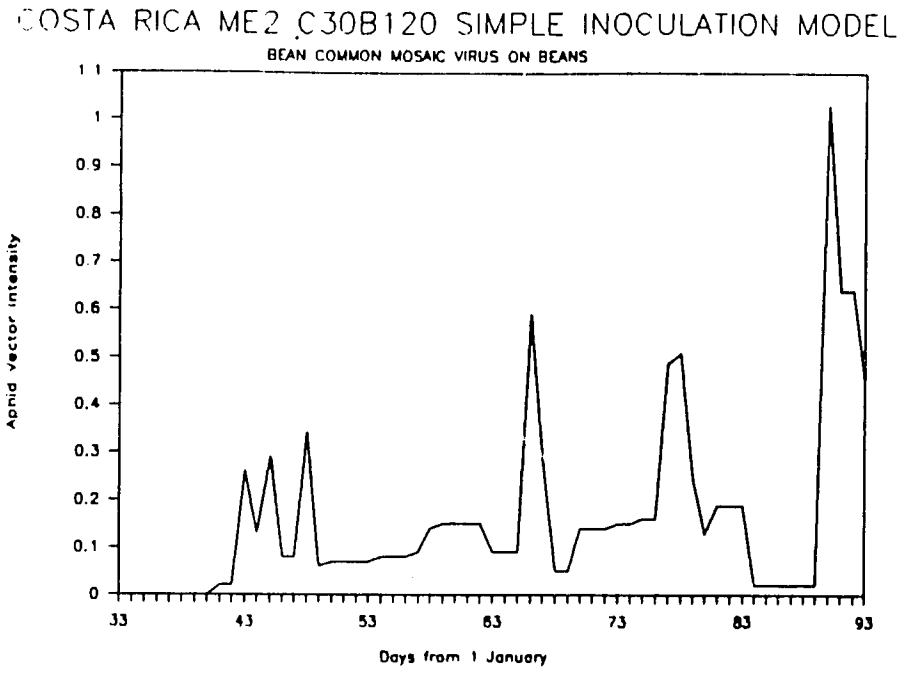


Figure 16. Plot of the daily vector intensity for the aphids trapped in the low density maize/bean biculture during Main Expt. #2 during the dry season of 1987 in Alajuela, Costa Rica.

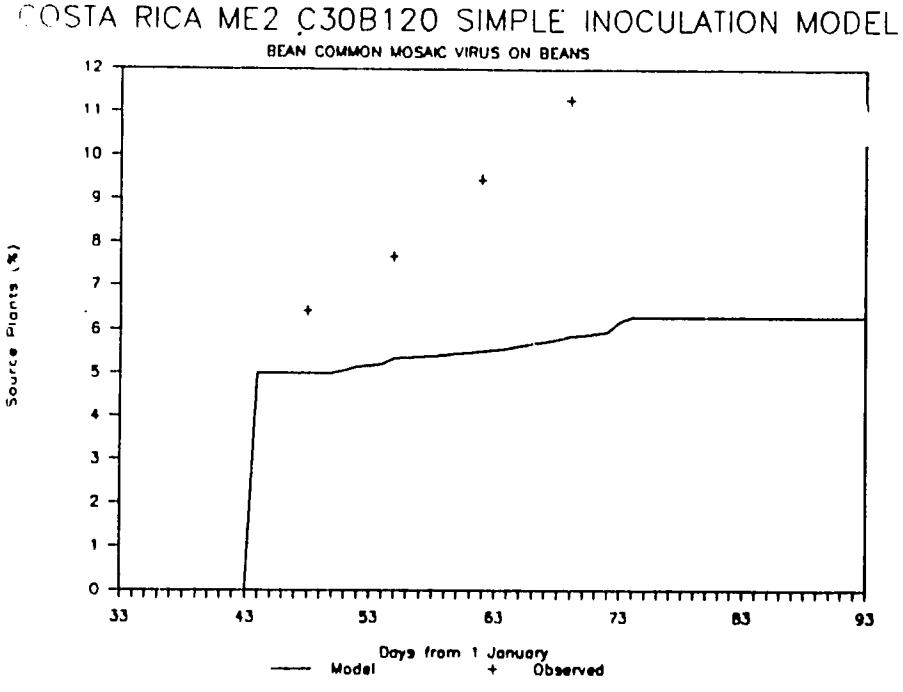


Figure 17. Observed and expected cumulative incidence of BCMV in the maize/bean low density biculture during the dry season 1987, Alajuela, Costa Rica.

