Evaluation of Leaf Spot Resistance in Wild *Arachis* Species of Section *Arachis*

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ABSTRACT

Wild diploid *Arachis* species are potential sources of resistance to early (ELS) and late (LLS) leaf spot diseases caused by *Passalora arachidicola* (syn. *Cercospora arachidicola* Hori), and *Nothopassalora personata* (syn. *Cercosporidium personatum* (Berk. & Curt.) Deighton), respectively. Within section *Arachis*, limited information is available on the extent of genetic variation for resistance to these fungal pathogens. A collection of 78 accessions representing 15 wild species of *Arachis* section *Arachis* from the U.S peanut germplasm collection was evaluated for resistance to leaf spots. Screening was conducted under field (natural inoculum) conditions in Dawson, Georgia, during 2017 and 2018. Accessions differed significantly ($P < 0.01$) for all three disease variables evaluated, which included final defoliation rating, ELS lesion counts, and LLS lesion counts. Relatively high levels of resistance were identified for both diseases, with LLS being the predominant pathogen during the two years of evaluation. This research documents new sources of resistance to leaf spot diseases selected from an environment with high inoculum pressure. The presence of ELS and LLS enabled the selection of resistant germplasm for further introgression and pre-breeding.

Key words: *Arachis sp.*, disease resistance, early leaf spot, groundnut, late leaf spot, *Nothopassalora personata, Passalora arachidicola*, peanut, wild *Arachis* species.

Early leaf spot (ELS) and late leaf spot (LLS) caused by *Passalora arachidicola* (Hori) U. Braun (syn. *Cercospora arachidicola*) and *Nothopassalora personata* (syn. *Cercosporidium personatum* (Berk. & Curt.) Deighton), respectively, are foliar fungal diseases of peanut (*Arachis hypogaea* L) responsible for significant yield losses. Wild *Arachis* species are potential sources of resistance to various peanut diseases including leaf spots (Abdou *et al.*,

1974; Stalker, 1984; Singh, 1986; Stalker and Moss, 1987; Tallury *et al.*, 2014a; Stalker *et al.*, 2017; Arias *et al*, 2018). Among the 81 wild species described in the genus, only taxa within section *Arachis* cross readily with cultivated peanut. Therefore, several studies have been focused on the screening of species within section *Arachis* and a number of resistant sources have been reported (Subrahmanyan *et al.*, 1985; Pande and Rao, 2001; Fávero *et al.*, 2009; Michelotto *et al.*, 2015). Most of these studies have been conducted in greenhouses or laboratory. However, screening of germplasm under natural infestation for a large number of accessions has been limited.

High levels of resistance or immunity to leaf spots have been identified in the wild diploid species *Arachis cardenasii* Krapov. & W.C. Gregory, *A. diogoi* Hoehne, and *A. stenosperma* Krapov. & W.C. Gregory (Stalker *et al.*, 1979; Simpson, 2001; Stalker *et al.*, 2017). These species have been extensively used in interspecific crosses to develop breeding materials for introgression. Multiple introgression lines from a *A. hypogaea* × *A. diogoi* interspecific derived population have demonstrated the potential of using wild *Arachis* species for peanut improvement (Hancock *et al.*, 2019). *Arachis cardenasii* derived introgression lines have been utilized as a major source of multiple disease resistances, including ELS (Chu *et al.*, 2019; Chu *et al.*, 2020; Stalker *et al.*, 2002; Tallury *et al.*, 2014b). More recently, major quantitative trait loci for resistance to early and late leaf spot diseases have been identified in a recombinant inbred line population (Florida-07 × GP-NC WS16) (Chu *et al.*, 2019). The resistant parental line, GP-NC WS16, is an interspecific breeding material with introgression from *A. cardenasii* (Stalker and Beute, 1993; Tallury *et al.*, 2014b). In the present study, 78 accessions representing 15 species of section *Arachis* from the U.S peanut germplasm collection were screened for resistance to leaf spots. The objective was to identify potential candidates for interspecific hybridization and pre-breeding.

