Current Research on Fusarium Wilt of Banana in Australia

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Abstract

*Two hundred and forty-five Australian isolates of **Fusarium oxysporum** f.sp. **cubense** (FOC) have been characterised using vegetative compatibility group (VCG) analysis and volatile (odour) production on starch substrates. Six VCGs exist amongst Australian isolates of FOC, and VCG correlates well with race and volatile production. All race 4 isolates (VCGs 0120, 0129, 01211) belong to the "odoratum" group. Race 1 (VCGs 0124, 0124/5, 0125) and race 2 (VCG 0128) isolates do not produce odour and have been placed in the "inodoratum" group.*

Race 1 is widespread, having been detected in northern and southern Queensland as well as northern New South Wales, where it limits the production of Lady Finger. Race 2, which affects Bluggoe, has a more limited distribution having only been found at two localities in northern Queensland. Race 4, which attacks the cultivars above as well as Cavendish, is present in northern New South Wales and southern Queensland.

***Musa** germplasm has been assessed for resistance to races 1 and 4 of FOC at two field screening sites in southeast Queensland. Williams (AAA), SH3142 (AA), SH3362 (AA), SH3481 (Prata ana x SH3142, AAAB), Pisang Susu (AAA), Pisang Ramo (AAB), Pisang Nangka (AAA),*

Kluai Khai Bong (AAA), Kluai Pa (AA), Mysore (AAB), TU8 (AAAA) and Kuma Kuma (AA) were highly resistant to race 1.

Most cultivars tested were susceptible to race 4 except Mysore (AAB), Dwarf Parfitt (AAA) and its putative mutant, Giant Parfitt (AAA), SH3362 (AA) and SH3142 (AA). In a preliminary test, SH3481 also appears resistant to race 4.

Dwarf Parfitt is the only member of the Cavendish subgroup with resistance to race 4. Relatively high chlorophyll concentrations and the effective photosynthetic activity the cultivar maintains during periods of cold stress may be key factors in its resistance to race 4 in Australia.

The Banana Industry in Australia

Banana production in Australia is concentrated in the coastal regions of northern and southern Queensland, and northern New South Wales, with smaller areas at Carnarvon and the Ord River in Western Australia. The total cultivated area is presently around 13,000 ha, which produces an annual market value of AUS$250 million. Bananas account for 15% of all fruit produced in Australia with Cavendish subgroup (AAA) cultivars Williams, Mons Mari, Grande Naine, and Dwarf Cavendish making up approximately 95% of the cultivars grown. Lady Finger (Pacha Naadan (AAB)) of the Pome subgroup is also a popular dessert cultivar but its production in southern Queensland and northern New South Wales is limited by the availability of Fusarium wilt-free soils. Ducasse (Pisang Awak (ABB)), Pacific Plantain (AAB), and Red Dacca (AAA) are also grown on a small commercial scale.

History of Disease

Fusarium wilt of banana (*Musa* spp.), caused by *Fusarium oxysporum* Schlect. f.sp. *cubense* (E.F. Smith) Snyder & Hansen (FOC), was first recorded in Australia by Bancroft in 1874 on Sugar (Silk (AAB)) bananas in the Brisbane area (Bancroft, 1876). It is interesting to note that Bancroft also observed apparently healthy Dwarf Cavendish plants growing near the infected Sugar plants. Fusarium wilt is currently very destructive in Lady Finger plantations in southern Queensland and northern New South Wales, and has been attacking Cavendish cultivars in southern Queensland since 1976 (Pegg and Langdon, 1986). A brief history of this disease in Australia was published recently (Pegg et al., 1991).

Pathogen Variability in Australia

Race and Their Distribution

Races 1, 2, and 4 of FOC are present in Australia. Race 1 is widespread in the eastern states, limiting Lady Finger production in coastal Queensland and New South Wales. Race 2 has been recorded at only 2 sites in northern Queensland. Race 4 has been identified in 42 Cavendish and 19 Lady finger plantations in southern Queensland, and at 3 sites in New South Wales, where it occurs alone or in mixed populations with race 1. Quarantine measures are in place to prevent the spread of this potentially devastating race of the pathogen. To date, race 4 has not been identified in the major Cavendish production areas of northern Queensland.

