Tropical Grasslands (1997) Volume 31, 408–416

Biodiversity, epidemiology and virulence of *Colletotrichum gloeosporioides*.
IV. Epidemiology of *Stylosanthes* anthracnose at the centre of host-pathogen diversity

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Abstract

Selected lines of *Stylosanthes guianensis*, *S. scabra*, *S. capitata* and *S. macrocephala* were established at field sites at Planaltina and Campo Grande in Brazil and at Carimagua and Caquetá in Colombia. Weather conditions at each site were monitored continuously using an automatic weather station. Data on anthracnose severity caused by *Colletotrichum gloeosporioides* were collected by visually assessing these lines at monthly intervals and analysed to study disease progress on susceptible and resistant lines in relation to weather variables. Anthracnose was most severe at Planaltina, followed by Carimagua, Campo Grande and Caquetá. *S. scabra* cv. Fitzroy, susceptible to all Australian races of *C. gloeosporioides*, was not the most susceptible at Carimagua and Caquetá. Relationships between anthracnose severity and weather variables were explored using multiple regression analysis. These explained between 30 and 95% of the variation in the severity of anthracnose on Fitzroy at the 4 sites. The study highlights the need for improved understanding of anthracnose epidemiology.

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Introduction

From its centre of origin in central and South America, *Stylosanthes* has been introduced to several other parts of the world. *Stylosanthes* are now the most widespread and successful tropical pasture legumes with several commercial cultivars available in Australia, central and South America and Asia. Commercial utilisation in Australia was severely constrained when several cultivars of *S. humilis* and *S. guianensis* were devastated by the anthracnose disease caused by *Colletotrichum gloeosporioides*. None of the current commercial cultivars in Australia is completely resistant to the pathogen.

Despite the earlier setbacks, Australia has been relatively successful in the commercial development of *Stylosanthes*. By comparison, the genus has not been used to any great extent at its centre of origin. Damage from anthracnose remains the major constraint to the productivity and persistence of *Stylosanthes*. Extensive germplasm evaluation has occurred in Colombia and Brazil and several cultivars have been released. Early testing included *S. guianensis* cultivars, Schofield, Endeavour and Cook, which were highly susceptible to anthracnose (Trutmann 1994). Evaluations in the llanos of Colombia have shown *S. capitata* as more resistant than many *S. guianensis* (Grof *et al.* 1979). A blend of 5 *S. capitata* ecotypes was released as cultivar Capica by Instituto Colombiano Agropecurio (ICA) for Colombia in 1983. In recent years, Capica has become susceptible at certain locations in Colombia (Trutmann 1994). More recently, some late-flowering and other breeding populations of *S. guianensis* from CIAT have shown resistance to anthracnose. Among the recent *S. guianensis* cultivar releases are Bandeirante, released in 1983 in Brazil, Pucallpa released in Peru, and Mineirâo, released in 1993 for the Brazilian Cerrados.

The wide range of pathogenic variation in *C. gloeosporioides* populations partly explains why anthracnose has been particularly damaging to *Stylosanthes* in central and South America. Evaluation of an extensive collection of *S. capitata* in Brazil and Colombia (Lenné *et al.* 1984) showed that over 85% of the accessions were susceptible in Brazil, compared with only 6% in Colombia. Evaluation of accessions, CIAT 1097 and CPAC 56, which showed promise during early evaluations, has been abandoned due to severe anthracnose damage during pre-release multiplication (Trutmann 1994). This indicates changes in pathogenic specialisation within the *C. gloeosporioides* population in the Brazilian Cerrados where *S. capitata* is endemic. Extensive qualitative and quantitative variation has been recorded in pathogenicity in the South American population (Miles and Lenné 1984; Lenné 1988). Use of isozyme (Lenné and Burdon 1990) and selection-neutral DNA-based genetic markers has revealed the extent of this variation in isolates from *S. guianensis*, *S. capitata*, *S. scabra* and *S. macrocephala* (Masel *et al.* 1993; He *et al.* 1995; Kelemu *et al.* 1997; Chakraborty *et al.* 1997).