Materials and Methods

A total of 78 accessions representing 15 wild species of *Arachis* section *Arachis*, including 72 diploids ($2n = 2x = 20$) and 6 tetraploids ($2n = 4x =$

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40) from the U.S. peanut germplasm collection were evaluated at the USDA-ARS National Peanut Research Laboratory at Dawson, Georgia, during 2017 and 2018. Additionally, six peanut runner cultivars, three susceptible ('Georgia-13M', 'TUFRunner 511', 'Georgia-09B') and three resistant cultivars ('Georgia-14N', 'Georgia-06G', 'TifNVHigh OL') were used as checks (Table S1). Seeds were planted in the greenhouse in 5.7 cm × 5.7 cm peat pots containing peat-based potting mix. After 5-6 weeks, plants were transplanted into the field at the Newman and Bolton farms in 2017 and 2018 growing seasons, respectively. The experimental design was a randomized complete block with two replications. Each block consisted of a single row with five plants separated 0.61 m apart and 1.83 m between rows. Plants were grown using common agricultural practices for peanut production in Southwest Georgia with supplemental irrigation. No fungicides were applied for prevention or control of leaf spots. Chemicals for weed and insect control were applied following manufacturer's recommendations. Weeds were also controlled by manual hoeing. Meteorological data were collected at the Newman farm, Terrell County, Georgia. This weather station was used as a reference for both farms (www.weather.uga.edu).

Screening was conducted under field (natural inoculum) conditions. Disease severity was evaluated by final defoliation rating (FD), early leaf spot lesion counts (ELC), and late leaf spot lesion counts (LLC). Defoliation was rated on whole plots at the end of the season using the proportional 1-9 scale, with 1 indicating no defoliation and 9 complete defoliation (Chiteka et al., 1988; Tallury et al., 2009). For lesion counts, five leaves were randomly chosen from a lateral branch of each plant in the plot. Lesions were examined under a stereomicroscope and the number of lesions were counted for ELS and LLS, separately. Images of leaf spot lesions were captured with a stereomicroscope Leica MZ16F (Leica, Wetzlar, Germany).

Data from FD, ELC, and LLC were subjected to analysis of variance (ANOVA), followed by Tukey's test for mean comparisons. Variables were transformed to the lambda power of 0.5 (FD) and log_{10} (ELC, LLC) to meet the assumptions of ANOVA. Phenotypic correlations among variables were calculated and plotted using the *corrplot* package (Wei et al., 2017). All statistical analyses were conducted in R environment (R Development Core Team, 2020).

Results and Discussion

Environmental conditions in 2017 and 2018 growing seasons (May-October) were favorable for leaf spot development, as indicated by the severe leaf spot symptoms observed in both susceptible and resistant checks (Table 1). Average maximum and minimum temperatures showed a similar trend both years, with the exception of June (maximum) and September (minimum/maximum) 2018, which were significantly higher ($P < 0.01$) (Fig. 1).

Correlation coefficients between variables were estimated based on the mean of two years. Final defoliation ratings were highly correlated ($r = 0.92$) with the total number of lesions (ELC + LLC) and moderately correlated ($r = 0.64$-0.66) with ELC and LLC when analyzed independently (Fig. 2). Results further showed that LLS was predominant in 70% of accessions, which can explain the low correlation ($r = 0.14$) between ELC and LLC (Fig. 2).

Accessions differed significantly ($P < 0.01$) for all disease variables evaluated (Table 1). Final defoliation rating and ELC also indicated significant effects of year ($P < 0.05$). Variable levels of FD, ELC, and LLC were detected among accessions of the same species. This highlights the importance of selecting germplasm at the accession level rather than species level. Similar findings have been reported in previous studies (Michelotto et al. 2015, Fravero et al. 2009, Pande and Rao, 2001).

