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Advances on Pod and Stem Blight of Soybean *(Diaporthe Phaseolorum* var. *Sojae* and *Phomopsis Longicolla)* in Argentina

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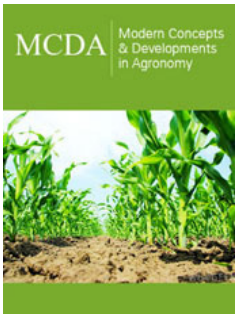

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Abstract

The *Diaporthe*/Phomopsis complex, composed of *D. phaseolorum* var. *sojae* and *P. longicolla*, causes the Soybean Stem Blight (SSB) and Seed Decay (SD), which affect seed quality worldwide. This study synthesizes recent advances in the taxonomy and epidemiology of the complex, identifying seeds and crop residues as main sources of primary inoculum. An integrated approach was employed, combining morphological characterization with molecular tools (ITS, RAPD and SNP), to resolve taxonomic ambiguities and validate the isolates. This research analyzed also pathogenic variability by GGE Biplot and allowed to detect markers associated with virulence patterns. Finally, the most recent advances regarding the identification of the resistance gene Rpsb1, which exhibits Mendelian inheritance, are discussed. It was demonstrated that stalk resistance (PSB) is genetically independent of the Rpsd genes linked to Seed Decay (SD). These advances provide a solid genetic foundation for plant breeding, enabling the development of cultivars with specific resistance to improving soybean crop health.

Keywords: Glycine max-phomopsis sp. interactions, F1 validation by SNP, Resistance to soybean stem blight and seed decay

Causal Agents

Diaporthe phaseolorum (Cke. & Ell.) Sacc. var. *sojae* (Lehman) Wehm. [teleomorph].

Phomopsis phaseoli var. *sojae* Leh. [anamorph].

Phomopsis longicolla (not detected *Diaporthe* Teleomorph)

Taxonomy

Domain: *Eukaryota*

Kingdom: *Fungi*

Phylum: *Ascomycota*

Class: *Ascomycetes*

Subclass: *Sordariomycetidae*

Order: *Diaporthales*

Family: *Valsaceae*

Introduction

Diaporthe phaseolorum var. *sojae* (Dps) and (Plo) were isolated from leaves, pods, seeds and stems of soybean and occasionally from flowers and roots [1-3]. According to data from the 2006-2009 period, the most frequent isolates obtained from soybeans with Pod and stem blight symptoms were identified as *P. longicolla* [4]. *Phomopsis longicolla* and *Phomopsis sojae* produce light brown spots on the cotyledons and lower stem. Later, pod and stem show blight and pycnidia on the main stem. Seeds infected with *P. longicolla* or *D. phaseolorum* var. *sojae* are frequently flattened, wrinkled, discolored and smaller than non-infected seeds [5]. They may also exhibit various degrees of cracking on the seed coat, shriveling, and frequently are covered with a white mold [6,7]. *D. phaseolorum* (Cke. & Ell.) Sacc. var. *sojae* (Lehm.) Wehm. *(D. sojae Lehm.), anamorph Phomopsis sojae (Lehm.)* or *Phomopsis phaseoli* var. *sojae*, was generally accepted as the cause of pod and stem blight. This specie is known to infect numerous host plants such as alfalfa stems, *Abelmoschus esculentus (Malvaceae), Arachis hypogaea (Fabaceae), Camptotheca acuminata (Nyssaceae), Capsicum annuum, Capsicum frutescens var. grossum (Solanaceae), Citrus spp. (Rutaceae), Cucumis melo (Cucurbitaceae), Glycine max (Fabaceae), Helianthus annuus (Asteraceae), Lespedeza spp. (Fabaceae), Solanum lycopersicum (Solanaceae), Melilotus spp. (Fabaceae), Phaseolus lunatus (Fabaceae), Phaseolus vulgaris (Fabaceae), Stokesia laevis (Asteraceae), Strophostyles helvola (Fabaceae), Vigna sinensis (Leguminosae), Vitis vinifera (Vitaceae)* [8-10].