In Australia, 2 types of anthracnose have been recognised since 1978. Type A attacks almost all species of *Stylosanthes* to produce discrete lesions on all aerial plant parts. Type B infects mainly *S. guianensis* to produce a blight of the terminal shoots (Irwin and Cameron 1978). This grouping could apply also to anthracnose in South America. Over 96% of isolates from *Stylosanthes* spp. other than *S. guianensis* produced typical Type A symptoms, and all of the 34 isolates from *S. guianensis* produced Type B symptoms in an international study of isolates from south-east Asia, Africa, Australia and South America (Davis *et al.* 1990).

Damage to *Stylosanthes* from anthracnose in the South American Savanna ecosystems is more severe than in the humid tropical forest regions. Lenné and Brown (1991) attributed this to weakly pathogenic isolates of *C. gloeosporioides* and bacterial antagonism in the humid tropical forests. Difference in weather conditions between these 2 contrasting ecosystems may partly explain the damage levels, especially if resistance in some of the cultivars is sensitive to environmental conditions (Boland 1994). Studies in Australia have shown that infection and inoculum dispersal of the anthracnose pathogen is dependent on favourable weather conditions (Chakraborty and Billard 1995). A surface wetness period of 36 h results in maximum severity (Irwin *et al.* 1984), although the pathogen can cause serious disease when surface wetness is interrupted for short periods (Chakraborty *et al.* 1990). Duration of relative humidity (RH) over 95% is critical to anthracnose development in the field with rainfall being a major influence. Heavy rain, however, can reduce disease severity (Davis *et al.* 1987), presumably by washing off inoculum. Moisture also plays a role in the survival of the pathogen between successive growing seasons. Anthracnose lesions on dead and senescent tissue can sporulate following periods of high RH (Boland *et al.* 1995) and the amount of initial inoculum available for infection in the new season is determined by weather conditions.

While variation in the pathogen population and the influence of biotic agents, such as antagonistic bacteria, have been studied to a limited extent, there is no published information on the influence of weather on anthracnose development in South America. In 1993, a collaborative project between CSIRO, Centro Internacional de Agricultura Tropical (CIAT) and Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) was initiated to examine this and other aspects of this disease. This paper presents preliminary results on anthracnose progress on susceptible and resistant lines of *Stylosanthes* at selected field sites in Brazil and Colombia in relation to prevailing weather conditions during 1995.

Materials and methods

Field sites

Four field sites, 2 in Brazil and 2 in Colombia, were established in the summer of 1994–95. The Centro de Pesquisa Agropecuária dos Cerrados (CPAC) research station of EMBRAPA at Planaltina, near Brasilia and the Centro Nacional de Pesquisa de Gado de Corte (CNPGC) of EMBRAPA in Campo Grande, Mato Grosso do Sul, were selected as the Brazilian sites. The Planaltina site has a long history of *Stylosanthes* research and development work and Campo Grande is at the heart of beef cattle country in Brazil. The 2 Colombian sites were at the CIAT field experiment stations in Carimagua and Caquetá. Carimagua, in the Colombian Savanna, has been a centre of extensive *Stylosanthes* research and development for many decades. The Caquetá station is located within the Colombian Amazon basin. Details on the sites are given in Table 1.

Stylosanthes lines and field plots

A range of accessions and cultivars of *S. guianensis*, *S. scabra*, *S. capitata* and *S. macrocephala* from EMBRAPA, CSIRO and CIAT was used at the 4 sites. These included a set of 6 *S. scabra* genotypes used as host differentials to distinguish the Type A pathogenic races of *C. gloeosporioides* in Australia. Cultivars, accessions and selections of local and regional significance totalled 72 genotypes at Planaltina, 44 at Campo Grande and 32 each at Carimagua and Caquetá. Details on the anthracnose resistance of some of these lines appear elsewhere (Cameron *et al.* 1997). Anthracnose progress on *S. scabra* cv. Fitzroy and 93116 (CIAT 1054), susceptible and resistant, respectively, to all known Type A races in Australia, was studied at all 4 sites. For *S. guianensis*, cultivar Mineirâo and GC 348, resistant and susceptible, respectively, were used for the Brazilian sites, and FM 9205 Parcela 5 and CIAT 1500, resistant and susceptible, respectively, were used for the Colombian sites. Four *S. capitata* from the Brazilian sites were included; these were accessions CPAC 1606 and CPAC 4367 at Planaltina and GC 2225 and GC 1468 at Campo Grande.