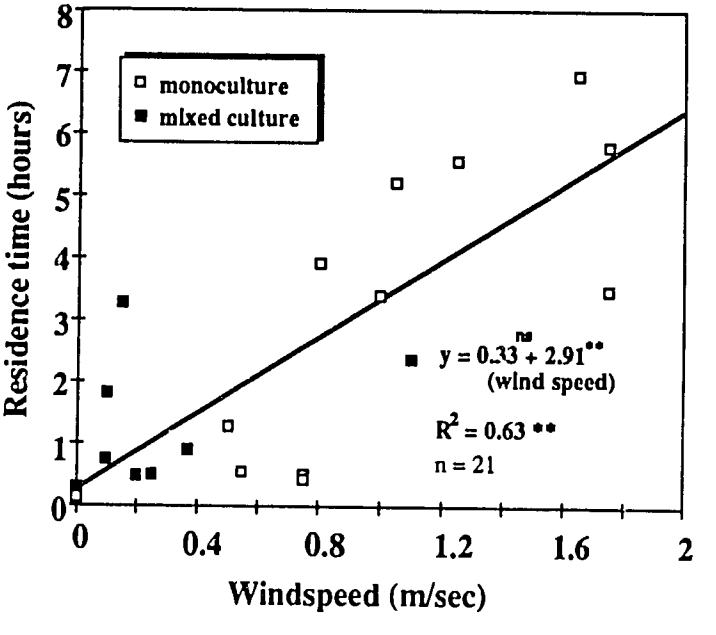


Figure 18. Relationship between mean staying time (hours) of *Uroleucon ambrosiae* alatae on bean plants in monocultures and mixed cultures of bean and maize, and windspeed (m/sec) at bean canopy level, Alajuela, Costa Rica, February - March, 1987.

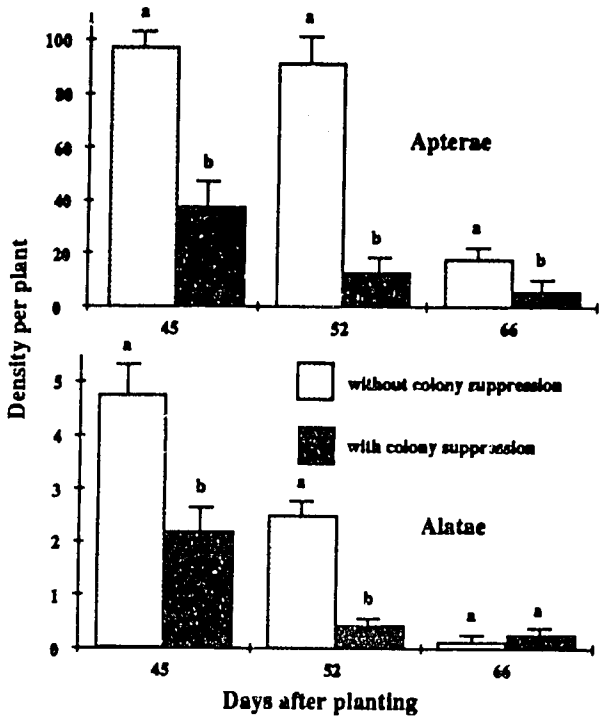


Figure 19. Effect of aphidicide treatment of sorghum whorls on density of *R. maidis* apterae and alatae, Illinois, 1987. Means within days followed by the same letter are not significantly different at P=0.05.

