

Stem, leaf and cotyledon resistance responses to a prevalent Sclerotinia sclerotiorum pathotype in Australia highlight new opportunities to improve white mould resistance in common bean

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ABSTRACT

Context. White mould (Sclerotinia sclerotiorum) inflicts major yield losses on common bean (Phaseolus vulgaris); yet, commercial cultivars known for their high yields and market-adapted grains lack physiological resistance to this disease. Aims. This study aimed to test diverse common bean genotypes for resistance in stem, leaf and cotyledon tissues. Methods. Thirty-four common bean genotypes with a wide range of agronomic traits and grain types, including genotypes noted previously for susceptible and resistant responses to white mould, were inoculated with the prevalent S. sclerotiorum isolate MBRS-1. Then they were assessed for resistance in stem, leaf and cotyledon tissues under controlled environment conditions, by inoculating plants with a 10⁵ mL⁻¹ hyphal fragment concentration. Key results. There was significant (P < 0.001) variation in resistance responses in stem, leaf and cotyledon tissues across the genotypes. Contender, ICA Bunsi, XAN 280 and Taisho-Kintoki showed the highest resistance in stems, whereas Norvell 2558, Pico de Oro, Sanilac, Othelo and Negro Argel exhibited notable resistance in leaves. Metis, Canario 107, Pico de Oro, Pogonion and Iubilejnaja 287 displayed the most resistance in cotyledons. Conclusions. This is the first reported attempt to determine the response of common bean germplasm to a prevalent pathotype of S. sclerotiorum in Australia. Bean genotypes exhibiting high-level resistance to white mould identified in this study can be used as parental lines for crosses in common bean breeding programs and/or directly as improved cultivars. Implications. The study highlighted both the value of screening under controlled environmental conditions to reliably locate new stem, leaf and/or cotyledon resistances and the possibility of using rapid cotyledon screening to indicate stem resistances because the expression of resistances in cotyledons generally correlated strongly with those in stems.

Keywords: common bean, common bean diseases, disease screening, host resistance, *Phaseolus vulgaris*, physiological resistance, *Sclerotinia* rot, stem rot, white mould.

Introduction

Common bean, *Phaseolus vulgaris*, is one of the most widely grown pulse crops for direct consumption in both tropical and temperate climates worldwide. The total worldwide production of dry bean and area harvested in 2020 was 27.5 million metric tonnes and 34.8 million hectares, respectively (FAO 2022). Asia contributes approximately 43% to the global production, followed by North, Central and South America (29%), and then Africa (26%), whereas Europe and Oceania contribute approximately 2% of total production (Uebersax *et al.* 2023). In addition to the use of dry bean for human consumption or animal feed, the immature pods are widely consumed as green or string beans. In Australia, green bean production occupies more arable land than any vegetable product, except potatoes and maize (Australian Bureau of Statistics 2021), and is commonly rotated with other major vegetables such as potato and pea (Jones *et al.* 2011).

White mould (*Sclerotinia sclerotiorum*) is a major global disease of common bean (del Río et al. 2004; Singh et al. 2014; Kamvar et al. 2017) and causes significant yield losses to both

irrigated and rain-fed bean production. For example, in the Americas, worst instances of yield losses of >90% occur under conducive weather conditions (Singh and Schwartz 2010; Schwartz and Singh 2013). Increased sowing density and irrigation, while necessary for high yields, increases the incidence of white mould (Mila et al. 2003; Abán et al. 2018; Robison et al. 2018). Because sclerotia of S. sclerotiorum can survive in soil for several years, crop rotation is often an ineffective form of management, making reliance on fungicidal sprays at flowering the most used means of disease control in many countries (McCaghey et al. 2019), including in Australia (Jones et al. 2012). However, owing to the cost with fungicide application, there has been increased use of wider row spacing and morphological characteristics that foster 'disease escape', such as enhanced standing ability as a means to lower canopy humidity and decrease contact among plants, and so reduce white mould infection (Miklas and Grafton 1992; Ando et al. 2007). However, although such traits are heritable and with associated quantitative trait loci (OTL) identified, they are generally also associated with reduced yield (Ender and Kelly 2005).