Therefore, Dps was identified as a species complex. Detailed descriptions of asexual and sexual morphs are available in Lehman [11] and Udayanga et al. [8]. Pathogenicity data on different hosts are available in Dissanayake et al. [9], Udayanga et al. [8]. In the phylogenetic tree of Norphanphoun et al. [12], *Diaporthe sojae* clustered in the *D. sojae species* complex. Regarding the *D. sojae* species complex observed in the same study, there is a possibility that this complex may comprise multiple complexes or encompass several distinct and well-delimited species. On the other hand, Kmetz et al. [13] gave evidence on a *Phomopsis spp*. related predominantly to soybean seed decay, recognized as a separate and distinct component of the pod and stem blight. Hobbs et al. [14] provided a full morphological description of *Phomopsis spp*. sensu Kmetz and established its name as *Phomopsis longicolla Hobbs*. Numerous morphological and physiological differences as size and shape of stromata, conidiomata formation, *picnidial locula apperance*, and *conidiophora* branches served, also, to separate *Phomopsis longicolla* from *Phomopsis soja* [15]. The teleomorph (perithecial stage) of *Phomopsis longicolla* has never been found [2,14,16,17]. It has several hosts as Abutilon *Theophrasti (Malvaceae), Ambrosia trifida (Asteraceae), Euphorbia maculate (Euphorbiaceae), Rumex crispus (Polygonaceae), Xanthium strumarium (Asteraceae), Arachis hypogaea (Fabaceae), Aster exilis (Compositae), Caperonia palustris (Euphorbiaceae), Desmanthus illinoensis (Fabaceae), Eclipta prostrata (Asteraceae), Euphorbia nutans (Euphorbiaceae), Glycine max (Fabaceae), Ipomoea lacunose (Convolvulaceae), Plectranthus scutellarioides (Lamiaceae), Polygonum aviculare (Polygonaceae), Sida spinosa (Malvaceae), Chamaesyce nutans (Euphorbiaceae).*

This species was introduced as *Phomopsis longicolla* by Hobbs et al. [14] from the seeds, pods, and stems of Glycine max in USA. The conidiomata are pycnidial, black, stromatic, solitary or aggregated, with an apical ostiole. Locules are uniostiolate or multiostiolate, globose and up to 500µm wide. Alpha conidia are hyaline, ellipsoid to fusiform, 5-9.5×1.5-3.5µm. *Phomopsis longicolla* was synonymized as *Diaporthe* by Santos et al. even though the teleomorph has not detected yet. Additionally, Zhang et al. [18] inferred the phylogeny of the *Diaporthe/Phomopsis* complex on soybean based on the nucleotide sequence divergence in the internal transcribed spacers of the ribosomal DNA. These authors suggested that *P. longicolla* is an individual species, meanwhile *D. phaseolorum* var. *caulivora* and *D. phaseolorum* var. meridionalis are varieties of *D. phaseolorum*, and *D. phaseolorum* var. *sojae* is either several varieties of *D. phaseolorum* or possibly several distinct species. Considering the intricate nature of this group, it would be valuable to conduct further investigations using GMYC, PTP analyses, and phylogenetic network approaches [12], including bio morphological characterization, as a necessary complement to establish the relationship between the observation of natural biological structures and molecular studies [19]. These methods can provide insights into the genetic relationships and boundaries of closely related taxa, helping to clarify the structure of the *D. sojae* complex.

Dissemination and Sources of Inoculum

Natural dispersal

Soybean seeds and crop residues were formerly recognized as sources of inoculum for *D. phaseolorum* var. *sojae* and *Phomopsis spp*. [11,20]. All colonized tissues are potential sources of primary inoculum, although the bulk of primary inoculum appears to originate from over-wintered or over-summered crop debris [21,22].=

Seedborne spread

An effective way to introduce Phomopsis into new areas fungus-free is the movement of infected potentially seeds [1,21]. However, seed-borne inoculum, even on 77% of incidence; was not related to infections on either seedlings or mature plants in fields with continuous soybean or corn-soybean rotation, which indicated that seeds were a minor inoculum source [21]. These results allowed us to infer that soybean infected residues with Phomopsis are the major inoculum sources for pod and stem blight [20,21,23]. Similar results were obtained in Santa Fe, Argentina where continuous-soybean rotation increased the incidence of Phomopsis when compared with corn-soybean rotation [24].