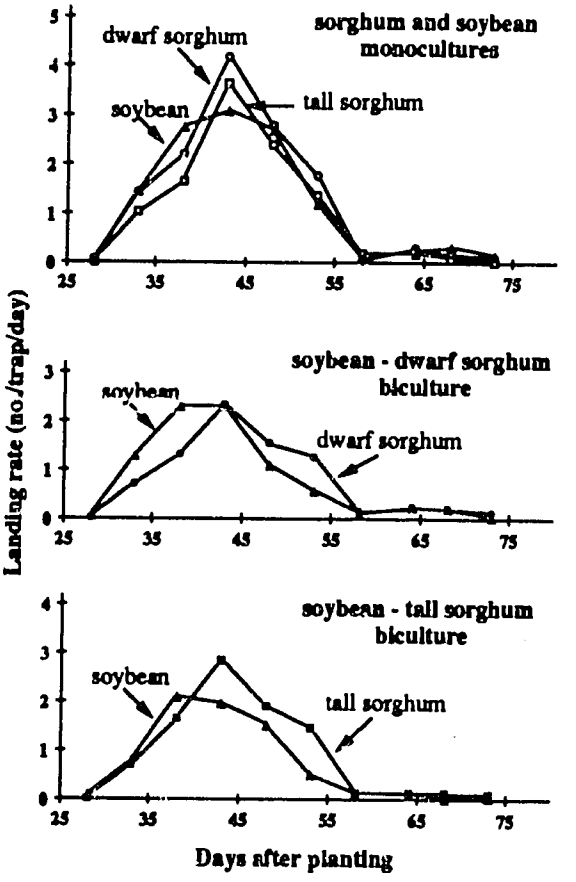


Figure 20. Change in landing rates over time of *Rhopalosiphum maidis* (Fitch) in soybean and sorghum monocultures and bicultures, Illinois, 1988.

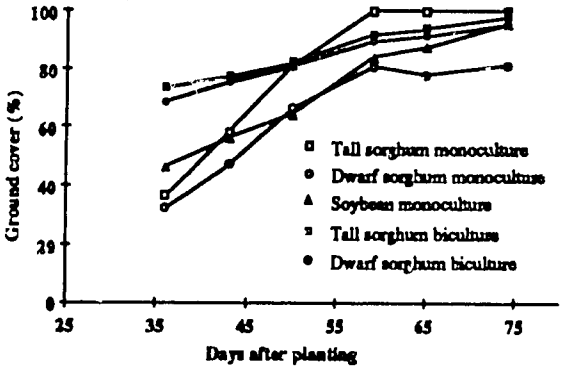


Figure 21. Change in ground cover (%) over time of monocultures and bicultures of soybean and sorghum, Illinois, 1988.

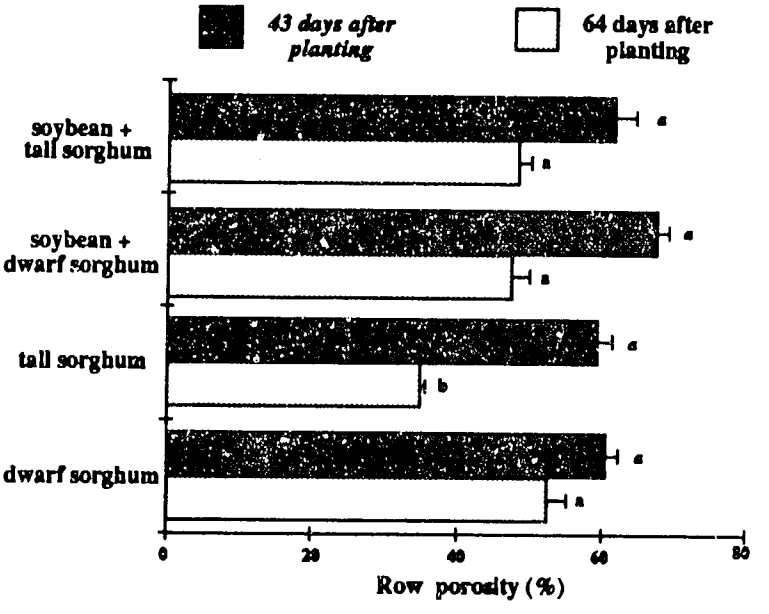


Figure 22. Sorghum row porosity at tillering (45 days after planting) and booting-heading stage (64 days after planting) in sorghum and soybean monocultures and bicultures. Means, within culture groups, followed by the same letter are not significantly different at P=0.05.