Three to five replicate plots of the selected lines were established at the 4 sites. Each plot constituted a single row of 5–10 plants of a given line with 1.5–2 m between rows.

Monitoring weather conditions and disease development

Environmental variables were logged continuously for each site using an automatic weather station (Monitor Sensors, Queensland, Australia). Sensors for air temperature and RH were housed in a meteorological screen, within 15–20 m of the field plots. Leaf wetness, canopy temperature and RH sensors were mounted 20 cm above ground level in the canopy, where they avoided direct sunlight for most of the day (Chakraborty *et al.* 1990). Data on radiation, temperature, RH and wind speed were recorded hourly. Rainfall and leaf wetness data were recorded at 6-min intervals, when these events occurred.

Anthracnose severity was assessed on a randomly selected branch on each plant within a plot at approximately monthly intervals. Plants were assessed visually for disease severity using a 10-point rating scale, where: 0 = disease free; 1 = 1–3% leaf area diseased; 2 = 4–6%; 3 = 7–12%; 4 = 13–25%; 5 = 26–50%; 6 = 51–75%; 7 = 76–87%; 8 = 88–94%; and 9 = 95–100% (Chakraborty 1990).

Data analysis

Data on anthracnose severity and prevailing weather conditions were summarised, plotted and Pearson's correlation coefficients determined for weather variables and severity on Fitzroy. Data for mean anthracnose severity for each site were $\log_e$(rating + 1) transformed to stabilise variance and analysed separately using analysis of variance. Quantitative relationships between severity on Fitzroy (dependent variable) and weather (independent variables) were determined using multiple regression analysis (SAS Institute Inc. 1988). The criteria used to select independent variables for regression analysis were: (i) significant correlation with severity; (ii) indication of a strong relationship from plots and other data summary; (iii) prior knowledge of the influence of certain factors on infection of

Table 1. Characteristics of the field sites used in this study

	Field site			
Characteristic	Caquetá	Carimagua	Campo Grande	Planaltina
Map reference: Latitude	1° 15′ N	4° 30′ N	20° 27′ S	15° 35′ S
Longitude	75° 41′ W	71° 19′ W	54° 37′ W	47° 42′ W
Annual rainfall (mm)	3552	2337	1526	1540
Soil type	Ultisol	Oxisol	Oxisol	Oxisol
Dominant native *Stylosanthes* species	None	*S. guianensis*	*S. guianensis, S. capitata, S. acutifolia, S. grandifolia*	*S. guianensis, S. macrocephala, S. capitata*

Fitzroy in the field (Chakraborty and Smyth 1995; Chakraborty and Billard 1995); and (iv) lack of significant correlation with other independent variables included in the regression equation.

Results and discussion

Anthracnose development at the field sites

Anthracnose was most severe at Planaltina with an overall mean rating of all lines of 3.18. This was followed in decreasing severity by Carimagua, Campo Grande and Caquetá (Table 2). At Planaltina, severe anthracnose damage, in combination with other biotic and abiotic stress, caused the death of a large number of *S. scabra* and *S. capitata* plants. These plants could not be assessed adequately for anthracnose damage for a large part of the year. As a result, anthracnose severity at this site was underestimated. With mean anthracnose severity ranging between 1 and 1.5, it was not possible to discriminate between the 44 lines grown at Campo Grande. This was also the case with the *S. scabra* lines at Caquetá (mean rating 0–0.29), although the *S. guianensis* lines could be separated into resistant and susceptible groups using the range in severity between 0 and 3.8. Planaltina and Carimagua sites provided the best separation between the various lines. The mean severity rating ranged from 0.6–6 at Planaltina and from 0.05–4.8 at Carimagua (data not given).

