Alternative hosts of Phakopsora pachyrhizi in the Americas: an analysis of their role in the epidemiology of Asian soybean rust in the continental U.S.

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Alternative hosts of *Phakopsora pachyrhizi* in the Americas: an analysis of their role in the epidemiology of Asian soybean rust in the continental U.S.

by

Oscar Pérez-Hernández

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Plant Pathology

Program of Study Committee:
Xiao Bing Yang, Major Professor
Mark L. Gleason
Eugene S. Takle

Iowa State University
Ames, Iowa
2007
I dedicate this work to God, for my life.

To my daughter, Daphne Gabriela, who, someday, when she can read and see her name written on this page, knows of Dady’s love for her. <Tú te convertiste en una de mis mayores motivaciones desde el momento en el que supe que existías. Te quiero mucho hija>.

To my parents, Felicitas and Miguel, who have always supported, encouraged, and trusted me, and who, despite their limited education, knew how to inculcate in myself, discipline, good values, and the spirit to be someone in life. <Ustedes son los cimientos sobre los que están fundados mi carácter y mi vida; han sido y serán siempre mi motivación. Les dedico este esfuerzo con todo mi amor y cariño>.

To my brothers: Hortencia, Nahúm, Alejandro, Arsenio, Miguel and Minerva, and to my nephews Benjamín, Edson and Joel, for their love.

To all relatives to whom a link of love, trust, hope, and caring keeps me joined.

To my Major Professor, Dr. Xiao-Bing Yang
# TABLE OF CONTENTS

ABSTRACT .......................................................................................................................................................... v

CHAPTER 1. GENERAL INTRODUCTION ................................................................. 1
  Thesis organization ................................................................................................................................. 1
  Introduction .......................................................................................................................................... 1
  References .......................................................................................................................................... 4

CHAPTER 2. LITERATURE REVIEW .................................................................................. 7
  General information on the life cycle pattern of a rust fungus ................................................. 7
  The disease: soybean rust .................................................................................................................. 7
    Causal agents .................................................................................................................................... 7
    Cycle, infection process and infection components ........................................................................ 8
    Symptoms ....................................................................................................................................... 9
  Epidemiology ...................................................................................................................................... 9
  Current world distribution of soybean rust ...................................................................................... 10
  Current distribution of soybean rust in the Americas ............................................................... 11
  The pathogen: *Phakopsora pachyrhizi* ............................................................................................ 12
    Morphology and taxonomy ............................................................................................................. 12
    Host range of *Phakopsora pachyrhizi* ......................................................................................... 13
  The host (s): ...................................................................................................................................... 17
    Soybean: the economically important host .................................................................................. 17
    Growth and development of soybean ............................................................................................ 17
  Kudzu: an additional host component in the soybean rust pathosystem .................................. 17
    Origin, botanical description and taxonomy .................................................................................. 18
    Habitat ............................................................................................................................................ 19
    History and distribution of kudzu in the U.S. ............................................................................... 20
  Green leaf area index: definitions and usefulness ........................................................................ 20
  Duration of the growing season of some suitable hosts of *P. pachyrhizi* .............................. 22
  References ........................................................................................................................................ 24
ABSTRACT

Role of susceptible hosts of *Phakopsora pachyrhizi* in the occurrence of epidemics of Asian soybean rust (ASR) in the U.S. was assessed. Phenology of kudzu (*Pueraria montana* var. *lobata*) along a ~800 km transect in the U.S. was characterized in 2003 and 2004 to assess the potential for kudzu to serve as an inoculum source for occurrence of ASR and subsequent spread to the north central soybean growing regions. Also, the occurrence, distribution, and growing periods of six potential hosts of *P. pachyrhizi* (including kudzu and soybean), in Central America, the Caribbean, and Mexico, were delineated. Sampling data revealed that bud break of kudzu plants in the two consecutive years of study occurred as early as April 7 from southern Louisiana (29.8 N latitude) to northern Mississippi (35.0 N latitude); kudzu green leaf area index decreased linearly with increasingly northern latitude ($R^2$ and regression coefficient = 0.750 & –0.097, respectively, for 2003 and 0.654 & –0.384 for 2004). Further, results of modeling predicted that in southern Mississippi (31.5 N latitude), kudzu plants broke dormancy in the second and first week of March in 2003 and 2004, respectively. Modeling also showed that kudzu vines may break dormancy prior to March 1st in areas of southern and central Florida and southern Louisiana. Amount of kudzu foliage increased abruptly from April to May and June. Five out of the six hosts investigated in Central America, the Caribbean, and Mexico, were found to occur in such regions. Occurrence of selected hosts in each region was documented and maps of distribution and cultivation period schemes were generated.
CHAPTER 1. GENERAL INTRODUCTION

Thesis organization

This thesis is organized in five chapters. The first chapter is a general introduction, which includes three sections: a description of the organization of the thesis itself, a brief introduction that deals with the importance of this study, and a list of the bibliographic references cited in this introduction.

The second chapter is a literature review in which I have compiled relevant topics that can help better explain the objectives and focus of this study. Information on the ecology of soybean rust, its causal agent, an update of its current global distribution, and recent findings reports in the U.S., has been included. Also, included in this chapter is some information concerning kudzu as an additional component in the pathosystem of soybean rust. A list of the references reviewed appears at the end of this chapter.

The third and fourth chapters are two separate studies. The first one is an analysis of the importance of kudzu plants in the epidemiology of soybean rust in the U.S., to be submitted to the Plant Health Progress Journal. The second study is a documentation of the occurrence, distribution, and growing periods of suitable hosts of *Phakopsora pachyrhizi* in Central America, the Caribbean, and Mexico.

The last chapter contains the general conclusions of this study and acknowledgments to institutions and people who provided assistance in this thesis study. A list of the examined web pages as well as the institutions and people who provided information to the second study (Chapter 4) is presented as an Appendix section, which, though included, was not categorized as a chapter.

Introduction

Soybean [*Glycine max* L. (Merr.)] is the most important oilseed crop in the world today (1,6). In the United States (U.S.), soybean is currently grown on almost 30 million hectares, predominantly in the northern states (13). This puts the U.S. as the current world leader in soybean production (1,6,13). The area planted to soybean in the U.S. has increased
in the last decade. In 2004, the area harvested was approximately 29,930 million ha (12), which was valued at $16.01 billion (7,12).

Soybean is vulnerable to numerous diseases that adversely affect production and yield (22). A prominent disease is Asian soybean rust (ASR), caused by the airborne fungus *Phakopsora pachyrhizi* Syd. On susceptible soybean cultivars and under favorable environmental conditions, ASR results in tremendous numbers of spores (2,11,28), which can cause severe plant defoliation (2,23). Large economic losses are reported in areas where the disease occurs each season (5,8,26,30). In the U.S., empirical yield loss models have been developed to estimate the effect of disease at different growth stages (29). Results show that ASR affects crop developmental stages and yield components by reducing the vegetative growth rate and reproductive stages up to 40%. A more recent analysis (3) indicated that the economic effects of soybean rust in the U.S. vary by region. After pathogen establishment in the continental U.S., expected net economic losses to growers and consumers are predicted to range from $640 million to $1.3 billion (3,10). Depending on the disease severity and geographic scope of the outbreaks, losses in subsequent years are projected between $240 million and $2.0 billion (3,10).

Asian soybean rust was first found and confirmed in the continental U.S. in Louisiana state at the end of the 2004 growing season (21). Confirmation of the disease presence was of big concern for the U.S. soybean growers and continues to represent a threat to them, especially to those in the major soybean producing regions. One of the biggest reasons for this concern is that most, if not all, soybean varieties grown here are thought to be susceptible to attack by the ASR pathogen. Considering the occurrence pattern of ASR in 2005 and 2006 growing seasons in the U.S., however, whether or not the disease will occur and reach epidemic proportions in the major soybean producing regions in upcoming seasons, still remains unpredictable. The occurrence of ASR seasonal epidemics in upper latitudes (above the 37°N parallel) in the U.S. is believed to depend on the built-up of inoculum in southern areas followed by its subsequent northward movement. Of great importance in this scenario is to determine overwintering zones for the pathogen (16) and distribution of alternative hosts for inoculum production. In the U.S., kudzu (*Pueraria montana* var. *lobata*) is an alternative host that may be important to the development of ASR epidemics (15), chiefly because it is
widely distributed in most of the southeastern states, where it is confirmed as being an overwintering host of *P. pachyrhizi* (USDA, 2005).

In this study, as a first goal, we describe the potential implications and importance of kudzu in the occurrence and expansion of ASR epidemics from southern into northern areas of the U.S.

The fact that the ASR fungus attacks many other legumes (2,4,9,14,17,19,20,25), many of which are thought to occur in continental regions below the 29°N parallel, complicates understanding of the dynamics of possible ASR epidemics in the U.S. Alternative hosts in regions where ASR may become endemic might constitute significant supplementary sources of inoculum production for aerial incursions of urediniospores in a season. Therefore, it is relevant to analyze the potential of geographic regions, such as Central America, the Caribbean, and Mexico, in the production of initial inoculum and dispersal of spores of ASR. The potential of regions in Central America, the Caribbean, and Mexico as source areas for the aerial introduction of other rust fungi into the U.S. is well documented from the introduction of other phytopathogenic fungi (16,18,24).

Identification of the location and strength of inoculum source areas, coupled with climatological information, can be useful if one attempt to assess the potential expansion of ASR by land bridging or the spore dispersal by single leaps over long distances. In modeling the movement of spores by simulation of air parcel trajectories, identification of where and when a source area is available is fundamental; inaccurate results can be obtained when the location and strength of the inoculum source is ignored (27).

Thus, a second goal of this study is to delineate and document the occurrence and distribution of several reported suitable alternative hosts of *P. pachyrhizi* in Central America, the Caribbean, and Mexico. The ultimate goal is to provide information of where and when alternative hosts are likely to occur in order to assist in future assessments of the occurrence of ASR in the continental U.S., based on seasonal incursions of spores from zones where the pathogen could persist year-round.
References


CHAPTER 2. LITERATURE REVIEW

General information on the life cycle pattern of a rust fungus

Rust fungi constitute a group of plant pathogens that attack numerous plant species (1,68). They have complex life cycles, which vary according to the genera and species. The complete life cycle of a rust fungus includes five successive spore stages (3,68), which are commonly designated with Roman numerals. Depending on the system of terminology used (ontogenic or morphologic), the designation of the stages in the life cycle of a rust fungus will vary. Based on Alexopoulos et al. (1996) the following different stages may be produced:

Stage 0: spermogonia bearing spermatia \( n \) and receptive hyphae \( n \)
Stage I: aecia bearing aeciospores \( n+n \)
Stage II: uredinia bearing urediniospores \( n+n \)
Stage III: telia bearing teliospores \( n+n \rightarrow 2n \)
Stage IV: basidia bearing basidiospores \( n \)

Based on the above reproductive stages, rusts are classified in three groups: (i) macrocyclic, (ii) demicyclic, and (iii) microcyclic (3,28). The first group refers to rusts that exhibit all five reproductive stages, the second group to rusts that lack the uredinial stage, and the third group to rusts that lack the aecial and uredinial stages while the teliospores are the only binucleate spores it produces (3).

Rusts that complete the five stages on a single host are called autoecious, while those rusts needing two hosts species for the completion of their cycle are termed heteroecious (3,28,68).

The disease: soybean rust

Causal agents

To date, two fungal species of the genus Phakopsora, Phakopsora pachyrhizi and Phakopsora meibomiae, are reported as the causal agents of soybean rust (84). Both pathogens are obligate parasites and have been described on the basis of the uredinial and telial stages. The more aggressive species, P. pachyrhizi, (9,11,17,18,115) has occurred in the eastern hemisphere for decades, predominantly in Asia and Australia (17,55,105). For this
reason, the rust on soybean caused by *P. pachyrhizi* is often referred to Asian soybean rust (ASR, as in this study) or Australasian soybean rust. The second fungal species (*P. meibomiae*), reported as having less epidemiological importance (16,17), appeared in the western hemisphere on several hosts in the 1970s and 1980s (16,23,92). The first formal distinction between the soybean rust fungi was established in 1992 on the basis of morphological differences between their anamorphs and teleomorphs (84). More recently, Frederick et al. (2002) developed classical and real-time fluorescent polymerase chain reaction (PCR) to detect and differentiate both species causing soybean rust (40).

**Cycle, infection process, and infection components**

The cycle of ASR has not been clearly elucidated (84). Only the uredinial and telial stages are known in *P. pachyrhizi*. The uredinial stage is observed throughout a season producing urediniospores, which are responsible for infections during the season. The telial stage is not commonly seen on soybean in the field, but has been observed on other infected hosts late in the season (17,20,55,129). The infection process begins when urediniospores germinate, forming a single, short, unbranched germ tube that grows across the leaf surface until an appressorium forms (61,72,89). From the appresorium, a penetration peg is formed. Typically, the penetration peg makes its way through the epidermal cells (10,60,61,72). Entry through joint of adjacent epidermal cells, however, has also been observed (10). When appressoria form on stomata, the “infecting hypha” penetrates the surface of the contacting guard cell instead of entering the leaf through the stomatal opening (60,61). The penetration peg develops into an initial infection structure often termed a “transepidermal vesicle” (55,72,97) and some times “penetration hypha” (60,61). This structure penetrates into the mesophyll, elongates into a hypha that septates to form a secondary hyphae, and finally cylindrical or globose haustoria (60,61,97).

Uredinia develop 5 to 8 days after inoculation (61,70,71) and new uredinia from a primary infection continue to form for 30 days (128). Mature urediniospores are produced as early as 9 days after infection (71,128). Successful infection depends on temperature and availability of wetness on the leaf or other affected plant organs. Temperature range for germination of urediniospores is between 15-27°C (63,70). Optimum range is unclear. Minimum wetness duration for infection is reported to be 6 hours and maximum infection
occurs within 10 to 12 hours of dew (70,74,76). Yet, in a histological study on the development of ASR infection, McLean and Byth (1981) found that some urediniospores germinated in the absence of dew and after dew periods; appressoria were formed and penetration also occurred (73).

