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Soybean Mosaic Virus Infection in Three Cultivars of Soybeans Intercropped with Corn at Three Planting Densities of Soybeans

Eman Ibrahim Abdel-Wahab^{1*}, Sherif Ibrahim Abdel-Wahab², Tamer Ibrahim Abdel-Wahab² and Sawsan Massoud Saied³

¹Food Legumes Research Department, Field Crops Research Institute, Agricultural Research Center, Giza, Egypt.

²Crop Intensification Research Department, Field Crops Research Institute, Agricultural Research Center, Giza, Egypt.

³Virus and Phytoplasma Research Department, Plant Pathology Research Institute, Agricultural Research Center, Giza, Egypt.

*Corresponding author

Eman Ibrahim Abdel-Wahab,

Food Legumes Research Department, Field Crops Research Institute, Agricultural Research Center, Giza, Egypt.

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Abstract

To evaluate the tolerance of soybean cultivars intercropped with corn for soybean mosaic virus (SMV) infection, a two year experiment was conducted at Giza Agricultural Research Station, ARC, Giza, Egypt during 2023 and 2024 summer seasons. Three soybean plant densities (50, 75, and 100 percent of solid soybean plant density) and three soybean cultivars (Giza 21, Giza 82, and Giza 111) under intercropping with corn were distributed in split-plot design with three replicates. The Pd1 and Pd2 genes, which control pubescence density, received particular attention. Giza 82 showed typical pubescence (recessive), whereas Giza 21 and Giza 111 showed dense pubescence (dominant Pd1/Pd2 expression). Giza 111, with 100% density, produced the maximum seed yield per plant (10.85 g), per hectare (2.56 t), and land equivalent ratio (LER, 1.65). Pd1/Pd2-mediated dense pubescence showed a negative correlation with aphid infestation and SMV infection but a positive correlation with seed yield, LER, and Jasmonic Acid (JA) production. Genotype-specific defense protein induction was validated by SDS-PAGE analysis. Intercropping four rows of Giza 111 in middle of corn raised beds increased seed yield, LER, with reduced SMV infection.

Keywords: Intercropping, Soybean cultivars, Soybean plant density, Pd1 and Pd2 genes, SMV, Protein banding patterns.

Introduction

A vital legume worldwide, soybeans (*Glycine max* L. Merrill) are severely limited in yield by biotic stressors, particularly soybean mosaic virus (SMV). SMV causes mosaic symptoms, stunting, and yield decreases of up to 35% (Liu et al., 2016; Eid et al., 2023). Aphids mostly spread it in a non-persistent way (Gadhav et al., 2019; Carr et al., 2020; Shi et al., 2021). An ecological method to reduce pest pressure and maximize land use efficiency, as measured by land equivalent ratio (LER), is to intercrop soybeans with corn (*Zea mays* L.). On the other hand, the overall yield and quality of the crop are largely determined by the soybean cultivar's genetic makeup and planting density (Gan et al., 2002; Li et al., 2024). Therefore, planting density and the genetic composition of soybean cultivar can play a major role in the system's effectiveness (Wang et al., 2023; Zhang et al., 2025). Leaf pubescence density, which is largely controlled by the Pd1 and Pd2 genes, is an important genetic predictor of aphid resistance and SMV tolerance (Gunasinghe et al., 1988; Liu et al., 2020; Abdel-Wahab et al., 2025a). While Pd2 affects trichome length and distribution, Pd1 controls trichome density (Tang et al., 2020). Dense pubescence is a physical barrier that prevents aphid probing and virus inoculation in cultivars expressing dominant Pd1/Pd2 alleles (Zhang