Developing cultivars with inherent physiological resistance is considered the most desirable avenue to manage this disease (Miklas et al. 2013; Singh et al. 2017). Despite ongoing efforts to pyramid high levels of physiological resistance from multiple other species in the Phaseolus secondary gene pool into common bean (Singh et al. 2014, 2017), commercial common bean cultivars with a combination of high yield, market-adapted size and colour, and high physiological resistance to white mould are not yet available (Robison et al. 2018; Campa et al. 2020). Screening the progeny of partially resistant genotypes crossed with commercially available cultivars of common bean has demonstrated that there is potential for breeding lines to contribute their resistance to new cultivars with favourable agronomic and seed characteristics (Miklas et al. 2004; Carvalho et al. 2013). However, regional variation in agronomic and market factors further complicates such efforts, as a successful commercial cultivar must be both adapted to the local climate in terms of high yield and meet the preference of local consumers in terms of grain attributes such as seed size and colour. Meeting consumer preferences for improved common bean cultivars can be an additional ongoing and large undertaking for breeding programs (Lehner et al. 2015; Lima et al. 2017). In addition, S. sclerotiorum has wide diversity, with isolates varying in their aggressiveness and interaction with host resistance in common bean. Hence, it is not surprising that resistant bean genotypes respond differently to different isolates at different stages of disease progression (Lehner et al. 2016; Abán et al. 2020).

Common bean germplasm is frequently screened using isolates specific to the region concerned (Singh *et al.* 2017), as is the case, for example, in Brazil (Lehner *et al.* 2016), Spain (Pascual *et al.* 2010) and Argentina (Abán *et al.* 2020). However, resistance in common beans to Australian isolates

of *S. sclerotiorum* has not been investigated. Hence, taking 34 common bean genotypes from various countries, including those for partial resistance or susceptibility (Miklas *et al.* 2004; Viteri and Singh 2015), the objective was to screen these for resistance under controlled environmental conditions by comparing their varietal resistance responses on cotyledons, leaves and stems.

Materials and methods

Pathogen isolate preparation and culturing

S. sclerotiorum isolate MBRS-1 was used to screen common bean breeding lines in this study. MBRS-1 was originally collected from canola (*Brassica napus*) in the Mount Barker region of Western Australia in 2004 (Li *et al.* 2006). This isolate was chosen because it is an aggressive strain belonging to Pathotype 76, the prevailing pathotype among broadleaf crops in Western Australia (Barbetti *et al.* 2014; Khan *et al.* 2020), particularly among lupin and *Brassica* crops (Ge *et al.* 2012). This isolate has been previously used to demonstrate differences in susceptible and resistance host responses across diverse *Brassicaceae* (Li *et al.* 2007; Garg *et al.* 2010). There has not been any previous characterisation of the pathogen associated with common bean.

Cultures were revived from dry-stored MBRS-1 sclerotia (Clarkson et al. 2003; Barbetti et al. 2014), briefly as follows. Dormant sclerotia were surface sterilised in 6% (v/v)sodium hypochlorite for 3 min and washed twice using sterile deionised water to ensure all hypochlorite was removed, then cut in half and placed face-down on a 2% potato dextrose agar (PDA) plate. Agar plugs 3 mm in diameter were cut from the original plate cultures when 7 days old and used to subculture the pathogen onto further freshly poured PDA plates, but containing 1% potato-derived peptone. Finally, 3-mm plugs from the growing edge of these colonies when 7 days old were used to produce inoculum for stem inoculations and/or for further subculturing as necessary. For cotyledon and leaf inoculations, hyphal inoculum was prepared in liquid culture by using the methodology of Garg et al. (2008). All cultures were incubated at 18°C.

Common bean cultivars

Thirty-three *P. vulgaris* genotypes were obtained from the international bean collection at the Australian Grains Genebank. Genotypes were chosen to represent the diversity of flowering time, seed weight and country of origin, and included available genotypes that had been used in previous studies involving *S. sclerotiorum*. Table 1 displays information about agronomic characteristics of bean genotypes used for this study. Some additional information was also extracted from Li *et al.* (2016). The selected genotypes included ICA Bunsi, a variety noted for moderate resistance to *S. sclerotiorum*