**Symptoms**

Symptoms of ASR can occur on all aboveground plant parts (17,104,121). On leaves, symptoms start as small chlorotic spots that are irregularly distributed. These chlorotic areas gradually increase in size and develop into gray to tan or brown polygonal lesions, usually about 0.5 mm large, and delimited by the leaf veins (17,102). Individual lesions continue to enlarge and may coalesce; the color of the lesions becomes darker (dark brown to reddish) because of the production of erumpent pustules, which eventually cause necrosis, premature yellowing and defoliation. Uredinia develop in the pustules and release urediniospores through a central pore (17). Typically, the number of uredinia is higher on the abaxial than on the adaxial leaf surface (17,104).

**Epidemiology**

The epidemiology of ASR has been studied by several researchers (17,21,107,109,122,126). Most epidemiological studies of ASR, however, have focused on the temporal analysis of disease at the local scale. The disease was reported to progress in a logistic-like fashion (108,109) in Taiwan. Infection rates have been reported to range from 0.114 to 0.209 units/day (107). Spatial distribution studies concerning macroscale patterns of ASR occurrence are scarce. Local spread rates in field experiments have been estimated (21). Casey (1981) found that within a field, rate of spread of ASR varied from 0.15-0.45 m/day with values of 0.045-0.050 for apparent infection rates. The ASR is reported to form small aggregations in the field followed by rapid spread with severity sometimes reaching 100% on lower leaves (20,116). In some regions of South America, Asia, and Africa, the disease is considered endemic (111,130,131).

Understanding the epidemiology of ASR requires careful consideration of all pathosystem components as well as the infection process and the effects of the environment.
In the disease triangle, alternative hosts of *P. pachyrhizi* may be considered as additional components of the factor “host” in the pathosystem. Studies on the role of alternative hosts in the epidemiology of ASR are scarce and more information on this matter would be crucial to quantify the intensity of ASR epidemics in a given locality or region based on contribution of inoculum from alternative hosts.

Climatic conditions strongly affect both the development of the soybean plants and ASR disease. Models have been developed in the past 15 years to describe climatic impact on disease components (123,126) and soybean crop losses (124,126). Rainfall is considered a determining factor in the establishment and triggering of epidemics of ASR (30,31). The differential effects of dew and rainfall on the soybean rust epidemics could explain differences of ASR severity and losses in different regions and years (117,124). Average daily temperatures were successfully used to simulate soybean and *Phakopsora pachyrhizi* development by physiological days (125). When moisture is available, the disease severity increases rapidly due to secondary infections (76). Environmental conditions directly affect the infection components. The latent period ranges between 7 and 14 days, depending on temperature regime, which allows several disease cycles within the growing season (63,70). The polycyclic nature of ASR helps to explain its potential for explosive development under favorable conditions.

The physiological age of soybean plants is also a relevant factor in the development of ASR epidemics (75,107). Another factor that makes the epidemiology of ASR more complex to characterize is that its causal agent has several alternative hosts (17,55,107). The existence of physiological races of the pathogen (42,120) and possible intra-specific genetic variability within host species further complicates the issue.

**Current world distribution of soybean rust**

The current global distribution of ASR includes several continents and countries of the eastern and western hemisphere (2,17,19,47,50,53,54,58,64,67,93,98,103,107,130). In the eastern hemisphere, it occurs in Australia (55,56,105), Asia (17,107,121), and Africa (2,53,54,66,67), and in the western hemisphere, it occurs in several countries of the Americas. The first report of ASR was from Japan in 1902 (17). In 1934, the disease was found in
several other Asian countries and Australia (17,55). By 1970, ASR was noticed on soybeans in India (104). The disease was found in Hawaii in 1994 on cultivated soybeans (58). The first confirmed report of the pathogen in Africa was in 1996 from Kenya, Rwanda, and Uganda (66,67). Since then, the disease spread to Zambia and Zimbabwe in 1998, Mozambique in 2001 (67), South Africa in 2001 (91) and Nigeria in 2001 (2). In the western hemisphere, ASR has been reported in Paraguay (79), Brazil (50,130,131), Argentina (93), Bolivia (130), Colombia (130), and in the continental U.S. in 2004 (98).

**Current distribution of soybean rust in the Americas**

In the Americas, ASR is spread in several countries of South America, including Paraguay (79), Brazil (50,130,131), Argentina (36,93), Bolivia, and Colombia (130). According to Yorinori (2005), ASR was first observed in South America on March 5, 2001 in Paraguay during the 2000-2001 growing season and in the Brazilian state of Paraná late in the same growing season. Other researchers in Brazil (50) affirm that ASR had been observed since 1998. However, it is not clear whether symptoms from these observations indeed corresponded to those induced by *P. pachyrhizi*. By the time of the first observations of ASR, soybean growing areas affected in Paraná were estimated at 10,000 ha. In the 2001-2002 growing season, the disease spread to all soybean-growing regions of Paraguay and many soybean-growing areas of south and west central Brazil. Economic losses caused by ASR epidemics in Brazil were estimated at $2.0 billion for 2004 (34). ASR was detected in experimental plots in the province of Misiones, Argentina at the end of the 2001/2002 growing season (93) and in Bolivia in a winter soybean crop in 2003 (130).

The first report of ASR north of the equator was in July 2004 when the disease was found in Colombia. In North America, the disease was first found in the mainland U.S. on November 6, 2004 in experimental soybean fields of the Louisiana State University in Baton Rouge (98). Thereafter, the disease appeared in Alabama, Arkansas, Florida, Georgia, Mississippi, Missouri, and South Carolina. In the 2005 growing season, ASR has been found in several counties in Florida, Alabama, Mississippi, Georgia, and South Carolina. All identifications of the disease have occurred on kudzu stands and soybean crops (112).
In Mexico, the disease was found in the state of San Luis Potosí in 2005. Presumably, ASR has not been found and reported in Central America and the Caribbean to date.

**The pathogen: Phakopsora pachyrhizi**

The ASR fungus, *P. pachyrhizi*, was first collected by Torama Yoshinaga in Japan in 1902 from infected wild plants of *Glycine soja* (17). That same year, Nakanishiki collected and identified the fungus in Japan from cultivated soybeans and named it *Uredo sojae*. According to Yang (1977), T. Yoshinaga sent his collected wild infected soybean specimen to Hennings in 1903 (in Europe) for identification. Henning’s identification agreed with that of Nakanishiki and confirmed that the species collected was *Uredo sojae*. In 1903, Hennings described the uredinial stage under that name and recorded it in the mycological literature for the first time (17). Subsequently, the name of the ASR fungus was changed several times. In 1914, the name *Phakopsora pachyrhizi* was first applied by H. Sydow and P. Sydow to designate a fungus they described from an infected leaf of yam bean (*Pachyrhizus erosus*) collected by Y. Fujikuro in Taipei, Taiwan (17). Still, different names for the ASR fungus were inadvertently used in later literature to refer to *P. pachyrhizi* (17,101).

**Morphology and taxonomy**

Spermogonial (or pycnial) and aecial stages of *P. pachyrhizi* are unknown. Only the uredinial and telial stages have been observed on infected host species (17,84). Reports of natural infections caused by basidiospores are nonexistent. However, teliospores have been germinated in the laboratory with subsequent formation of a basidium bearing basidiospores (62,95). More recently, Carmona and Gally (2005) reported the presence of the telial stage in soybean plants collected from soybean fields in several provinces of Argentina (20). There, the ASR fungus had been previously confirmed by polymerase chain reaction.

Most of the descriptions of *P. pachyrhizi* have been based on the uredinial stage since the telial stage is usually absent. The telial stage is an important criterion in the taxonomy of ASR (27) since the morphology of the uredinia is very similar to that of other rusts (127,128). Teliospore formation has been reported on several hosts in the field (17,20,56) and in controlled experiments in the laboratory (62,89,95,127,128) in different regions. Germination
of teliospores has been accomplished in the laboratory alternating wet and dry cycles (95). The first report of successful basidiospores formation from teliospores was in 1987 by Koch and Hoppe (62).

**Uredinial stage:** (uredinial anamorph: *Malupa sojae* [syn. *Uredo sojae*]). Uredinia are small (about 100-200 µm in diameter), usually in groups, occurring on the abaxial surface of the leaves. They are light tan to reddish brown in color, subepidermal, and erumpent.

**Telial stage:** (teleomorph: *Phakopsora pachyrhizi*). The fungus *P. pachyrhizi* forms crustose telia with 2 to 7 irregular layers of teliospores. Teliospores are more or less oblong with pale yellowish brown to colourless walls and equally 1 µm thick or slightly thickened apically to 3 µm in the outermost spores (84).

**Taxonomy:** The Latin name, *Phakopsora pachyrhizi*, has appeared in the literature under different synonyms (101). It was first applied by H. Sydow and P. Sydow in 1914 to designate a fungus from an infected leaf of yam bean (*Pachyrhizus erosus*) collected in Taipei, Taiwan (17). At present, the name *Phakopsora pachyrhizi* is generally accepted as the name for the fungus that causes ASR (17). Based on current authoritative sources (12,22,59), *P. pachyrhizi* is taxonomically classified as indicated below:

<table>
<thead>
<tr>
<th>Kingdom Fungi</th>
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<tbody>
<tr>
<td>Phylum Basidiomycota</td>
</tr>
<tr>
<td>Class Uredioniomycetes</td>
</tr>
<tr>
<td>Order Uredinales</td>
</tr>
<tr>
<td>Family Phakopsoraceae</td>
</tr>
</tbody>
</table>

The family Phakopsoraceae is composed of 12 genera (84), including the genus *Phakopsora*. The genus *Phakopsora* includes more than 90 species that occur on over 150 plant genera (84).

**Host range of Phakopsora pachyrhizi**

In the 1970s and 80s, when epidemics of soybean rust -known now to have been caused by the fungal species *P. meibomiae*- were observed in the western hemisphere (15,16,23,92,101,113,114,115), the alternative hosts of rust screened in those regions were
considered to be hosts of the species *P. pachyrhizi* (17,113,114,115). Common lists of hosts for *P. pachyrhizi* and *P. meibomiae* (including legumes reported in the eastern and western hemisphere) continued to appear in the literature until 1992, when Ono *et al* (1992) identified that the species occurring in the western hemisphere was *Phakopsora meibomiae*. The hosts for both species of fungi differ at somewhat, though 24 species in 19 genera are reported as common hosts for both pathogens (48).

To date, more than 90 cultivated and wild plant species are reported as hosts of *P. pachyrhizi* (17,29,83,90,106,107). Most species reported (17,56,90,106,107), are legumes that are closely related taxonomically (49). Approximately 31 species have been recorded as natural hosts and 60 species as artificial hosts (infections produced by artificial inoculations) (45,107). Reported lists of alternative hosts of *P. pachyrhizi* can be found in Sinclair (1982) (100), Tschanz (1982)(107), and Bromfield (1984)(17). However, due to inconsistencies observed in the results of experiments and studies on the compatibility of legumes as hosts of *P. pachyrhizi* (17,56,94,97,107), any list of hosts is still tentative and incomplete. Bromfield (1984)(17) pointed out the importance of carefully interpreting the meaning of the term “host” in any list of reported studies. He also suggested that in order to determine whether or not a given host has significance in the epidemiology of ASR, hosts should be tested locally against endemic populations of *P. pachyrhizi*.

Based on observations and past reports on specific experiments with alternative hosts, several legumes have been consistently and repeatedly cited at allowing symptoms expression and sporulation of *P. pachyrhizi* (Table 1). In such reports, ASR occurrence was observed in areas where at least one specific pathogenic race of the fungus and one species or intra-specific type of host legume coexisted. These species of legumes are considered functional in the epidemiology of ASR.
Table 1. Host species reported to be suitable to the infection by *Phakopsora pachyrhizi* in the eastern and western hemispheres. Hosts listed have been consistently observed to allow the symptom expression and sporulation of the pathogen of ASR both in field occurrences and artificial inoculations.

**Eastern Hemisphere**

<table>
<thead>
<tr>
<th>Continent and country where disease was observed or reported</th>
<th>Field occurrences (natural infections)</th>
<th>Artificial inoculations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Artificial inoculations</strong></td>
<td><strong>Greenhouse</strong></td>
<td><strong>Laboratory</strong></td>
</tr>
<tr>
<td><strong>Eastern Hemisphere</strong></td>
<td></td>
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<tr>
<td><strong>Australia</strong></td>
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<tr>
<td></td>
<td><strong>Cajanus cajan</strong></td>
<td><strong>Canavalia maritima</strong></td>
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<td></td>
<td><strong>Crotalaria spp</strong></td>
<td><strong>Crotalaria linifolia</strong></td>
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<td></td>
<td><strong>Desmodium spp.</strong></td>
<td><strong>Desmodium spp.</strong></td>
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<td></td>
<td><strong>Glycine max</strong></td>
<td><strong>Glycine max</strong></td>
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<tr>
<td></td>
<td><strong>Kennedia rubicunda</strong></td>
<td><strong>Kennedia rubicunda</strong></td>
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<td></td>
<td><strong>Kennedia prostrata</strong></td>
<td><strong>Lotus pedunculatus</strong></td>
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<td></td>
<td><strong>Macroptilium atropurpureum</strong></td>
<td><strong>Lupinus angustifolius</strong></td>
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<td></td>
<td><strong>Macrotyloma axilare</strong></td>
<td><strong>Pachyrhizus erosus</strong></td>
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<td></td>
<td><strong>Pueraria lobata</strong></td>
<td><strong>Phaseolus vulgaris</strong></td>
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<td></td>
<td><strong>Lotus pedunculatus</strong></td>
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<td><strong>Asia</strong></td>
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<td><strong>China</strong></td>
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Table 1. continuation

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<td><strong>Mexico</strong></td>
<td>Glycine max</td>
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*In the continental U.S., ASR and its causal agent, _P. pachyrhizi_, have been observed only on kudzu and soybeans plants in field occurrences.

In Hawaii, ASR has been observed on soybeans.

*Pueraria lobata and _Pueraria montana var. lobata_ are synonyms.*
The host(s):

Soybean: the economically important host

Soybean, *Glycine max* L. (Merr.) (Fabaceae: Papilionoidae) is a leguminous plant native to north and central China (8). It is a short-day, nitrogen-fixing plant that adapts well to tropical and temperate regions. Soybean maturity is mostly influenced by maturity group and not as much so by planting date. Today, soybean is the most important oilseed crop in the world (35).