et al., 2022). Recessive alleles, on the other hand, increase vulnerability by causing normal or scanty pubescence (Zhao et al., 2016; Kato et al., 2026). Plant hormones, such as jasmonic acid (JA), mediate basal defense responses brought on by viral infections and insect feeding in addition to mechanical barriers (Li et al., 2022; Zhu et al., 2026). Planting density further modulates these genetic defenses (Douma and Noordhoek, 2025; Luo et al., 2026). High-density intercropping alters the microclimate, affecting light interception, water consumption, and canopy architecture (Duan et al., 2026; Kou et al., 2026). While dense canopies may reduce light availability, they can also suppress viral diseases by modifying vector behavior (Hill and Whitham, 2014; Abdel-Wahab et al., 2025). Furthermore, biochemical defenses, including JA biosynthesis and the expression of pathogenesis-related proteins, are genetically regulated and environmentally responsive (Todd et al., 2022; Bredow et al., 2025). The tripartite relationship between Pd1/Pd2 expression, planting density, and SMV epidemiology is still poorly understood, despite the established functions of Pd genes and intercropping. The objective of this study is to evaluate the resistance of soybean cultivars to SMV infection through Pd1/Pd2 gene expression.

Materials and Methods

To evaluate the tolerance of soybean cultivars to SMV infection through Pd1/Pd2 gene expression, a two-year experiment was conducted at Giza Agricultural Research Station (Lat. 30°00'30' N, Long. 31°12'43' E, 26 m a.s.l.), Agricultural Research Center, during two summer seasons (2023 and 2024). Nine treatments were used in this study: three soybean plant densities (2, 3, and 4 rows per ridge were expressed as 50, 75, and 100 percent of solid soybean plant density, respectively) and three soybean cultivars (Giza 21, Giza 82, and Giza 111) under intercropping with corn (Figure 1).

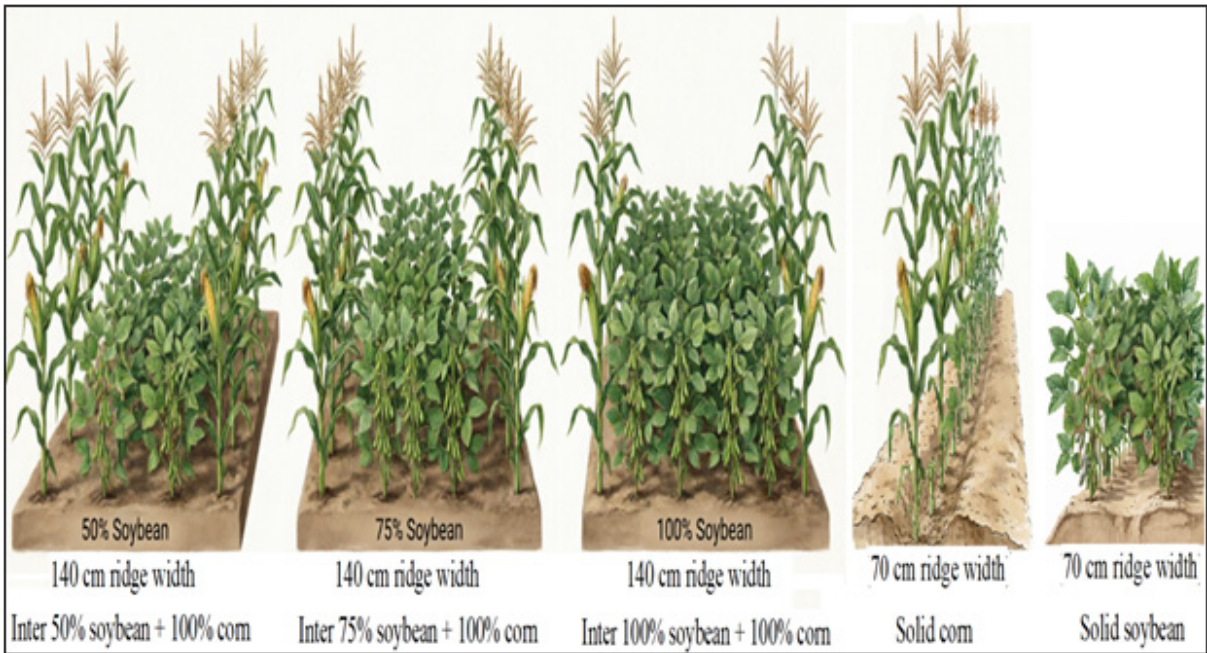


Figure 1: Intercropping soybean with corn under three soybean plant densities and solid plantings of both crops

Additionally, corn and soybean were planted separately (solid planting). Corn (T.W.C. 321) was the intercrop companion. A split-plot design in randomized complete blocks with three replicates was used. Main plots were three soybean planting densities. Meanwhile, subplots were planted with three soybean cultivars. Table 1 displays the pedigree, Pd1/Pd2 gene expression, pubescence length (µm), and MG.