With the exception of *A. villosa*, all perennial/semi-perennial accessions of the A-genome species showed the highest level of resistance with FD values between 1 and 2, and lesion counts lower than 2.5 (Table 1). Among these were *A. cardenasii*, *A. correntina*, *A. diogoi*, *A. helodes*, *A. herzogii*, *A. kempff-mercadoi*, *A. kuhlmannii*, *A. simpsonii*, and *A. stenosperma*. *Arachis stenosperma*, although described as annual or semi-perennial (Krapovickas et al., 2007), all plants in the field showed a perennial-like growth habit.

Accessions of *A. villosa* (PI 298636, PI 666104, PI 666106, PI 666108) had moderate levels of resistance to LLS with final defoliation ratings not significantly different from those of the B-genome species *A. magna* and *A. hoehnei*. All accessions of *A. villosa* were susceptible to ELS (Table 1, Fig. 3). The accession from Argentina (PI 298636) was comparatively more resistant than accessions from Uruguay (PI 666104, PI 666106, PI 666108). Plants of this accession showed similarities, but also distinctive morphological characteristics (e.g., pubescence, leaflet shape), suggesting a genetically different germplasm.

Among the non-A genome species evaluated, *A. hoehnei*, *A. benensis*, and *A. magna* had the lowest

Table 1. Accession means for all disease variables measured on 78 wild *Arachis* accessions and five runner cultivar checks.

Accession	Species	Final defoliation rating	Tukey's test[a]	Early leaf spot lesion counts	Late leaf spot lesion counts
'TufRunner 511'	*A. hypogaea*	8.5	a	2	46.7
'Georgia-09B'	*A. hypogaea*	8.25	ab	14	29.95
'TifNVHigh OL'	*A. hypogaea*	8	abc	1.3	21.95
'Georgia-14N'	*A. hypogaea*	8	abc	1.95	27.45
'Georgia-06G'	*A. hypogaea*	7.5	abcd	7.9	15.25
'Georgia-13M'	*A. hypogaea*	7.25	abcde	2	29.25
PI 497260	*A. monticola*	7	abcde	1.75	17.7
PI 468329	*A. batizocoi*	7	bcde	0	11.5
PI 468196	*A. monticola*	6.75	cde	5.1	15.6
PI 219824	*A. monticola*	6.75	cde	3.15	21.2
PI 686979	*A. batizocoi*	6.75	de	7.7	0.85
PI 468199	*A. monticola*	6	de	2.5	20.95
PI 263393	*A. monticola*	6.25	de	4.95	14.85
PI 468326	*A. batizocoi*	6	ef	0	6.55
PI 468327	*A. batizocoi*	6	ef	0	6.5
PI 686976	*A. batizocoi*	6	ef	1	9.05
PI 688943	*A. batizocoi*	6	ef	7.8	1.45
PI 688944	*A. batizocoi*	6	ef	8.05	1.4
PI 405933	*A. monticola*	6	ef	5.15	17.2
PI 666108	*A. villosa*	5	fg	4.8	1.5
PI 666104	*A. villosa*	5	fg	4.3	1.7
PI 666106	*A. villosa*	5	fg	4.75	1.2
PI 688954	*A. hoehnei*	4	g	5.4	0
PI 666086	*A. hoehnei*	4	g	4.95	0
PI 468340	*A. magna*	4	g	6.3	0
PI 599183	*A. magna*	4	g	0	4.1
PI 475877	*A. benensis*	3	h	0.7	3.5
PI 681081	*A. hoehnei*	3	h	3.75	0
PI 468338	*A. magna*	2.75	hi	2.95	0
PI 298636	*A. villosa*	2.75	hi	3.2	0
PI 262808	*A. correntina*	2	ij	0.45	1.7
PI 666091	*A. kuhlmannii*	2	ij	0.5	2.5
PI 475873	*A. kempff-mercadoi*	2	jk	0.05	0.65
PI 468159	*A. kuhlmannii*	2	jk	1.3	1.3
PI 674406	*A. kuhlmannii*	2	jk	0.45	1.7
PI 666089	*A. kuhlmannii*	1.75	jk	1.65	1.3
PI 497579	*A. stenosperma*	1.75	jk	1	0
PI 475998	*A. cardenasii*	1.5	jkl	0	1.55
PI 468334	*A. kempff-mercadoi*	1.5	jkl	0.1	0.75
PI 476119	*A. kuhlmannii*	1.5	jkl	0.45	0.5
PI 666094	*A. kuhlmannii*	1.25	jkl	0.55	0.45
PI 476008	*A. herzogii*	1.25	kl	0	1.35
PI 666095	*A. kuhlmannii*	1.5	kl	0.6	0.55
PI 666090	*A. kuhlmannii*	1.5	kl	0.75	1.3
PI 591359	*A. stenosperma*	1.25	kl	0.25	0.85
PI 591350	*A. stenosperma*	1.75	kl	1.25	0.35
PI 591351	*A. stenosperma*	1.75	kl	1.15	0.4
PI 475994	*A. cardenasii*	1	l	0.45	0.2
PI 475997	*A. cardenasii*	1	l	0	0.35
PI 476011	*A. cardenasii*	1.75	l	0	1.05
PI 476013	*A. cardenasii*	1	l	0	0.5
PI 681078	*A. cardenasii*	1	l	0.65	0
PI 262141	*A. cardenasii*	1	l	0.65	0
PI 475880	*A. correntina*	1	l	0.3	0.6
PI 261871	*A. correntina*	1	l	0.45	1
PI 261868	*A. correntina*	1	l	0.15	0.55