Growth and development of soybean

Soybean grows well in different soil types, except in sandy soils with poor water retention capacity (8). Varieties of soybean are classified into 13 maturity groups (000 to X) on the basis of their response to photoperiod. In the U.S., maturity groups grown are 00 to IX, each adapted to certain latitudinal ranges (86). Group 00 corresponds to the earliest maturity group and group IX to the latest (86). Based on the growth pattern, soybeans are generally classified into two groups: indeterminate and determinate. Varieties of indeterminate growth habit continue their vegetative growth after the initiation of flowering (86). Most of the varieties within the maturity group 00 to IV exhibit the indeterminate growth habit and are typically grown in north central regions. In soybean varieties with determinate growth habit, the vegetative growth ceases before flowering begins (86). Soybean varieties with this growth habit are grown in the southern U.S., Mexico, and South America. Planting dates of soybean in the U.S. vary, but generally they occur earlier in southern states in order to avoid stress caused by drought (46,70).

Soybean was introduced into the U.S. in 1765. Today, it is grown in more than 25 states of the U.S., which makes it the second largest crop in cash sales and the number one crop in terms of the value of exports (6,81).

Kudzu: an additional host component in the soybean rust pathosystem

Many legume species are reported as hosts of the ASR fungus (17,29,56,107). Only some hosts, however, are functional in the epidemiology of this disease. Kudzu, reported as a suitable host in several regions where ASR occurs (17,56,131), is confirmed now as an overwintering host in the U.S. This fact, coupled with its wide distribution in southern U.S,
puts kudzu as a potential additional component in the study of the ASR pathosystem. The perennial nature of kudzu in areas where it can tolerate low temperatures and remain with green foliage all year-round (as in south and central Florida) is another relevant aspect of kudzu as a host of the ASR fungus in the U.S. (87).

**Origin, botanical description and taxonomy**

Kudzu (*Pueraria montana* [Lour.] Merr. var. *lobata* [Willd.] Maesen & Almeida), is indigenous to subtropical and temperate regions of Asia (38,51,69). The genus *Pueraria* comprises about seventeen described species currently distributed in many regions of the world, from China, Japan, Korea, Micronesia, India, and Australia, to South, Central, and North America (14,38). In southeast Asia, three varieties of kudzu are found: *Pueraria montana* var. *chinensis*, *P. montana* var. *montana*, and *P. montana* var. *lobata* (51). This was confirmed recently by Jewett *et al.* (2003) using genetic markers. *Pueraria montana* var. *lobata* is the species that was introduced in the U.S. in 1876 and the only one identified to exist in the U.S. to date (51,118). Nonetheless, despite being the sole species, high intra-specific genetic variability in populations of it has been detected (85), which is attributed to repeated introductions of kudzu from the 1880s to the 1930s (85). In Central and South America, two species of kudzu are reported to occur: *Pueraria lobata*, and *Pueraria phaseoloides* or tropical kudzu (25,32,33,36). The former species is reported from Panama, Argentina, Brazil and Paraguay, and the latter from many other countries of Central and South America and several states of Mexico.

**Botanical description.** Kudzu is a herbaceous to semi-woody, nitrogen-fixing vine. It can exhibit two types of growth habits, prostrate and climbing, depending on site conditions of occurrence (77). In both growth habit types, the growth rate in initial phenological stages is extremely high; vines can elongate from 10 to 30 cm a day (77,119).

Kudzu plants produce a tap root system. Its tuberous roots can reach diameters of 18 cm and reach depths up to 3 m, hence it is difficult to control with herbicides (44). Stems are herbaceous to semi-woody; leaves and growing vines are covered by abundant bronze-colored trichomes (32). Leaves are deciduous, alternate, compound (trifoliate), peduncled, and suborbicular to ovate, entire or lobed, varying in size from 10 to 25 cm at maturity.
Flowers are clustered in axillary racemes, purple in color, and appear in late summer (77). Seeds are kidney-shaped, 3 to 4 cm long, grouped in pods, which are several seeded, hairy, and mate in early fall (49). Pods are produced only on vertically growing vines and bear a few seeds that are viable (77).

**Taxonomy.** Kudzu belongs to the Fabaceae family, tribe Phaseoleae, subtribe Glycininae (69). It was first named *Dolichos lobatus* (69). The species *Pueraria montana* var. *lobata* is the one identified to exist in the U.S. (51,118). The most common synonyms found in the literature for this species are *P. lobata* and *P. thumbergiana* (49). Common names include mile-a-minute vine, foot-a-night vine, and the vine that ate the south, porch vine, telephone vine, and wonder vine in Alabama (14,49,69,88).

**Habitat**

Kudzu can occur in diverse ecological environments (38,77). In the southern U.S., it is commonly seen in exposed areas, along roads, abandoned fields, abandoned cars, fencerows, overtopping trees, or in dense shaded sites within a forest (38). Kudzu grows well in different soil types. However, its growth can be reduced significantly with high concentration of salts in the soil (4). Its rapid growth (photosynthetic rate) and efficiency to colonize new environments have been attributed to the external and internal characteristics of its leaves (32). Fluctuations of air temperature cause changes on the assimilation of nitrate nitrogen of kudzu. De Pereira-Netto *et al.* (1998)(33) found that nitrate reductase activity was reduced significantly with air temperature below 21.8 or above 33.6°C. Photosynthetic rate of kudzu leaves depends on the influx of sunlight: its maximum photosynthetic rate is higher in leaves from exposed stands than in shaded stands (38). Despite its adaptation to a wide climatic range, kudzu is very sensitive to frost. Leaves drop after the first frost, and new leaves are not produced until next spring. In the U.S., kudzu remains with green foliage year-round in frost-free areas such as south and central Florida.

Maximum green leaf area index (GLAI) of kudzu can surpass 8.0 units (41). It reaches a GLAI peak in late June in midsouthern areas (119). Kudzu is highly efficient in CO₂ allocation (96,110). Tsugawa *et al.* (1992) reported that kudzu shifts its priority of carbon
allocation from growth of primary branches to growth of the main stem as it changes from a prostrate to climbing growth habit (110).

**History and distribution of kudzu in the U.S.**

Kudzu was originally brought to the United States from Japan in 1876 at the Centennial International Exhibition (first official world's fair in the United States) held in Philadelphia, Pennsylvania (37). As part of the celebration of the 100th anniversary of the foundation of the U.S., visiting countries were invited to build exhibits. The Japanese constructed a garden at their pavilion, which included kudzu and other native plants brought from Japan. Kudzu was again exhibited at the New Orleans exposition of 1883. In 1902, kudzu was planted by the botanist David Fairchild as an ornamental plant in Washington, D.C. In subsequent years, kudzu was used increasingly as an ornamental vine in southern states. In 1905, C.E. Pleas in Chipley, FL noticed the potential of kudzu as forage after seeing his chickens feeding on kudzu leaves. Later kudzu started being used as forage crop. During the 1930s and 40s, it was promoted in a program to control soil erosion in several regions of the south. About 73 million kudzu seedlings were produced in nurseries and 1.2 million acres were planted (14). In 1950, kudzu was recognized as a weed and later declared as a noxious weed for several states (14,88).

At present, kudzu is distributed throughout most of the southeastern states of the U.S. It extends from as far south as Florida and Texas and as far north as Connecticut, Oregon, Missouri and Pennsylvania (37,39).

**Green leaf area index: definitions and usefulness**

Green leaf area index (GLAI), commonly referred to as “leaf area index” (24,26,52,65), is a measure of the amount of area of all green leaves in a plant canopy per unit of ground surface. For broadleaf canopies, GLAI is defined as the total one-sided green leaf area per unit ground area (24,52). For needle canopies or other types of irregular foliage elements, it is defined as the maximum projected leaf area per unit ground area (80). The GLAI is a dimensionless quantity, hence it can be used in a wide variety of spatial scales.
Commonly, however, “m^2” is the unit of area used to define and estimate the amount of foliar area index that a plant canopy contains (43,65).

The amount of foliage expressed as GLAI describes a fundamental property of the plant canopy in its interaction with the atmosphere, especially concerning radiation, energy, momentum and gas exchange (26). The ability to estimate leaf area index is relevant in understanding and characterizing ecological processes such as photosynthesis and transpiration. Leaf area index can be a good descriptor of canopy architecture, disease-affected foliar area, and climatic change (7,13,26).

Methods to determine GLAI. Methods to determine GLAI can be classified into two general types: direct and indirect methods. The first group is based on the collection of leaves within a unit area, which typically requires harvest of foliage (destructive sampling), litter-fall collection, or point contact sampling (24). Given the principle and practicability of direct methods, they are more easily applicable in agricultural crops and grassland areas. Direct methodologies are the most accurate, but they are usually time-consuming and labor-intensive. Other operational constraints, like the error accumulation due to frequently repeated measurements, make the direct methodologies less compatible for monitoring GLAI dynamics spatio-temporally. Nonetheless, direct methods are useful to calibrate or validate indirect methods.

The second group or indirect methods involves optical devices and models. In these methods, the amount of leaf area is estimated from observations of other variables. Indirect methods are faster to perform and allow determinations in larger samples.

The amount of GLAI in crops or other types of short stature vegetation is calculated dividing the leaf surface area measured by the ground area selected. For example, if a 1 m^2 of ground area is selected and the total leaf area adds up to 4 m^2, the index of green leaf area is: GLAI = 4 m^2 / 1 m^2 = 4.

Fluctuation of green leaf area index in the developmental stages of leguminous plants. The increase or decrease of the GLAI varies with plant species or crop type. In leguminous crops, GLAI increases during active growth, especially from emergence to beginning of flowering, then peaks at end of flowering and starts declining when grain filling
begins (13); at physiological maturity GLAI stops. In soybeans, a similar GLAI fluctuation pattern was found by Moreira et al. (2003) using a multiespectral radiometer (78).

**Duration of the growing season of some suitable hosts of* P. pachyrhizi***

i) Cowpea [*Vigna unguiculata* (L.) Walp. Fabaceae: Papilionoidea]. Basionym: *Dolichos unguiculatus* L. Common synonyms include: *Dolichos sinensis* and *Vigna sinensis*. It is an erect or suberect, annual, herbaceous plant that reaches up to 80 cm tall or more. Cowpea is a tropical grain legume commonly grown as a subsistence crop. There exist early and late maturity groups and determinate and indeterminate variety types. Early maturing varieties produce pods in 50 days and seeds in 90 days whereas late maturity cultivars mature seed in 240 days. Varieties are sensitive to photoperiod and temperature. Normally, the growing cycle of cowpea lasts around six months. When used as cover crop, cowpea is usually harvested three months after planting to allow the accompanying crop to grow well (25). Cowpea is consumed as green vegetable, used for pasturage to some extent, hay, ensilage, as a cover crop to control soil erosion, and as green manure.

ii) Hyacinth bean [*Lablab purpureus* (L.) Sweet. Fabaceae: Papilionoidea]. Basionym: *Dolichos purpureus* L. Most common synonyms are *Dolichos lablab* L., *Lablab vulgaris*, and *Lablab lablab*. It is a tropical, short-lived perennial or annual legume of semi-determinate growth. Hyacinth bean grows as a vine producing purple or white flowers and scarlet colored pods. Its growing cycle varies from three to seven months depending on the cultivar. Short cycle varieties require three months, semi-late varieties are three to five months, and late ones are longer than six months. As cover crop it is usually cut four months after planting. Hyacinth bean is used as food crop, ornamental, forage, or as a cover crop.

such as south Florida, kudzu can remain green all year and loss its foliage gradually. In zones
where frost occurs, kudzu foliage is killed by the first frost of the season and vines enter into a
dormancy period. It is hypothesized that kudzu distribution is limited by cold temperature.

iv) Pigeon pea \([Cajanus cajan\, (L.)\, Millsp.\, Fabaceae:\, Papilionoidea]\). Basionym:
\(Cytisus cajan\, L.\) Common synonyms are \(Cajan cajan\) and \(Cajanus bicolor\). It is an erect bush
that grows between 0.5 and 4 m tall (usually 1-2 m). Pigeon pea is traditionally cultivated in
intercropping systems either as an annual or semipernennial crop. Growing cycle or crop
duration depends on the maturity group, varying from 80 to 450 days. Most common grown
cultivars are intermediate to long duration, which usually take from six to 12 months from
planting to harvesting (5,99). Early maturity or short duration cultivars are harvested three to
five months after planting. The uneven maturation and perennial habit of the short day
duration pigeon peas, enables multiple harvests during the growing season. Pigeon pea plants
are tolerant to drought and high temperatures; the photoperiod sensitivity of pigeon pea
varieties allows to grow pigeon pea in mild winter environments. Pigeon pea is used as
consumption grain, forage, cover crop, and green manure.

v) Soybean \([Glycine max\, (L.)\, Merr.\, Fabaceae:\, Papilionoidea]\). Basionym: \(Phaseolus
max\, L.\) Synonyms: \(Dolichos soja\, L.,\, Glycine hispida\, (Moench)\, Maxim.,\, Glycine soja\,).
Soybean is a short-day, herbaceous plant with two general growth habits types: determinate
and indeterminate (86). Regardless of the growth habit, cultivated soybeans are generally
annual plants. The length of the growing cycle of soybean crops varies according to the
cultivar and maturity group, but usually ranges from four to six months. Developmental rate
of the vegetative and reproductive stage of soybean is significantly influenced by the
temperature, photoperiod or daylength, and water availability (6). Temperature is the major
factor that determines the early vegetative development of soybeans; higher temperatures
hasten emergence and vegetative growth. Photoperiod or number of hours of light, in its turn,
promotes the floral induction; short days (long nights or dark periods) initiate flowering.

vi) Yam bean \([Pachyrhizus erosus\, (L.)\, Urban.\, Fabaceae:\, Papilionoidea]\). Basionym:
\(Dolichos erosus\, L.\) Most common synonyms: \(Pachyrhizus angulatus\, Rich.\, ex\, DC.,\, Dolichos
erosus\, L.,\, Stizolobium bulbosum\, (L.)\, Spreng.\) It is a tropical, semi-erect, herbaceous to
somewhat lignified plant that produces one or more edible tuberous roots. Cultivated yam
bean species are grown as annual crops, although they have a perennial habit (25). The growing cycle of yam bean goes from four to seven months depending on the climate and region where it is grown. Commonly, yam bean is harvested when tubers reach a determined size. In areas where yam bean is grown, it is common to find yam bean volunteer plants in between seasons. Yam bean is traditionally intercropped, or monocropped when grown in commercial scale. In some regions, it is pruned two months after planting to increase the size of the tubers. Sometimes, a third of the vegetative shoots are also removed.