S. guianensis showed significantly higher anthracnose severity at Planaltina and Caquetá. *S. scabra* had significantly higher severity than the other species at Campo Grande and Carimagua. *S. capitata* lines were included only at Planaltina and Campo Grande and there was no significant difference in severity between these and the *S. scabra* lines at these 2 sites (Table 2).

Anthracnose progress on a resistant and susceptible line for the main species grown at the 4 sites is presented in Figures 1 and 2. At Planaltina, Fitzroy and Q10042 were among the most severely diseased genotypes of *S. scabra*. In general, *S. scabra* plants did not survive for more than a few months at Planaltina. This is partly due to severe anthracnose. Many other factors such as a stem borer (*Caloptilia* sp.) and a putative mycoplasma are known to affect the vigour of plants towards the end of a season at this site. Therefore, interpretation of data on anthracnose severity and weather influence beyond a certain time point becomes equivocal. Several *S. guianensis* lines, including CPAC 4239, 4160 and 4226 had higher anthracnose severity than Fitzroy. CPAC 1606 and 4367 were the most resistant and susceptible *S. capitata* lines, respectively, at this site. *S. macrocephala* was the most resistant of the species with a mean severity rating of less than 1 for all 4 lines.

At the 2 Colombian sites, Accessions 93116, 36260 and several *S. scabra* selections from Australia developed moderate levels of anthracnose at Carimagua. Fitzroy was not the most severely affected line at Carimagua and it was anthracnose-free at Caquetá. For *S. guianensis*, FM 9205 Parcela 1, 2, and 3 were among the most susceptible lines at Carimagua, Caquetá and Planaltina. Of the 17 *S. scabra* and 8 *S. guianensis* lines common to all 4 sites, several, including *S. guianensis* FM9205 Parcela 1, 2 and 3, were uniformly susceptible at 3 of the sites where severe disease developed. Some of the other *S. guianensis* lines, such as CIAT 1500 (FM 9D) and CIAT 1927 (FM 2E), however, were resistant at Carimagua and/or Caquetá, but susceptible at Planaltina. Differential susceptibility was also noted for *S. scabra* cv. Fitzroy and 93116. Differences in reaction between sites may

Table 2. Mean anthracnose severity (with standard error in parenthesis) on lines of *S. guianensis, S. scabra, S. capitata* and *S. macrocephala* at 4 field sites in Brazil and Colombia.

	Field site			
Species	Caquetá	Carimagua	Campo Grande	Planaltina
S. guianensis	1.10 (0.03) a[1]	1.74 (0.08) a	1.01 (0.003) a	3.69 (0.05) a
S. scabra	0.16 (0.01) b	2.18 (0.07) b	1.06 (0.01) b	2.88 (0.06) b
S. capitata			1.07 (0.01) b	2.84 (0.09) b
S. macrocephala				0.80 (0.04) c
Overall mean	0.61 (0.02)	1.98 (0.05)	1.05 (0.006)	3.18 (0.04)

[1]Within a column, values followed by different letters are significantly ($P < 0.05$) different.