Table 1: Pedigree, Pd1/Pd2 gene expression, pubescence length (µm), and MG of Egyptian soybean cultivars under the study.

Soybean cultivar	Pedigree	Pd1/Pd2 Gene Expression	MG	Pubescence length (µm)
Giza 21	Crawford x Forrest	Dominant	IV	299.95 (dense)
Giza 82	Crawford x Maple Presto	Recessive	III	133.93 (normal)
Giza 111	Crawford x Celeste (Late)	Dominant	IV	393.19 (dense)

In both seasons, wheat was the previous winter crop, and the soil was clay. A split plot distribution in randomized complete blocks design with three replicates was used. Soybean plant density were randomly assigned to the main plots, soybean cultivars were allocated in sub-plots. Plot area was 12.6 m². Each plot consisted of three raised beds, 3.0 m long and 140 cm wide (in case of solid plantings, each plot consisted of six ridges, 3.0 m long and 70 cm wide). During the two summer seasons, 357 kg of calcium superphosphate (15.5% P₂O₅) was sprayed per hectare for soil preparation. Gum Arabic was used as a sticking agent to inoculate soybean seeds with *Bradyrhizobium japonicum*. In the 2023 and 2024 seasons, soybean seeds were sown on May 30 and May 22, respectively. Fifteen days later, corn was sown. For corn, two equal doses of mineral N fertilizer were applied prior to the first and second irrigations, respectively, at a rate of 285.6 kg N per ha as ammonium nitrate (33.5% N) under intercropping

and solid plantings. Additionally, before the initial irrigation under intercropping and solid plantings, mineral nitrogen (N) fertilizer was applied to soybeans at a rate of 35.7 kg N per ha as ammonium nitrate (33.5% N). In a mixed intercropping system with raised beds (140 cm ridge width), three different densities of soybean plants were planted: corn plants were grown on both sides of the ridge, and two rows of soybean seeds (100% corn + 50% soybean) were drilled in the center of the ridge. Soybean seeds were drilled in three rows in the center of the ridge (100% corn + 75% soybean), and corn plants were growing on both sides of the raised beds. Soybean seeds were drilled in four rows in the center of the raised beds (100% corn + 100% soybean), and corn plants were grown on both sides of the raised beds. Regarding the solid plantings of both crops, two rows of soybeans were drilled into a ridge (70 cm width) for the solid planting of soybeans, while corn plants were grown in one side of the ridge. LER were estimated using

solid plantings of both crops. Under intercropping and solid plantings, corn was grown in hills spaced 25 cm apart, with one plant per hill. Soybeans were thinned to 20 plants per one meter under intercropping and solid plantings. The irrigation system used in this study was furrow irrigation. Soybean cultivars Giza 21 and Giza 111 were harvested on October 7 and 2, respectively, in 2023 and 2024, while Giza 82 was harvested on September 4 and 1, respectively, in 2023 and 2024. On September 30 and 25 of the 2023 and 2024 seasons, respectively, corn plants were harvested.

The Studied Traits

Jasmonic acid (JA) in soybean leaves: JA was quantified in soybean cultivars' leaves using HPLC 60 days after soybean planting to evaluate biochemical defense responses. The Food Technology Research Institute of the Agricultural Research Center in Giza, Egypt, conducted this analysis.

Features of soybean leaf pubescence: Three soybean cultivars with varying degrees of pest infestation and pubescence ratings were used to measure pubescence attributes 60 days after soybean planting. Singh (2010) classified pubescence density into two phenotypes: dense and normal. Pubescence length (μm) was used to estimate pubescence features. The Egyptian Mineral Resources Authority Central Laboratories Sector used the SEM Model Quanta 250 FEG (Field Emission Gun) to evaluate pubescence features as a sign of direct resistance to insect infestation. In accordance with Bandillo et al. (2017), phenotypes were categorized as "Dense" (dominant Pd1/Pd2 expression) or "Normal" (recessive pd1/pd2 expression).