Genotype	Country origin United States	Stem disease index (%)		Cotyledon disease index (%) ^A		Leaf disease index (%)		Days to flowering	Seed weight (g/100) ^B	Seed type
Contender		9.7	(1)	-		52.I	(33)	34	54.2	Shiny mottled cream
ICA Bunsi	Colombia	16.0	(2)	47.9	(21)	13.9	(19)	42	15.8	Dull white
XAN 280	Colombia	21.5	(3)	44.9	(18)	17.4	(26)	49	_	Black
Taisho Kintoki	Japan	23.6	(4)	_		12.9	(16)	36	58.7	Dull mottled red
ARS-R93003	United States	32.6	(5)	48.1	(22)	12.9	(16)	38	41.2	Shiny pink
Radical	Colombia	33.3	(6)	34.9	(7)	5.9	(10)	49	63.2	Shiny red
Centralia	Canada	34.0	(7)	43.1	(17)	5.4	(8)	44	_	White
BAT 1217	India	34.0	(7)	37.7	(9)	39.5	(32)	42	21.4	Shiny purple
Royal Red	Colombia	34.0	(7)	45.3	(19)	59.0	(34)	36	_	Shiny red
Burter's Blight Proof	United States	34.0	(7)	38.0	(11)	22.4	(28)	34	16.5	Shiny white
Light Red Kidney	United States	35.4	(11)	32.5	(6)	30.0	(30)	40	44.5	Shiny brown
Teebus	South Africa	40.3	(12)	50.3	(23)	10.0	(12)	39	23	Shiny white
Swedish Brown	Canada	41.0	(13)	39.3	(12)	5.5	(9)	38	33	Shiny yellow
A55 (a)	Colombia	42.2	(14)	41.2	(14)	20.0	(27)	46	-	Dull black
Othelo	Colombia	44.4	(15)	41.4	(16)	2.7	(4)	36	43.4	Shiny striped cream
A55 (b)	India	44.4	(15)	41.2	(14)	16.2	(24)	44	27.2	Dull black
A54	India	45.I	(17)	-		30.0	(30)	46	21.8	Dull buff
Kingaroy 53	Australia	45.8	(18)	54.3	(24)	26.4	(29)	41	41.2	White
Negro Argel	Chile	45.8	(18)	62.6	(27)	2.8	(5)	49	18.9	Shiny black
Tweed Wonder	Australia	45.8	(18)	_		14.9	(21)	40	52.7	Shiny red
Sanilac	United States	46.5	(21)	55.3	(25)	1.4	(3)	36	22	Shiny white
SEA 2	Colombia	49.3	(22)	37.9	(10)	10.2	(14)	42	-	Dotted buff
Metis	Colombia	50.0	(23)	19.7	(1)	14.9	(21)	34	14	Shiny white
Norvell 2558	Guatemala	50.0	(23)	46.7	(20)	0	(1)	46	28.1	Dull black
Pogonion	Colombia	52.1	(25)	26.8	(4)	5.3	(7)	36	61.8	Shiny yellow
PP 1088	Turkey	56.9	(26)	40.8	(13)	9.4	(11)	38	41.8	Shiny yellow
A99	India	59.0	(27)	56.2	(26)	15.9	(23)	38	27.4	Dull buff
Canario 107	Colombia	60.4	(28)	24.0	(2)	10.9	(15)	36	_	Shiny yellow
Jubilejnaja 287	Russian Federation	64.6	(29)	29.2	(5)	9.9	(12)	38	24.5	Shiny white
Borlotti	Colombia	64.6	(29)	-		16.4	(25)	40	41.2	Mottled brown
Pico de Oro	Brazil	65.3	(31)	24.3	(3)	0	(1)	42	-	Dull buff
XPB 155	India	66.0	(32)	35.8	(8)	13.8	(18)	38	22.4	Dull white
Seaway	United States	66.0	(32)	64.3	(28)	14.4	(20)	36	17.4	Shiny white
Hebar	Bulgaria	70.1	(34)	-		3.9	(6)	36	26.4	White
C' 'C				0.001		0.001				

Table I. Percentage stem disease index following colonised mycelial plug inoculation; percentage cotyledon and leaf disease index follow hyphal inoculation, origin and varietal traits for common bean (*Phaseolus vulgaris*) genotypes infected with *Sclerotinia sclerotiorum* isolate MBRS-1.

^AMissing cotyledon disease index values are due to slow germination, making cotyledons on some genotypes inaccessible for inoculation. ^BHistorical data for seed weight were not available for all genotypes.