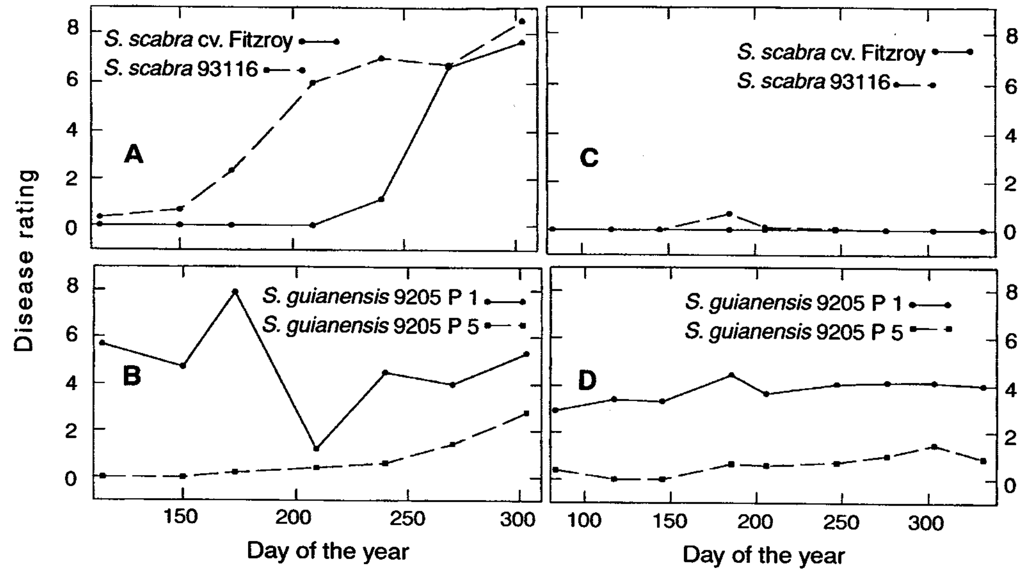

Figure 1. Anthracnose progress on selected lines of *Stylosanthes scabra* and *Stylosanthes guianensis* at Carimagua (A, B) and Caquetá (C, D). Disease rating: 0 = disease free; 9 = 100% of leaf area diseased.

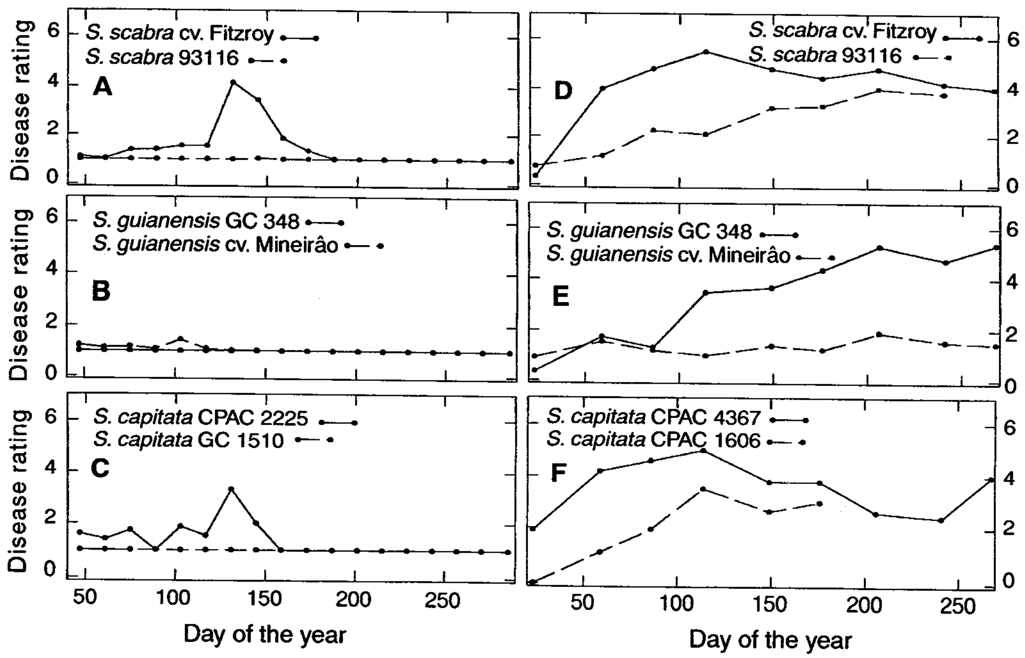

Figure 2. Anthracnose progress on selected lines of *Stylosanthes scabra, S. guianensis* and *S. capitata* at Campo Grande (A–C) and Planaltina (D–F). Disease rating: 0 = disease free; 9 = 100% of leaf area diseased.

be due to differences in pathogenic variation between *C. gloeosporioides* populations and/or differences in biotic and abiotic environment. A thorough understanding of pathogenic specialisation among isolates at these sites is needed urgently.

All Australian isolates of Type A *C. gloeosporioides* cause severe to very severe damage to Fitzroy, but are avirulent on 93116. The moderate to low levels of damage to Fitzroy, recorded at some sites in this study, suggest that Fitzroy may possess resistance towards some isolates of the pathogen in South America. However, results may have been confounded by other forms of stress at some sites. Experiments under more controlled conditions will be necessary to determine the levels of resistance in Fitzroy to isolates from the different sites.