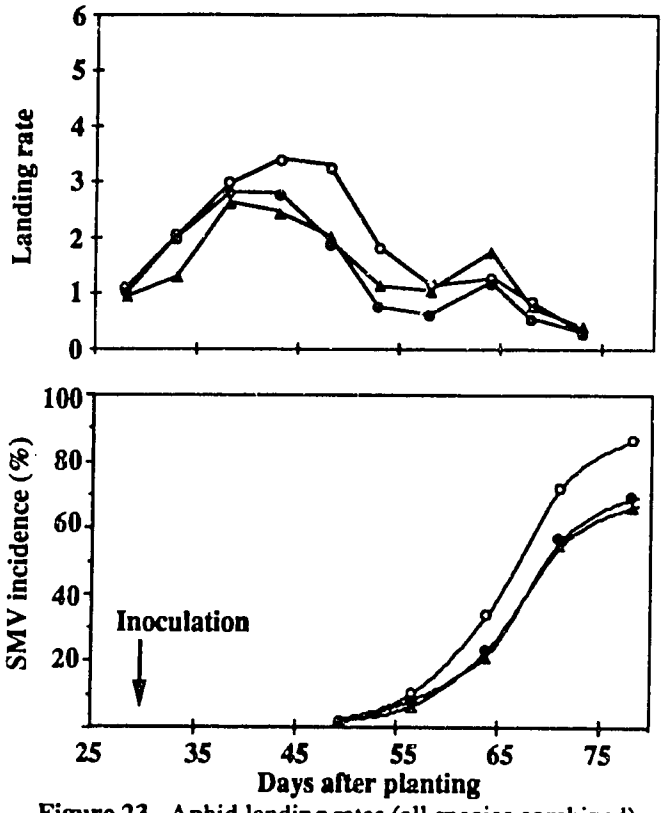


Figure 23. Aphid landing rates (all species combined) and spread of SMV in soybean monocultures, soybean-dwarf sorghum, and soybean-tall sorghum mixtures, Illinois, 1988.

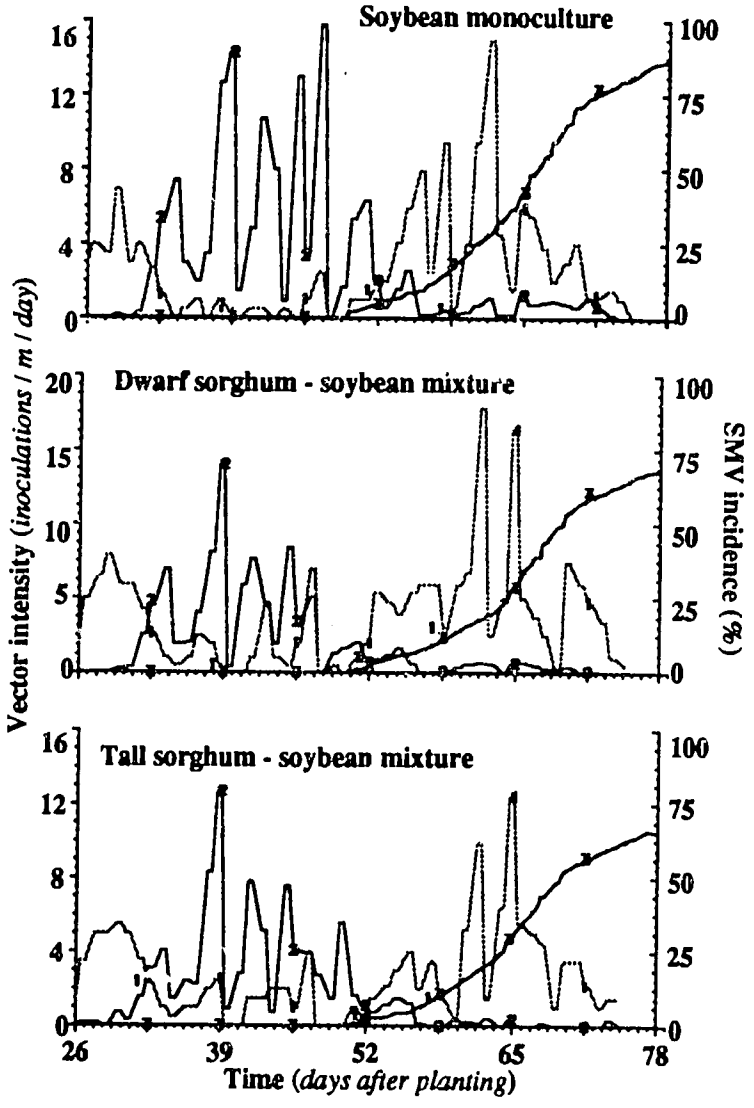


Figure 24. Daily change in vector intensity rates of *Aphis* spp. (1), and *R. maidis* (2) and incidence of SMV (3), Illinois, 1988.