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25


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Hershman, eds.


CHAPTER 3. KUDZU (Pueraria montana var. lobata) PHENOLOGY AND ITS IMPLICATIONS FOR OCCURRENCE AND SPREAD OF ASIAN SOYBEAN RUST IN THE U.S.

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ABSTRACT

Phenology of kudzu (Pueraria montana var. lobata) was characterized along a ~800 km long transect to assess the potential for kudzu to serve as a source of inoculum for the onset and development of Asian soybean rust epidemics in the U.S. Along the transect, 22 kudzu stands were selected and leaves sampled once in the spring, summer and autumn of 2003 and 2004. Five subsamples were collected from each location using a round 1858-cm² quadrat arbitrarily thrown into the kudzu stand. Foliar area measurements were made in a laboratory using a leaf area meter and then, GLAI was calculated. Linear regression was used to describe the foliar growth of kudzu in early spring for both years. Analysis showed that kudzu foliage appearance potentially precedes that of soybean crops for about one month in zones as far north as 35º latitude. Kudzu GLAI decreased linearly with increasingly northern latitude ($R^2$ and regression coefficient = 0.750 & –0.097, respectively, for 2003 and 0.654 & –0.384 for 2004). Results of this study provide the first quantitative description of the phenology of kudzu along a transect that may be a logical route for the seasonal northward spread of Asian soybean rust.
Introduction

Asian soybean rust (ASR), caused by the fungus *Phakopsora pachyrhizi* Syd., is a disease of major economic importance in many soybean-growing regions of the world (3,10,22,32). In Uganda and Brazil, for example, losses caused by the disease have been estimated at 60 to 80% and up to 100%, respectively (5,10,32). In the U.S., an analysis indicated that the expected economic losses to U.S. growers and consumers would be $640 million to $1.3 billion annually, after pathogen establishment (4).

The symptoms caused by ASR can appear on all aboveground plant parts, but they are more significant on leaves. On leaves, symptoms start as small, irregularly distributed chlorotic spots that gradually enlarge and develop into gray to brown lesions. Lesions soon become dark brown to reddish because of the production of erumpent pustules in which abundant uredinia, bearing urediniospores, develop (3). Eventually, pustules result in necrosis, premature yellowing and severe defoliation (3,26). At temperatures between 22 and 27ºC and a minimum of 6 h of continuous wetness, urediniospores can be produced as early as 9 days after infection (14). Then, upon release, urediniospores can be easily dispersed by wind over short or long distances (18). The large amount of urediniospores produced by the ASR pathogen and the rapidity in completing its cycle confer ASR a high potential for spread and devastation. These conditions are evident from the global spread pattern and effects caused by the disease in several geographic regions in the last two decades (12,22,28,32).

In the U.S., ASR was first detected in November 2004 in Louisiana (24) and subsequently found in several other southern states that year (28). The disease reappeared in the 2005 and 2006 growing seasons in several southern states, reaching as far as north as Illinois and Indiana in 2006 (28). As of the middle of July in the 2007 growing season, the disease presence has been confirmed in 46 counties in AL, FL, GA, LA, MS and TX. Outbreaks of ASR in the U.S. in the 2005, and 2006 growing seasons have been mild and confined predominantly to zones below 38.0 N latitude. Likely factors for the restricted range in the U.S. are the lack of host availability caused by seasonal dieback of foliage, summer drought conditions in the south, and limited survival of *P. pachyrhizi* due to winter temperatures that prevail in most areas of the U.S., particularly, where the major soybean-producing areas are concentrated.
Using climate modeling, Pivonia and Yang (2004) predicted that in the U.S., winter temperatures would restrict survival and persistence of *P. pachyrhizi* to central and southern FL and TX or other frost-free zones situated below 29.0 N latitude (21). Moreover, as the ASR pathogen in an obligate parasite and produces no functional survival structures, it cannot overwinter in the absence of live host tissue. Host availability, thus, needs to be addressed to better assess ASR risk, as *P. pachyrhizi* has more than 90 hosts, including wild and cultivated plants (11,20,23,25).

Several alternative hosts of *P. pachyrhizi* occur in the continental U.S. (2,28). However, their importance in ASR epidemiology, especially assessments of phenology and distribution in relation to inoculum build up and long-distance transport of urediniospores, have not been carried out.

Kudzu (*Pueraria montana* [Lour.] Merr. var. *lobata* [Willd.] Maesen & Almeida) (13), a fast growing and invasive weed, is considered a major alternative host for ASR in the U.S. because of its wide distribution and abundance and its confirmed suitability to host *P. pachyrhizi* (11,26,28,30). Kudzu is a herbaceous to semi-woody plant that exhibits prostrate and climbing growth habits, in both of which vine elongation rate in initial phenological stages can be from 10 to 30 cm/day (7,16,29). The U.S. area occupied by kudzu, as reported by extension agents from 27 states in 2001, is estimated at 617,872 ha (1.53 million acres) (Jewett, unpublished data). The twelve states that contain 95% of the reported coverage are Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, South Carolina, Tennessee, and Virginia.

The susceptibility of kudzu to *P. pachyrhizi*, its invasive weed nature, and the extensive area it covers in the U.S. implicate it as a potential alternative host for occurrence of ASR epidemics, especially for production and long distance dispersal of inoculum. The objective of this research was to characterize the phenology of kudzu in the U.S. in order to assess the potential for kudzu to serve as inoculum source for occurrence and spread of ASR from southern to the north central soybean growing areas of the U.S. Characterization of phenology was centered on a likely route for urediniospore transport that was previously determined for this study.
Materials and methods

Selection of monitoring route and establishment of sampling sites

In establishing the sampling sites, we first determined a likely route for the south-to-north dispersal of ASR spores in the U.S. and then identified strategic sites along this route to monitor the phenology of kudzu. In order to achieve this, we examined the distribution of kudzu and soybean in the U.S. as well as the reported dispersal pathways of other plant pathogenic fungi from southern to northern areas of the U.S. Distribution maps of kudzu and soybean directed our focus to areas of central Louisiana (LA) and western Mississippi (MS), Tennessee (TN), and Kentucky (KY), where both kudzu and soybean are abundant (Fig. 1, A and B).

As with the historical dispersal routes of plant pathogenic fungi, we focused on three economically important plant diseases spread by airborne inoculum: southern corn leaf blight, caused by *Bipolaris maydis*; wheat stem rust, caused by *Puccinia gramminis* f. sp. *tritici*; and tobacco blue mold, caused by *Peronospora tabacina*. The first two diseases are reported to spread into the northern Great Plains and Midwest areas from foci in the south, including the MS delta region (6,8,17) (Fig. 2). Tobacco blue mold spreads primarily towards northeastern areas, typically from infested cropping areas of Florida (FL) and Georgia (GA) (1,31) (Fig. 2). In view of this, areas of FL and GA and dispersal routes that may originate from such zones were regarded as of low risk for the spread of ASR to the Midwest and hence as no suitable for the monitoring purpose sought in this study.

We selected an approximately 800-km-long transect extending from south-central LA (29.5 N latitude) to southwest KY (37.0 N latitude) (Fig. 3). Along this transect, we determined positioning of numerous sampling sites based on the USDA map of plant hardiness zones. Subsequently, driving along the selected sampling route, we identified readily accessible kudzu stands in which to monitor kudzu growth. In total, 22 stands in prostrate growth and varying approximately from 0.2 to 10 ha, were selected to sample leaves throughout our study (Fig. 3). At least two sampling sites within a different plant hardiness zone, and spaced at 30 to 40 km between each other, were established. The geographic location of each site was recorded using a handheld global positioning system device.
Sampling dates

Growth of kudzu along the transect was assessed once in spring, summer, and autumn of 2003 and 2004. For the length of the transect, it took 5 to 6 days to drive through it and collect the samples in all sites. Spring assessment was carried out from 7-11 April in 2003 and 2004. Summer and autumn assessments were carried out from 7-12 May and 7-12 October, respectively, in 2003 and from 25-30 June and 7-12 September in 2004.

The dates for the first assessment in both years of study were fixed at early April in an attempt to monitor not only the foliar growth, but also the bud break of kudzu plants at different latitudes along the sampling route. According to kudzu botanical references (7,16) and feedback from weed scientists acquainted with the kudzu phenology, it was determined that early April was a suitable time to capture bud break of kudzu plants at different latitudes.

Sample collection, foliar area measurements, and green leaf area index calculation

On each sampling date, samples of kudzu leaves were collected from each location. A round 1858-cm² quadrat was arbitrarily thrown into the kudzu stand; live kudzu leaves within it were handpicked, placed in labeled plastic bags, and transported in coolers to an Iowa State University laboratory; five subsamples were obtained per location. Foliar area measurements were determined in the laboratory using a leaf area meter (Li-Cor Model LI-3100, Lincoln, NE). Measurements of foliar area from the five subsamples were averaged to obtain a mean value of foliar area per location and date. Then, green leaf area index (GLAI) was calculated as FA/1858, where FA is the mean foliar area (in cm²) per location, and 1858 corresponds to the area of the quadrat in cm².

Bud break of kudzu plants and seasonal variation of green leaf area index

During the 2003 and 2004 April sampling periods, kudzu mats in some of the northern latitude sites of the transect were encountered exhibiting little or no growth. Often, dormant vines or hardly sprouting shoots were observed. In the latter situation, we recorded number and length of new shoots and number of opened trifoliate leaves. Kudzu leaves for foliar area measurements were collected whenever well developed leaves were present. Data
of GLAI from the spring, summer and autumn samplings in 2003 and 2004 were plotted against latitude to characterize the seasonal foliar fluctuations and compare them for both years of study. Scatter plots of GLAI from the first sampling period for both years suggested a linear trend when excluding the sites in which kudzu vines had not broken dormancy and no grown shoots or leaves were observed. Discarding such observations, linear regression was used to describe the dynamics of GLAI versus latitude in early spring for the two years of study.

Assessment of the role of kudzu in onset and spread of ASR epidemics

A theoretical assessment of the role of kudzu in the occurrence and northward spread of ASR in the U.S. was made from estimations of kudzu foliage appearance time, seasonal GLAI increments, and potential amount of urediniospores produced per kudzu area. We analyzed the data of GLAI of kudzu from Wechsler’s work (29) in relation to accumulated growing degree days (GDD) to investigate relationship between these two variables and explore a possible GDD predicting potential. Daily average temperature data were obtained from the National Climatic Data Center for the closest weather station to Athens, GA for year 1976, where and when Wechsler’s work was carried out. Daily GDD were calculated using a base temperature = 5°C. Plots of both raw and logarithmically transformed data suggested a curvilinear relationship between GDD and GLAI. Then, a quadratic or second degree polynomial model of the form $Y = \beta_0 + \beta_1X_i + \beta_2X_i^2 + e_i$ was adjusted to these data to predict the GLAI as a function of GDD. Parameters of the model were estimated using the method of least squares in a SAS program (ver. 9.1; SAS Institute, Cary, NC). We anticipated use of this model to enable monthly estimations of GLAI for our 2003 and 2004 data sets, and to validate kudzu bud break and GLAI increments in some regions of the U.S.

The potential amount of ASR urediniospores produced per unit of kudzu leaf area was estimated under assumptions derived from previous works on ASR epidemiology (Table 1). This information was coupled with kudzu coverage (ha) in U.S. southern regions to delimit areas with potential for ASR occurrence in early spring.
Results

Bud break and seasonal development of kudzu green leaf area index

Between 7 and 11 April, in both years of study, kudzu plants had already sprouted and produced some foliage in several locations of the transect. New shoots of 2.0 ± 0.35 m long with several well-developed trifoliate leaves (GLAI between 0.1 and 1.0; Fig. 4. A and B) were observed during this period in southern LA and southern MS. Kudzu vines with one or two developing trifoliate leaves were observed at sites up to 34.0 N latitude in 2003 and up to 35.0 N latitude in 2004 (Fig. 5-A). Between the latitudinal range 35 and 37.0 N, kudzu vines remained dormant during the April sampling period in both years of study (Fig. 5-B).

Linear regression described well the variation of GLAI with latitude in the April surveys in the two years of study. Kudzu GLAI decreased linearly with increasingly northern latitude (R^2 and regression coefficient = 0.750 & –0.097 for 2003, and 0.654 & –0.384 for 2004) (Fig. 6). Rate of GLAI decrease was higher in 2004 than in 2003, as indicated by the regression coefficients. Kudzu GLAI in early spring of 2003 was < 1.0 at all locations of the transect while in 2004 GLAI reached 2.5 in southern LA.

In summer, kudzu GLAI increased in all locations, reaching values larger than 2.0 in both years (Fig. 7-A and B). Maximum GLAI observed in 2003 was 4.2 in a location in southern MS, while in 2004 maximum value was 5.1 and corresponded to a location of northern MS. In autumn, although the GLAI slightly increased, the GLAI variation with increasing latitude was minimal in both years of study (Fig. 7 A and B). Maximum values of GLAI were identified around 35.0 N latitude.

Prediction of kudzu bud break and GLAI, and estimation of urediniospore production

The polynomial equation that emerged from the analysis of kudzu GLAI data from Wechsler’s work was y = -2E-06x^2 + 0.0087x – 2.5296. This model was effective (R^2 = 0.90) at predicting the GLAI with accumulated GDD (Fig. 8). Model fitness was verified with the graph of residual versus predicted values (no defined pattern of points was evident), standard error value, and p-value (p = 0.02). With this equation it was predicted that kudzu shoots start breaking dormancy when accumulated GDD reaches 313 units. First derivative of the equation indicated that kudzu GLAI reaches the maximum value at 2175 accumulated GDD
and then starts decreasing. Using this model, it was determined that kudzu vines could break dormancy prior to March 1\textsuperscript{st} in areas of southern and central FL and southern LA (Table 2). The daily amount of ASR urediniospores produced per 1m\(^2\) of kudzu foliage covered area was estimated at 1.54 x 10\(^6\) (Table 1).