Table 1. Continued.

Accession	Species	Final defoliation rating	Tukey's test[a]	Early leaf spot lesion counts	Late leaf spot lesion counts
PI 262881	*A. correntina*	1	1	0.15	0.55
PI 681079	*A. correntina*	1	1	0.15	0.55
PI 468141	*A. diogoi*	2	1	0	1.1
PI 468142	*A. diogoi*	1	1	0	1
PI 476044	*A. diogoi*	1	1	0	0.9
PI 276235	*A. diogoi*	1	1	0	0.9
PI 468144	*A. helodes*	1	1	0	0.55
PI 468146	*A. helodes*	1	1	0	0.45
PI 476043	*A. helodes*	1	1	0.12	0.75
PI 476045	*A. helodes*	1	1	0	0.45
PI 468331	*A. kempff-mercadoi*	1	1	0	0.5
PI 468333	*A. kempff-mercadoi*	1	1	0	0.65
PI 476108	*A. kuhlmannii*	1	1	0.25	0.85
PI 476126	*A. kuhlmannii*	1	1	0	0.55
PI 681082	*A. kuhlmannii*	1	1	0	0.65
PI 686982	*A. kuhlmannii*	2	1	0.25	1.75
PI 688955	*A. kuhlmannii*	1	1	0.85	0
PI 688957	*A. simpsonii*	1	1	0.45	0
PI 688958	*A. simpsonii*	1	1	0	0.15
PI 338279	*A. stenosperma*	1	1	0.15	0.55
PI 497578	*A. stenosperma*	1	1	0.6	0
PI 497580	*A. stenosperma*	1	1	0.8	0
PI 497581	*A. stenosperma*	1	1	0.35	0
PI 666097	*A. stenosperma*	1	1	0.1	0.55
PI 666098	*A. stenosperma*	1	1	0.75	0.15
PI 591352	*A. stenosperma*	1	1	0	0.55
PI 599180	*A. stenosperma*	1	1	0	0.85
PI 599185	*A. stenosperma*	1	1	0.35	0.05