Impact of Disease

Economic impact

Human consumption of cooked soybeans and soy flour may help alleviate global protein deficiency, especially in high populating developing countries [25]. Therefore, soybean seed quality, judged by germination and general appearance of the seed has been relevant aspects to consider in many of the soybean-growing

areas of the world. However, tropical areas with high rainfall and temperature favor the development of seed-borne *Diaporthe phaseolorum* var. *sojae (Phomopsis sojae)* and *P. longicolla,* their broad distribution and high frequency deserve careful attention. Formerly, pod and stem blight was cited as a common disease in Illinois, Iowa, Indiana, USA, and Ontario, Canada [26-29]. Later, in Midwestern Maryland and Delaware this fungus was considered the predominant organism associated with low seed quality [6]. Louisiana, bio-assayed for internally borne pathogens, showed 97% infection with *D. phaseolorum* var. *sojae* [5]. In Illinois, seeds of soybean with symptoms of stem pod blight infection were smaller in size and volume, lower in density, produced lower quality oil and flour and had lower viability and durability than symptomless seeds. Oil from infected seeds had rancid off smell, and a high peroxide value, indicating oil deterioration [30]. Phomopsis seed decay and stem canker constitute diseases that more severely affect soybean seed quality and yield, and they are present in almost every region of soybean production in the world [22]. In South America *Phomopsis sojae* was identified on naturally infected soybean plants in Argentina (Memoria anual 1979), in Brazil (Castro and Kimati, 1981; Almeida, 1981; Berger and Hinson, 1984), and pathogenicity was confirmed in Venezuela (Sanabria de Albarracin, 1993). Other studies also reported the importance of *Phomopsis spp. (P. sojae, P. longicolla, Phomopsis spp.)* as seed-borne pathogen associated to green seed soybean *(eda mamé)* [31]; native forest species [32] and the epidemiological role of the infection progress and colonized tissues by this fungus in the core of soybean area [3,33].

Effect on seed quality

Infection of soybean seeds by the *Diaporthe/Phomopsis* complex decreases physiological quality and viability leading to significant losses in germination [34]. Oil extracted from infected seeds typically has a lower quality, characterized by a rancid smell and a high peroxide value, which indicates oil deterioration [30,35]. And the quality of the produced flour was also diminished. For horticultural use such as vegetable soybean or edamame, infected pods and seeds are considered unsuited for consumption due to these qualitative defects [17,31,36]. Consequently, the presence of these pathogens impacts not only on the seed's health but also on its overall weight, industrial utility, and commercial value [17,22].

Phytosanitary risk

Prior to 1960 *Phomopsis sojae* was considered of little importance to soybean production [26,29,37,38]. Since that time significant germination losses have been reported in heavily infected seed lots in the USA and Canada [5,39-41]. Later *Phomopsis sojae* was recognized as a major cause of moldy, poorly germinating soybean seeds in Brazil, Canada, and USA [42-46]. *Phomopsis seed* infection often exceeds 50% on susceptible cultivars when the harvest is delayed [34,40,42]. Latent infection by Phomopsis sojae has also been found in symptomless soybean plants [33]. It contributes to the fungus capacity to over-winter on crop debris and would have epidemiological importance. Also, as seeds are important source of inoculum that may perpetuate the pathogen, seed treatment was considered necessary even for good quality asymptomatic seeds [30]. In this context, *Diaporthe/Phomopsis* (DP) is a complex that comprises over 900 species characterized by high genetic diversity and a broad host range, including industrial crops and native forests. As hemi-biotrophic pathogens, these fungi establish versatile nutritional strategies-transitioning between endophyte, necrotrophy, saprophytism, and parasitism-often maintaining a latent endophytic phase before manifesting symptoms [17,33].

In Argentina, *Phomopsis longicolla* (Plo) and *P. phaseoli* var. *sojae* (Pps) (Teleomorph *Diaporthe phaseolorum* var. *sojae*, Dps) are the primary species associated with soybean, as well as horticultural varieties intended for fresh consumption or edamame [31]. Their interaction leads to Stem and Pod Blight and Seed Decline (TTVyS), drastically reducing seed weight and quality. While Pps possesses a known teleomorph (sexual) stage, Plo has only been observed in its anamorphic form. Both species utilize stubble and seeds as primary inoculum sources, and their biological plasticity allows them to colonize diverse agro-ecosystems, even affecting the seed germination of tree species like *Schinopsis balansae* [32,33]. The biological plasticity of this complex has facilitated its expansion into diverse agro-ecosystems, the transmission through seeds and long-distance transport increasing the epidemiological risk; thus constituted the main pathways to introduce inoculum into plots previously free of the disease [17]. Molecular studies revealed significant genetic variability within the complex, favoring the emergence of new physiological races with enhanced parasitic capacity. This diversity in both fungal and plant germplasm complicates disease management. Consequently, Argentine research has pivoted toward characterizing specific sources of resistance to Stem Blight.