Examination of soybean plants infected by viruses: In each row of a plot, samples of naturally occurring soybean plants exhibiting symptoms of soybean mosaic diseases were counted. The afflicted plants had labels. Visual inspection for virus symptoms was used to assess the percentage of infestation. The number of SMV-infected plants divided by the total number of plants in the plot was used to determine the percentage of infected soybean plants. The obtained samples were transported in labeled plastic bags to the Plant Pathology Research Institute's Virus and Phytoplasma Research Department at the Agricultural Research Center in Giza. SMV was detected via indirect ELISA. Each plot's diagonals were represented by three plants, which were then analyzed to determine the viral population density.

Studies on biochemical genetics (SDS-protein analysis):

At 60 days of soybean planting, the banding patterns of the investigated soybean cultivars were examined using SDS-PAGE. For this investigation, young and fresh leaves were gathered from each treatment. Protein fractionation was carried out using Laemmli (1970) method, as modified by

Studier (1973), on a vertical slab (16.5 cm x 18.5 cm, Hoefer E600, Amersham Pharmacia Biotech). The Cairo University Research Park, Faculty of Agriculture, Cairo University, Giza, Egypt, was the location of this analysis.

Productivity: Ten guarded plants from each subplot had their seed yield per plant measured at harvest. Based on the experimental plot, the seed yield per plot (kg) was measured and converted to tons per hectare (t/ha).

LER: According to Mead and Willey (1980), LER is the ratio of the area required for solid cropping to that required for intercropping at the same management level to achieve an equivalent yield. LER is calculated as follows: $(Y_{ab} / Y_{aa}) + (Y_{ba} / Y_{bb})$, where Y_{aa} is the pure stand yield of crop a (corn), Y_{bb} is the pure stand yield of crop b (soybean), Y_{ab} is the intercrop yield of crop a (corn), and Y_{ba} is the intercrop yield of crop b (soybean).

Correlation analysis: To assess the relationships between the measured quantitative traits—seed yield per plant, seed yield per hectare, LER, JA content, and SMV infection—and the Pd1 and Pd2 gene expressions (coded as a binary variable: 1 for dominant/dense, 0 for recessive/normal), simple correlation coefficients were calculated.

Statistical analysis: The homogeneity of variances over the course of the two growth seasons (2023 and 2024) was assessed using Bartlett's test. Because the experimental site in Giza, Egypt, has a stable environment with low interannual change in weather patterns, data were combined for analysis once variance homogeneity was confirmed ($p > 0.05$). The impacts of soybean plant density and soybean cultivars on the measured variables were examined using analysis of variance (ANOVA) (Freed, 1986). Mstat Software (version 8.0.1, URL link: Mstat version 8.0.1 for Windows-14.8 M) was used to conduct an ANOVA. For mean comparisons, the least significant differences (L.S.D.) test was employed (Gomez & Gomez, 1984).

Results

Soybean cultivars Giza 21 and Giza 111 have intense pubescence (299.95 and 393.19 μm , respectively) due to dominant Pd1/Pd2 alleles, while Giza 82 has recessive alleles with normal pubescence (133.93 μm), according to cultivar features (Table 1). The interaction had a considerable impact on biochemical defensive responses as determined by JA content. Compared to normal-pubescence Giza 82 (305 $\mu\text{g}/100\text{g}$ FW), dense-pubescence cultivars Giza 111 and Giza 21 accumulated high JA levels at 100% plant density (429 and 421 $\mu\text{g}/100\text{g}$ FW, respectively) (Figure 2).