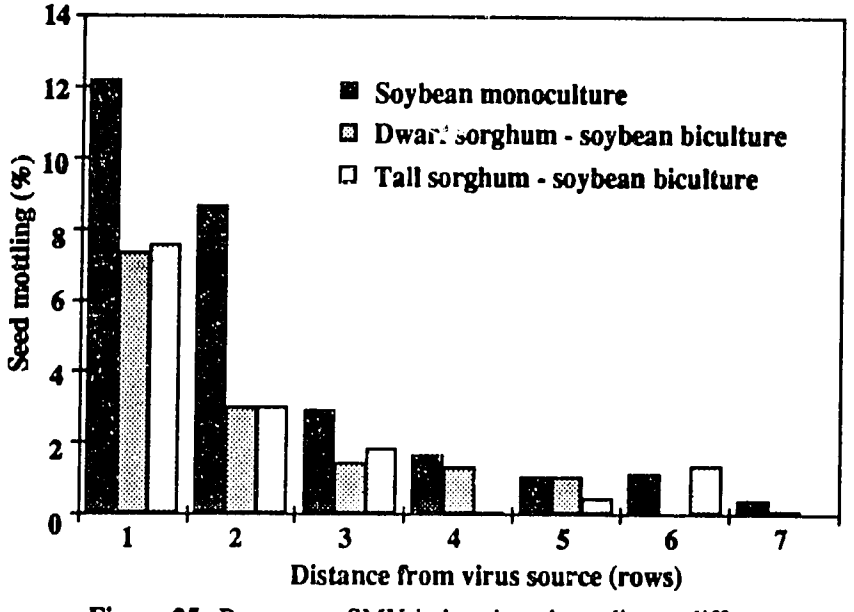


Figure 25. Percentage SMV-induced seed mottling at different distances from a central inoculum source in soybean monocultures and soybean-sorghum mixtures, Illinois, 1988.

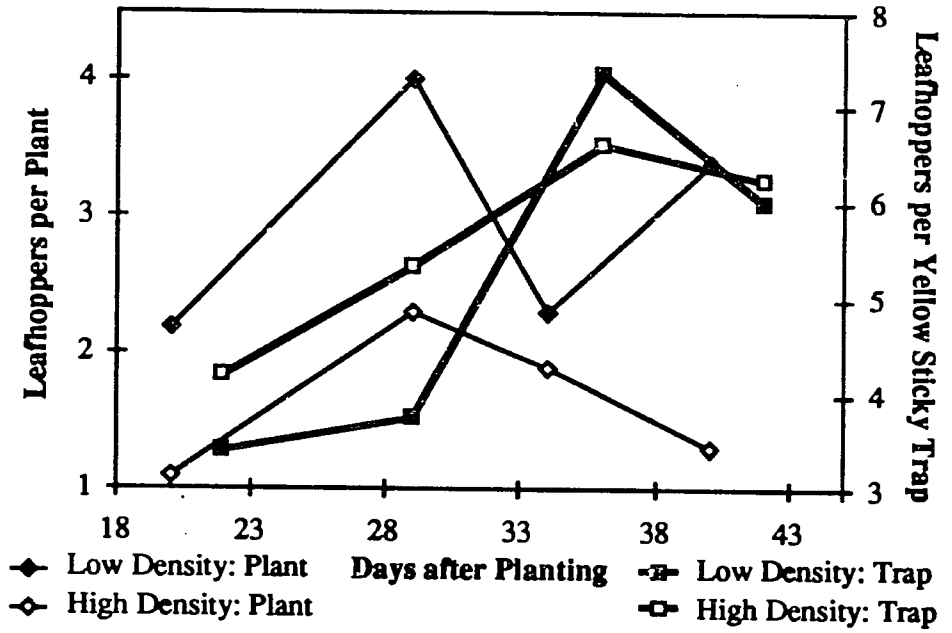


Figure 26. *Dalbulus maidis* leafhoppers found per plant and on yellow sticky cards in low and high density planted corn.