A previous international study has shown that most isolates from *S. capitata* produced a Type A-like symptom while isolates from *S. guianensis* produced Type B-like symptoms (Davis *et al.* 1990). The Type A pathogen may have co-evolved with the endemic *S. capitata* in the Brazilian Cerrados. This may explain the high level of anthracnose damage to many *S. capitata* and *S. scabra* lines at Planaltina. Severe anthracnose damage to the relatively large collection of *S. guianensis* at Planaltina suggests that there is also an extensive pathogenic specialisation in the Type B population at this site.

Relationship between anthracnose severity and weather

Data on anthracnose severity on Fitzroy and the most susceptible *S. guianensis* line at Planaltina and Carimagua were plotted with selected weather variables to examine visually their relationship (Figures 3 and 4). At Caquetá, only data on *S. guianensis* FM 9205 Parcela 1 were plotted because anthracnose did not develop on Fitzroy. Similarly, at Campo Grande, very little anthracnose developed on the *S. guianensis* lines, and therefore, only Fitzroy severity data were plotted. Selection of weather variables for plotting was based on Pearson's correlation coefficient with the mean severity on Fitzroy. The relationship between rainfall, leaf wetness and hours of RH > 95% at Planaltina and Campo Grande (Figure 3) clearly demonstrates the role of moisture availability in anthracnose development. Anthracnose severity at Campo Grande was mainly low except for a major increase following a rainfall event in April. At Planaltina, moderate and frequent rain fell during the early part of the year which contributed to the development and maintenance of high anthracnose severity levels for most part of the year. Continuous data from Carimagua and Caquetá weather stations were not available. As a result, data on anthracnose severity and weather were recorded (Figure 4) on only a limited number of days.

At most sites, variables associated with moisture availability, temperature and wind speed were among the significant independent variables in the regression equations. Temperature and wetness duration have been the major variables to influence disease development by *C. gloeosporioides* in *Stylosanthes* (Chakraborty and Billard 1995; Chakraborty and Smyth 1995) and other plants, including tomato (Dillard 1989) and strawberry (Wilson *et al.* 1990).

From an epidemiological standpoint, anthracnose development depends on the interaction between: (i) the level of host resistance; (ii) prevalence, appearance and proliferation of damaging pathogen races; and (iii) conduciveness of prevailing weather conditions. Within a relatively short time scale, this collaborative study has contributed to the understanding of anthracnose epidemiology at its centre of diversity. The preliminary results reported in this paper need to be confirmed and strengthened through a continuation of these studies. Several aspects require further attention. There is an indication of a differential influence of weather on Type A and B anthracnose at the Carimagua and Caquetá sites (data not given). Anthracnose severity on susceptible lines at 2 of the 4 sites was low to moderate and a continuation of the research will ensure that anthracnose development is studied under a wide range of weather conditions. In Australia, the weather-based model for anthracnose has been developed using data on *S. scabra* (Chakraborty and Billard 1995). The sites used in this study represent the native range for *S. guianensis* and *S. capitata*. *S. scabra* is more prevalent in the Minas Gerais and Bahia states in Brazil. For a comparative assessment of anthracnose progress in Australia and Brazil, future studies should include one or more sites in areas where *S. scabra* is naturally distributed. A targeted collection and characterisation of *C. gloeosporioides* isolates is vitally important to monitor the prevalence and