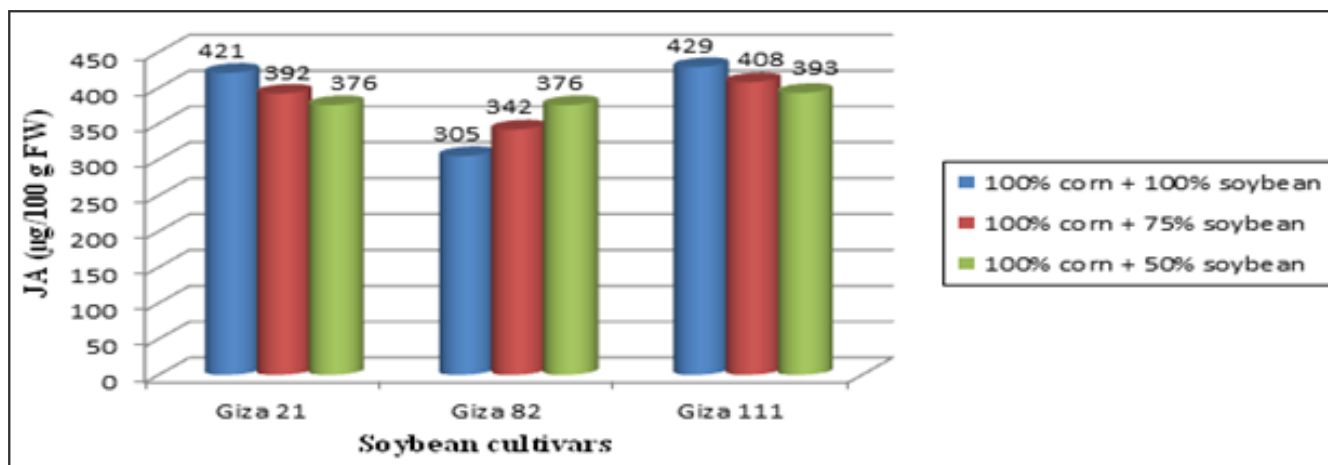


Figure 2: JA content in leaves of the studied soybean cultivars under different soybean plant densities at 60 days from soybean planting

Genotype-specific protein production at 100% plant density was verified by SDS-PAGE analysis (Figure 3, Table 2). Soybean cultivar Giza 111 specifically produced a 75 kDa band, indicating significant tolerance, while Giza 21 induced six defense proteins (35–245 kDa). Giza 82, on the other hand, lost the 35 and 75 kDa bands, indicating susceptibility. SMV infection rates showed a highly significant interaction (Table 3). While soybean cultivar determined overall tolerance, soybean plant density often decreased SMV in dominant cultivars. Soybean cultivars Giza 21 and Giza 111 had the lowest SMV infection rates at 100% plant density (7.40% and 8.05%, respectively). On the other hand, soybean cultivar Giza 82 at 100% plant density showed the highest infection incidence (19.30%), suggesting that viral susceptibility is increased by high density in the absence of genetic pubescence protection. Soybean cultivar Giza 21 (12.00%) and soybean cultivar Giza 111 (12.40%) performed better overall than soybean cultivar

Giza 82 (15.36%), according to cultivar averages. Soybean plant density, soybean cultivars, and their interaction had a significant impact on productivity and LER (Table 4). For all cultivars, raising plant density from 50% to 100% increased yield and LER. Soybean cultivar Giza 111 with 100% plant density was more compatible, maximizing LER (1.65), seed yield per hectare (2.56 t), and seed yield per plant (10.85 g). Soybean cultivar Giza 82 produced 2.25 t/ha with an LER of 1.61 at 100% plant density. For comparison, intercropped corn yields varied from 8.63 to 8.65 t/ha (solid corn: 8.75 t/ha), while solid planting yields for Giza 21, Giza 82, and Giza 111 were 2.86, 3.56, and 3.80 t/ha, respectively. Lastly, Pd1/Pd2 expression (Dense=1) is strongly positively correlated with seed yield per hectare ($r=0.92^{**}$), LER ($r=0.88^{**}$), seed yield per plant ($r=0.85^{**}$), and JA content ($r=0.79^{*}$), but strongly negatively correlated with SMV infection ($r=-0.87^{**}$), according to Pearson correlation analysis (Table 5).