Glasshouse pathogenicity tests with Australian isolates of *Fusarium oxysporum* from *Heliconia* spp., have not confirmed the existence of race 3 FOC in Australia.

The genetic relationships of populations of FOC in Australia have been assessed using vegetative compatibility group (VCG) analysis, production of volatile compounds on starch substrates, and the DNA based technique RAPD-PCR (Random Amplification of Polymorphic DNA - Polymerase Chain Reaction).

Vegetative Compatibility

Vegetative compatibility is a useful technique for studying the genetic relationships between isolates of asexually reproducing fungi such as FOC. Characterisation of 245 Australian isolates of FOC using this technique, which was developed by Cove (1976) and refined by Puhalla (1985) and Correll et al. (1987), has clearly defined 6 VCGs within Australian populations of FOC (Brake et al., 1990; Moore et al., 1992). Correlations between VCG and pathogenicity have also been demonstrated for Australian isolates of FOC in field reactions and glasshouse pathogenicity tests using 6- to 8-month-old plants with large, well-developed rhizomes (Brake et al., 1990; Moore et al., 1992).

Isolates in VCGs 0124 and 0125 possess race 1 virulence whereas isolates from VCGs 0120 and 0129 exhibit race 4 virulence. Only two isolates have been placed in the uniquely Australian VCG 01211. These were recovered from SH3142 (AA), an improved diploid from the FHIA breeding program, and *Musa acuminata* subspecies *banksii* (AA) at a germplasm screening site in southern Queensland which is heavily

infested with race 4 (VCGs 0120 and 0129). On the basis of volatile production and RAPD-PCR analysis (see below) it is assumed that isolates in VCG 01211 also possess race 4 virulence.

Isolates of FOC recovered from Bluggoe and Blue Java (ABB) in northern Queensland were identified as race 2 and were found to belong in VCG 0128.

Several isolates within the race 1 VCGs 0124 and 0125 show vegetative cross-compatibility. This is consistent with findings from other collections of FOC and it has been suggested by Ploetz (1990) that these VCGs represent diverging subpopulations of a common VCG which are losing the ability to form heterokaryons consistently. Recently a small number of isolates in VCG 0120 displayed cross-compatibility with one of the isolates in VCG 01211. These "bridging" isolates provide evidence that VCG 01211 has probably evolved in Australia from VCG 0120, and that although the VCG 0120 population is very stable in Australia, localised evolution can occur.

Volatile Production

In 1962 Stover classified isolates of FOC according to the production of volatile substances from cultures on starch substrates (Stover, 1962). Using this technique he divided isolates into either the "odoratum" or "inodoratum" group. Similar studies have been conducted with Australian isolates of FOC (Moore et al., 1991). Gas chromatographic analysis of the head space above the cultures, which were grown on sterile, steamed rice, enabled chromatogram profiles of the volatile odours to be obtained. Absolute correlation between odour production and VCG has been found for isolates tested so far. Isolates in the race 1 VCGs 0124 and 0125, and the race 2 VCG 0128 do not produce volatile compounds nor chromatograms with peaks. Isolates in the race 4 VCGs 0120, 0129, and 01211 all produce distinctive volatile odours. The volatile products of isolates in VCGs 0120 and 01211 were very similar and gave identical chromatogram profiles with 6 significant peaks (Figure 1). The volatile odour produced by isolates in VCG 0129 differed from that produced by isolates in VCGs 0120 and 01211 and gave chromatograms with 1 significant peak (Figure 1). It is tempting to speculate that the genes conferring race 4 virulence are linked to those governing the production of volatile compounds. Identification of the volatile compounds is continuing.