[a]FD means followed by the same letter were not significantly different ($P < 0.05$) according to Tukey's test.
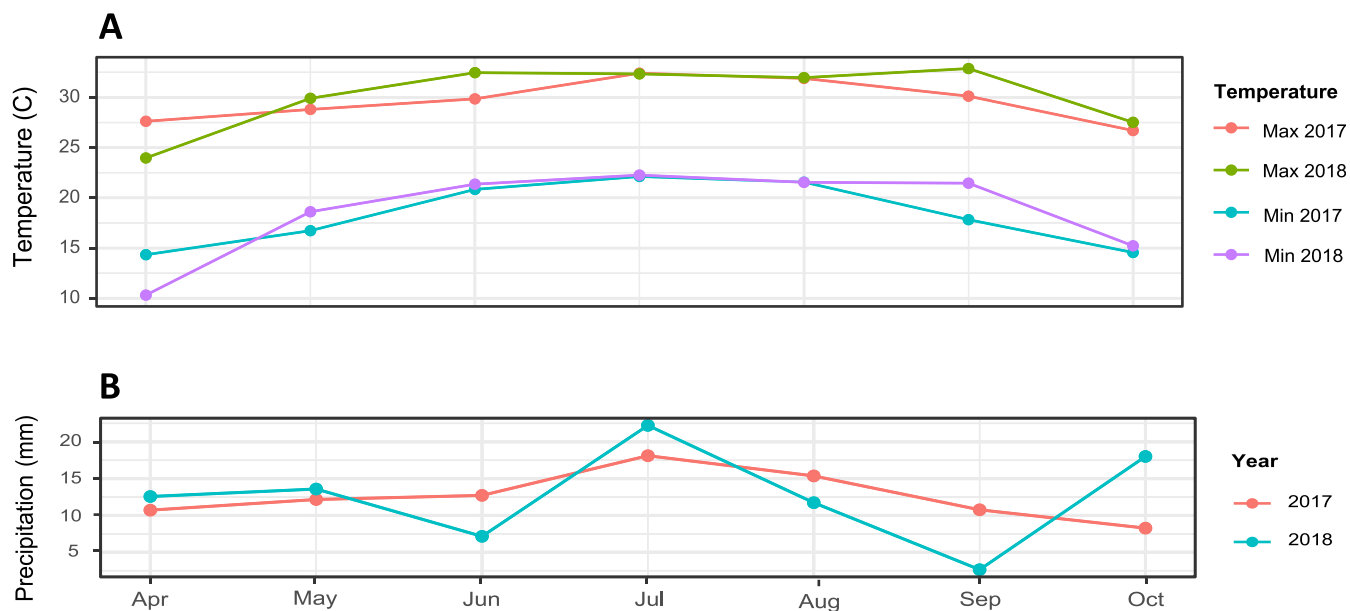