**Discussion**

The information collected in this study constitutes the first quantitative description of the phenology of kudzu along a likely route for spread of ASR from southern to the Midwestern soybean growing areas in the U.S. The basic questions aimed to answer were: when, where, and how much foliar area of kudzu would be available for infection with *P. pachyrhizi* in a season along a potential pathway for spore transport from southern to northern regions of the U.S. Sprouting and growth of kudzu were monitored at several latitudinal zones in an attempt to answer such questions. Sampling data revealed that bud break of kudzu plants in the two consecutive years of study occurred as early as April 7 (day of year 97) from southern LA (29.8 N) to northern MS (35.0 N). Further, results of modeling predicted that bud break of kudzu plants occurs when accumulation of GDD is around 313 units (base T=5°C: minimum temperature that kudzu plants can withstand). It was predicted that in southern MS (31.5 N latitude), kudzu plants broke dormancy in the second and first week of March in 2003 and 2004, respectively. Evidently, in areas of further south, such as central and southern FL (28.0 and 26.0 N, respectively), kudzu plants break dormancy earlier in the season as higher temperatures occur earlier in the year in those regions. Moreover, depending on the mildness of the winter, kudzu plants in central and southern FL could remain with green foliage year round.

The importance of the early kudzu foliage availability in the occurrence of ASR can be better comprehended with the understanding of two additional relevant aspects: (i) the interaction soybean-*P. pachyrhizi* and subsequent field occurrence of ASR at different phenological phases) and, (ii) the timing when developmental stages of soybean crops occur in the U.S. based on planting and harvesting dates. Susceptibility of soybean plants to the attack of the ASR fungus is reported as being related to plant and leaf age (15) and maturity
duration (27); consistently, field appearance of ASR has been associated to the development stage R1 (beginning of flowering) and later maturation stages (26). In the U.S., soybean is a summer crop whose planting dates in major production regions vary from early May to late June (19), except in the southern states of AR, LA, GA, MS, and AL, where planting dates vary from late March through June (9). Regardless of maturity group, soybean crops reach stage R1 at 42 days after planting, on average (9). This means that if a soybean cultivar is planted as early as March 31, it would reach R1 by approximately May 12. In more northerly soybean-producing states, reproductive stage R1 occurs later in the season, ranging from early June to early July. If ASR occurrence in the field indeed appears at the beginning or during reproductive stages of soybean, then mid-May could be a critical period for epidemic occurrence in the earliest planted soybean crops. Large amounts of inoculum produced early in the season on kudzu or other alternative hosts would therefore represent a considerable risk of disease spread to northern areas. The present study provides a clearer picture of the amount of foliar area of kudzu available in early spring for *P. pachyrhizi* activity in the corridor (lower Mississippi valley) along which the pathogen may disseminate northward.

To our knowledge, data of kudzu GLAI fluctuations along different latitudinal zones are nonexistent. We found that GLAI in early spring decreases linearly with increasing northern latitude, and it increases abruptly from April to May in southern LA and MS.

Increase in the amount of initial inoculum will be a key factor in future severe ASR epidemics, if any occur in the U.S. (21). Therefore, identification of source areas for inoculum build up and early spore deposition is crucial to assess disease risk for the major U.S. soybean growing regions. Our work provides a more solid basis to help in the identification of potential areas for inoculum increase, based on areas where kudzu foliage is more likely to become available early in the season. Using the quadratic model selected in this study, for example, a major risk zone for urediniospores deposition on kudzu patches would correspond to kudzu areas in which the accumulated GDD surpasses 313.0 units in early March (considering a base T=5°C). This range would encompass southern and central FL and southern LA. Considering that there are > 5000 ha covered by kudzu in FL and that the weather is favorable for ASR occurrence early in the season, FL areas are determinant in
the increase of ASR inoculum. Our results add some host quantitative information to the assessment carried out by Pivonia and Yang, who found that stress indices would allow overwintering of the pathogen in southern FL.

In summary, this study focused on the description of the phenology of kudzu, an abundant and widely distributed weed whose suitability to host *P. pachyrhizi*, causal agent of ASR, has been confirmed in the U.S. Our assessments indicate that kudzu foliage development precedes that of soybean crops in the U.S. That is, developed kudzu foliage becomes available for ASR onset when soybean crops are not still even planted. Particularly, in southern and central FL, high amounts of kudzu foliage (GLAI>1.0) could be observed as early as January 25 (Table 2), depending on the mildness of the winter. Our data are insufficient to make exact assessments of the extent of ASR spread risk to the Midwestern regions. However, they provide a clear picture of the GLAI of kudzu that can be available for ASR foci initiation and inoculum build up in regions like FL, from where the pathogen could move to southern and central LA and the MS valley. These latter areas could be the starting point of a potential route for a rapid spread of the disease to the north central soybean growing regions of the U.S., as evident from the ASR spread pattern in the 2006 growing season.

**Acknowledgments**

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Literature cited


Table 1. Assumptions and description of variables used in this study to estimate the amount of Asian soybean rust spores produced per kudzu area in early spring (April 1 to 15) in Natchez, MS (31.6 N latitude).

| i) | Kudzu leaves are susceptible to infection by *P. pachyrhizi* at any developmental stage and kudzu plants in all stands are equally susceptible. |
| ii) | GLAI of kudzu by April 10 in central LA and southern MS is 1.0. |
| iii) | By the time GLAI reaches 1.0, all the ground in a kudzu stand is covered by foliage, thus the probability of ASR urediniospores landing on kudzu foliage into a kudzu patch = 100%. (probability of spore interception after a spore shower). |
| iv) | Average amount of viable spores per lesion per day = 200 (Based on Yeh *et al.*, 1982). |
| v) | Estimated % of disease severity in the upper canopy layer = 0.5 % |
| vi) | Infection efficiency at highest disease level = 5% |

If GLAI = 1.0, \( \Rightarrow \) total area available for infection in 1 m\(^2\) = 1,000,000 mm\(^2\)

\[
\text{% of diseased area} = \left( \frac{1,000,000}{0.65} \right) = 5000 \text{ mm}^2
\]

Lesion size = 0.65 mm\(^2\)

Number of active lesions = 5000 mm\(^2\) / 0.65 mm\(^2\) = 7692.308

Number of spores.m\(^2\).day\(^{-1}\) = 7,692.308 x 200 = 1,538,462 \(\approx\) 1.54 \(\times\) 10\(^6\)

Production of spores.ha\(^{-1}\).day\(^{-1}\) (rate of spore release) on the upper canopy:

\[
1 \mu\text{g} = 400 \text{ spores}
\]

1,538,462 spores = 3846.154 \(\mu\text{g}\)

\(\Rightarrow\) 10,000 x 3846.154 \(\mu\text{g}\) = 38.5 grams

Production of spores.km\(^{-2}\).day\(^{-1}\) = 3.85 kg
Table 2. Weekly accumulation of growing degree days (GDD) and predicted increments of kudzu green leaf area index (GLAI) in U.S. southern regions. Predicted GLAI was calculated with the polynomial equation developed in this study.

<table>
<thead>
<tr>
<th>Regions and approximate latitude and altitude</th>
<th>Accumulated growing degree days (GDD) and predicted green leaf area index (GLAI) at weekly intervals in March</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>March 1</td>
</tr>
<tr>
<td>southern FL 26.06 N, 3.0 m</td>
<td>GDD 879.7</td>
</tr>
<tr>
<td></td>
<td>GLAI 3.58</td>
</tr>
<tr>
<td>central FL 28.43 N, 27.4 m</td>
<td>GDD 655.2</td>
</tr>
<tr>
<td></td>
<td>GLAI 2.31</td>
</tr>
<tr>
<td>southern LA 30.033 N, 7.6 m</td>
<td>GDD 389.5</td>
</tr>
<tr>
<td></td>
<td>GLAI 0.56</td>
</tr>
<tr>
<td>southern MS 31.62 N, 82.9 m</td>
<td>GDD 274.23</td>
</tr>
<tr>
<td></td>
<td>GLAI 0.0</td>
</tr>
</tbody>
</table>

- Temperature data correspond to year 2004. Daily temperatures data were obtained from the National Climatic Data Center.
- Base temperature used to calculate GDD = 5°C and accumulation counted from January 1st.
- Kudzu is reported in the counties where selected weather stations are located.
**Figure headings**

**Figure 1.** A) Distribution of kudzu (*Pueraria montana* var. *lobata*) and B) soybean (*Glycine max*) in the U.S. Data sources: for kudzu: Jewett Daryl, USDA, unpublished data. For soybean: NASS, 1997).

**Figure 2.** Reported spread pathways of wheat stem rust (*Puccinia graminis* f. sp. *tritici*) (solid blue arrows), southern corn leaf blight (*Bipolaris maydis*) (solid red arrow), and tobacco blue mold (*Peronospora tabacina*) (dashed green arrow) in the U.S.

**Figure 3.** Monitoring route and location of sampling sites where kudzu leaves were collected for measurements of green leaf area index (GLAI) in this study. Each location corresponds to an area of a kudzu stand of minimum 0.2 ha.

**Figure 4.** A) Kudzu plants at a location in southwestern Mississippi in April 7, 2004 (30.5 N latitude). B) Kudzu leaf showing size reached by April 7, 2004 in same location.

**Figure 5.** A) Kudzu shoots and developing trifoliate leaf in a location of northern MS (35.0 N latitude) in April 9, 2004. B) Kudzu patch in a location of TN (37.0 N latitude) on April 10, 2004. All vines were still dormant, kudzu plants had not broken dormancy.

**Figure 6.** Variation of kudzu green leaf area index in early April explained by linear regression.

**Figure 7.** Dynamics of kudzu green leaf area index in spring, summer and autumn of 2003 (A) and 2004 (B) along a transect situated within the latitude range 29.5 and 37.0 N. Arrows indicate the latitudinal range in which no kudzu developed leaves were observed during first sampling period (April 9-11, for those particular sites). Three sites that were close to each other were averaged for better graphic representation.
Figure 8. Graph and equation of quadratic polynomial model adjusted to data of kudzu GLAI collected in Athens, GA, in 1976 (29).
Figure 1. A and B.
Figure 4. A and B.
Figure 5. A and B.
Figure 6.

\[ y = -0.0973x + 3.3207 \quad R^2 = 0.7504 \]

\[ y = -0.384x + 13.147 \quad R^2 = 0.6543 \]
Figure 7. A and B.
Figure 8.

\[ y = -2E-06x^2 + 0.0087x - 2.5296 \]

Accumulated growing degree days

Green leaf area index
CHAPTER 4. DELINEATION OF THE OCCURRENCE, DISTRIBUTION, AND ANNUAL AVAILABILITY OF POTENTIAL HOST OF *Phakopsora pachyrhizi* IN CENTRAL AMERICA, THE CARIBBEAN, AND MEXICO.

ABSTRACT

More than 90 legume species have been reported as hosts for *Phakopsora pachyrhizi*, the causal agent of Asian soybean rust (ASR). Only a few of the reported host species, however, are suitable to infection, symptom induction, and abundant sporulation of the pathogen and therefore, considered to be functional in the epidemiology of ASR. Occurrence, distribution and annual availability of six legumes species, reported as suitable hosts for *P. pachyrhizi*, were investigated for Central America, the Caribbean, and Mexico. A total of thirteen countries were examined for the presence of cowpea (*Vigna unguiculata*), hyacinth bean (*Lablab purpureus*), kudzu (*Pueraria montana var. lobata*), pigeon pea (*Cajanus cajan*), soybean (*Glycine max*), and yam bean (*Pachyrhizus erosus*). Information on occurrence, growing areas, and growing periods for each host was obtained from perusal of bibliographic sources, online databases, reports from agricultural agencies and institutions, as well as from direct communication with Agronomists familiar with these plant species in the investigated countries. With the exception of kudzu, all the legumes considered in this study were found to occur in Central America, the Caribbean, and Mexico. Presence of other hosts, regarded as being of minor importance in the epidemiology of ASR, was also confirmed and documented. In this work, maps of growing areas, generated in ArcGIS 9.0, and cultivation period schemes of each of the six hosts investigated are presented and the importance of these legumes species in the likely seasonal reintroductions of ASR to the U.S. is discussed.
Introduction

Asian soybean rust (ASR) is a polycyclic disease caused by *Phakopsora pachyrhizi*, a biotrophic fungus that attacks more than 90 cultivated and wild hosts (10,18,33,38,41,56). The disease has caused significant economic losses in many soybean-producing regions of the world (10,40,86,87). In Uganda and Brazil, for example, losses from total harvest have been estimated at 60 to 80% and up to 100%, respectively (40,87). In the U.S., expected economic losses to U.S. growers and consumers were estimated at $640 million to $1.3 billion annually, after pathogen establishment (16).

In the continental U.S., ASR was first detected in November 2004 in Louisiana (71). The disease reappeared in the 2005 and 2006 growing seasons in several southern states and as far as north as Illinois and Indiana (81). As of the middle of July in the 2007 growing season, the disease has been found in Alabama, Florida, Georgia, Louisiana, Mississippi and Texas (81). Nonetheless, all outbreaks of the disease have been mild and confined to zones below 38ºN latitude. Likely factor for the restricted range in the U.S. are the lack of live hosts caused by seasonal dieback of foliage due to winter temperatures.

Using climate modeling, Pivonia and Yang (2004) predicted that in the U.S., winter temperatures would restrict survival and prevalence of *P. pachyrhizi* to a few southern states, such as Florida and Texas. Yet, they also found that the pathogen can survive and establish year-round in Central America, the Caribbean and Mexico regions (60). Annual prevalence of ASR in these regions may be one risk factor for severe ASR epidemics in the U.S. since it would constitute inoculum sources that could supplement early and continuous incursions of urediniospores to target areas of the U.S. each season (76). Moreover, the seasonal reintroduction or migrations of pathogenic races of *P. pachyrhizi* to the U.S. could be a factor complicating efforts to develop durable resistance in soybean varieties, which up to now, is one of the most promising methods to cope with ASR. The potential of areas in Central America, the Caribbean, and Mexico as origin points for the aerial introduction of plant pathogenic fungi into the U.S. is confirmed from the introduction of other phytopathogenic fungi (37,62,76,85).

For a better delimitation of pathogen establishment regions and assessment of likely reintroductions, identification of host areas is fundamental, since *P. pachyrhizi* affects many
plant species (41, 61, 67, 77). Among the more than 90 legumes that have been reported as hosts for *P. pachyrhizi* (10, 80), only a few are suitable to infection, symptom induction, and abundant sporulation of the pathogen and therefore, considered to be functional in the epidemiology of ASR (10).