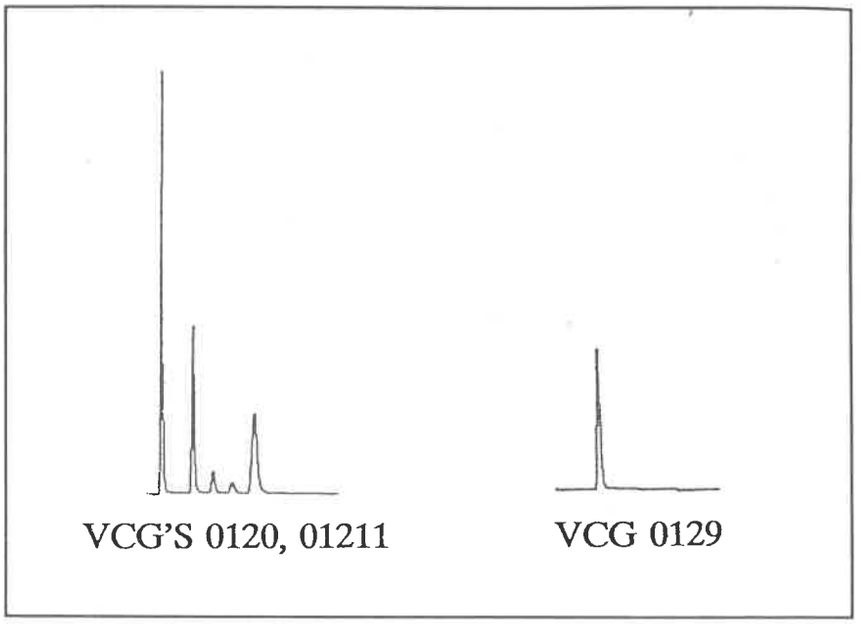

Fig. 1. Typical gas chromatograms of Australian isolates representing race 4 VCGs of *Fusarium oxysporum* f. sp. *cubense*.

DNA Analysis

Although VCG and volatile analyses have been highly successful in defining and characterising populations of FOC in Australia the diversity or relatedness of isolates within these groups cannot be ascertained by these methods alone. DNA analysis allows comparative studies of the DNA sequences of isolates within and among VCGs and may allow an understanding of the evolutionary relationships of the races of FOC. In Australia, RAPD-PCR has been used to generate DNA "fingerprints" for isolates of FOC (see paper by Sorensen et al. these proceedings) These results agreed with classifications based on host range, VCG and chromatogram profiles of volatile products.

Based on VCG analysis, Australian populations of FOC have been shown to be very stable. Results have been obtained from the germplasm screening programs where *Musa* germplasm of various genomic constitutions has been deployed in fields infested with either race 4 or race 1. To date, 160 isolates of FOC recovered from many different host genotypes at these sites indicate that FOC populations at each site do not change over time.

Screening Germplasm for Resistance to Fusarium Wilt

Due to the lack of reliable glasshouse or growth cabinet assays, resistance evaluation of *Musa* germplasm is carried out in the field. There are two field screening sites in Australia. The first site has been at Wamuran in southern Queensland (latitude 27°S) for six years and is heavily infested with race 4 FOC (VCGs 0120 and 0129) A second screening site at Ormeau has been relocated to Pimpama in southern Queensland (latitude 27°49'S) and is infested only with race 1 FOC (VCGs 0124 and 0125).

The objectives of the screening program in Australia with respect to Fusarium wilt are as follows:

1. To identify a race 1-resistant dessert cultivar to replace Lady Finger in areas where only race 1 occurs. While agronomically less productive than the Cavendish varieties, the AAB clones have much to offer in terms of drought and cold tolerance, longer shelf-life and pleasant acid taste.

2. To identify a race 4-resistant dessert variety to replace Cavendish, particularly in southern Queensland and northern New South Wales where the climate is more subtropical and race 4 is prevalent.

It is necessary that standardised procedures be followed when screening germplasm at field sites. For these trials, sites were selected where >75% of the Lady Finger or Cavendish plants had succumbed to Fusarium wilt. The FOC population at each site was intensively sampled and characterised using VCG and volatile analysis to ensure that a uniform population of FOC was present. A representative isolate from each screening site was cultured on sterile sorghum grains, which were used to infest each planting site. After planting, regular observations were made for plants showing external symptoms of Fusarium wilt. Such plants were destructively sampled to determine the degree of internal discoloration of the rhizome. Isolations were made from each diseased plant and the isolates characterised to ensure that the pathogen population remained stable and that no contamination of the site by other populations of FOC had occurred. After the plant crop, harvest plants which remained healthy were destructively sampled to assess internal discoloration.

