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Research Papers

Yields and resistance of strawberry cultivars to crown and root diseases in the field, and cultivar responses to pathogens under controlled environment conditions

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Summary. Devastating outbreaks of crown and root diseases have impacted severely on commercial strawberry production in Western Australia (W.A.). Studies were conducted to evaluate the yields, and resistance of three commercial strawberry cultivars to crown and root diseases, both in fumigated and non-fumigated field beds, and to determine the responses of eight commercial cultivars to individual pathogens under controlled conditions. In the field, cv. Camino Real showed the greatest fruit yield both in fumigated and non-fumigated beds, and was the most disease-resistant cultivar. Each cultivar had a greater fruit yield and a lower amount of plant decline in fumigated beds, compared with non-fumigated beds. Both for fumigated and non-fumigated beds, the amount of plant decline increased from August to November, particularly in non-fumigated beds. Under controlled conditions, cv. Festival was most resistant and cv. Camarosa most susceptible to wilt-causing *Fusarium oxysporum*. Against binucleate *Rhizoctonia* AG-A, *Cylindrocarpon destructans* and *Phoma exigua*, cv. Festival was most resistant and cv. Aromas most susceptible. Cultivar Camino Real was the most resistant to *Gnomonia fructicola* and *Phytophthora cactorum* and cv. Festival most resistant to *Pythium ultimum*. Against *Macrophomina phaseolina*, cv. Albion was the most resistant with cv. Camarosa the most susceptible. Cultivar Camarosa, the most widely grown cultivar in W.A., was most susceptible to *F. oxysporum*, while cv. Camino Real was resistant to *F. oxysporum* both in the field and the controlled environment conditions. Cultivar Festival is the most resistant cultivar to *F. oxysporum* and a range of different pathogens. The Australian bred cv. Juliette was as susceptible as cv. Camarosa to *F. oxysporum*, but relatively resistant to binucleate *Rhizoctonia* AG-A. This is the first study, not only to define the relative yield potentials of different cultivars in a situation where crown and root disease prevails in the field, but also to demonstrate differential resistance of current cultivars to specific pathogens associated with crown and root disease in W.A. For the first time, growers can now make informed choices about the cultivars they can deploy to minimise losses caused by diseases.

Key words: *Fragaria* × *ananassa*, *Fusarium oxysporum*, binucleate *Rhizoctonia*, fumigation, plant decline.

Introduction

Strawberry is a high-value export crop grown in Western Australia (W.A.), constituting up to 72% of Australia's strawberry exports (Phillips and Golzar, 2008). Devastating outbreaks of crown and root diseases in W.A. have impacted severely on commercial strawberry production (Golzar *et al*., 2007; Phillips and Golzar, 2008; Fang *et al*., 2011a). The surveys in recent growing seasons of the largest strawberry farms in W.A. confirmed up to 50% plant losses on the worst-affected properties (Phillips and Golzar,

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2008; Fang *et al*., 2011a). W.A.'s position in Australia as a major and reliable exporter of strawberry fruit is currently threatened by losses from crown and root diseases.

Crown and root diseases of commercial strawberry plants are endemic in North America (Urena-Padilla *et al*., 2001; Mertely *et al*., 2005), South America (Tanaka and Passos, 2002; Latorre and Viertel, 2004), Europe (Cal *et al*., 2004), Asia (Zhao *et al*., 2009) and Western Australia (Golzar *et al*., 2007; Fang *et al*., 2011a). These diseases can be caused by single, or combinations of, fungal and/or oomycete pathogens, including one or more species of *Fusarium* (Golzar *et al*., 2007), *Rhizoctonia* (Martin, 1999), *Cylindrocarpon* (Manici, 2005), *Macrophomina* (Mertely *et al*., 2005), *Pythium* (Martin, 1999), *Gnomonia* and *Phoma* (Morocko, 2006), *Phytophthora* (Duncan, 2002) and/or *Colletotrichum* (Urena-Padilla *et al*., 2001). *Fusarium oxysporum* and binucleate *Rhizoctonia* are the most frequently occurring and damaging pathogens associated with crown and root diseases of strawberry in W.A. (Fang *et al*., 2011a, b). The predominant recovery of these pathogens from affected plants is in the spring months of the year, and with the frequent occurrence of *Macrophomina phaseolina* when temperatures exceed 30°C (Fang *et al*., 2011b). Other pathogens, including *Cylindrocarpon destructans*, *Phoma exigua*, *Gnomonia fructicola*, *Phytophthora cactorum* and *Pythium ultimum*, can also cause significant crown and/or root disease on strawberry (Fang *et al*., 2011b).

Several methods have been used to reduce the impact of crown and root diseases in disease-prone areas, including use of healthy and certified runner plants for establishment, various crop rotations, minimization of soil compaction, incorporation of organic matter, avoidance of heavy and water-logged soils, improved soil drainage by planting on raised beds and, in particular, by utilization of pre-plant fumigation of soil (Himerlick and Dozier, 1991; Martin and Bull, 2002). The phase-out of methyl bromide for fumigation has forced development of alternative fumigants and other means for management of strawberry soilborne pathogens (Easterbrook *et al*., 1997). Identifying and deploying resistant strawberry cultivars is considered the most cost effective and sustainable strategy for control of crown and root diseases of strawberry (Particka and Hancock, 2005; MacKenzie *et al*., 2006). While a range of commercial cultivars is available for planting in W.A., including cv. Albion, Aromas, Camarosa, Camino Real, Festival, Gaviota, Selva and Juliette, there is no information on their relative resistances to crown and root diseases.

Studies were therefore undertaken to evaluate the yield and resistance of the three most commonly grown commercial cultivars of strawberry in W.A. to crown and root disease, both in fumigated and non-fumigated field beds across a production season, and to determine the response of eight commercial cultivars of strawberry to the specific fungal and oomycete pathogens associated with crown and root diseases under controlled environmental conditions.

Materials and methods

Strawberry cultivars

Strawberry cultivars (viz. Albion, Aromas, Camarosa, Camino Real, Festival, Gaviota and Selva) were purchased as certified commercial runners from Toolangi Certified Strawberry Runner Grower's Co-Op Ltd, Victoria, Australia. The strawberry cv. Juliette was purchased as certified commercial runners from Perry Certified Strawberry Runner Growers, Victoria, Australia.

Field experiment

A field experiment to assess yields of three strawberry cultivars (viz. Albion, Camarosa and Camino Real) in relation to their resistance to crown and root diseases was conducted at a commercial strawberry field in Wanneroo, W.A. (Latitude/Longitude: -31.8/115.8). This was a location where plants experienced serious crown and root disease caused by *F. oxysporum* during field surveys in previous years (2006 and 2007), across a growing season from planting in April (mid-autumn) until the end of the season in November (late-spring) 2008. The three cultivars represent the main commercial cultivars grown in W.A., constituting approximately 99% of the total strawberry area planted and grown in the state at that time (W.A. Agricultural Produce Commission, unpublished report).