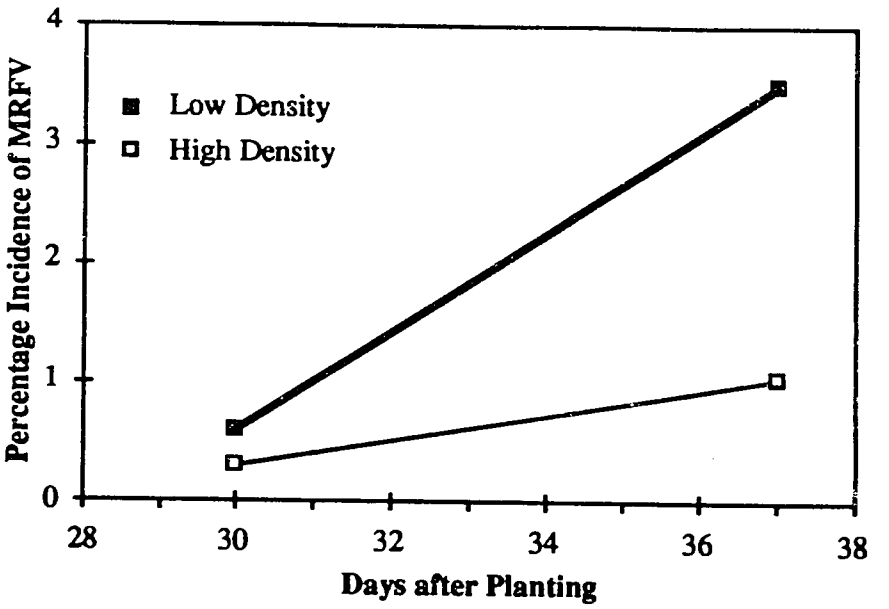


Figure 27. Percentage incidence of maize rayado fino virus (MRFV) in low and high density planted corn.

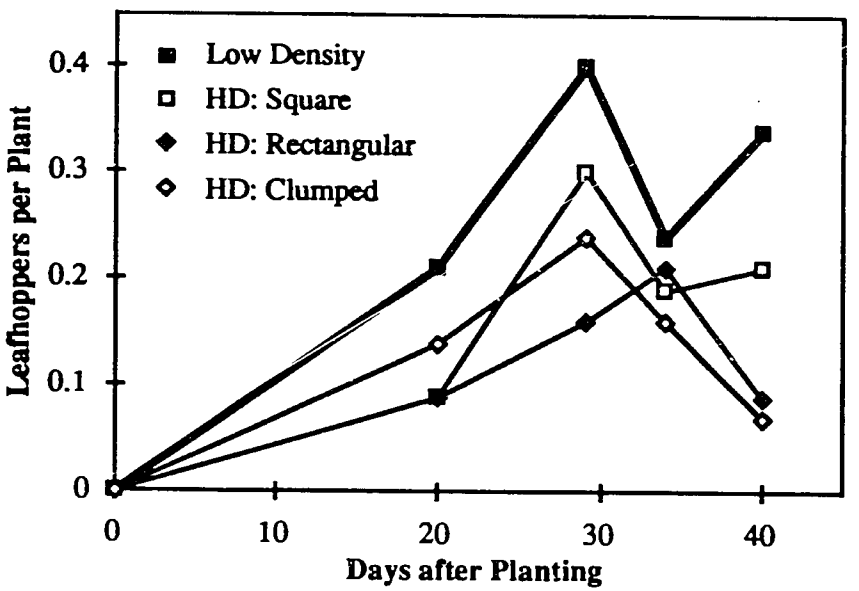


Figure 28. *Dalbulus maidis* leafhoppers found per plant in low density planted corn, high density square, high density rectangular, and high density clumped planting arrangements.