Resistance evaluations for germplasm screened at the race 1 site to date are summarised in Table 1. The most promising cultivar to show

Table 1. Resistance evaluation of Musa germplasm to Race 1 of *Fusarium oxysporum* f. sp. *cubense* (VCGs 0124 and 0125) at Pimpama, Australia.

Cultivar	Genomic Constitution	Resistance Evaluation
Lady Finger (Pacha Naadan)	AAB	S
Pisang Lampeneng	AAB	S
Pisang Gajih Merah	AAB	S
Pisang Kosta Hijau	AAB	S
Pacific Plantain	AAB	S
Hua Moa	AAB	S
Pisang Raja Sereh	AAB	S
Vunamami (PNG acc # 144)	AAA	S
Kalapua (PNG acc # 145)	ABB	S
Kandrian (PNG acc # 148)	ABB	S
Kluai Pa	AA	R
Kluai Khai Bong*	AAA	R
Kluai Niu Mue Nang	ABB	R
Pisang Nangka	AAB	R
Pisang Ramo*	AAB	R
Mysore*	AAB	R
Cavendish (cv Williams)	AAA	R
Pisang Susu	AAB	R
SH3481	AA	R
Kuma Kuma*	AAAA	R
SH3436	AAAA	R
TU8	AAAA	R

S = susceptible reaction: severe leaf yellowing and internal discoloration of rhizome and pseudostem.

R = resistant reaction: externally healthy plant with no internal discoloration of rhizome or pseudostem.

* denotes surviving cultivars with apparent resistance to banana weevil borer (*Cosmopolites sordidus*).

resistance to race 1 for the Australian industry is SH3481 (Prata ana X SH3142), an elite hybrid from the FHIA breeding program.

In excess of 20,000 plants have been evaluated for resistance at the race 4 screening site. Of these, only Mysore (AAB), SH3362 (AA), SH3142 (AA), Dwarf Parfitt (AAA) and its putative mutant, Giant Parfitt (AAA) have displayed resistance to race 4. In a preliminary test, six plants of SH3481 (AAAB) established in a nearby race 4-infested site have also remained healthy.

Occasionally, when established from tissue culture, the parent plant of Mysore succumbs to both races 1 and 4 Fusarium wilt. However, ratoons from the susceptible parent plants rarely succumb and intenal investigations have revealed that infection in the followers is confined to the rhizome. It is interesting to note that Banana Streak Virus has been identified in Mysore accessions in Australia. The presence of this virus may contribute to the initial susceptibility which has been observed in this cultivar, and may also influence fruit size and yield.

Recent investigations have revealed that after 2 years in tissue culture some plantlets of the Honduran and Jamaican accessions of Mysore do not show symptoms of Banana Streak Virus and give negative results in ELISA tests. These symptomless Mysore have been planted in a replicated experiment in a race 1-infested field with plants which show virus symptoms and give positive ELISA tests, to compare their reactions to Fusarium wilt as well as the influence of the virus on fruit size and yield.

Giant Parfitt was obtained by subjecting micropropagated plants of Dwarf Parfitt, an extra dwarf Cavendish, to gamma-irradiation (see paper by Smith et al. these proceedings). Giant Parfitt appears to have retained the race resistance and dark green leaves of the parent plant while producing a commercially acceptable bunch. Approximately 1,500 plants of Giant Parfitt have recently been planted in a field heavily infested with race 4 FOC in southern Queensland to further evaluate the Fusarium wilt resistance and agronomic characteristics of this variety.

Susceptibility of Cavendish Cultivars to Fusarium Wilt

The successful colonisation of plants by pathogen can, in some cases, be attributed to the development of stress in the host. For instance, charcoal and Fusarium rots of sorghum are exacerbated by water and/or photoassimilate stress (Eastin et al., 1983; Mughogho and Pande, 1983). Preliminary investigations in Australia provide evidence that physiological stresses related to environmental conditions may be predisposing Cavendish cultivars to lethal infection by race 4 of FOC.