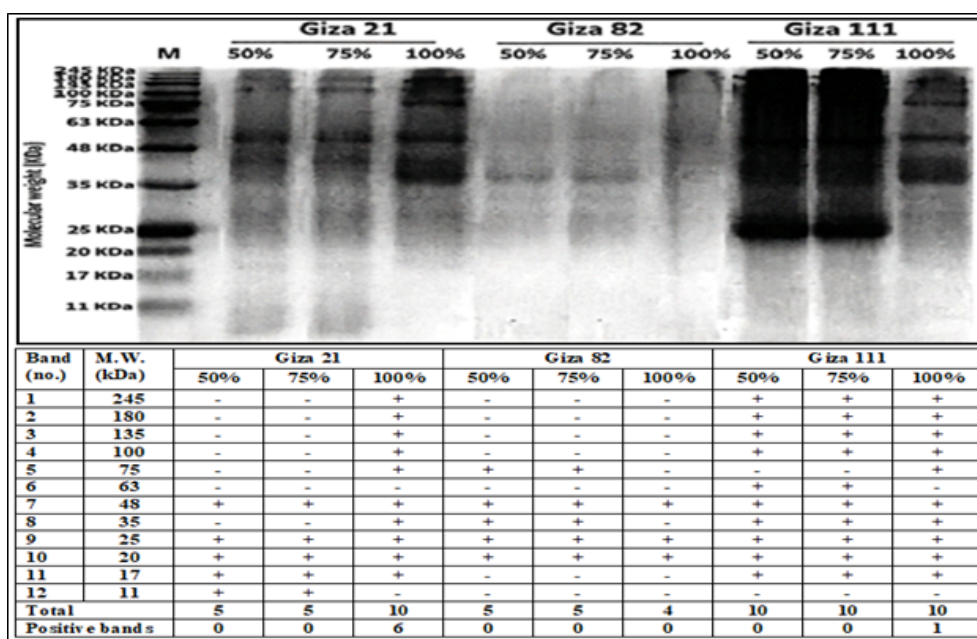


Figure 3: Leaf protein banding patterns under varying soybean plant densities for intercropping soybean cultivars with corn

Table 2: SDS-PAGE defense protein banding patterns at 100% plant density.

Soybean cultivar	Molecular weights of induced/lost bands (kDa)	Defense response
Giza 21	35, 75, 100, 135, 180, 245 (induced)	High
Giza 82	35, 75 (lost)	Susceptible
Giza 111	75 (induced)	High

Table 3: The effects of soybean plant densities, soybean cultivars, and their interactions on SMV infection at 60 days from soybean planting.

Soybean plant density	Soybean cultivar	SMV infection/plant (%)
100% corn + 100% soybean	Giza 21	7.40
	Giza 82	19.30
	Giza 111	8.05
Mean		11.58
100% corn + 75% soybean	Giza 21	13.10
	Giza 82	16.40
	Giza 111	11.90
Mean		13.80
100% corn + 50% soybean	Giza 21	15.50
	Giza 82	10.40
	Giza 111	17.25
Mean		14.38
Average of soybean cultivar	Giza 21	12.00
	Giza 82	15.36
	Giza 111	12.40
LSD (0.05) Soybean plant density		1.29
LSD (0.05) Soybean cultivar		1.26
LSD (0.05) Interaction		2.33

Table 4: The effects of soybean plant densities, soybean cultivars, and their interactions on soybean seed yield at harvest.

Soybean plant density	Soybean cultivar	Seed yield per plant (g)	Seed yield per hectare (t)	LER
100% corn + 100% soybean	Giza 21	7.97	1.82	1.62
	Giza 82	9.06	2.25	1.61
	Giza 111	10.85	2.56	1.65
Mean		9.29	2.21	1.63
100% corn + 75% soybean	Giza 21	9.37	1.23	1.41
	Giza 82	11.38	1.56	1.41
	Giza 111	8.19	1.75	1.44
Mean		9.64	1.51	1.42
100% corn + 50% soybean	Giza 21	9.65	0.96	1.30
	Giza 82	12.13	1.10	1.31
	Giza 111	12.64	1.34	1.33
Mean		11.47	1.13	1.31
Average of soybean cultivar	Giza 21	8.99	1.33	1.44
	Giza 82	10.85	1.63	1.44
	Giza 111	10.56	1.88	1.47
LSD (0.05) Soybean plant density		ns	0.19	0.19
LSD (0.05) Soybean cultivar		1.51	0.10	ns
LSD (0.05) Interaction		ns	0.21	0.26

Table 5: Simple correlation coefficient: Agronomic traits vs. Pd1/Pd2 gene expression.