Identification based on morphological and molecular tools

To resolve taxonomic ambiguities, an approach combining morphological characterization with molecular tools was employed to evaluate Argentine isolates of Plo and Pps from different environments. For morphological analysis: Macro-attributes (colony texture, stroma/pycnidia distribution) and micro-attributes (conidia, asci, and ascospore dimensions) were evaluated. Whilst several molecular analyses validated the identity of isolates where morphology was limited. Thus, 12 isolates were selected and categorized into four taxa: Ten as *P. longicolla*; one as *D. phaseolorum* var. *sojae* (or Pps); and to use as experimental control: one *D. phaseolorum* var. *caulivora* (Dpc) and two *D. phaseolorum* var. meridionalis (Dpm). The combination of phenotypic and molecular tools is essential for the accurate identification of species within the DP complex. These findings enhance the understanding of fungal plasticity, host expansion mechanisms, and biological relationships (such as (homo or heterothallism and hybridization), providing a critical foundation for managing genetic variability and preserving fungal biodiversity in agricultural systems [33].

Pathogenic diversity of *phomopsis sp*. causal agent of soybean (glycine max) stem and pod blight

Molecular studies applied on Dps and Plo demonstrated a remarkable genetic variability within this fungal group [22], that

gave rise to the appearance of new physiological races [8,47]. Resistant genotypes to SPB-SD were obtained by breeding programs worldwide, but not particularly to SB. Therefore, although in Argentina it was possible to characterize and select some potential sources of resistance [48], it was relevant to deepen the study of these diseases. In this case, the objective was to study genetic and pathogenic variability of Phomopsis in interactions with cultivars of varied resistance or susceptibility, and to study the association between molecular and pathogenic profiles in the analyzed interactions. The hypothesis was that the existence of genetic variability in both fungus and plant materials increases the biodiversity in specific reactions during the development of SB. For contrasting this hypothesis, a new approach of the widely known statistical methods GGE Biplot was proposed for measuring the correlation among pathogenic attributes (phenotypic expression of the plant pathology) and molecular markers. Six isolates of Plo and one of Pps were inoculated to six soybean cultivars. Genetic variability in the fungi was evaluated at the molecular level by RAPD and ITS markers and at the phenotypic level by their pathogenic performance through the severity (S%) of the pathology caused in soybean cultivars. Molecular characterization separated the Plo isolates from the Pps isolate. Specific interaction between each isolate-cultivar combination evidenced differential pathogenic performances in respect to resistance/susceptibility. Biplot GGE analysis allowed visualization of specific interactions where certain isolates express their maximum virulence on specific cultivars, demonstrating that genetic variability in both fungal and plant germplasm is associated with the diversity of specific reactions during disease development. Using this tool, specific polymorphic fragments (generated by the OP-AA01 primer) were identified, the presence or absence of which correlated with the ranking of Phomopsis isolates that cause SB in G. max, differentiated by severity, detecting molecular markers potentially associated with virulence [33].

Inheritance of resistance genes to SSB caused by Plo

In recent years, some soybean genotypes carrying Rpsd genes that confer resistance to soybean seed decay, caused by the same agents that cause SSB, have been reported. However, it was not known whether the Rpsd genes were also effective for Soybean Stem Disease (SSB). Therefore, in this case, the objective was the characterization of various soybean genotypes, carriers of Rpsd genes and others of interest, to evaluate their behavior against local strains of Phomopsis (Pps and Plo) that caused SSB, detecting eventual resistance genes (Rpsb) and determining their mode of inheritance. From these parents, crosses between RxS and RxR genotypes (Ge) were carried out during two planting seasons, 2015/16 and 2016/17. Of a total of 203 hybridizations performed (RxS and RxR), 43 fertile combinations producing pods and seeds were obtained, corresponding to a 21% cross effectiveness [49]. To identify truly hybrid individuals (with heterozygous complement) and ensure the accuracy of the resulting segregating generations, SNP-type molecular markers were used to evaluate the F1. Due to their robustness and greater accessibility thanks to reduced costs, SNP markers are currently the most widely used and promising class of markers. Based on the importance and progress achieved by applying these biotechnological tools to plant breeding, this thesis proposed the early and innovative application of specific molecular markers to characterize the first generation (F1), making the selection process more efficient from the beginning of soybean breeding work [33]. The use of SNP molecular markers in the initial stages of selection and genetic improvement allowed for obtaining F1 individuals who's heterozygous and hybrid makeup was molecularly validated, ensuring safe progress in subsequent segregating generations [50].