Cavendish cultivars rarely succumb to Fusarium wilt in tropical regions (Ploetz, 1990). When disease does occur, only restricted areas are affected with little subsequent spread (Stover, 1990). However, Fusarium wilt is a much more serious threat to Cavendish cultivars in subtropical regions (Australia, Canary Islands, South Africa and Taiwan) where diseased plantations can rapidly lose commercial variability.

The edible bananas are believed to have evolved in the tropical regions of Asia (Purseglove, 1972) which is reflected in the 22-31°C temperature range for optimum growth and production of banana (Robinson, 1990). The assimilation of CO_2 and rate of leaf emergence have been shown to decrease when the mean temperature falls below 22°C, with growth ceasing in the plant at = 14°C (mean) (Robinson, 1990). Such conditions occur during winter in the subtropical banana production areas of Australia (Figure 2) where Fusarium wilt reaches epidemic proportions in race 4-infested plantations following winter (K.G. Pegg unpublished). Hence, it is suggested that the sensitivity of cultivars to stress induced by cold temperatures, and the associated disruption of the photoassimilation mechanisms, contributes to susceptibility to race 4 in the subtropics.

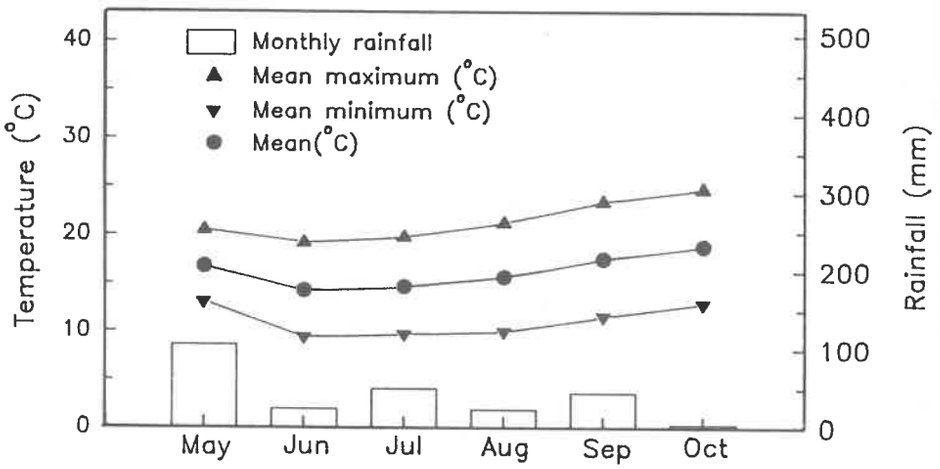

Fig. 2 Monthly rainfall and mean temperature at Wamuran, Australia (Latitude 27° S) during winter, 1992.

Host defence mechanisms (ie: formation of gels, tyloses and phenolic infusions), which block invasion by the pathogen (Beckman, 1990) are primarily driven by photoassimilates, either from storage or current photosynthesis. Therefore, a decrease in the carbon assimilation capacity of a banana plant may reduce its ability to block invasion by the pathogen.

Preliminary studies in Australia during the winter of 1992 have investigated changes in leaf chlorophyll concentrations, rates of CO_2 assimilation (*A*), chlorophyll flourescence induction, total plant leaf area