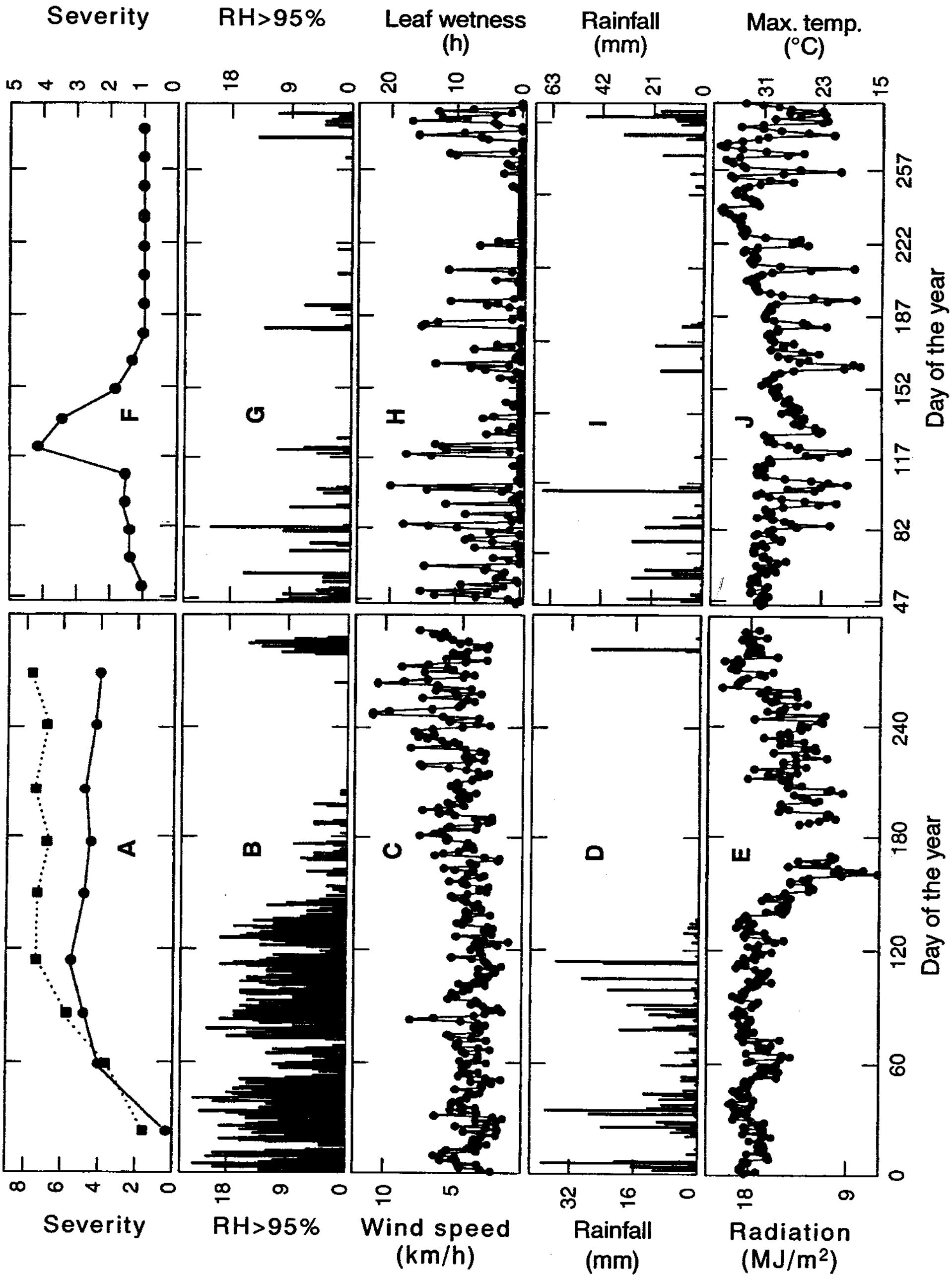

Figure 3. Anthracnose progress on susceptible lines of *Stylosanthes scabra* cv. Fitzroy (●) and *S. guianensis* CPAC 4239 (■) in relation to weather variables at Planaltina (A–E) and Campo Grande (F–J). Severity rating: 0 = disease free; 9 = 100% of leaf area diseased.