<0.001

18.6

<0.001

4.21

<0.001

26.9

(Tu and Beversdorf 1982; Miklas *et al.* 2004), and the Canadian cultivar Centralia descended from it (Park *et al.* 1988). Two genotypes known to exhibit susceptibility to the disease were included as susceptible checks A55 (Miklas *et al.* 2001;

Significance

l.s.d. (P < 0.05)

Singh *et al.* 2003) and Othello (Singh *et al.* 2014; Viteri and Singh 2015). Two separate batches of A55 germplasm were obtained from the Genebank and utilised but noted to have been supplied from different countries (India and Colombia).

All selected genotypes had an upright growth habit (Type I or II) that is suitable for mechanical harvesting. Whereas this habit is considered to offer some reduction in the incidence of white mould under field conditions (Schwartz and Singh 2013), Othello growth habit was Type III (i.e. indeterminate prostate). An additional commercial cultivar, 'Borlotti', that is widely utilised in Australia (Yates Australia), was included as a comparison, totalling 34 test genotypes.

Plant establishment

Four seeds per each of the 34 selected genotypes were sown into each pot (pots $10 \times 10 \times 20$ cm depth) at a depth of 3 cm. Pots were filled with modified University of Western Australia potting mix consisting of 50% composted pine bark, 20% coco peat and 30% fine river sand that together had been pasteurised at 65°C for 90 min. Throughout experiments, all plants were kept in a controlled environment room maintained at 24°C by day, 18°C by night, constant 70% humidity and with a 12-h photoperiod. This temperature range is considered optimal for Australian common bean production. Plants were fertilised with Thrive All-Purpose fertiliser (N:P:K ratio of 25:5:8.8, Yates Australia) according to manufacturer recommendations.

Inoculation of cotyledons and disease assessment

Seven 3-mm plugs of PDA were cut from the growing edge of each *S. sclerotiorum* colony. These were used to inoculate 75-mL batches of liquid potato dextrose medium (24 g L⁻¹ potato dextrose) containing 10 g L⁻¹ potato peptone. Cultures were then incubated in 250 mL flasks at room temperature for 72 h on a rotary shaker at 120 rpm at 25°C. The resulting mycelial mat was removed and washed twice with sterile deionised water to remove any residual fungal metabolites from the liquid medium, then resuspended in 125 mL of liquid medium. Mycelium was macerated for 5 min using a sterilised stick-blender and then filtered using four layers of muslin cloth. Using a haemocytometer counting chamber (Superior), liquid medium was used to dilute samples until a hyphal fragment concentration of 10^5 mL^{-1} was achieved.

Cotyledons were inoculated, with a single $10-\mu$ L droplet applied by micropipette to the surface of each fully opened cotyledon 8 days after sowing. During inoculation, the mycelial suspension was regularly mixed by handshaking to prevent clumping of hyphae. Plants were maintained for 72 h post-inoculation (hpi) in translucent sealed plastic boxes containing water to a depth of 2 cm, so as to maintain high humidity. This ensured both reduced lighting and high humidity, which together favour *S. sclerotiorum* infection (Garg *et al.* 2008).

Cotyledons were assessed 72 hpi. Lesions were rated according to their length (mm) as a proportion of cotyledon size, from 0 (0% lesion coverage) to 5 (100% lesion coverage) and the mean lesion score across all plants in each pot was

taken to be a single replicate score. Ratings were converted into a mean percentage cotyledon disease index (%CDI) on the basis of the method of McKinney and Davis (1923), as follows:

$$\label{eq:CDI} \begin{split} & \text{\%CDI} = \{ [(a \times 0) + (b \times 1) + (c \times 2) + (d \times 3) + (e \times 4) \\ & + (f \times 5)] \times 100 \} / [(a + b + c + d + e + f) \times 5 \end{split}$$

where *a*, *b*, *c*, *d*, *e* and *f* are the number of plants with leafdisease scores of 0, 1, 2, 3, 4 and 5, respectively, as widely used for cotyledon infection studies (Murtza *et al.* 2021).