Strawberry plants were grown using standard commercial practices on drip irrigated raised beds (1.2 m wide, 8.0 m long and 0.3 m high at the edge) with black plastic cover. Each raised bed consisted of four rows of strawberry plants with 0.3-m spacing between rows and 0.3-m spacing between plants within rows (25 plants per row, 100 plants per bed). The distance

between the raised bed centers was 2.1 m. For each cultivar, there were replications with three fumigated raised beds and three non-fumigated raised beds arranged in a randomised complete block design. Before planting, the fumigated beds were treated with Telone C-35® at 350 kg ha^{-1}. Water was applied by drip irrigation as needed to maintain proper growth. Calcium nitrate and soluble N–P–K (10–10–10) fertilisers were applied once every month via drip irrigation.

For the period from 30 June to 11 November 2008, all ripe fruits of the strawberry plants on each raised bed of each cultivar were harvested at 3 to 5 d intervals. All fruits were sorted based on marketability criteria, and only marketable fruits were weighed. The severity of plant top decline on all raised beds of each cultivar was assessed three times, on 5 August, 21 October and 11 November 2008. The plant top decline was assessed on a 0–4 severity scale as used by Fang *et al.* (2011a), where: 0 = healthy plant; 1 = beginning of wilt symptoms; 2 = pronounced wilt symptoms; 3 = majority of leaves wilted/dead, plants generally very small; 4 = dead plant.

Isolations of pathogens were made from segments of freshly harvested diseased root, crown and/or crown vascular tissues to indentify the organisms responsible for disease symptoms in the field trial. The isolated pathogen was firstly indentified morphologically to be *F. oxysporum* and then confirmed by species-specific primers for *F. oxysporum* (Williams *et al*., 2002) and by PCR amplification of rDNA gene fragments using universal primers ITS1 and ITS4 (White *et al*., 1990).

Controlled environment experiments

Fungal and oomycete pathogens

A representative isolate each of *F. oxysporum* (WUF-ST-FO35), binucleate *Rhizoctonia* AG-A (WUF-ST-Rhw2), *C. destructans* (WUF-ST-CD29), *M. phaseolina* (WUF-ST-M3), *P. cactorum* (WUF-ST-PhyC2), *P. ultimum* (WUF-ST-PyU1), *P. exigua* (WUF-ST-PhE9) and *G. fructicola* (WUF-ST-GnF1) was selected for this test. These isolates were obtained from diseased crown and/or root tissues of strawberry collected from the major commercial strawberry fields in 2008 in W.A. (Fang *et al*., 2011a), and were selected on the basis of their occurrence in declining plants in the field, their morphological and molecular characteristics and our previous pathogenicity tests (unpublished data; Fang *et al*., 2011b).

Inoculum production

For the isolate of *F. oxysporum*, conidial suspension inoculum was prepared from 5 to 7 d old colonies growing on potato dextrose agar (PDA) maintained at 24°C under continuous fluorescent light. The inoculum suspension was prepared in sterile deionised (DI) water, filtered through four layers of cheesecloth to remove any agar contamination, and diluted to 1×10^6 conidia mL^{-1}.

For isolates of binucleate *Rhizoctonia* AG-A, *C. destructans*, *P. cactorum*, *P. ultimum, P. exigua* and *G. fructicola*, millet seed colonised by mycelia of each isolate was prepared using a modified procedure of Barbetti (1989). Colonised sterilised moist millet seeds (*Panicum miliaceum*) were prepared by soaking 200 g millet seeds in DI water in a 1 L flask for 12 h, draining excess water and then autoclaving at 121°C for 20 min on three consecutive days. One to 2-week-old colonies of each isolate growing on PDA or corn meal agar (CMA) plates were cut to plugs of 2 mm^2 and 20 pieces added in each flask containing the prepared sterilised moist millet seed. Flasks were shaken every 2 d to ensure uniform colonisation and incubated in the dark at 24°C for 2 weeks.

For the inoculum of the isolate of *M. phaseolina*, toothpicks colonised by mycelia were prepared using a modified procedure of Mertely *et al*. (2005). The isolate was grown on CMA at 24°C for 5 d and then allowed to colonise sterilised toothpicks (previously autoclaved twice at 121°C for 20 min in DI water and a third time in V8 juice agar) placed on the surface of the medium for an additional 5 d.

Response of seven strawberry cultivars to specific pathogens

All controlled environment experiments were conducted on 8-week-old plants of seven strawberry cultivars, viz. Albion, Aromas, Camarosa, Camino Real, Festival, Gaviota and Selva. The response of these cultivars to *F. oxysporum,* binucleate *Rhizoctonia* AG-A, *C. destructans*, *P. exigua*, *P. cactorum* and *P. ultimum* was evaluated under controlled environment conditions where air temperature was maintained at 22 (±1)°C and a 12 h photoperiod of 280 μE m^{-2} s^{-1}. The response of these cultivars to *M. phaseolina* was evaluated under controlled environment conditions where air temperature was maintained at 27 (±1)°C and a 12 h photoperiod of 372 μE m^{-2} s^{-1}. For each pathogen, the temperature selected was that which mimics that commonly experienced in the field

when crown and root diseases first become evident. University of Western Australia potting mix (finely crushed pine bark : coco peat : sand at 2.5 : 1.0 : 1.5 w/w), treated with aerated steam for 90 min at 65°C, was used in this test.

For the isolate of *F. oxysporum,* plants were inoculated by dipping cut roots in the conidial suspension for 10 min before planting; control plants for comparison were dipped in sterilised DI water for 10 min before planting. For isolates of binucleate *Rhizoctonia* AG-A, *C. destructans*, *P. exigua*, *P. cactorum* and *P. ultimum*, plants were inoculated by mixing millet seed colonised by mycelia of each isolate with the steamed potting mix at a rate of 0.5% (w/w); control plants for comparison were planted in uninoculated soil only. Uninoculated sterilised millet seed was deliberately not used as a control comparison as it is known to have a 'baiting-out' effect on any other potential pathogens present in the soil, especially *Pythium* species, when introduced uncolonised into soil (Barbetti and Sivasithamparam, 1987). For the isolate of *M. phaseolina*, plants were inoculated by inserting a single toothpick colonised by mycelia into the lower half of the crown region of each plant; control plants for comparison were inoculated by inserting a sterilised V8 juice-infused toothpick into the lower half of the crown region of each plant.