In the U.S., kudzu is considered a major host in the epidemiology of ASR because of its abundance and wide distribution (9, 31), and confirmed susceptibility to *P. pachyrhizi* (7, 81). In other regions, such as Central America, the Caribbean, and Mexico, several hosts of *P. pachyrhizi* are known to occur, but research or documented information regarding the species that are present, growing areas, and growing periods, is inexistent or incomplete.

The **objective** of this study was to delineate and document the occurrence, distribution, and annual availability of cowpea (*Vigna unguiculata*), hyacinth bean (*Lablab purpureus*), kudzu (*Pueraria montana var. lobata*), pigeon pea (*Cajanus cajan*), soybean (*Glycine max*), and yam bean (*Pachyrhizus erosus*) in Central America, the Caribbean, and Mexico. Such hosts are reported to be suitable hosts for *P. pachyrhizi*.

**Materials and methods**

**Definition of concepts**

In this section, we introduce definitions of a few particular terms, most of which will be used hereafter in this paper. The purpose is to make clear distinctions between such terms, inasmuch as the meaning and usage of each can be sometimes confusing in the reading of literature on soybean rust.

**Host.** Biologically, “host” is defined as an organism that lodges a parasite and provides the nutrients for a parasite to develop and multiply (42, 51). In a phytopathological context, “host” is defined as a plant species on which a plant pathogen lodges or harbors (2). Often, the term “host” is used in the sense of susceptibility (42) and sometimes only to refer to a plant that a pathogen infects. In this study, the term “host” is used as a generic term to refer to a plant species on which the fungus *Phakopsora pachyrhizi*, causal agent of ASR, can lodge, whether or not the host will allow the development of sporulating lesions or cause a delay or interruption in the duration or completion of the disease developmental stages.
Alternate host. One of the two botanically unrelated hosts of a heteroecious rust on which the rust fungus develops to complete its life cycle (2,42). Typically, the host of non-economic importance is called “alternate host” while the host of economic importance is called “primary host” (2,42). Alexopoulos et al. (1996) refer to “primary host” as the host on which the telial stage is produced (3).

Alternative host. One of the few or many hosts that certain species of pathogens can have and that is attacked when other hosts are not present.

Suitable host. The term “suitable host” has not been previously discussed in the phytopathological literature. In this study, we follow Bromfield’s rationale (10) and conventionally use the term “suitable host” to designate a plant species reported to allow establishment of infection by \emph{P. pachyrhizi}, support normal ASR symptom development and subsequently, abundant sporulating lesions of the pathogen. Thus, a suitable host has epidemiological importance, which means it can be functional in the initiation and development of an epidemic of ASR (10).

Selected hosts and selection criteria

Six legume species: cowpea (\emph{V. unguiculata}), hyacinth bean (\emph{L. purpureus}, formerly known as \emph{Dolichos lablab}), kudzu (\emph{P. montana} var. \emph{lobata} = \emph{P. lobata}), pigeon pea (\emph{C. cajan}), soybean (\emph{G. max}), and yam bean (\emph{P. erosus}) were considered for this study (Fig. 1). Two major criteria in selection of these species were that (i) they are confirmed to be suitable hosts of \emph{P. pachyrhizi} (10). Suitability has been consistently observed not only in artificial inoculations (68,70), but also in natural occurrences (18,33,41,84). The second criterion for selection was that, with the exception of kudzu, all of them are cultivated species, so if they indeed occur in Central America, the Caribbean, or Mexico the appearance of ASR on any of these hosts would be more likely to be reported.

Geographic regions examined

Three geographic units: Central America, the Caribbean, and Mexico (13 countries in total), were investigated for the presence of the six selected hosts in this study (Fig. 2). For Central America, investigation encompassed Panama, Costa Rica, Nicaragua, Honduras, El Salvador, Guatemala, and Belize (Fig. 3). For the Caribbean, research focused on Cuba,
Dominican Republic, Haiti, Jamaica, and Puerto Rico (Fig. 4). For Mexico, search emphasis was put on the following six southern and central eastern states: Campeche, Chiapas, Quintana Roo, Yucatán, Tabasco, Veracruz and Tamaulipas (Fig. 5).

**Data collection**

Bibliographical sources were searched for reports or information that suggested the occurrence (presence), cultivation areas (local and regional acreage), and cultivation periods (annual availability) of each selected host in the 13 countries considered. Focus was on books of the flora of each country, botanical manuals, compendia of leguminous plants, agronomical bulletins, scientific reports, and scientific journals from the countries considered. Complementary information on distribution, local and regional acreage, and growing seasons was obtained from online databases of FAO and the Department of Agriculture of each investigated country, as well as from other agricultural agencies and institutions. Direct communication with agronomists and botanists from several of the regions investigated, and familiar with the local flora and crops, helped obtain additional data and verify information such as planting dates, growing season of each crop, and local acreage. The period for which data, reports, and information were collected was 1995-2005.

The information collected was organized in a MsExcel database that contained name of localities (geographically equivalent to U.S. counties) where hosts were found to be reported. Respective approximate geographic coordinates were obtained using ArcGIS 9.0 computer program. Subsequently, maps of distribution of each host were generated using ArcMap from ArcGIS 9.0 software. Schematic representations of the range of planting and harvesting dates of each legume in each region were also created.

**Results and discussion**

**Occurrence of selected hosts in the continental units examined**

Five out of the six hosts considered in this study were found to be reported in Central America, the Caribbean, and Mexico: cowpea (*V. unguiculata*), hyacinth bean (*L. purpureus*), pigeon pea (*C. cajan*), soybean (*G. max*), and yam bean (*P. erosus*). Kudzu (*P.
montana var. lobata) is not reported in any of those geographic regions. In such regions, these hosts are known with different common Spanish names (Table 1).

**Occurrence and distribution of selected hosts in Central America**

Cowpea, hyacinth bean, pigeon pea, soybean, and yam bean are reported to occur in all the Central American countries examined (15,19,28,35,45,46,58,66,74,78)(Table 2). Precise delimitation of the distribution of these hosts is complicated since the species are spread throughout many zones and localities of each country.

Cowpea is grown extensively in Panama as a regular crop each season, being grown on almost 13,000 ha (23,24,25). Hyacinth bean is grown in most of the Central American countries as a sustainable crop (15,30,34,44,54,64). Records about its distribution and abundance were not available. Pigeon pea occurs in all the countries of Central America (13,43,50,65,79,88), but only in Panama is it grown every season (24). According to FAO (27), 4169.0 ha of pigeon pea were planted in Panama in 2004. Soybean is also reported to occur in all countries (1,4,5,12), but only in Guatemala is it grown commercially. In Costa Rica, soybean is not produced commercially to date, though it is currently acquiring importance as forage crop and is grown in some zones of the Provinces of Heredia and Guanacaste (8,52, Rodríguez, personal communication). In Panama, there are no recent reports on soybean production. Based on FAO databases (27), 130 ha of soybean were planted in 2004. Information about localities where growing area occurs was not available.

Yam bean (P. erosus) is reported to occur in all the Central American countries (11,26,29,49,53,73,82,89), except in Panama (Fig. 6). Three cultivated species of yam bean are reported in Central America: Pachyrhizus erosus, P. ahipa, and P. tuberosus (73). The species P. erosus, also known as Mexican yam bean, is the most abundant of the three species and occurs mainly from Costa Rica to Belize either as a crop or wild populations. The major zones where yam bean occurs are concentrated mainly in the Pacific side areas of Costa Rica, Honduras, El Salvador and Guatemala (Fig. 6). Only in the latter two countries is it regularly planted each season. In addition to the three cultivated species, two wild species of yam bean (P. ferrugineous and P. panamensis) occur also in some regions of Central America (73). The latter species (P. panamensis) is native to Panama (73).
Other species of legumes, reported in the past as hosts of *P. pachyrhizi* (38,41,67,80), were found to occur in many areas of the Central American countries. These species include common beans (*Phaseolus vulgaris*), lima bean (*Phaseolus lunatus*), tropical kudzu (*Pueraria phaseoloides*), royal ponciana (*Delonix regia*), velvet bean (*Mucuna* spp.), canavalia bean (*Canavalia ensiformis* and *Canavalia* spp.) and desmodium (*Desmodium* spp.) (6,34,39,49,69,75,83). Within this additional list, common beans are grown extensively in all the countries. The rest of the crops are used as cover crops, green manures or as forage in some cropping seasons. Tropical kudzu for example, is used as cover crop in oil palm plantations in Costa Rica and intercropped with citrus in Honduras (15).

**Occurrence and distribution of selected hosts in the Caribbean**

With the exception of kudzu (*P. montana var. lobata*), the other five hosts considered in this study are grown in the Caribbean islands examined (Table 3). Cowpea and pigeon pea are the predominant hosts in terms of the area grown, particularly in the Dominican Republic, Haiti and Puerto Rico (Fig. 7) (27). In 2004, grown area of cowpea and pigeon pea in the Dominican Republic was reported at 45,000 and 13,000 ha, respectively (27). In Haiti and Puerto Rico, grown area of pigeon pea in 2004 was estimated at 6,500 and 750 ha, respectively (27). In Cuba, pigeon pea is used as forage (57) and medicinal plant (32). Hyacinth bean and yam bean are minor crops in the five Caribbean islands examined and are marginally adapted in a few areas and seasons. As far as soybean is concerned, Cuba is the only country in the Caribbean where soybean is large-scale cultivated, either for grain for the national market and for forage (21,22,48,55). Information about the soybean grown area in Cuba was unavailable, but it was found that soybean is cultivated in several provinces of the country. In Central and southern provinces, the major producing areas, soybean is grown three seasons per year (Despaigne-Olguin, personal communication). Soybean in the western part of Cuba is used as forage. In Puerto Rico, soybean is not grown commercially, but only in experimental stations.
Occurrence and distribution of selected hosts in Mexico

Cowpea, hyacinth bean, pigeon pea, soybean, and yam bean are reported to occur in Mexico (20,47) (Table 4). The species of kudzu P. montana var. lobata, is not reported in the country, though the tropical kudzu species (P. phaseoloides), reported in the past as a host of P. pachyrhizi (18), is grown in some zones of Peninsula of Yucatan and Veracruz for forage purposes (59) or implemented as cover crop (Martinez-Rivera, personal communication). Cowpea, hyacinth bean, and pigeon pea are crops generally adapted to marginal growing conditions for subsistence purposes and in other instances they are used as cover crops (36,63). All of them are grown in a small scale (Fig. 8).

From all of the hosts investigated, soybean is the only crop that is grown commercially and in the largest scale. In the country, soybean is grown in the north central part in Tamaulipas and San Luis Potosi states, in the southern part in Campeche and Chiapas and in the northwestern part in Sinaloa state (Fig. 9). In the country, Tamaulipas is the largest soybean producing state.

Growing periods of selected hosts in Central America, the Caribbean, and Mexico

The following schemes represent the most likely growing periods of the leguminous crops considered in this study, based on the ranges of planting and harvesting dates, in the Central American and Caribbean countries, and Mexico. It is difficult to determine with accuracy the dates on which these crops are planted since that varies from region to region and from locality to locality, even within a same country. This aspect is strongly influenced by the latitude and rain regimes in zones where the crops are established. In Honduras, for example, in the Atlantic coast, some of these species are intercropped with corn in December, while in central regions they are established in June at the latest to harvest their seeds in March (Flores-Barahona, personal communication). Also, some of the crops are only adopted in certain seasons by a few farmers in sustainable agriculture systems. Therefore, it is possible to find them in a growing season of the year in a certain locality and not in the next year season.
Central American countries

Belize

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</table>


Note: in Belize, climatic conditions allow to plant soybean from June to September for the first season and from October to November for the second or less important growing season, which is destined mainly for seed production.

Fig. 10-A. Growing season (likely period of host availability) of the selected hosts in this study, in Belize, based on range of planting and harvesting dates.
### Costa Rica

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<th>Nov</th>
<th>Dec</th>
<th>Grown area (ha)</th>
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</thead>
<tbody>
<tr>
<td>Cowpea</td>
<td>![Range of planting dates]</td>
<td>![Range of harvesting dates]</td>
<td>![Likely period of host availability]</td>
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<td></td>
</tr>
<tr>
<td>Hyacinth bean</td>
<td>![Range of planting dates]</td>
<td>![Range of harvesting dates]</td>
<td>![Likely period of host availability]</td>
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<tr>
<td>Pigeon pea</td>
<td>![Range of planting dates]</td>
<td>![Range of harvesting dates]</td>
<td>![Likely period of host availability]</td>
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<tr>
<td>Soybean</td>
<td>![Range of planting dates]</td>
<td>![Range of harvesting dates]</td>
<td>![Likely period of host availability]</td>
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<tr>
<td>Yam bean</td>
<td>![Range of planting dates]</td>
<td>![Range of harvesting dates]</td>
<td>![Likely period of host availability]</td>
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</table>

**Sources:** SEPSA, 2003 (Secretaría Ejecutiva de Planificación Sectorial Agropecuaria); Carlos Rodríguez, University of Costa Rica.

**Note:** Pigeon pea varieties grown in Costa Rica are early maturing type and are used for cover crop and forage; soybean is grown for forage.

**Fig. 10-B.** Growing season (likely period of host availability) of the selected hosts in this study, in Costa Rica, based on range of planting and harvesting dates.
El Salvador

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<th>Grown area (ha)</th>
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<td>Soybean</td>
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<td>NA</td>
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</tbody>
</table>

Range of planting dates
Range of harvesting dates
Likely period of host availability
NA Not available

Sources: Ministry of Agriculture, El Salvador (2005); FAO (2005).
Note: pigeon pea corresponds to early maturing varieties.

Fig. 10-C. Growing season (likely period of host availability) of the selected hosts in this study, in El Salvador, based on range of planting and harvesting dates.
Guatemala

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<td>Pigeon pea</td>
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<td>Yam bean</td>
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<td>NA</td>
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</tbody>
</table>

Range of planting dates
Range of harvesting dates
 Likely period of host availability
NA Not available

Sources: Ministry of Agriculture, Guatemala (2005).
Note: pigeon pea corresponds to early maturing varieties.