Leaf and stem inoculations and disease assessments in adult plants

Leaves

To screen common bean breeding lines, for leaves, liquid inoculum was prepared using the method described above for cotyledons. Forty days after sowing, when visible flower buds were present on >50% of plants and flowers had begun to open on each plant, the uppermost fully opened and expanded leaf was inoculated in two locations (both leaf lobes) with a 10-µL droplet applied using a micropipette and allowed to dry slightly to ensure adhesion to the leaf surface. High humidity was maintained post-inoculation by hand-misting inoculated plants with deionised water and covering them with a translucent plastic cover for 72 h. At 72 hpi, leaf lesion diameter was measured on all inoculated leaves using calipers and a mean leaf lesion diameter computed on a 0-9 scale, where 0 = n0disease symptoms; 1 = <1 mm; 2 = 1 - <3; 3 = 3 - <6; 4 = 6 - <9; 5 = 9 - < 12; 6 = 12 - < 15; 7 = 15 - < 18; 8 = 18 - < 21; and 9 = >21 mm. Ratings were converted into a mean percentage leaf disease index, as described for cotyledon disease above, but modified to include the greater number of score categories.

Stems

Forty days after sowing, when visible flower buds were present on >50% of plants and flowers had begun to open on each plant, stems were inoculated using the method described for canola screening by Barbetti et al. (2015). This involved taking S. sclerotiorum-colonised 5-mm plugs from freshly cultured peptone-PDA. Petri dishes of S. sclerotiorum and attaching a single colonised agar plug to each stem directly below the 1st node, by using Parafilm. This method roughly approximates the 'straw test' commonly used to test P. vulgaris disease response in the field (Singh and Terán 2008). High humidity post-inoculation was provided as for leaf studies, and stem infection was recorded at 72 hpi. The nine-point scale described by Terán et al. (2006) and modified by Singh et al. (2014) for cut-stem and straw test screenings of common bean infection was adapted to compute stem disease severity scores as follows: Scores 1-3 represented a resistant response in which the fungus failed to progress past any node; Scores 4-6 represented moderate infection proceeding past the first post-inoculation node; and Scores 7–<9 represented infection past the second post-inoculation node. Score 0 indicated no infection, whereas any plant destroyed by stem collapse because of infection was assigned a score of 9. These scores were converted to mean percentage stem disease index, as described above for cotyledons, but modified to include the greater number of score categories.

Data analysis

The experiment was fully repeated once. Each experiment had six single pot replications per genotype, with a total of 204 pots arranged as a 'fully randomised design', generated by using the 'Generate a Standard Design' function of GenStat 18.1 (18th edition, Lawes Agricultural Trust, Rothamsted Research, UK). Normality of data and homogeneity of the original and repeat experiments were tested before conducting analyses. Data from the original and the repeat experiments were not significantly (P > 0.05) different by using a Student's *t*-test nor when comparing cultivar responses across the duplicate experiments when compared using an F-test for equality of two variances. Therefore, data from the original and repeat experiments were combined, and analysed together as a single data set, using completely randomised ANOVA function in GenStat. Fisher's least significant difference (l.s.d. at $P \le 0.05$) test was used to highlight differences among genotypes in relation to the three different disease assessment parameters (percentage cotyledon, leaf or stem disease indices). Where appropriate, correlation gradients were plotted and R^2 values calculated using Microsoft Excel.

Results

Cotyledon inoculations

Cotyledons developed characteristic lesions and significant differences in %CDI were observed (P < 0.001) (Table 1, Fig. 1*a*-*c*). The disease index of the cotyledon ranged between 19.7% (Metis) and 64.3% (Seaway). Other than Metis, genotypes also showing high level of cotyledon resistance included Canario 107, Pico de Oro, Pogonion and Jubilejnaja 287, with index values of 24.0, 24.3, 26.8 and 29.2, respectively. Whereas no significant difference was observed in %CDI between ICA Bunsi (47.9), Othello (41.4) and A55a,b (both 41.2), these three genotypes had significantly greater %CDI values than did the most resistant genotype Metis (19.7).