Analyzing the SNP molecular characterization of each parental pair yielded information on four interesting aspects: the degree of polymorphism between parents, residual heterozygosity, the conversion of an allele to one of the parents (maternal effect), and the advantages and limitations of characterizing the first generation (F1) solely through observation of morphological traits [51]. Regarding the degree of polymorphism detected between parents, it emerged that the germplasm of some genotypes was more closely related to each other, as observed, for example, in Ge(1) and Ge(2), which are considered almost isolines, and some authors still debate whether they are the same genotype, where out of 1100 amplified SNPs, only 1 SNP was polymorphic for both. Meanwhile, other more divergent genotypes allowed the identification of up to 405 polymorphic SNPs between the parents, as in the case of Ge (1) and Ge (5). Regarding the residual heterozygosity detected in the parents through the loci characterized by polymorphic SNPs for 10 parents, it was observed that the Ge (6) and Ge (4) genotypes, which are stabilized cultivars used in various breeding programs, showed practically no loci in a state of residual heterozygosity (2 and 1, respectively). While the Ge (3) genotype registered 22 out of 564 residual heterozygous events, this may be due to a problem with seed purity, which could be associated with seed handling; however, in none of the cases it was higher than 4%. Likewise, when characterizing the F1 individuals, in a few cases a proportion of non-heterozygous loci were observed, which duplicated one of the alleles of one of the parents. Although this study observed a low proportion of loci like maternal parent, a phenomenon known as the "maternal effect" or gene conversion heterozygous genotypes, individuals with this percentage exceeding 10-12% were excluded [52-56]. A particular case was found for the crosses resulting from the white-flowered Ge(6) and purple-flowered Ge(1) genotypes, where the three F1 individuals from such a cross (Ge(6) x Ge(1).1A; Ge(6) x Ge(1).1B; Ge(6) x Ge(2).2), molecularly validated as heterozygous hybrids, presented white flowers as the maternal genotype Ge(6), contrary to what was expected based on the molecular analysis using SNPs [57]. This could be due to a residual heterozygosity effect from the paternal genotype Ge (1), in which, of the 1224 total SNPs, 920 amplified for this genotype, 848 were found in homozygosity and 72 in heterozygosity [10]. Within these 72 heterozygous SNPs, 6 were located on chromosome 13, the site of the allele coding for flower color (dominant purple W1, recessive white w1) [58].

The results obtained demonstrated that the additional and complementary application of molecular markers, combined with

classical controls (morphological and structural-histological), provides rigor and relevant additional information about each of the parents involved in the crosses, enriching and strengthening the results and their biological significance. However, it is important to note that this same protocol simultaneously generated a significant reduction in diversity compared to the numerous original combinations and their respective RxS, RxR, and reciprocal crosses [59]. Thus, one of the proposed objectives has been met: to have molecularly validated F1 populations and their respective heterozygous and hybrid parents from the first filial generation (F1), that is, from the F1 individuals, and to allow for safe progress in the segregating F2 populations and their respective F3 generations and F2:3 families. Through inoculations, the reaction against SSB of the parents, the F1, F2 individuals and the F3 plants distributed in the F2:3 families (Progeny Tests) were characterized [60]. Through the observed phenotypic ratios, it was possible to infer the expected genotypic ratios in the F2 parents, allowing the identification of the first SSB resistance gene (Rpsb1) to SSB, carried by one of the resistant genotypes, without ruling out the possibility of carrying other associated genes [61]. By evaluating Resistance / Susceptibility as a dichotomy qualitative trait, different types of epistatic interactions were detected in each different cross.

Conclusion

The preliminary results obtained by classic genetic improvement and molecular assistance contribute and strengthen the current studies for identifying resistance genes (Rpsb) to SSB-Plo and their inheritance way. It was also demonstrated that stalk resistance (PSB) is genetically independent of the Rpsd genes linked to Seed Decay (SD). These advances provided an understanding about the effectiveness of the strategies applied and perspectives of plant improvement aimed at incorporating resistance to diseases in soybean crops.

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