There were eight single plant replicates for each treatment (one plant per 9 cm × 18 cm pot) arranged in a completely randomised block design, and all the experiments were repeated once. Plants were watered each day with DI water to free draining. For all tests, 1 week after inoculation and weekly thereafter, plants were fertilised with the complete range of nutrients required for plant growth (Thrive, Yates®, New SouthWales, Australia) at the recommended rate. For strawberry cultivars inoculated with *F. oxysporum*, plants were harvested for final assessment 6 weeks after inoculation. For strawberry cultivars inoculated with all the other isolates, plants were harvested for final assessment 8 weeks after inoculation.

Response of strawberry cultivar Juliette to F. oxysporum *and binucleate* Rhizoctonia *AG-A*

Developing Australian cultivars suitable for W.A. conditions could allow an industry for the propagation of strawberry plants to be developed locally, and this would lessen the current reliance on interstate propagators who have exclusive Australian licenses with breeders outside of Australia. Cultivar Juliette is a strawberry variety that has been developed locally in Australia. However, this variety was still in at the pre-commercial-release stage when we screened the other varieties for resistance to the main root and crown pathogens isolated, and for this reason we were not able to access commercial runners of this variety in time to include them in the studies on the other seven varieties. Therefore, an additional experiment was conducted when cv. Juliette became available to determine its response to *F. oxysporum* and binucleate *Rhizoctonia* AG-A, the major pathogens causing crown and root disease, respectively, under the same conditions as described above. The cultivars Camarosa (most susceptible to *F. oxysporum*) and Festival (most resistant to both *F. oxysporum* and to binucleate *Rhizoctonia*) were included for comparison.

Disease severity assessment

For all controlled environment room studies, prior to harvesting, symptoms on plant tops were evaluated weekly based on a 0–5 disease severity scale as used previously by Fang *et al*. (2011b), where: 0 = the plant well developed, no disease symptoms; 1 = the plant slightly stunted; 2 = the plant stunted and yellowing; 3 = the plant severely stunted and wilting; 4 = majority of leaves of the plant wilted or dead; 5 = plant dead.

At harvest, plants were removed from each pot and thoroughly washed under running tap water to remove all attached soil and then floated in a shallow tray of DI water. The top, crown, vascular tissue and/or root symptoms of each plant were scored separately. Plant tops were assessed as above. Root disease was assessed on a 0–5 disease severity scale as used previously by Fang *et al*. (2011b), where: 0, root well developed, no discolouration; 1, <25% root discoloured; 2, ≥25%, <50% root discoloured; 3, ≥50%, <75% root discoloured; 4, ≥75% root discoloured; 5, all root discoloured (rotted), plant dead. Crown disease was assessed based on a 0–5 disease severity scale as used previously by Fang *et al*. (2011b), where: 0, no crown tissue discoloured; 1, <25% crown tissue discoloured; 2, ≥25%, <50% crown tissue discoloured; 3, ≥50%, <75% crown tissue discoloured; 4, ≥75% crown tissue discoloured; 5, all crown tissue discoloured (rotted), plant dead. After sectioning, vascular tissue in crowns was assessed on a 0-5 disease severity scale as used previously by Fang *et al*. (2011b), where: 0, no vascular

tissue discoloured; 1, <25% vascular tissue discoloured; 2, ≥25%, <50% vascular tissue discoloured; 3, ≥50%, <75% vascular tissue discoloured; 4, ≥75% vascular tissue discoloured; 5, all vascular tissue discoloured, plant dead. Following harvest, the length of new roots emerged was also measured; and the dry weight (DW) of the plant top, crown and roots of each plant were also recorded following air drying in an oven at constant 69°C.

Re-isolations were made from segments of freshly harvested diseased root, crown and/or vascular tissues onto PDA and/or CMA, as appropriate, to confirm that disease symptoms observed were caused by the isolates inoculated. Further, for *P. cactorum*, 2 cm root segments were excised from diseased roots and floated in Petri dishes containing sterilised DI water for 2 d at 22°C and then examined microscopically for typical sporangia of the pathogen.

Data analysis

In the field studies, plant decline indices (% DI) were used to describe the level of plant decline caused by crown and root diseases. The 0–4 rating scale scores for each plant on each raised bed were converted into % DI based on the method described by McKinney (1923), where:

$$\%DI = \frac{(a\times 0)+(b\times 1)+(c\times 2)+(d\times 3)+(e\times 4)}{(a+b+c+d+e)\times 4}\times 100$$

and where a, b, c, d, and e are the number of plants with decline scores of 0, 1, 2, 3 and 4, respectively. Multiple factor analyses of variance were conducted using GenStat (11th edition, Lawes Agricultural Trust, Rothamsted Experimental Station, UK) to determine the effects of fumigation, cultivar and harvest date on yield of strawberry cultivars, and to determine the effects of fumigation, cultivar and assessment date on the level of plant decline of the cultivars. Fisher's least significant differences (LSD) at $P<0.05$ were used to test the differences between treatment means. In all the controlled environment studies, for disease scores of plant top, crown, crown vascular tissue and root, the values of the disease scores of uninoculated plants were subtracted from those of the inoculated controls; for the reduction in root length, the values of root length of inoculated plants were subtracted from those of the uninoculated controls; for the reduction in DW of plant top, crown and root, the values of the DW of inoculated plants were subtracted from those of the uninoculated controls. The data from control treatments are not presented and were excluded from the analysis. Analyses of variance were also conducted to determine the response of strawberry cultivars to crown and root diseases caused by different pathogens. Correlation coefficients between the different parameters assessed and probabilities were also calculated and tested. Delineations for resistance/susceptibility were made as by Purwantara *et al.* (2001) and Li *et al.* (2009) for other host-pathogen combinations, where cultivars with the disease severity score of the plant top, crown, root or vascular tissue <2.5 were considered as resistant and those ≥2.5 were considered as susceptible. Means of all assessed parameters are presented.

Results

Field experiments

Yields of three strawberry cultivars

Yields of cvs Albion, Camarosa and Camino Real for fumigated and non-fumigated field beds were recorded at 3–5 d intervals from 30 June to 11 November 2008 in the field experiments in Wanneroo, Western Australia (Table 1). There were statistically significant effects ($P<0.001$) of fumigation, cultivar and harvest date, and significant two-way interactions ($P<0.001$) of fumigation × cultivar, fumigation × harvest date and cultivar × harvest date, and a significant three-way interaction ($P<0.001$) of cultivar × fumigation × harvest date in relation to the strawberry yields (Table 2). For each of the three cultivars, the yield of plants in fumigated beds was greater than that in non-fumigated beds, with the greatest difference being for cv. Camarosa; both in fumigated and non-fumigate beds, cv. Camino Real showed the greatest total yields of strawberries, followed by cv. Camarosa and cv. Albion (Table 1).