Figure 1. (A) Average maximum and minimum temperatures and (B) cumulative monthly precipitation at Newman, Terrell County, Georgia weather station.
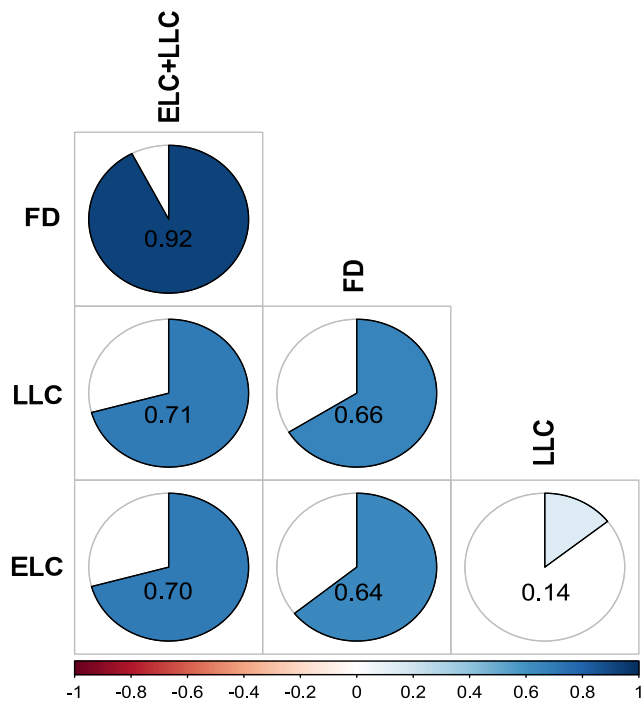
Figure 2. Correlations between disease variables based on means of two years. FD: Final defoliation rating. ELC: Early leaf spot lesion count. LLC: Late leaf spot lesion count. ELC+LLC: Combined lesion counts. Spearman correlation coefficients are indicated within cells.
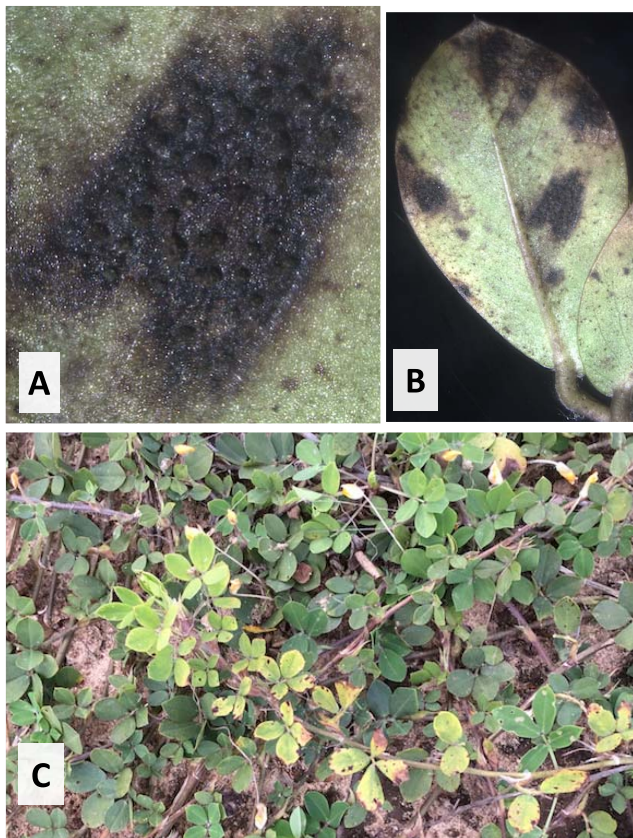

Figure 3. Late leaf spot in *Arachis kempff-mercadoi*. (A) Lesion with spores on the abaxial leaf surface observed under stereomicroscope. (B) Leaflet with lesions. (C) Late season LLS symptoms in field plots.
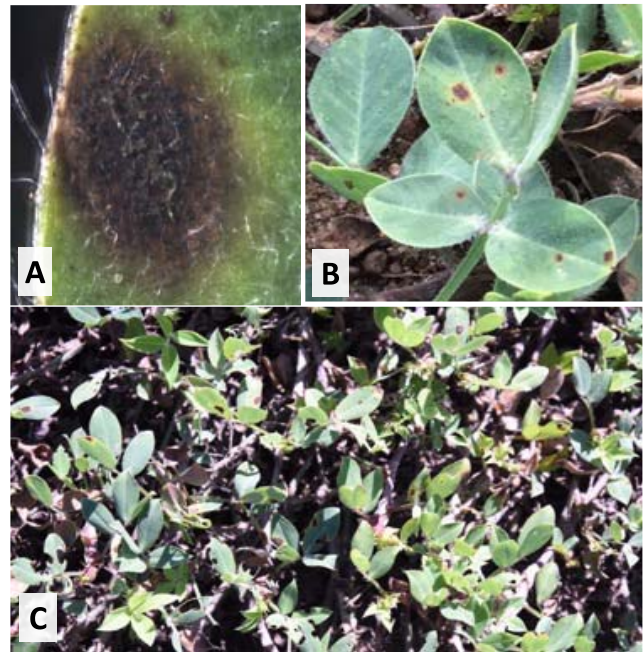

Figure 4. Early leaf spot in *Arachis villosa*. (A) Lesion with spores on the adaxial leaf surface observed under stereomicroscope. (B) Early season ELS symptoms. (C) Late season ELS symptoms in field plots.