Fig. 10-D. Growing season (likely period of host availability) of the selected hosts in this study, in Guatemala, based on range of planting and harvesting dates.
**Honduras**

<table>
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<td>Hyacinth bean: NA</td>
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<td>Pigeon pea: NA</td>
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<td></td>
<td></td>
<td>1450</td>
<td>Soybean: 1450</td>
</tr>
</tbody>
</table>

- Range of planting dates
- Range of harvesting dates
- Likely period of host availability
- NA Not available

Sources: Ministry of Agriculture, Honduras (2005).

Fig. 10-E. Growing season (likely period of host availability) of the selected hosts in this study, in Honduras, based on range of planting and harvesting dates.
Nicaragua

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<th>Grown area (ha)</th>
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<td>NA</td>
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</tbody>
</table>

Sources: Direction of Statistics of the Ministry of Agriculture, Animal Research, and Forestry (MAGFOR).
Note: pigeon pea corresponds to early maturing varieties type and is used for cover crop and forage, Hyacinth is used as forage.

Fig. 10-F. Growing season (likely period of host availability) of the selected hosts in this study, in Nicaragua, based on range of planting and harvesting dates.
## Panama

<table>
<thead>
<tr>
<th>Grown area (ha)</th>
<th>Jan</th>
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<tbody>
<tr>
<td>Cowpea</td>
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<td>12.980</td>
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<tr>
<td>Hyacinth bean</td>
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<td>4169</td>
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<td>Soybean</td>
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<td>NA</td>
<td>130</td>
</tr>
</tbody>
</table>

- **Range of planting dates**
- **Range of harvesting dates**
- **Likely period of host availability**
- **NA** = Not available

### Sources:
- For cowpea and pigeon pea: Ministry of Agriculture of Panama, VI National Agricultural and Animal Census, Final results, 2003, General Direction of Statistics and Census, Panama.
- For soybean grown area: FAO (2005).
- Note: planting dates correspond to the dry region of Panama (Los Santos).
- Cultivated pigeon pea is early maturing varieties type.
- First planting dates of cowpea (Aug-Sep) correspond to the region of the country (Central provinces); second correspond to the province of Chiriquí.

### Fig. 10-G.
Growing season (likely period of host availability) of the selected hosts in this study, in Panama, based on range of planting and harvesting dates.
The Caribbean (includes all the countries that were investigated in this unit)

<table>
<thead>
<tr>
<th>Month</th>
<th>Cowpea</th>
<th>Hyacinth bean</th>
<th>Pigeon pea</th>
<th>Soybean</th>
<th>Yam bean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
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</tr>
<tr>
<td>Dec</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Acreage</th>
</tr>
</thead>
<tbody>
<tr>
<td>45,360</td>
</tr>
<tr>
<td>NA</td>
</tr>
<tr>
<td>20,600</td>
</tr>
<tr>
<td>NA</td>
</tr>
</tbody>
</table>

Sources: FAO (2005), Ministry of Agriculture of The Dominican Republic, and Census of Agriculture for Puerto Rico.

Note: Area grown of cowpea corresponds to Haiti (45,000 ha) and Jamaica (360 ha). Pigeon pea data are for the Dominican Republic (13,000 ha), Haiti (6500 ha), Jamaica (1100 ha), and Puerto Rico (750 ha). Soybean corresponds to Cuba.

Fig. 11. Growing season (likely period of host availability) of the selected hosts in this study, in the Caribbean (Cuba, Dom. Republic, Haiti, Jamaica, and Puerto Rico), based on range of planting and harvesting dates.
### Mexico (includes the five states on which focus was placed)

<table>
<thead>
<tr>
<th></th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Area Grown (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cowpea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Hyacinth bean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Pigeon pea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>39,403</td>
</tr>
<tr>
<td>Yam bean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1963</td>
</tr>
</tbody>
</table>

Sources: for area grown to of soybean: Service of Agricultural and Livestock Information, Department of Agriculture (SAGARPA, 2005).

Fig. 12. Growing season (likely period of host availability) of the selected hosts in this study, in southern and central eastern states of Mexico, based on range of planting and harvesting dates.

In Tamaulipas, current leader state in soybean production in Mexico, soybean-growing areas are concentrated in south central and southeastern part of the state (Fig. 9-B).
Two cropping seasons of soybean occur in Tamaulipas: spring-summer and autumn-winter season. The spring-summer growing season starts at the end of June and ends in November (Fig. 13). It is in this season when the heaviest production occurs. The autumn-winter cropping season is from December to April, which is basically for seed production. The acreage planted in this season is minimum compared with that of the spring-summer season.

1) Spring–Summer Cropping season

<table>
<thead>
<tr>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>35 000 hectares</td>
</tr>
</tbody>
</table>

Range of planting dates

Likely period of host availability

2) Autumn-Winter Cropping season

<table>
<thead>
<tr>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>439 hectares</td>
</tr>
</tbody>
</table>

Range of planting dates

Likely period of host availability

Note: range of planting dates represents the grand average of the most common dates in the state.

Fig. 13. Soybean cropping seasons, range of planting and harvesting dates, and grown area in Tamaulipas state, Mexico.
Summary

This study documents for the first time, the occurrence, distribution and cultivation periods of cowpea (*V. unguiculata*), hyacinth bean (*L. purpureus*), pigeon pea (*C. cajan*), soybean (*G. max*) and yam bean (*P. erosus*) in regions of Central America, the Caribbean, and Mexico. Such leguminous crops are reported to be important hosts in the initiation and development of ASR epidemics in several regions where the disease is endemic (10).

To date, ASR has not been reported to occur on any of the hosts considered in this study, in Central America and the Caribbean, though the disease was found in soybean crops in Mexico in San Luis Potosí state in 2005 (14). Confirmation of the occurrence of the selected hosts in the regions investigated indicates that such regions could indeed constitute niches for Overseasing of *P. pachyrhizi*. Local and regional grown area of cowpea, hyacinth bean, pigeon pea, soybean, and yam bean also shows that the carrying capacity of these host areas could be sufficient for inoculum production for ASR to spread to the continental U.S. each year. One known case supporting this assertion is the introduction of sugarcane rust into the U.S. in 1979 (17) (introduction and seasonal reintroductions of tobacco blue mold to Florida from Cuba is another documented example (85)). Using backward trajectory analysis, it was convincingly elucidated that sugarcane rust introduction originated from the transoceanic movement of spores from the Dominican Republic (62), where a 1.6-ha sugarcane plantation was the presumed initial source of inoculum. Results of our study show that in the Dominican Republic, for example, more than 20,000 ha of cowpea are grown each year (27) and that the planted area to other legumes of ASR epidemiological importance exceeds 100,000 ha -at least one suitable crop is grown in a season each year.-

Overall, the potential of the examined regions in serving as source areas for inoculum production for ASR to spread to the U.S., either in a land bridging fashion or long-distance transport, is related to an overlapping of cropping and rainy season in each region. Further, potential should be assessed in terms of several other factors, including position of these crop areas with respect to prevailing winds or climatic events for spore take off, nearness to other host areas or sources for spore deposition, continuous availability of host during the year, and advance direction of a disease front. Susceptibility of host at a given locality is another factor
that should be quantified to estimate the amount of spores that can overcome the dilution caused by wind during a flight spore event to target areas.

The information presented in this study could serve as a reference guide to locate places to set up experiments with ASR alternative hosts, disease scouting efforts, as well as a guide to direct studies focusing in ASR spread or assessment of seasonal reintroductions to the U.S. Our study has also delineated some of the information needed for a more precise identification of areas for ASR establishment. If the risk of ASR reintroductions to the U.S. is to be assessed, this information would enable researchers to make better predictions of disease spread. Our findings particularly help in facilitating information concerning where initial inoculum sources would be more likely to be present each season, where disease outbreaks would occur, and how much inoculum could be produced in a given source area. The ability to identify and quantify potential zones for inoculum production would enhance our capability of predicting future incursions of ASR epidemics each season.

**Literature cited**


erosus) en la zona sur de Intibucá Honduras, C.A. Centro Internacional de Información sobre cultivos de cobertura. Tegucigalpa, Honduras.


73. Sorensen, M. 1996. Yam bean (*Pachyrhizus* DC.). Promoting the conservation and use of underutilized and neglected crops. 2. Institute of Plant Genetics and Crop Plant Research, Gatersleben/ International Plant Genetic Resources Institute, Rome, Italy.


and O. Toshiyuki-Hamawaki, eds. Uberlandia, Mato Groso, Brazil.


List of tables

Table 1. Most common local Spanish names of selected hosts in this study in the Central American countries, Mexico, Cuba, and Puerto Rico.  

Table 2. Record of the occurrence of the hosts of *P. pachyrhizi* selected for this study in the Central American countries.  

Table 3. Record of the occurrence of the hosts of *P. pachyrhizi* selected for this study in the Caribbean countries.  

Table 4. Record of the occurrence of the hosts of *P. pachyrhizi* selected for this study in southern and central eastern states of Mexico.
<table>
<thead>
<tr>
<th><strong>List of figures</strong></th>
<th><strong>Page</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 1. Images of the legume species considered for this study. A. cowpea, B. hyacinth bean, C. kudzu, D. pigeon pea, E. soybean, and F. yam bean.</td>
<td>94</td>
</tr>
<tr>
<td>Fig. 2. Geographic units in which the occurrence, distribution, and growing periods of the six selected hosts in this study were investigated.</td>
<td>95</td>
</tr>
<tr>
<td>Fig. 3. Countries that integrate Central America and on which investigation on the selected host species was focused.</td>
<td>95</td>
</tr>
<tr>
<td>Fig. 4. Countries of the Caribbean on which investigation on the selected host species was focused.</td>
<td>96</td>
</tr>
<tr>
<td>Fig. 5. Mexico and states in the country where investigation on the selected host species was focused.</td>
<td>96</td>
</tr>
<tr>
<td>Fig. 6. Distribution of selected hosts of <em>P. pachyrhizi</em> in this study, in the Central American countries.</td>
<td>97</td>
</tr>
<tr>
<td>Fig. 7. Distribution of selected hosts of <em>P. pachyrhizi</em> in this study, in the Caribbean countries examined.</td>
<td>97</td>
</tr>
<tr>
<td>Fig. 8. Distribution of selected hosts of <em>P. pachyrhizi</em> in this study, in southern and central eastern states of Mexico.</td>
<td>98</td>
</tr>
<tr>
<td>Fig. 9. A. Soybean-growing areas in Mexico, B. Soybean-growing areas in Tamaulipas state, Mexico.</td>
<td>99</td>
</tr>
<tr>
<td>Fig. 10. Growing season (likely period of host availability) of the selected hosts in this study, in Central America, based on range of planting and harvesting dates. A. Belize, B. Costa Rica, C. El Salvador, D. Guatemala, E. Honduras, F. Nicaragua, and G. Panama.</td>
<td>69</td>
</tr>
<tr>
<td>Fig. 11. Growing season (likely period of host availability) of the selected hosts in this study, in the Caribbean (Cuba, Dom. Republic, Haiti, Jamaica, and Puerto Rico), based on range of planting and harvesting dates.</td>
<td>76</td>
</tr>
<tr>
<td>Fig. 12. Growing season (likely period of host availability) of the selected hosts in this study, in southern and central eastern states of Mexico.</td>
<td>77</td>
</tr>
<tr>
<td>Fig. 13. Soybean cropping seasons, range of planting and harvesting dates, and grown area in Tamaulipas state, Mexico.</td>
<td>78</td>
</tr>
</tbody>
</table>
Table 1. Most common local Spanish names of selected hosts in this study in the Central American countries, Mexico, Cuba, and Puerto Rico.

<table>
<thead>
<tr>
<th>Cowpea</th>
<th>Hyacinth bean</th>
<th>Kudzu</th>
<th>Pigeon pea</th>
<th>Soybean</th>
<th>Yam bean</th>
</tr>
</thead>
<tbody>
<tr>
<td>caupí</td>
<td>frijol jacinto</td>
<td>kudzú</td>
<td>arveja</td>
<td>frijol soya</td>
<td>jicama</td>
</tr>
<tr>
<td>frijol caupí</td>
<td>frijol mungo</td>
<td></td>
<td>frijol arveja</td>
<td>soja</td>
<td></td>
</tr>
<tr>
<td>frijol alacín</td>
<td></td>
<td></td>
<td>frijol caballero</td>
<td>soya</td>
<td></td>
</tr>
<tr>
<td>frijol de bejuco</td>
<td></td>
<td></td>
<td>frijol de árbol</td>
<td></td>
<td></td>
</tr>
<tr>
<td>frijol de vara</td>
<td></td>
<td></td>
<td>frijol de palo</td>
<td></td>
<td></td>
</tr>
<tr>
<td>frijol de vaca</td>
<td></td>
<td></td>
<td>gandú or gandul</td>
<td></td>
<td></td>
</tr>
<tr>
<td>frijol vigna</td>
<td></td>
<td></td>
<td>guandú or guandul</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Record of the occurrence of the hosts of *P. pachyrhizi* considered in this study, in the Central American countries.

<table>
<thead>
<tr>
<th>Country</th>
<th>Cowpea</th>
<th>Hyacinth bean</th>
<th>Pigeon pea</th>
<th>Soybean</th>
<th>Yam bean</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Belize</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>1,2,3,4, 5,6,7</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>1,2,3,4, 5,6,7</td>
</tr>
<tr>
<td>El Salvador</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Present</td>
<td>1,2,4,5, 6,7</td>
</tr>
<tr>
<td>Guatemala</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Present</td>
<td>1,2,4,5, 6,7</td>
</tr>
<tr>
<td>Honduras</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>1,2,3,4, 5,6,7</td>
</tr>
<tr>
<td>Nicaragua</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>1,2,3,4, 5</td>
</tr>
<tr>
<td>Panama</td>
<td>Present</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>Absent</td>
<td>1,2,3,4, 5,6</td>
</tr>
</tbody>
</table>

Present. Indicates that the species is grown or has been reported to occur, at least within the last 11 years (1995-2006). Information about growing areas, growing season and abundance (hectares) was always available.

Reported. Indicates that the species is grown or has been reported to occur at least within the last 11 years (1995-2006), but information about growing areas, growing season, and/or abundance was not always available.