Resistance of three strawberry cultivars to crown and root diseases

There were statistically significant effects ($P<0.001$) of fumigation, cultivar and assessment date, and significant two-way interactions ($P<0.001$) of fumigation × cultivar, fumigation × assessment date, and cultivar × assessment date, and a significant three-way interaction ($P<0.001$) of fumiga-

Table 1. Yields of strawberry cultivars for fumigated (F) and non-fumigated (NF) field beds (100 plants per bed) harvested at 3–5 d intervals from 30 June to 11th November 2008 in the field experiments in Wanneroo, Western Australia.

Harvest date	Total yield per harvest date (g)						Mean
	Albion		Camarosa		Camino Real		
	F	NF	F	NF	F	NF	
30 June	200	239	233	329	50	166	203
4 July	827	338	807	468	200	235	479
10 July	531	423	645	587	605	295	514
15 July	1872	1162	2272	1608	2486	809	1702
19 July	1483	938	1700	1463	2683	1293	1593
23 July	1200	1233	1450	1193	2350	1617	1507
27July	1527	1625	2013	2241	2127	2134	1944
1 August	521	452	687	622	726	593	600
5 August	1421	707	2731	1302	2793	2203	1859
11 August	957	428	1074	967	1213	1537	1029
17 August	679	372	1447	1066	1099	1304	995
23 August	1433	867	1567	1500	1270	1250	1314
29 August	1940	1422	2250	1517	1943	1437	1751
4 September	4150	2833	6000	2883	5233	4850	4325
10 September	1667	2000	2233	1733	2230	3317	2197
16 September	2617	2100	2350	2167	2667	3083	2497
22 September	3333	2000	4833	2550	3833	3117	3278
28 September	2667	1617	5667	2050	4833	2983	3303
4 October	3167	1917	5000	2333	5833	4333	3764
10 October	3167	2333	3667	3067	4667	5267	3694
16 October	4833	2583	10200	4633	12833	10000	7514
21 October	3167	1500	8400	1553	8500	9833	5492
24 October	1333	417	3833	500	4500	2167	2125
27 October	1917	280	4583	617	5083	2167	2441
31 October	1383	100	2767	333	2500	1392	1412
5 November	1677	83	5230	383	4943	1523	2307
11 November	1720	7	4850	247	4080	497	1900
Total yield per season (g)	51389	29976	88489	39912	91280	69402	61739
Mean	1903	1110	3277	1478	3381	2570	2287

tion × cultivar × assessment date in relation to the amount of plant decline (Table 3). For each of the three cultivars, taken as a mean of the % DI across the fumigated and non-fumigated beds, the amount of plant decline increased significantly from August to November, with the largest increase being for cv.

Table 2. Analysis of variance for yields of strawberry cultivars in relation to fumigation, cultivar and harvest date in the field experiment in Wanneroo, Western Australia.

Source of variance	df	*F* value	*P*>*F*
Fumigation	1	769.7	<0.001
Cultivar	2	435.3	<0.001
Harvest date	26	234.4	<0.001
Fumigation × cultivar	2	66.2	<0.001
Fumigation × harvest date	26	31.2	<0.001
Cultivar × harvest date	52	27.9	<0.001
Fumigation × cultivar × harvest date	52	7.8	<0.001
Residual	324		
Total	485		

Table 3. Analysis of variance for plant decline indices (% DI) of strawberry cultivars in relation to fumigation, cultivar and assessment date in the field experiment in Wanneroo, Western Australia.

Source of variance	df	*F* value	*P*>*F*
Fumigation	1	3868.0	<0.001
Cultivar	2	115.5	<0.001
Assessment date	2	1539.0	<0.001
Fumigation × cultivar	2	163.3	<0.001
Fumigation × assessment date	2	101.5	<0.001
Cultivar × assessment date	4	46.5	<0.001
Fumigation × cultivar × assessment date	4	33.6	<0.001
Residual	36		
Total	53		

Albion where the % DI increased from 0.9 to 52.8 (Figure 1a). Both for fumigated and non-fumigated beds, taken as a mean of the % DI across the three cultivars, the level of plant decline increased significantly, particularly in non-fumigated beds where the % DI increased from 5.1 to 90.3; on each assessment date, there was a significant (P<0.001) difference in the amount of plant decline between fumigated and non-fumigated beds, with the largest difference in November where the % DI for fumigated and non-fumigate beds was 8.8 and 90.3, respectively (Figure 1b). For each of the three cultivars, taken as a mean of the % DI across the three assessment dates, there was a significant (P<0.001) difference in the amount of plant decline between fumigated and non-fumigated beds, particularly for cv. Camarosa where the % DI for fumigated and non-fumigated beds was 1.4 and 58.7, respectively; cv. Camino Real was the most resistant cultivar in non-fumigated beds, followed by cv. Albion and cv. Camarosa (Figure 1c). After the morphological and molecular identification of the fungi and oomycetes isolated, the pathogen responsible for disease symptoms in field trial was confirmed to be *F. oxysporum*.

Controlled environmental experiments

Response of seven strawberry cultivars to Fusarium oxysporum

For plants inoculated with *F. oxysporum*, there were statistically significant effects (P<0.001) of cultivar in relation to disease severity of plant top and crown vascular tissue, significant effects (P<0.01) of cultivar in relation to disease severity of root and the reduction in root length, and significant effects (P<0.05) of cultivar in relation to disease severity of crown, the reduction in DW of plant top and root (Table 4). Cultivars Festival, Aromas and Camino Real were relatively resistant to *F. oxysporum*, and in particular, Festival was the most resistant with disease scores for plant top, crown, root and vascular tissue all ≤1.0 and with the smallest reduction in root length (1.2 cm). The others were relatively susceptible to *F. oxysporum*, and in particular, cv. Camarosa was the most susceptible with disease scores for plant top, crown, root and vascular tissue all ≥2.8, and with the largest reduction in root length (12.6 cm) (Table 4, 8). Overall, across cultivars inoculated with *F. oxysporum*, there were significant positive correlations between disease scores for plant top, root, crown and vascular tissue, and the reduction in DW of plant top (data not presented).