Trait	Correlation with Pd1/Pd2 (Dense=1)	Significance
Seed yield per plant	+0.85**	Strong positive
Seed yield per hectare	+0.92**	Strong positive
LER	+0.88**	Strong positive
JA content	+0.79*	Moderate positive
SMV infection	-0.87**	Strong negative

Discussion

Soybean plant density, soybean cultivar, and their interaction significantly affect both the agronomic performance of corn-soybean intercropping systems and the epidemiology of SMV. Our results highlight that morphological traits (especially Pd1/Pd2-mediated leaf pubescence) serve as the primary physical barrier against aphid vectors, reducing the spread of non-persistent SMV. Due to their thick trichomes and dominant Pd1/Pd2 alleles, cultivars Giza 21 and Giza 111 were consistently more resistant to SMV infection than the recessive, normal-pubescence Giza 82. Thick pubescence physically hinders aphid probing and stylet penetration, lowering the inoculation rate of viruliferous aphids. SDS-PAGE protein banding patterns further support this morphological defense, showing that dense-pubescence cultivars produced specific defense proteins (such as the 75 kDa band in Giza 111 and several bands in Giza 21) under high-density intercropping. In contrast, Giza 82 lost these essential defense proteins, making it extremely susceptible. These findings are consistent with earlier research that found a correlation between pubescence density and leguminous crop tolerance to viral diseases (Srikant et al., 2025; Sun et al., 2026). The possession of particular defensive proteins emphasizes how crucial this characteristic is for offering organic resistance against diseases and pests (Jain et al., 2022; Shobade et al., 2025). The microclimate and canopy architecture were separately influenced by the density of soybean plants, which in turn had an impact on pest dynamics and resource competition (Abdel-Wahab et al., 2024). The LER and total seed yield per hectare were greatly increased when the soybean density in the corn intercrop was increased from 50% to 100%. This is consistent with the idea that the best spatial configurations for intercropping maximize both land use efficiency and light interception (Metwally et al., 2021). The impact of density on SMV infection, however, was solely genotype-dependent, indicating a crucial connection between soybean plant density and soybean cultivar. The 100% density canopy in Pd1/Pd2-dominant cultivars (Giza 111 and Giza 21) probably formed a microclimate that reduced aphid mobility or changed vector behavior, working in concert with the physical trichome barrier to lower SMV infection to negligible levels (7.40% and 8.05%). In contrast, the 100% density canopy produced the highest SMV infection (19.30%) in the susceptible Giza 82. This implies that in the absence of the hereditary pubescence barrier, a dense canopy can raise humidity or decrease air circulation, which could encourage aphid colonization. Alternatively, it could be that