Absent. The species has not been grown or reported to occur within the last 11 years (1995-2006). The species may be present or have been reported in the past, but based on our examination, no recent records and information of any type regarding the presence of the plant species were found.

Other hosts. Includes common beans (*Phaseolus vulgaris*)¹, lima bean (*P. lunatus*)², tropical kudzu (*Pueraria phaseoloides*)³, royal ponciana (*Delonix regia*)⁴, velvet bean (*Mucuna spp.*)⁵, canavalia (*Canavalia spp.*)⁶ and desmodium species (*Desmodium spp.*)⁷.
Table 3. Record of the occurrence of the hosts of *P. pachyrhizi* considered in this study in the Caribbean countries.

<table>
<thead>
<tr>
<th>Country</th>
<th>Cowpea (<em>V. unguiculata</em>)</th>
<th>Hyacinth bean (<em>L. purpureus</em>)</th>
<th>Pigeon pea (<em>C. cajan</em>)</th>
<th>Soybean (<em>G. max</em>)</th>
<th>Yam bean (<em>P. erosus</em>)</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cuba</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>1,2,3,4,</td>
</tr>
<tr>
<td>D. Republic</td>
<td>Present</td>
<td>Reported</td>
<td>Reported</td>
<td>Absent</td>
<td>Reported</td>
<td>1,2,3</td>
</tr>
<tr>
<td>Haiti</td>
<td>Present</td>
<td>Reported</td>
<td>Present</td>
<td>Absent</td>
<td>Reported</td>
<td>2,3,4</td>
</tr>
<tr>
<td>Jamaica</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Absent</td>
<td>Absent</td>
<td>1,2,4,5,6,7</td>
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<tr>
<td>P. Rico</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>Reported</td>
<td>1,2,4</td>
</tr>
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</table>

Table 4. Record of the occurrence of the hosts of *P. pachyrhizi* considered in this study in southern and central eastern states of Mexico.

<table>
<thead>
<tr>
<th>State</th>
<th>Cowpea (<em>V. unguiculata</em>)</th>
<th>Hyacinth bean (<em>L. purpureus</em>)</th>
<th>Pigeon pea (<em>C. cajan</em>)</th>
<th>Soybean (<em>G. max</em>)</th>
<th>Yam bean (<em>P. erosus</em>)</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Campeche</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>1,2,3,4,5,</td>
</tr>
<tr>
<td>Chiapas</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
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<td>Reported</td>
<td>1,2,3,4,5,</td>
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<td>Reported</td>
<td>Present</td>
<td>Present</td>
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</tr>
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<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Present</td>
<td>1,2,4,5,6,</td>
</tr>
<tr>
<td>Veracruz</td>
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<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>1,2,3,4,5,</td>
</tr>
<tr>
<td>Yucatán</td>
<td>Reported</td>
<td>Reported</td>
<td>Reported</td>
<td>Present</td>
<td>Reported</td>
<td>1,2,3,4,5,</td>
</tr>
</tbody>
</table>

*Present.* Indicates that the species is grown or has been reported to occur, at least within the last 11 years (1995-2006). Information about growing areas, growing season and abundance (hectares) was always available. *Reported.* Indicates that the species is grown or has been reported to occur at least within the last 11 years (1995-2006), but information about growing areas, growing season, and/or abundance was not always available. *Absent.* The species has not been grown or reported to occur within the last 11 years (1995-2006). The species may be present or have been reported in the past, but based on our examination, no recent records and information of any type regarding the presence of the plant species were found. *Other hosts.* Includes common beans (*Phaseolus vulgaris*), lima bean (*P. lunatus*), tropical kudzu (*Pueraria phaseoloides*), royal ponciana (*Delonix regia*), velvet bean (*Mucuna spp.*), canavalia (*Canavalia spp.*), and desmodium species (*Desmodium spp.*).
Figure 1. Images of the legume species considered for this study. A. cowpea, B. hyacinth bean, C. kudzu, D. pigeon pea, E. soybean, and F. yam bean. Image sources: cowpea (www.fsagx.ac.be/pc/images/vigna_ungui_re.jpg); hyacinth bean (tolweb.org/.../Lablab_purpureus1111.200a.JPG); kudzu (picture taken by author in Central Florida); soybean (courtesy of Carlos Rodríguez, Costa Rica); yam bean (http://www.conabio.gob.mx/malezasdemexico/fabaceae/pachyrhizus-erosus/imagenes/habitat1.jpg).
Figure 2. Geographic units in which the occurrence, distribution, and growing periods of the six selected hosts in this study were investigated.

Figure 3. Countries that integrate Central America and on which investigation on the selected host species was focused.
Figure 4. Countries of the Caribbean on which investigation on the selected host species was focused.

Figure 5. Mexico and states in the country where investigation on the selected host species was focused.
Figure 6. Distribution of selected hosts of *P. pachyrhizi* in this study, in the Central American countries.

Figure 7. Distribution of selected hosts of *P. pachyrhizi* in this study, in the Caribbean countries examined.
Figure 8. Distribution of selected hosts of *P. pachyrhiz* in this study, in southern and central eastern states of Mexico.
Figure 9. A. Soybean growing areas in Mexico, B. Soybean growing areas in Tamaulipas state, Mexico. Adapted from SIAP, SAGARPA (2005).
CHAPTER 5. GENERAL CONCLUSIONS

Asian soybean rust (ASR) has occurred in the continental U.S. since autumn 2004. Although disease outbreaks in the U.S. have been mild and confined predominantly to zones below 38.0 N latitude, future severe epidemics, if any occur, may have a significant impact to U.S. soybean growers and consumers. Accurate identification of areas of survival and establishment of *Phakopsora pachyrhizi*, causal agent of ASR, is crucial to assess the disease onset potential and inoculum build up. Increase in the amount of initial inoculum will be key factor for occurrence of the disease and subsequent risk of spread to the major U.S. soybean producing regions. The objective of this research presented in this thesis was to characterize and assess the role of susceptible hosts of *P. pachyrhizi* from several regions in the occurrence of ASR epidemics in the U.S.

The study conducted provides valuable insights about the role of kudzu in the occurrence and subsequent spread of ASR to the north central areas of the U.S. Solid basis on the amounts of kudzu foliage, expressed as green leaf area index, in southern regions early in a growing season as well as along a likely route for northward transport of urediniospores were provided. Kudzu plants in southern and Central Florida can indeed harbor the ASR fungus year-round or become available for infection prior to the planting of soybean crops in the U.S.

Confirmation of the presence, distribution and growing periods of several legume species, reported as susceptible hosts to the ASR fungus, in regions of Central America, the Caribbean, and Mexico shows that those regions can constitute niches for overseasoning of *P. pachyrhizi*. The inoculum carrying capacity of these host areas, once they are impacted by ASR, can be sufficient for them to be potential sources that could supplement incursions of ASR urediniospores into the U.S. every growing season. Migrations or reintroductions of pathogenic races of *P. pachyrhizi* could complicate efforts to control disease using durable resistance.
Acknowledgments

I thank immensely my major professor, Dr. Xiao-Bing Yang, for having offered me the opportunity to study in his research program. Thanks for his support and generosity during my studies and for providing the freedom and encouragement for me to be able to develop ideas and thoughts all this time. Thanks also for his suggestions to improve the quality of this work.

Likewise, I thank greatly Dr. Mark L. Gleason, for his accurate comments, thorough review, critiques, and advice. Moments of interaction with him have often been a space for learning and educative growth.

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Finally, I am grateful to those individuals who have generously shared their knowledge and talent with me and whose names are not included in these acknowledgments accounting.
APPENDICES

List of people who assisted the author by providing information on occurrence and distribution of hosts of *P. pachyrhizi* in Central America, the Caribbean, and Mexico.

### Central America

<table>
<thead>
<tr>
<th>Name</th>
<th>Country</th>
<th>Institution name</th>
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<tbody>
<tr>
<td>Amy Wang (M.S.)</td>
<td>Costa Rica</td>
<td>Universidad de Costa Rica</td>
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<tr>
<td>Carlos Rodriguez (Agronomist)</td>
<td>Costa Rica</td>
<td>Universidad de Costa Rica</td>
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<tr>
<td>Enrique Villalobos (Dr.)*</td>
<td>Costa Rica</td>
<td>Universidad de Costa Rica</td>
</tr>
<tr>
<td>Rodolfo Araya V. (M.S.)</td>
<td>Costa Rica</td>
<td>Estación Exp. Fabio B., Universidad de Costa Rica</td>
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<td>Ana Gloria Flores (Agronomist)</td>
<td>El Salvador</td>
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<td>Fredy Romero (M.S.)</td>
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<td>Iowa State University</td>
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<td>Francisco Viteri (M.S.)</td>
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<td>Milton Flores Barahona</td>
<td>Honduras</td>
<td>Director of Cover Crops International Clearinghouse</td>
</tr>
<tr>
<td>Pablo E. Paz (Prof. of Agronomy)</td>
<td>Honduras</td>
<td>Escuela Agrícola Panamericana Zamorano</td>
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<tr>
<td>Moises Blanco</td>
<td>Nicaragua</td>
<td>Ministry of Agriculture</td>
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<tr>
<td>Jose A. Yau Quintero (Agronomist)</td>
<td>Panamá</td>
<td>Animal and Agricultural Research Institute</td>
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<tr>
<td>Mireya Correa (Botanist)</td>
<td>Panamá</td>
<td>Universidad de Panama (P), director of the herbarium, UP</td>
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### The Caribbean

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<td>Fernando Despaigne (Agronomist)</td>
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<td>Universidad de Santiago</td>
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<td>Cosme, J. Guzmán</td>
<td>Puerto Rico</td>
<td>Ag. Reliant Genetics Exp. Station</td>
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<tr>
<td>Pedro E. Márquez M. (M.S.)</td>
<td>Puerto Rico</td>
<td>Administrative Director of Agricultural Experimental Substation of Isabela. Universidad de Puerto Rico.</td>
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### Mexico

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<td>Antonio Morales Maza (M.S.)</td>
<td>México</td>
<td>Plant Science, Chapingo University</td>
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<tr>
<td>Fernando Urzua Soria (Dr.)</td>
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<td>Plant Parasitology, Chapingo University</td>
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<td>Hector Torres (Dr.)</td>
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<td>Julian Carrillo (Agronomist)</td>
<td>México</td>
<td>Farmer’s advisor in Tamaulipas state</td>
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<td>Moises Ramirez (M.S.)</td>
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<td>Narciso Martinez (Agronomist)</td>
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<td>Chapingo University</td>
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<td>Nicolás Maldonado M. (Agron.)</td>
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<td>INIFAP, Tamaulipas</td>
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<tr>
<td>Roberto Dzib (M.S.)</td>
<td>México</td>
<td>INIFAP, Estación Experimental Península de Yucatán</td>
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Online resources examined (includes Agricultural Research and Academic Institutions; some with translation into English)

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<tr>
<td>Brazil</td>
<td>EMBRAPA. Empresa Brasileira de Pesquisa Agropecuaria</td>
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FAO Statistical Databases (Agricultural data)


CAB International-Crop Protection Compendium

[http://www.cabi.org/index.asp]
[http://www.cabicompendium.org/NamesLists/CPC/lists/g1.htm]

Latin American Network Information Center (LANIC)

MetaBase: Bibliografía en red. A bibliographic source available in several libraries and documentation centers in Central America. It is an internet database that contains all bibliographic records of multiple Centers of Information of the participating countries.

Comisión Económica para Latin América y el Caribe (CEPAL). [http://www.eclac.cl/]
Economic Commission for Latin American and the Caribbean (ECLAC).
[http://www.eclac.cl/default.asp?idioma=IN]
Sistema de Información y Documentación Agropecuario de las Américas (SIDALC)
[http://orton.catie.ac.cr/default.htm]
In English: Agricultural Information and Documentation System of the Americas

Costa Rica
Centro Agronómico Tropical de Investigación y Enseñanza (CATIE)
INBio in internet

Honduras
Instituto Nacional de Estadística Honduras (INE)

Panama
Dirección de Estadística y Censos. Contraloría General de la República
Resultados finales Julio de 2003.

Corredor Biológico Mesoamericano del Atlántico Panameño (CBMAP).

Autoridad Nacional del Ambiente (ANAM)

Direccion de Estadistica y Censo, Panama
URL of the Ministry or Department of Agriculture of countries of Central America, the Caribbean, and Mexico examined in this study.

CENTRAL AMERICA

Belize
Ministry of Agriculture, Fisheries and Cooperatives
[http://www.agriculture.gov.bz/]

Costa Rica
Ministerio de Agricultura y Ganadería gobierno de Costa Rica (MAG)
[http://www.mag.go.cr/]

El Salvador
Ministerio de Agricultura y Ganadería El Salvador (MAG), C.A.
[http://www.mag.gob.sv/]

Centro Nacional de Tecnología Agropecuaria y Forestal (CENTA)
[http://www.centa.gob.sv//index.html]

Honduras
Secretaria de Agricultura y Ganadería, Honduras (SAG), C.A.
[http://www.sag.gob.hn/?CodSeccion=4]

Nicaragua
Ministerio Agropecuario y Forestal. República de Nicaragua
[http://www.magfor.gob.ni/ministerio/ministerio.html]

Centro Nacional de Información y Documentación Agropecuaria (CENIDA)-UNA.
[http://www.una.edu.ni/Cenida_sitio/index.html]
Panama
Ministerio de Desarrollo Agropecuario (MIDA)
[http://www.mida.gob.pa/]
IDIAP. Instituto de Desarrollo Agropecuario

THE CARIBBEAN
Dominican Republic
Secretaría de Estado de Agricultura (SEA)
[http://agricultura.gov.do/mestad.htm]
Estadísticas Agropecuarias

Haiti
[Ministère de l'Agriculture, des Ressources Naturelles et du Développement Rural]

MEXICO
Secretaría de Agricultura Ganadería Desarrollo Rural Pesca y Alimentación (SAGARPA)
[http://www.sagarpa.gob.mx/sdr/]
Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP)
[http://www.inifap.gob.mx/]
In English: National Institute of Forestry, Agricultural and Animal Research

Sistema de Información y Estadística Agroalimentaria y Pesquera (SIAP)
[http://www.siap.sagarpa.gob.mx/ar_comdeagr.html]

Anuario Estadístico de la Producción Agrícola (Fuente: SIACON)