Responses of seven strawberry cultivars to binucleate Rhizoctonia *AG-A,* C. destructans, P. exigua, P. cactorum *and* P. ultimum

For plants inoculated with binucleate *Rhizoctonia* AG-A, *C. destructans, P. exigua, P. cactorum* or *P. ultimum,* there were significant effects (P<0.001) of pathogen in relation to the disease severity on root and the reduction in root length, and also significant

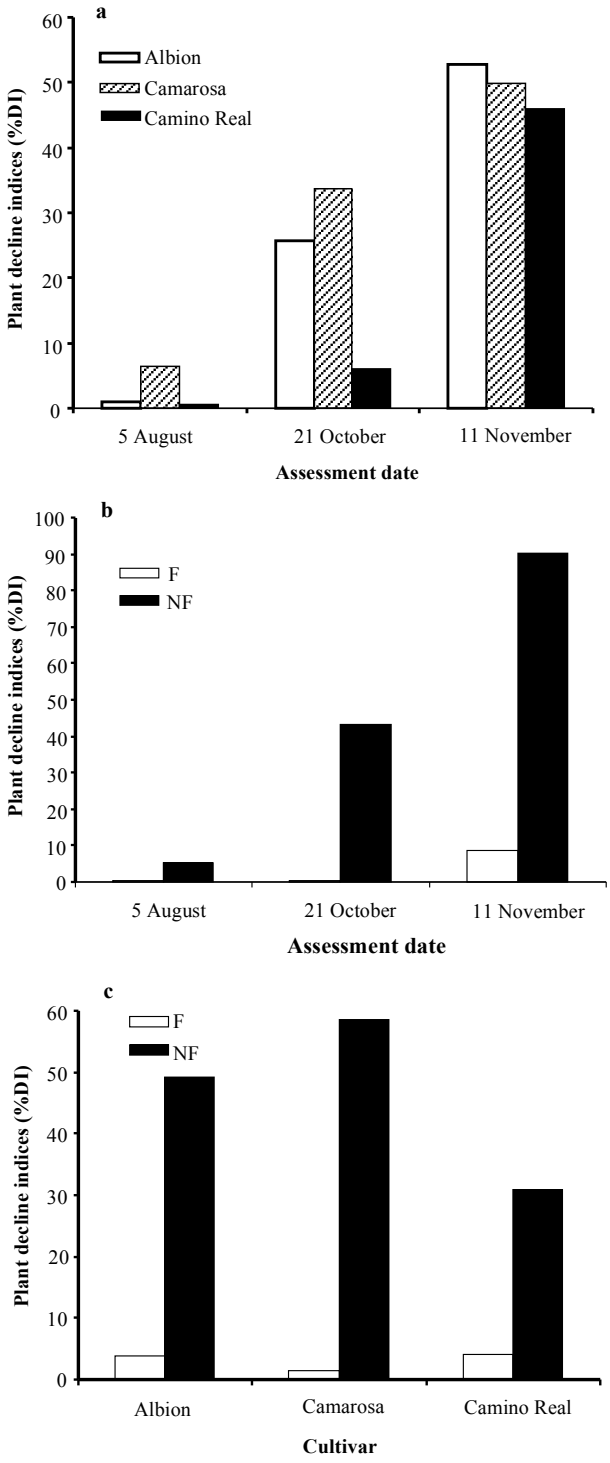

Figure 1. Mean plant decline indices (% DI): (a) for each of the strawberry cultivars on each assessment date taken as means of the % DI across the fumigated and non-fumigated beds; (b) for fumigated (F) and non-fumigated (NF) field beds on each assessment date taken as means of the % DI across the three cultivars; and (c) for fumigated (F) and non-fumigated (NF) field beds for each of the cultivars taken as means of the % DI across the three assessment dates; field experiments at Wanneroo, Western Australia.

Table 4. Response of strawberry cultivars to *Fusarium oxysporum* (WUF-ST-FO35) assessed as disease scores for plant top (0–5 scale where 0 = the plant well developed, no disease symptoms and 5 = plant dead), root (0–5 scale where 0 = root well developed, no discolouration and 5 = all root discoloured (rotted), plant dead), crown (0–5 scale where 0 = no crown tissue discoloured and 5 = all crown tissue discoloured (rotted), plant dead) and crown vascular tissue (0–5 scale where 0 = no crown vascular tissue discoloured and 5 = all crown vascular tissue discoloured, plant dead), reduction in root length (cm), reduction in dry weight (DW) (g) of plant top, crown and root under controlled enrironment conditions and analysis of variance for each parameter assessed in relation to cultivar.

Cultivar	Mean disease score[a]				Mean reduction in root length (cm)[b]	Mean reduction in DW (g)[c]		
	Plant top	Root	Crown	Crown vascular tissue		Plant top	Crown	Root
Albion	2.8	2.0	0.5	2.8	6.7	0.63	0.24	0.17
Aromas	1.1	1.3	1.3	1.5	5.8	0.25	0.24	0.14
Camarosa	4.4	2.9	2.8	3.3	12.6	0.67	0.58	0.45
Camino Real	1.9	2.9	1.0	0.0	8.4	0.33	0.32	0.37
Festival	1.0	0.9	0.9	0.0	1.2	0.23	0.02	0.08
Gaviota	3.5	2.4	1.5	0.1	10.8	0.37	0.08	0.19
Selva	4.3	2.6	2.5	3.1	12.2	0.37	0.29	0.22
Analysis of variance[d]	P<0.001 (6, 49, 72.59)	P<0.01 (6, 49, 6.72)	P<0.05 (6, 49, 3.89)	P<0.001 (6, 49, 82.60)	P<0.01 (6, 49, 10.03)	P<0.05 (6, 49, 2.61)	n.s. (6, 49, 1.47)	P<0.05 (6, 49, 2.57)

[a] The values of the disease scores of uninoculated plants were subtracted from those of the inoculated controls.
[b] The values of root length of inoculated plants were subtracted from those of the uninoculated controls.
[c] The values of the DW of inoculated plants were subtracted from those of the uninoculated controls.
[d] The number in parenthesis represents the degrees of freedom of cultivar, the degrees of freedom of residual and F value; n.s., non-significant at P<0.05.

effects (P<0.01) on disease severity of the crown. There were significant effects (P<0.001) of cultivar on all the parameters assessed apart from the disease severity of plant top. There were significant two-way interactions of pathogen × cultivar (P<0.001) in relation to the disease severity of root and the reduction in root length, and a significant effect (P<0.05) in relation to the disease severity of crown (Table 5).

For cultivars inoculated with binucleate *Rhizoctonia* AG-A, only cv. Aromas and Albion were relatively susceptible with root disease scores ≥2.6, and in particular, cv. Aromas was most susceptible with a root disease score of 3.6. Cultivar Festival was the most resistant with a root disease score of 0.8. For cultivars inoculated with *C. destructans*, cv. Festival was the most resistant with a root disease score of 0.3, and cv. Aromas was the most susceptible with a root disease score of 2.9. For cultivars inoculated with *G. fructicola*, cv. Camino Real was the most resistant, while cv. Albion, Aromas and Festival were relatively susceptible with root disease scores ≥2.9, and in particular, Festival was the most susceptible. For cultivars inoculated with *P. exigua*, cv. Festival was the most resistant with a root disease score of 0.5, and cv. Aromas was the most susceptible with a root disease score of 2.6. Cultivar Camino Real was the most resistant to *P. cactorum,* with a root disease score of 0.6 and without any disease on crown, while cv. Festival was the most resistant to *P. ultimum* with a disease score of 0.1 for root and 0.5 for crown (Tables 5 and 8). Overall, across all cultivars, there were significant positive correlations between disease scores for root and plant top (data not presented).