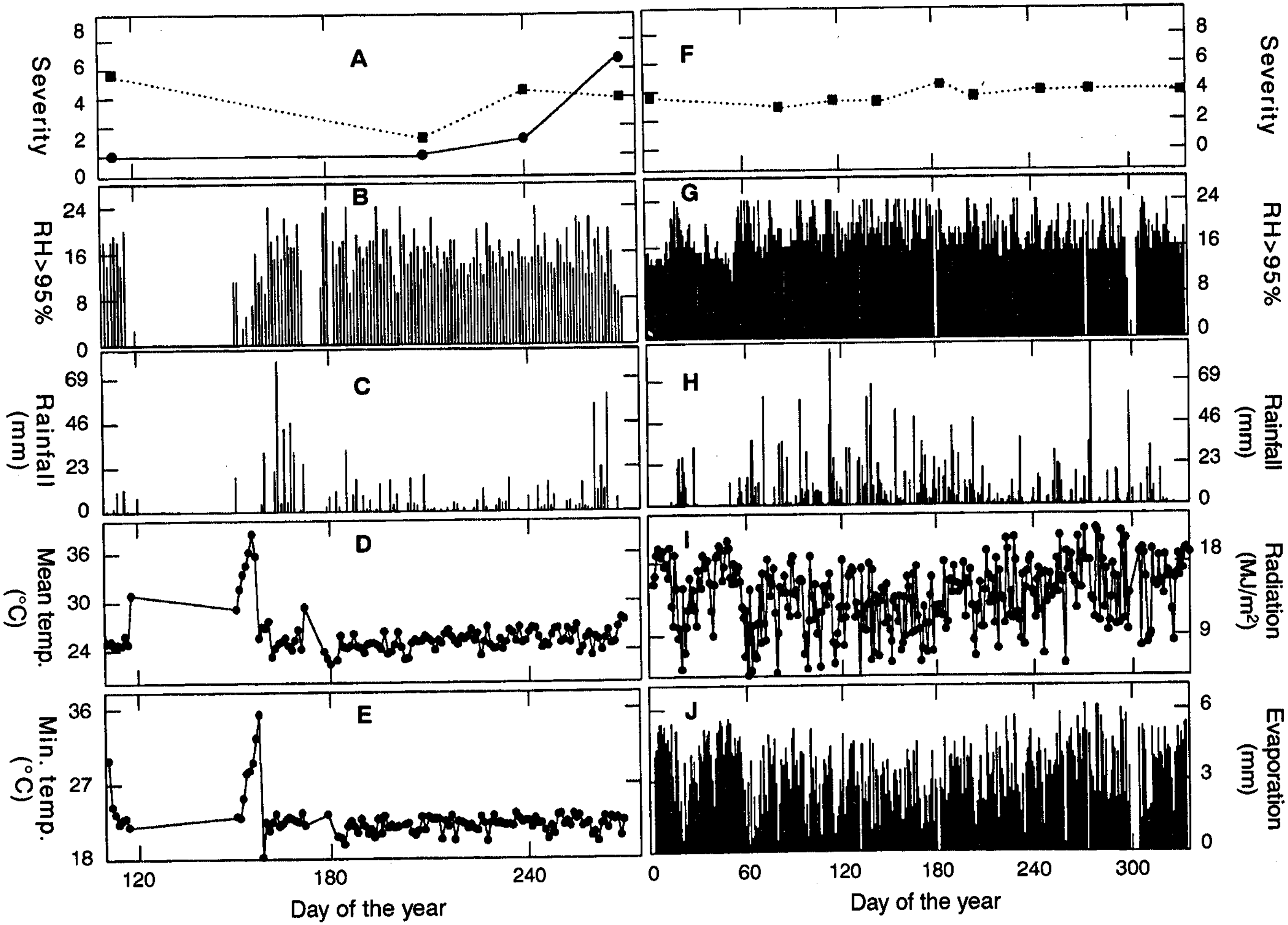

Figure 4. Anthracnose progress on susceptible lines of *Stylosanthes scabra* cv. Fitzroy (●) and *S. guianensis* FM 9205 Parcela 1 (■) in relation to weather variables at Carimagua (A–E) and Caquetá (F–J). Severity rating: 0 = disease free; 9 = 100% of leaf area diseased.

evolution of pathotypes and genotypes in the pathogen population. This is part of the current collaborative project and needs to continue.

Acknowledgements

Research reported in this review was made possible through funding from the CRC for Tropical Plant Pathology and the Australian Centre for International Agricultural Research. Technical assistance from Antonio Carlos Gomez, Jorge Badel, Ross Perrott, Raylee Trevorrow, Murray Anderson and Richard Ross is gratefully acknowledged.

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