Leaf inoculations

There were significant (P < 0.05) differences in %LDI across the test genotypes (Table 1, Fig. 1*d*, *e*). Percentage leaf disease index values ranged from 0 (Norvell 2558, Pico de Oro) to 59.0 (Royal Red). Other genotypes showing a high level of leaf resistance included Sanilac (1.4), Othelo (2.7) and Negro Argel (2.8). The %LDI for Othelo (2.7) was significantly lower than that for ICA Bunsi (13.9), the latter, in turn, being significantly lower than that for A55a (20.0) but not for A55b

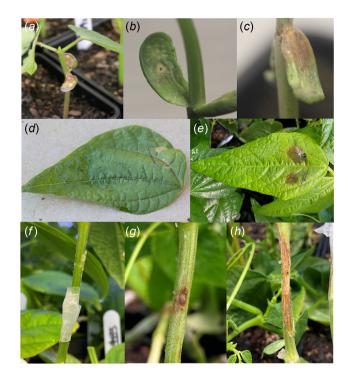


Fig. 1. Symptoms of S. sclerotiorum infection in common bean cotyledon, stem and leaf tissue. (a) Typical seedling, with the growing tip removed to maintain cotyledon attachment and cotyledons with typical white mould infection; (b, c) cotyledon of resistant and susceptible genotypes, respectively; (d, e) leaf of resistant and susceptible genotypes, respectively; (f) how Sclerotinia sclerotiorum colonised agar plug is attached using Parafilm to inoculate stems; (g, h) stem lesions on resistant and susceptible genotypes, respectively.

(16.2). The latter three genotypes had significantly greater %LDI values than the most resistant genotypes Norvell 2558 and Pico de Oro (both 0), Sanilac (1.4), Othelo (2.7) and Negro Argel (2.8).

Stem inoculations

There were significant (P < 0.001) differences in %SDI (Table 1, Fig. 1*f*–*h*), ranging from 9.7 (Contender) to 70.1 (Hebar). Genotypes other than Contender showing a high level of stem resistance included ICA Bunsi (16.0), XAN 280 (21.5) and Taisho Kintoki (23.6). Contender had a significantly lower %SDI than did both Othello (44.4) and A55a,b from both origins (44.4, 42.2), but ICA Bunsi (16.0) was not significantly different from Othello or the A55a,b genotypes.

Correlations

Percentage stem disease index correlated strongly and positively with %CDI ($R^2 = 0.7$; n = 28; P < 0.001) and seed weight ($R^2 = 0.7$; n = 28; P < 0.001). There were no other significant correlations between any of the disease or other factors considered in this study.

Discussion

This is the first reported attempt to determine the response of common bean germplasm to a prevalent pathotype of S. sclerotiorum in Australia. The most resistant responses in stems were Contender, ICA Bunsi, XAN 280 and Taisho-Kintoki, in leaves were Norvell 2558, Pico de Oro, Sanilac, Othelo and Negro Argel, and in cotyledons were Metis, Canario 107, Pico de Oro, Pogonion and Jubilejnaja 287. Bean genotypes exhibiting partial resistance to white mould identified in this study can be used as parental lines for crosses in common bean breeding programs and/or directly as improved cultivars where no resistance currently exists. Of the three plant components assessed, resistance to white mould in terms of stem resistance is considered the most critical towards effective management of white mould. The level of stem resistance found in Contender was similar to that of the moderately resistant variety ICA Bunsi, which in turn significantly outperformed A55a,b and Othello. Contender (also marketed as Buff Valentine) was developed in South Carolina, released in 1950, and has been well studied in the context of its genetic diversity within P. vulgaris and as a worldwide reference variety for production studies (Gepts et al. 1986; Nienhuis and Sass 2016; Meena et al. 2018). However, for this variety, there has not been any previous expression of physiological or morphological resistance on any plant component to white mould.

In previous studies, ICA Bunsi has consistently outperformed Othello, despite not being considered highly resistant (Viteri and Singh 2015). Although the difference in response between these two cultivars is not always large (Viteri and Singh 2015), in the current study ICA Bunsi showed much greater stem resistance to white mould. Resistance to white mould is known to be highly variable across common bean cultivars (Schwartz and Singh 2013), being similar to a wide range of host resistances/susceptibilities noted in previous studies across diverse Brassicaceae screened against this same isolate of S. sclerotiorum (Uloth et al. 2013, 2015; Barbetti et al. 2014; You et al. 2016). Interestingly, in previous studies, individual Othello plants have been identified as resistant to some isolates of S. sclerotiorum, even when the mean response is overall susceptible (Singh et al. 2014). Furthermore, Othello displays a Type III growth habit (indeterminate prostrate), a growth habit that is known to generally be more susceptible to white mould in the field than the more upright types of common bean (Ando et al. 2007; Schwartz and Singh 2013).