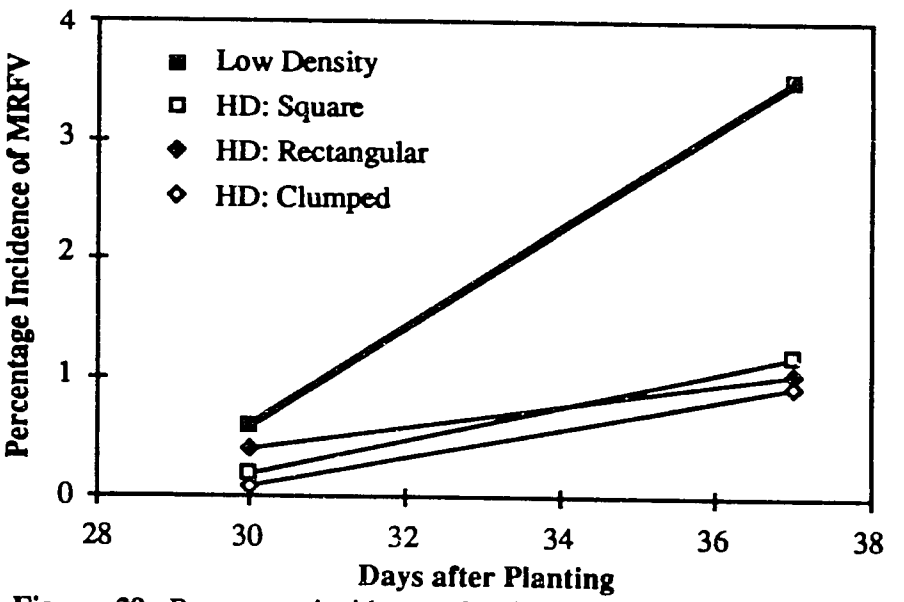


Figure 29. Percentage incidence of maize rayado fino virus (MRFV) in low density planted corn, high density square, high density rectangular, and high density clumped planting arrangements.

APPENDIX A

NEOTROPICAL WORKSHOP ON PLANT VIRUS/MOLLICUTE EPIDEMIOLOGY AND CONTROL

(DRAFT -- PRELIMINARY AGENDA)

THE SETTING
- Components Needed to Produce Epidemics
  - The Plant
  - The Virus/Mollicute Pathogens
  - The Vector
  - The Environment

- The Plant-Pathogen Component
  - How Crop and Non-Crop Species are Affected by Pathogenic Viruses
  - Systemic Nature of Infections
  - Effects on Crop Yields

- The Pathogen-Vector Component
  - Plant Virus/Mollicute Classification and Characteristics
  - Virus/Mollicute Vector Classification and Characteristics
  - Mechanisms of Transmission

- The Environment
  - Interactions with Plants
  - Interactions with Viruses
  - Interactions with Vectors
  - Primary Inoculum Sources
  - Alternate Hosts of Pathogens
  - Alternate Hosts of Vectors
  - Meteorological Factors that Influence Epidemics
  - Seasonal Influences and Plant Growth

EXAMPLES OF EPIDEMICS (disease and vector cycles, economic importance)
- Beetle-Transmitted Viruses
  - Cowpea Severe Mosaic Virus
  - Squash Mosaic Virus
  - Maize Chlorotic Mottle Virus

- Whitefly-Transmitted Viruses
  - Bean Golden Mosaic Virus
  - Cotton Crumple Virus
  - Soybean Yellows Virus

- Leafhopper- and Planthopper-Transmitted Viruses and Mollicutes
  - Maize Rayado Fino Virus
  - Maize Stripe Virus
  - Maize Mosaic Virus
  - Corn Stunt Spiroplasma
  - Maize Bushy Stunt Mycoplasma

Aphid-Transmitted Viruses
- Barley Yellow Dwarf Virus
- Potato Leafroll Virus
- Bean Common Mosaic Virus
- Soybean Mosaic Virus
- Sugarcane Mosaic Virus
- Potato Virus Y
- Watermelon Mosaic Virus
- Citrus Tristeza Virus

Thrips-Transmitted Viruses
- Tobacco Ringspot Virus

METHODOLOGY FOR STUDYING PLANT VIRUS EPIDEMIOLOGY

Working Session on Virus/Mycoplasma Identification in Crops, Weeds, and Vectors
- Symptomatology
- Light and Electron Microscopy
- Serology
- Molecular Techniques

Working Session on Vector Identification
- Aphids
- Leafhoppers and Planthoppers
- Beetles
- Whiteflies and Thrips

Working Session on Sampling Techniques
- Pathogens
- Vectors
- Crop, Weed, and Natural Systems Growth
- Crop Yield Components
- Meteorological Parameters

Working Session on Experimental Design
- Field and Laboratory Layouts
- Statistical Analyses

Working Session on Describing Epidemics
- Spatio-Temporal Patterns
  - Disease Progress Curves
  - Disease Gradients
- Simulation Models
- Disease Forecasting

MANAGEMENT STRATEGIES FOR CONTROLLING PLANT VIRUS/MYCOPLASMA EPIDEMICS
- Chemical Tactics
- Biological Control Tactics
- Host Plant Resistance Tactics
- Cultural Tactics
- Sanitation
- Novel Tactics (Reflective Mulches, Pheromones, Oil Sprays, etc.)
- Legal Control and Quarantine
- Integration of Control Measures