Response of seven strawberry cultivars to Macrophomina phaseolina

For plants inoculated with *M. phaseolina*, there were significant effects (P<0.001) of cultivar in relation to the disease severity of root and the reduction in root DW, a significant effect (P<0.01) in relation to the reduction in crown DW, and a significant effect (P<0.05) in relation to disease severity of crown (Tale

Table 5. Response of strawberry cultivars to different fungal and oomycete pathogens assessed as disease score (0–5 scale) for plant top, root and crown, reduction in root length (cm), reduction in dry weight (DW) (g) of plant top, root and crown under controlled enrironment conditions, and analysis of variance for each parameter assessed in relation to pathogen and cultivar.

Pathogen	Cultivar	Mean disease score[a]			Mean reduction in root length (cm)[b]	Mean reduction in DW (g)[c]		
		Plant top	Root	Crown		Plant top	Crown	Root
Binucleate *Rhizoctonia* AG-A (WUF-ST-Rhw2)	Albion	0.0	2.6	0.5	7.6	1.41	1.17	1.36
	Aromas	0.0	3.6	0.4	5.8	0.80	1.42	1.32
	Camarosa	0.6	1.3	1.4	8.1	1.18	1.31	1.12
	Camino Real	0.0	1.3	0.0	3.1	0.71	1.30	0.70
	Festival	0.0	0.8	0.5	4.8	0.71	1.06	0.04
	Gaviota	0.6	1.8	0.6	3.0	0.27	1.13	0.94
	Selva	0.6	1.4	1.9	5.6	0.91	1.19	0.79
Cylindrocarpon destructans (WUF-ST-CyD29)	Albion	0.0	2.1	0.1	7.8	1.62	1.11	1.37
	Aromas	0.0	2.9	0.5	4.3	0.93	1.60	1.26
	Camarosa	0.0	0.9	2.0	4.6	0.63	1.23	1.09
	Camino Real	0.0	0.9	0.5	3.7	0.37	1.21	0.81
	Festival	0.0	0.3	1.5	3.5	0.64	1.04	0.69
	Gaviota	0.0	0.9	0.4	3.1	0.02	1.19	0.35
	Selva	0.6	1.1	1.1	3.5	1.04	0.74	0.94
Gnomonia fructicola (WUF-ST-GnF1)	Albion	0.0	2.9	0.6	6.6	1.53	1.21	1.27
	Aromas	0.0	3.3	0.4	6.3	1.05	1.56	1.08
	Camarosa	0.0	0.9	0.9	5.4	0.75	0.99	1.14
	Camino real	0.0	0.6	2.0	3.2	0.46	1.23	0.83
	Festival	0.0	1.5	3.6	4.3	0.40	0.81	0.54
	Gaviota	0.0	0.8	0.4	5.1	0.40	1.25	1.10
	Selva	0.0	0.6	1.9	5.5	0.58	0.61	0.01
Phoma exigua (WUF-ST-PhE9)	Albion	0.0	1.3	0.1	7.6	1.79	1.52	1.67
	Aromas	0.0	2.6	0.5	6.0	0.93	1.41	1.22
	Camarosa	0.0	0.8	1.0	8.0	0.94	0.99	1.33
	Camino Real	0.0	1.3	1.4	5.1	0.62	1.07	0.92
	Festival	0.0	0.5	2.0	4.1	0.28	0.64	0.81
	Gaviota	0.0	1.1	2.4	3.8	0.18	0.85	0.63
	Selva	0.0	0.8	1.0	9.4	1.95	1.05	1.44
Phytophthora cactorum (WUF-ST-PhyC2)	Albion	0.0	1.6	0.1	8.0	1.95	1.54	1.64
	Aromas	0.0	1.9	0.4	4.1	1.14	1.59	1.28
	Camarosa	0.6	1.9	0.3	6.6	0.07	0.45	0.86
	Camino Real	0.0	0.6	0.0	4.4	1.03	1.21	1.07
	Festival	0.0	0.8	1.4	4.3	0.41	1.18	0.83

(*Continued*)

Table 5. *Continues.*

Pathogen	Cultivar	Mean disease score[a]			Mean reduction in root length (cm)[b]	Mean reduction in DW (g)[c]		
		Plant top	Root	Crown		Plant top	Crown	Root
	Gaviota	0.0	2.0	0.6	7.4	1.01	0.94	1.27
	Selva	0.6	1.9	1.9	5.1	1.26	1.10	1.07
Pythium ultimum (WUF-ST-PyU1)	Albion	0.0	1.8	0.4	6.5	1.67	1.23	1.42
	Aromas	0.0	1.5	0.1	9.0	0.86	1.61	1.27
	Camarosa	0.6	1.3	2.1	7.4	1.02	1.15	0.88
	Camino Real	0.0	0.6	0.9	4.2	0.08	0.87	0.34
	Festival	0.0	0.1	0.5	4.6	0.32	1.08	0.39
	Gaviota	0.0	0.8	1.0	1.9	0.26	1.05	0.67
	Selva	0.0	1.3	0.6	6.9	0.97	0.65	0.84
Analysis of variance	Pathogen[d]	n.s. (5, 294, 1.17)	$P<0.001$ (5, 294, 3.37)	$P<0.01$ (5, 294, 2.64)	$P<0.001$ (5, 294, 4.25)	n.s. (5, 294, 0.52)	n.s. (5, 294, 0.53)	n.s. (5, 294, 2.13)
	Cultivar[e]	n.s. (6, 294, 2.00)	$P<0.001$ (6, 294, 18.39)	$P<0.001$ (6, 294, 8.73)	$P<0.001$ (6, 294, 16.36)	$P<0.001$ (6, 294, 10.41)	$P<0.001$ (6, 294, 6.70)	$P<0.001$ (6, 294, 8.55)
	Pathogen × Cultivar[f]	n.s. (30, 294, 0.57)	$P<0.001$ (30, 294, 2.26)	$P<0.05$ (30, 294, 1.59)	$P<0.001$ (30, 294, 2.66)	n.s. (30, 294, 0.93)	n.s. (30, 294, 1.03)	n.s. (30, 294, 1.03)

[a, b, c] See Table 4.
[d] The number in parenthesis represent the degrees of freedom of pathogen, the degrees of freedom of residual and *F* value; n.s., non-significant at $P<0.05$.
[e] The number in parenthesis represent the degrees of freedom of cultivar, the degrees of freedom of residual and *F* value.
[f] The number in parenthesis represent the degrees of freedom of pathogen × cultivar, the degrees of freedom of residual and *F* value.