and dry matter accumulation in two cultivars of the Cavendish subgroup, Dwarf Parfitt (resistant to race 4 FOC) and Williams (susceptible to race 4 FOC). Total chlorophyll concentration and *A* were determined at four-week intervals from May to October, on three plants of each cultivar. The most recently unfurled leaf was selected on each plant when measurements were commenced and all measurements throughout the study were made on this leaf or the next youngest leaf where the original leaf was lost through damage or senescence. Chlorophyll extracts were made by placing discs of leaf tissue in 85% acetone solution which was incubated in darkness ar 25°C for 48 hr. The absorbance of the solution was read on a spectrophotometer at wavelengths 642.5 and 660 nm and the total chlorophyll concentration calculated using the formula of Proctor (1981). *A* of leaves was measured with a LiCor Li-6200 portable photosynthetic meter on each side of the selected leaf at temperatures greater than 19°C and photon flux densities (PFD) greater than 1200 umol quanta $m^{-2}s^{-1}$. Chlorophyll flourescence induction, expressed as the variable flourescence/maximal flourescence (F_v/F_m) ratio (Oquist and Wass, 1988), was measured with a BioMonitor AB Plant Stress Meter in August and October. Leaves were dark adapted for 10 min and then exposed to actinic light for 5 sec at a PFD of 400 umol quanta $m^{-2}s^{-1}$ (Table 2). In non-stressed plants the ratio falls between 0.8 and 0.9. The lower the ratio, the greater the level of stress.

Table 2. Chlorophyll fluorescence induction (F_v/F_m ratio) of Dwarf Parfitt and Williams in winter and spring in subtropical Australia.

Cultivar	F_v/F_m Ratio August	October
Dwarf Parfitt	0.520 ± 0.038	0.722 ± 0.013
Williams	0.354 ± 0.061	0.653 ± 0.018

Total plant leaf area and biomass were determined by monthly destructuve sampling of 3 randomly selected plants of each cultivar. The CO_2 assimilation efficiency per kg dry weight of total plant biomass was calculated from *A*, leaf area and plant dry weight.

This study confirms previously reported results of reduced chlorophyll concentration and *A* when mean temperatures fall below 22°C (Robinson, 1990) (Figure 2). It also shows that Dwarf Parfitt maintained higher chlorophyll concentrations and *A* than Williams during the winter

months (Figure 3). Furthermore, Dwarf Parfitt maintained its leaf area during winter while that of Williams significantly declined during the latter months of the study (Figure 4). These factors resulted in a higher threshold of *A* efficiency in Dwarf Parfitt than in Williams during the latter part of winter and early spring. Similarly, Dwarf Parfitt was able to maintain a higher F_v/F_m ratio (Table 2) indicating that it was less affected by cold temperatures during winter and able to make a more rapid recovery in spring, when mean temperatures increased to more favourable levels for growth.