APPENDIX B

Summary of experiments completed:

Experiment	Dates Conducted	Location
Cultivation of CSS from Chapingo, Mexico	July 1984	Stillwater, OK
Antiserum produced to Mexican CSS isolate	Feb.-June 1985	Stillwater, OK
Development of ELISA to Mexican CSS isolate	July-Aug. 1985	Stillwater, OK
Preliminary Cropping Experiment	May-July 1986	Alajuela, C.R.
Cultivation of CSS from Costa Rican maize	March 1986	Stillwater, OK
Propensity Experiment	May-July 1986	Alajuela, C.R.
Testing of light microscopic staining procedures for detection of MBSM or CSS in plants	Sept. 1986	Wooster, OH
Main Expt. #1	Sept.-Dec. 1986	Alajuela, C.R.
Movement of *Dalbulus maidis* in mono- and polycultures I	October 1986	Alajuela, C.R.
Relation of on-plant counts to sticky trap data for *Dalbulus maidis* I	October 1986	Alajuela, C.R.
Survey of aphids on weeds	Sept.-Dec. 1986	Alajuela, C.R.
Comparative polyacrylamide gel electrophoresis fingerprinting of CSS and other spiroplasmas	Sept.-Dec. 1986	Stillwater, OK
Development of Serological dot-immunobinding assay for detection of CSS	Sept.-Dec. 1986	Stillwater, OK
Main Expt. #2	Jan.-April 1987	Alajuela, C.R.
Movement of *Dalbulus maidis* in mono- and polycultures II	March 1987	Alajuela, C.R.
Relation of on-plant counts to sticky trap data for *Dalbulus maidis* II	March 1987	Alajuela, C.R.
Staying time & spatial movement of winged aphids	Feb.-April 1987	Alajuela, C.R.
Microclimatic profiles above crop canopy	Jan.-April 1987	Alajuela, C.R.
Release Expt.	Feb.-April 1987	Alajuela, C.R.
Cultivation of Costa Rican CSS onto new and better medium (old isolates no longer viable)	June 1987	Stillwater, OK
Plot Size Expt.	May-July 1987	Alajuela, C.R.
Effect of maize planting pattern on abundance & movement of *Dalbulus maidis* & consequent disease spread	June-July 1987	Alajuela, C.R.
Aphid dispersal and virus spread in mono/polycultures I	June-Oct. 1987	Urbana, IL
BCMV Propensity I	July-Aug. 1987	Urbana, IL
Main Expt. #3	Sept.-Dec. 1987	Alajuela, C.R.
Constant level microclimatic measurement above crop canopy	Sept.-Dec. 1987	Alajuela, C.R.
Main Expt. #4	June-Sept. 1988	Alajuela, C.R.
Microclimatic profiles inside crop canopy	June-Sept. 1988	Alajuela, C.R.
Aphid dispersal and virus spread in mono/polycultures II	June-Aug. 1988	Urbana, IL

Predators in Mono/Polycultures	June-Aug. 1988	Urbana, IL
BCMV Propensity II	July-Aug. 1988	Urbana, IL
Serial transmission by aphids in lab	Sept.-Nov. 1988	Urbana, IL

Main Experiments #1-4 included the monitoring of bean common mosaic virus, maize rayado fino virus, corn stunt spiroplasma, maize bushy stunt mycoplasma, aphid and *Dalbulus maidis* populations, and measurement of crop phenology and yield parameters. Climatic measurements were also recorded for all of these experiments.

APPENDIX C

Aphids Reported* to Transmit BCMV

Acyrthosiphon pisum
Aphis craccivora
Aphis euonymi
Aphis fabae
Aphis gossypii
Aphis nasturtii
Aphis pomi
Aphis rumicis
Aphis spiraecola
Brevicoryne brassicae
Drepanaphis minutus
Hayhurstia atriplicis
Lipaphis erysimi
Macrosiphum euphorbiae
Myzus persicae
Megoura viciae
Myzocallis coryli
Pemphigus populicaulis
Phyllaphis fagi
Rhopalosiphum padi
Uroleucon ambrosiae
Uroleucon pseudoambrosiae

* modified from p. 373, in J. R. Edwardson and R. G. Christie, 1986. *Viruses Infecting Forage Legumes*, Vol. II. Agr. Exp. Stn. Univ. Florida, Monograph #14.