6). Of the cultivars tested, cv. Albion and Aromas were relatively resistant to *M. phaseolina*, both with a root disease score of 1.3, and in particular, cv. Albion was more resistant with a crown disease score of 1.1. The other cultivars were susceptible to *M. phaseolina*, and in particular, cv. Camarosa was the most susceptible with a disease score of 4.1 for root and 2.5 for crown (Table 6, 8). Overall, across all cultivars inoculated with *M. phaseolina*, there were significant positive correlations between disease scores for crown and plant top (data not presented).

Response of strawberry cultivar Juliette to F. oxysporum *and binucleate* Rhizoctonia *AG-A*

Cultivar Juliette was as susceptible as cv. Camarosa to *F. oxysporum*, with the disease score for plant top, root, crown and vascular tissue ≥2.9, and a 18.5 cm reduction in root length. Cultivar Juliette was much more resistant to binucleate *Rhizoctonia* AG-A compared with cv. Camarosa, but less resistant compared with cv. Festival (Table 7).

Discussion

This is the first study to determine the yield potentials of commercial strawberry cultivars in a field situation where crown and root disease prevails and the first to demonstrate differential resistance of currently available commercial strawberry cultivars to specific fungal and oomycete pathogens associated with crown and root diseases in W.A. Together, these findings will allow strawberry growers to make informed choices about specific cultivars they can deploy in order to minimise losses from crown and root diseases in W.A.

Table 6. Response of strawberry cultivars to *Macrophomina phaseolina* (WUF-ST-MP3) assessed as disease scores (0–5 scale) for plant top, root, and crown, reduction in root length (cm), reduction in dry weight (DW) (g) of plant top, root and crown for seven strawberry cultivars under controlled enrironment conditions, and analysis of variance for each parameter assessed in relation to cultivar.

Cultivar	Mean disease score[a]			Mean reduction in root length (cm)[b]	Mean reduction in DW (g)[c]		
	Plant top	Root	Crown		Plant top	Crown	Root
Albion	0.0	1.3	0.4	0.5	0.21	0.06	0.48
Aromas	0.0	1.3	1.1	0.4	0.15	0.02	0.06
Camarosa	1.3	4.1	2.5	6.4	0.42	0.17	0.01
Camino Real	0.0	2.6	1.0	1.5	0.36	0.10	0.34
Festival	0.0	2.9	1.0	2.2	0.16	0.06	0.09
Gaviota	0.0	2.8	1.5	1.5	0.15	0.11	0.33
Selva	0.6	2.8	1.8	3.4	0.55	0.12	0.08
Analysis of variance[d]	n.s. (6, 49, 1.52)	$P<0.001$ (6, 49, 5.02)	$P<0.05$ (6, 49, 2.16)	$P<0.001$ (6, 49, 4.33)	n.s. (6, 49, 2.14)	$P<0.01$ (6, 49, 4.07)	n.s. (6, 49, 1.06)

[a, b, c] See Table 4.
[d] The number in parenthesis represent the degrees of freedom of cultivar, the degrees of freedom of residual and *F* value; n.s., non-significant at $P<0.05$.

Table 7. Response of strawberry cv. Juliette, Camarosa and Festival to *Fusarium oxysporum* (WUF-ST-FO35) and binucleate *Rhizoctonia* AG-A (WUF-ST-Rhw2) assessed as disease scores (0–5 scale) for plant top, root, crown and vascular tissue, reduction in root length (cm) under controlled enrironment conditions, and analysis of variance for each parameter assessed in relation to cultivar.

Cultivar	*Fusarium oxysporum* (WUF-ST-FO35)					Binucleate *Rhizoctonia* AG-A (WUF-ST-Rhw2)			
	Mean Disease score[a]				Mean reduction in root length (cm)[b]	Mean Disease score[a]			Mean Reduction in root length (cm)[b]
	Plant top	Root	Crown	Vascular tissue		Plant top	Root	Crown	
Juliette	4.8	3.7	2.9	4.0	18.5	0.3	0.9	0.8	5.1
Camarosa	4.1	2.4	2.2	3.1	12.3	0.9	1.4	1.6	8.5
Festival	0.6	0.3	0.3	0.0	1.8	0.0	0.6	0.4	3.7
Analysis of variance[c]	$P<0.001$ (2, 21, 104.33)	$P<0.001$ (2, 21, 50.25)	$P<0.001$ (2, 21, 248.11)	$P<0.001$ (2, 21, 58.90)	$P<0.001$ (2, 21, 329.85)	$P<0.001$ (2, 21, 15.08)	$P<0.01$ (2, 21, 8.17)	$P<0.001$ (2, 21, 12.49)	$P<0.001$ (2, 21, 11.70)

[a, b] See Table 4.
[c] The number in parenthesis represent the degrees of freedom of cultivar, the degrees of freedom of residual and *F* value.

In the field, cv. Camino Real had the least disease and showed the highest yield of strawberries. Cultivar Camarosa was susceptible to crown and root diseases and the yield was lower compared with Camino Real. Cultivar Camarosa is a short-day variety first grown in W.A. in 1998 and has been the predominant cultivar grown since 2000. Cultivar Camino Real is a new short-day variety for W.A.,

Table 8. Summary matrix of the response of the eight strawberry cultivars to eight different fungal and oomycete pathogens ('S' = susceptible and 'R' = resistant).

Cultivar	*Fusarium oxysporum*	Binucleate *Rhizoctonia* AG-A	*Cylindrocarpon destructans*	*Gnomonia fructicola*	*Phoma exigua*	*Phytophthora cactorum*	*Pythium ultimum*	*Macrophomina phaseolina*
Albion	S	S	R	S	R	R	R	R*
Aromas	R	S*	S	S	S	R	R	R
Camarosa	S*	R	R	R	R	R	R	S*
Camino Real	R	R	R	R*	R	R*	R	S
Festival	R*	R*	R*	S*	R*	R	R*	S
Gaviota	S	R	R	R	R	R	R	S
Selva	S	R	R	R	R	R	R	S
Juliette	S	R	—	—	—	—	—	—

* Represents the most resistant or the most susceptible cultivar of the eight cultivars against each particular pathogen.

later maturing, but less vigorous and with smaller root structure compared with cv. Camarosa (Phillips and Reid, 2008). This being so, cv. Camino Real still normally produces a higher proportion of marketable fruit than cv. Camarosa and is reputed to have resistance to Verticillium wilt, Phytophthora crown rot and anthracnose crown rot (Phillips and Reid, 2008). Previous studies in W.A. also showed that cv. Camino Real was the only variety to match cv. Camarosa in yield (Phillips and Reid, 2008). Hence, it was not surprising that cv. Camino Real showed the highest yields of strawberries both in fumigated and non-fumigated beds, and was also the most resistant in the field.