the close proximity of plants makes it easier for vectors to move quickly between susceptible hosts. These results are consistent with earlier research demonstrating the significance of plant spacing and canopy density in the dynamics of disease transmission (Douma & Noordhoek, 2025). All things considered, these results demonstrate how intricately plant characteristics, environmental variables, and vector behavior interact to determine crops' susceptibility to disease (Dara et al., 2026). Biochemically, the JA signaling system mediates the tolerance observed in Giza 111 and Giza 21. JA is an essential phytohormone that controls basal defensive mechanisms against aphids and other phloem-feeding insects as well as ensuing viral infections. An improved, environmentally responsive metabolic resistance is indicated by the much increased JA accumulation in dense-pubescence cultivars at 100% density. As long as the genetic basis (Pd1/Pd2) is there, ideal agronomic techniques (100% density) can upregulate genotype-specific biochemical defenses, as demonstrated by the induction of the 75 kDa defense protein in Giza 111 at maximum density. By allocating resources to both competitive canopy growth and antiviral/anti-herbivore defenses without suffering a yield penalty, these cultivars successfully negotiate the growth-defense trade-off. These findings are consistent with earlier research indicating that by encouraging the expression of defensive mechanisms, higher plant density can improve tolerance to pests and diseases (Abdel-Wahab et al., 2025b; Koca, 2026; Kumaraswamy & Huang, 2026). The negative correlation between Pd1/Pd2 and SMV infection stands in stark contrast to the strong positive correlations between Pd1/Pd2 expression and agronomic characteristics (yield, LER). This shows that biotic stress tolerance and yield optimization are two advantages of selecting for dense pubescence. The biological and financial benefits of the intercropping system over solid cropping are confirmed by the LER values above 1.0 in every intercropping treatment. Due to the cultivar's capacity to sustain high individual plant output (10.85 g/plant) in spite of the competitive intercropping environment, Giza 111 obtained a maximum LER of 1.65 at 100% density, indicating a 65% land-saving benefit. Additionally, intercropped corn yields (8.63–8.65 t/ha) remained highly competitive with solid-planted corn (8.75 t/ha), demonstrating that the companion cereal crop was not negatively impacted by the soybean density modifications. These findings are in line with earlier research that has shown the possible advantages of intercropping corn and soybeans in terms of total crop productivity and land use efficiency (Metwally et al., 2021; Te et al., 2023; Metwally et al., 2026). Our work clarifies the three-way relationship between SMV epidemiology, planting density, and Pd gene expression. It demonstrates how agronomic factors like crop density dynamically alter both morphological defenses (pubescence) and biochemical defenses (JA, defense proteins). It is advised not to use sensitive cultivars in high-density intercropping systems because of Giza 82's inability to produce defense proteins and its consequent high SMV susceptibility at 100% density. Rather, in legume-cereal intercropping systems, matching particular genetic features (Pd1/Pd2 dominance) with ideal spatial arrangements (100% density) is crucial for optimizing land use efficiency and guaranteeing sustainable viral disease management.

Summary of the Mechanisms for Tolerance of Soybean Cultivars to SMV Infection

This study explains the role of the Pd1 and Pd2 genes in providing SMV tolerance under varying planting conditions, including intercropping and solid planting (Figure 4). Key points include: 1) Morphological Defense: Pd1 and Pd2 regulate leaf trichome characteristics, where dominant alleles produce dense pubescence that forms a physical barrier against aphids, reducing SMV transmission. Recessive alleles lead to sparse pubescence, allowing greater virus spread. 2) Biochemical Protection: The JA pathway is activated in dense-pubescence cultivars, enhancing tolerance to aphids and virus infection. High-density intercropping cultivars like Giza 21 and Giza 111 shows increased defense protein production, unlike the susceptible Giza 82. 3) Plant Density Effects: The study highlights how intercropping significantly impacts disease control. In a 100% intercropped environment, Pd1/Pd2 cultivars reduce SMV infection rates, while recessive cultivars suffer increased rates due to favorable conditions for aphids. The synthesis emphasizes that a successful intercropping system requires selecting Pd1/Pd2-dominant cultivars at optimal densities to maximize soybean productivity and land use efficiency while minimizing disease susceptibility.

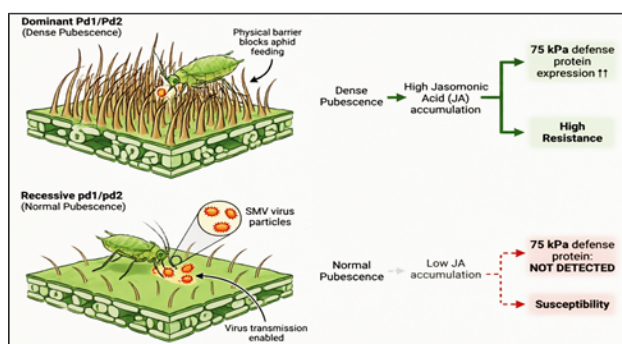


Figure 4: Mechanism for tolerance of soybean cultivars to SMV infection

Conclusion

This work shows that Pd1/Pd2-mediated pubescence and planting density interact to control SMV tolerance and land use efficiency in corn-soybean intercropping. A strong morphological and biochemical defense against aphids is produced when the dense-pubescence cultivar Giza 111 is grown at 100% soybean density, which ideally induces JA production and 75 kDa defense protein induction. This particular combination of soybean plant density and cultivar maximizes seed yield (2.56 t/ha) and LER (1.65) while minimizing SMV infection, providing a sustainable approach for robust agroecosystems.

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