The four genotypes that showed significantly smaller stem lesions than did A55a or A55b in the current study also included ICA Bunsi, but not its derived cultivar, Centralia. The other three, being Contender, breeding line XAN 280 and the Japanese landrace Taisho-Kintoki, have not previously been noted for resistance to *S. sclerotiorum*. However, XAN 280 has been previously noted for its high resistance to bacterial blight (*Xanthomonas campestris*) in the field (Rodriguez *et al.* 1999). Hence, XAN 280 may be particularly useful for locating combined disease resistance where both white mould and bacterial blight co-occur. Whereas Taisho-Kintoki has been noted for low yield, its seed quality and early maturation have led to the development of higher-yielding cultivars of Kintoki bean such as Fukura Kintoki, which may be a worthwhile inclusion in future resistance-screening studies (Narikawa 1972; Ebe *et al.* 2005).

S. sclerotiorum is capable of damaging beans in the field at all stages of growth (Schwartz and Singh 2013). However, yield loss from white mould primarily occurs once a canopy has developed, encouraged by both the rising humidity around the stems and the senescent leaf and flower tissues that act as additional inoculum. In addition, airborne ascospores of *S. sclerotiorum* frequently land on and directly infect leaves in addition to flowers, as found in *Brassicaceae* even when not flowering (Uloth *et al.* 2013; M. J. Barbetti, unpubl. data). Such infested leaves collapse around stems and this leads to additional severe stem disease (Uloth *et al.* 2013; M. J. Barbetti, unpubl. data). Ideally, combining stem and leaf resistances into new commercial cultivars would significantly improve overall management of white mould.

Percentage stem disease index correlated strongly and positively with percentage cotyledon disease index and with seed weight. This suggests that there is scope for using a rapid cotyledon test as a preliminary screen for stem resistance to white mould. Conversely, it appears that resistance expressed in leaves is under separate genetic control to that in stems, such that separate searches are required for determining stem and leaf resistances. The correlation between %SDI and seed weight is interesting, with large-seeded beans being seemingly more susceptible to severe white mould. Perhaps this could relate to subsequent stem diameter, because Li *et al.* (2006) showed that stem diameter was an important determinate of the severity of *Sclerotinia* stem rot in *Brassicaceae*.

Phaseolus is a genetically diverse genus and has two major gene pools, the Andean and Mesoamerican, which reflect its multiple centres of origin and subsequent hybridisation (Gepts 1998; Bitocchi *et al.* 2017). ICA Bunsi and its derivatives are derived from the Mesoamerican gene pool (Miklas *et al.* 2004), as are A55a,b and Othello (Seo 2003; Singh *et al.* 2003). However, Contender is derived from the Andean gene pool, and is further assigned to a subgroup of the pool because of its uncommon phaseolin banding pattern (de la Fuente *et al.* 2012). Further study into stem, leaf and cotyledon resistance to white mould displayed by Andean and hybrid beans by using more wide-ranging Australian *Sclerotinia* isolates of varying aggressiveness and across different pathotypes would be useful.

Common bean canopy architecture and growth habit can be important determinants of *S. sclerotiorum* disease severity and their influence could be different under controlled environment versus field conditions (Schwartz and Singh 2013). However, stem inoculations under controlled conditions are known to provide more consistent results than are field trials (Kull *et al.* 2003). Despite this, additional field studies would allow assessment of the impact of any field environment and morphological 'disease avoidance' mechanisms on partial physiological resistances highlighted in the current study.

Conclusions

These present studies have reported the first response of common bean genotypes to a prevalent pathotype of S. sclerotiorum in Australia. Genotypes identified with highlevel stem or leaf resistance are of particularly significant value for developing new white mould-resistant cultivars of common bean. Even genotypes identified with moderate levels of resistance in this study can be used as parental lines aimed at increasing resistance levels in common bean breeding programs. If deployed commercially, these resistances offer significant prospects for improving current integrated disease management strategies, as compared with current reliance on cultural and/or chemical controls utilised with cultivars generally lacking 'useful' resistance. Finally, as resistance was identified for the first time across some of these genotypes, it is likely that they could constitute new sources and/or types of host resistance not previously identified.

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Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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