Effective application of soil fumigant provides an essential foundation for management of this disorder in W.A (Fang *et al*., 2011a). For each cultivar tested in the field, plants in fumigated beds showed less disease and higher yields compared with those in the non-fumigated beds, and the greatest difference was evident for cv. Camarosa, which showed the highest level of disease in non-fumigated beds, but showed the least disease in fumigated beds. This is consistent with reports that soil fumigant is especially important for the susceptible cultivars (e.g., Subbarao *et al.,* 2007). However, effects of fumigation can gradually wear-off, allowing pathogen populations to re-establish over time (Particka and Hancock, 2005), and this may be one explanation for the marked increase in levels of plant decline even in fumigated beds from August to November in the present study.

The amount of plant decline increased significantly from August to November in the field experiments and was consistent with our field surveys (Fang *et al*., 2011a). This may have been associated with the rise in the average soil temperature from August to November, rising from 10/20°C to 18/31°C (min/max) (Unpublished data from the Department of Agriculture and Food, W.A.). Wilt-inducing *F. oxysporum* and binucleate *Rhizoctonia* were not only the most common pathogens isolated from declining strawberry plants in W.A. (Fang *et al*., 2011a), they are also the most damaging pathogens (Fang *et al.,* 2011b). There is a strong relationship between higher temperature and increased disease severity on strawberry plants affected by *F. oxysporum* and binucleate *Rhizoctonia* (Fang *et al*., 2011b).

Our studies showed that strawberry cultivars vary in their responses to infection by different fungal and oomycete pathogens. Takahashi *et al*. (2002) developed strawberry cultivars that showed useful resistance to Fusarium wilt in Japan. Cultivars Camarosa, Candonga and Ventana have been reported to show differences in their resistance to crown and root rot caused by *M. phaseolina* depending on the isolate (Avilés *et al*., 2008). Strawberry cultivars have been reported to vary in resistance to crown rot caused by *P. cactorum* (Eikemo *et al*., 2000). MacKenzie *et al*. (2006) showed that resistance of strawberry cultivars to crown rot caused by *C. gloeosporioides* from Florida was nonspecific, with significant differences among cultivars and isolates, but without significant cultivar

× isolate interactions. Our studies suggest that the differential responses of cultivars observed in relation to the incidence and severity of disease reflect significant effects of relative cultivar resistance or susceptibility to these individual pathogens.

A potentially useful strategy for resistance screens could be to utilise a combination of isolates with different levels of aggressiveness for each pathogen (MacKenzie *et al.*, 2006). An advantage of this strategy is that moderately aggressive isolates could differentiate between cultivars with low or moderate resistance, while aggressive isolates could be used to differentiate between cultivars with high levels of resistance (MacKenzie *et al.*, 2006). However, in our study, we evaluated the response of strawberry cultivars using pathogenic isolates associated with crown and root diseases of strawberry, and these isolates clearly differentiated the resistance levels of the cultivars tested. The current study showed that cv. Festival was most resistant and cv. Camarosa most susceptible to *F. oxysporum*, which is the most important pathogen, particularly associated with crown disease in W.A. (Fang *et al*., 2011a, b). Severe disease caused by *F. oxysporum*, often described as Fusarium wilt, was first reported on strawberry in eastern Australia in 1965 (Winks and Williams, 1965) and has since been reported in W.A. (Golzar *et al*., 2007), Korea (Nagarajan *et al*., 2006), China (Zhao *et al.*, 2009), Spain (Arroyo *et al*., 2009) and California (Koike *et al*., 2009). Of the cultivars we tested, cv. Festival was also the most resistant to binucleate *Rhizoctonia* AG-A, an important pathogen mainly associated with root disease of strawberry in W.A. (Fang *et al*., 2011a, b). *Rhizoctonia* spp. are important root pathogens in intensively cultivated strawberry, which rapidly colonise roots and can be recovered at a frequency of up to 60% or more of all pathogens recovered from roots of strawberry (Manici *et al*., 2005). *Rhizoctonia* spp. have also been reported as the major pathogens contributing to root disease development on strawberry in the USA (Martin, 2000), South Africa (Botha *et al.*, 2003) and Italy (Manici and Bonora, 2007). Cultivar Festival was most resistant to *C. destructans*, which is a frequently occurring and important pathogen associated with root disease of strawberry in W.A. (Fang *et al.*, 2011a, b). This fungus has been reported previously from roots of strawberry in Italy (Manici *et al.*, 2005) and Sweden (Morocko, 2006). Cultivar Camino Real was the most resistant cultivar to *G. fructicola* and *P. cactorum* while cv. Festival was the most resistant to *P. exigua*. *G. fructicola*, *P. exigua,* and to *P. ultimum*. These pathogens were components of the complexes associated with crown and root diseases of strawberry in W.A. (Fang *et al*., 2011b). Against *M. phaseolina,* cv. Albion was the most resistant and with cv. Camarosa the most susceptible.

It was evident from our study that cv. Camarosa was the most susceptible cultivar to Fusarium wilt both in the field and the controlled enrironment conditions. Continued commercial cultivation of this cultivar is heavily dependent upon maintaining effective soil fumigation procedures. It is clearly hazardous for growers to deploy this cultivar without effective fumigation, particularly in areas where *F. oxysporum* is prevalent, because of the significant losses likely to be incurred from diseases. Besides, it is important to identify resistance to the most significant pathogens prior to deploying new cultivars so that buildup and spread of pathogens in strawberry fields, especially in production nurseries, is minimised (MacKenzie *et al*., 2006). Cultivar Camino Real was resistant to wilt-causing *F. oxysporum* both in the field and the controlled enrironment conditions, and has a broad spectrum of resistance to a range of different pathogens tested. Cultivar Festival is the most resistant cultivar to a range of different pathogens in addition to *F. oxysporum*, including binucleate *Rhizoctonia* AG-A, *C. destructans, P. exigua* and *P. ultimum*. Therefore, cvs. Camino Real and Festival are expected to be more widely deployed in the future seasons in W.A., especially in situations where soil fumigation has not been fully effective in the past. It is not surprising that Festival has been the major cultivar deployed in Florida, the USA, and now in Queensland, Australia (Phillips and Reid, 2008). The Australian locally bred cv. Juliette was highly susceptible to wilt-causing *F. oxysporum*, but relatively resistant to binucleate *Rhizoctonia* AG-A. This study provides information giving strawberry growers in W.A. a range of useful cultivar resistances that can be deployed where particular pathogens predominate, especially where *F. oxysporum* and binucleate *Rhizoctonia* prevail.

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