FD levels (2.75-4). *Arachis magna* has been suggested as a potential candidate for introgression and pyramiding of resistant genes into cultivated peanut (Michelotto *et al.*, 2015). However, further evaluation is needed to select the appropriate *A. magna* germplasm, as different levels of leaf spot resistance have been reported, and also observed in this study (GKSSc 30093, GKSSc 30097, BRA 33821) for the same accessions when evaluated under different experimental conditions (greenhouse/field inoculation assays) (Subrahmanyan *et al.*, 1985, Favero *et al.*, 2009, Michelotto *et al.*, 2015).

It is suggested that field evaluations are likely to be influenced by canopy microclimates due to the effect of plant architecture on disease development (Coffelt and Porter, 1982; Akem *et al.* 1992; Chappell *et al.* 1995). These studies have shown that plants with the upright growth habit and less dense canopy, characteristic of Spanish-type peanut (*A. hypogaea* ssp. *fastigiata*) have more resistance to *Sclerotinia blight* than dense, spreading-type canopy of Virginia-type cultivars (*A. hypogaea* ssp. *hypogaea*). However, little is known about the effects of canopy architecture on the development of peanut foliar diseases, or whether the less dense canopy typical of wild *Arachis* species is more or less conducive for the invasion of some pathogens. Recent studies showed that it was possible to maintain superior disease resistance introgressed from wild *Arachis* species in a cultivated-type canopy architecture (Leal-Bertioli *et al.* 2016; Chu *et al.* 2019). In the present study, all wild species were

Figure 5. Aerial view of the canopy of wild *Arachis* species in field plots. Newman farm, GA, July 2017.

characterized by a single erect main stem and procumbent lateral branches (Krapovickas and Gregor, 2007). The length, number and branching of lateral branches defined different canopy patterns across species and accessions (Fig. 5). However, despite canopy differences, no apparent correlation was observed between canopy type and disease resistance. For example, accessions of *A. batizocoi*, characterized by sparse branching, and likely less favorable for fungal invasion, were more susceptible to leaf spots than accessions with dense canopies, such as those of *A. cardenasii* and *A. correntina* (Table 1, Fig. 5). Although field experiments were not designed to test the effect of canopy architecture, observations of susceptible and resistant genotypes in adjacent plots indicated that the microclimate created within the canopy of susceptible runner type peanut cultivars did not affect the resistance of wild *Arachis* genotypes (Fig. 6, A and B). Overall, these observations suggest that canopy architecture may not be a major factor, although this requires further investigations.

Summary and Conclusions

The present study reports the identification of peanut germplasm with resistance to leaf spot diseases which were selected from an environment with high inoculum pressure. As resistance was identified across a diverse *Arachis* germplasm representing different species, genome type, life cycle, and geographic distribution, it is likely that this resistance encompasses novel genetic sources. Therefore, the highly resistant (nearly immune) accessions of the A-genome species, including *A. cardenasii*, *A. correntina*, *A. diogoi*, *A. helodes*, *A. kuhlmannii*, *A. kempff-mercadoi*, *A. simpsonii*, and *A. stenosperma*, along with the moderately resistant accessions of the non-A genome species, including *A. benensis* (PI 475877), *A. hoehnei* (PI 681081), and *A. magna* (PI 468338) could contribute to durable resistance through introgression and gene pyramiding. Further, these novel resources can be leveraged in traditional peanut breeding approaches through the use of marker assisted selection methods to increase introgression efficiency, while minimizing linkage drag.

Acknowledgments

Figure 6. Resistant and susceptible peanut plants in adjacent plots. (A) A. *cardenasii* (PI 475997). (B) Susceptible check. White arrows indicate healthy leaves of the resistant *A. cardenasii* from lateral branches spreading under the canopy of a susceptible check.

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