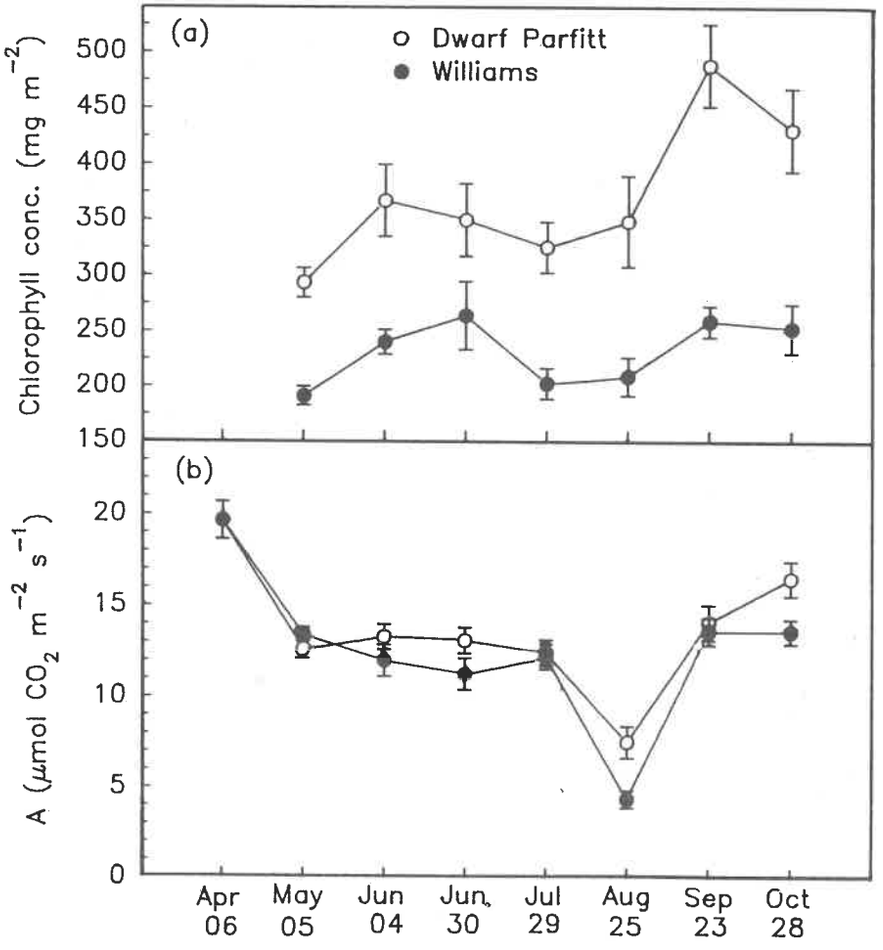

Fig. 3. Seasonal changes in (a) chlorophyll concentration and (b) CO_2 assimilation (A) of cvs. Dwarf Parfitt and Williams growing at Wamuran, Australia (Latitude 27°S). Vertical bars indicate ± Standard Error (n=3).

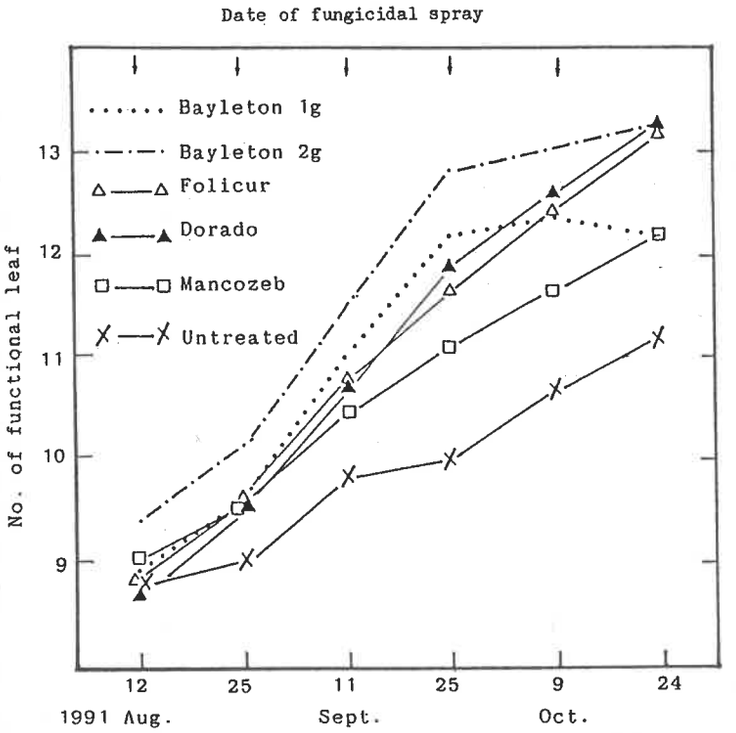

Fig. 4. Changes during winter in (a) leaf area and (b) CO2 assimilation efficiency (A) per kg DW of total plant biomass of cvs. Dwarf Parfitt and Williams growing at Wamuran, Australia (Latitude 270S). Vertical bars indicate ± Standard Error (n=3).

These preliminary data support the hypothesis that cold stress comprises resistance to race 4 in Williams when grown in subtropical environments. However, more rigorous testing is required to understand the mechanisms involved in preventing lethal infection by race 4. Epidemiological studies are currently being undertaken at the Wamuran site to correlate disease development with physiological changes in the plants. Photosynthetic response curves for light, temperature and CO_2 are also being determined for resistant and susceptible cultivars for future controlled environment glasshouse studies where environmental conditions will be manipulated in the presence of the pathogen and the colonisation of the host tissues studied. In addition, chloropyhll flourescence will be evaluated as a tool for indicating cold tolerance in cultivars. This approach may prove useful in Fusarium wilt resistance evaluation, particularly where large numbers of plants have been generated, as in mutation breeding programs.

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