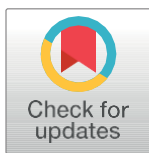


Research Article

Co-segregation of resistance genes to *Colletotrichum lindemuthianum* and *Pseudocercospora griseola* in common bean recombinant inbred lines

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Abstract

Anthraxnose and angular leaf spot, caused by *Colletotrichum lindemuthianum* and *Pseudocercospora griseola*, respectively, are among the most destructive diseases affecting common bean (*Phaseolus vulgaris* L.) worldwide, leading to severe yield losses and posing major challenges to breeding programs due to the high variability of pathogen populations. The identification of resistance loci and their genetic relationships is essential for the development of cultivars with durable and broad-spectrum resistance. In this study, we investigated the inheritance and co-segregation of resistance to race 73 of *C. lindemuthianum* and race 63-39 of *P. griseola* using 56 F_{2:8} recombinant inbred lines derived from the cross between Awauna UEM (resistant) and IPR88 Uirapuru (susceptible). Phenotypic evaluations revealed clear segregation patterns for both diseases, fitting a 1:1 ratio, consistent with monogenic inheritance. Resistance to anthracnose was associated with the *Co-4²* allele, while resistance to angular leaf spot was controlled by a major locus herein designated as *PhgPv08^{AW}*. The observed segregation fitted the expected 1RR:1SS ratio, with a χ^2 value of 0.071 and a *P*-value of 0.78, indicating monogenic dominant resistance to race 73 of *C. lindemuthianum*. Similarly, segregation for race 63-39 of *P. griseola* also fitted the 1RR:1SS ratio ($\chi^2 = 0.64$ and *P* = 0.42). Co-segregation analysis showed that 50 out of 56 lines exhibited identical resistance responses to both pathogens, with only six recombinant lines, indicating tight genetic linkage between *Co-4²* and *PhgPv08^{AW}*. These results suggest that resistance to both diseases is controlled by closely linked loci, likely located within a resistance gene cluster. From a breeding perspective, the co-segregation of resistance to two major diseases represents a highly advantageous genetic configuration, enabling simultaneous selection and facilitating gene pyramiding strategies. Overall, this study provides new insights into the genetic architecture of disease resistance in common bean and highlights the potential of exploiting linked resistance loci to accelerate the development of cultivars with durable and broad-spectrum resistance.

Keywords: Recombinant inbred population; allelic association; mendelian segregation; disease resistance breeding; protein; carbohydrates; dietary fiber; essential micronutrients; iron; zinc.

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Introduction

Common bean (*Phaseolus vulgaris* L.) is the most important grain legume for direct human consumption worldwide, serving as a major source of protein, carbohydrates, dietary fiber, and essential micronutrients such as iron and zinc, particularly in developing countries (Nay et al., 2019). In many regions of Latin America and Africa, common bean constitutes a fundamental component of daily diets, contributing significantly to food security and nutritional balance. Molecular and genomic evidence indicates that common bean originated in Mesoamerica, followed by the establishment of two major domestication centers, the Mesoamerican and Andean gene pools, which underpin the extensive genetic diversity observed in the species today (Bitocchi et al., 2012; Bitocchi et al., 2013; Schmutz et al., 2014). In Brazil, the Mesoamerican gene pool predominates and forms the basis of most commercial cultivars, particularly the carioca and black bean market classes.

Despite its agronomic and nutritional importance, common bean production is severely constrained by a wide range of diseases. Among these, anthracnose, caused by *Colletotrichum lindemuthianum*, and angular leaf spot (ALS), caused by *Pseudocercospora griseola*, are among the most destructive and widespread diseases affecting the crop. Under favorable environmental conditions, these pathogens can lead to yield losses of up to 100% and 80%, respectively (Gonçalves-Vidigal et al., 2020).

The wide diversity of virulence exhibited by both pathogens, coupled with the continuous emergence of new races, constitutes one of the main challenges for genetic improvement programs, frequently resulting in the overcoming of previously observed resistance in cultivars considered resistant (Nunes et al., 2021). In this context, recent studies have highlighted the importance of identifying new sources of resistance and understanding the genetic mechanisms involved in disease resistance, aiming at the development of common bean cultivars with more durable and efficient resistance (Frias et al., 2016; Nanami et al., 2017).

The genetic interaction between *P. vulgaris* and its pathogens reflects a dynamic co-evolutionary process. The diversity of *C. lindemuthianum* and *P. griseola* populations mirrors the differentiation of the Andean and Mesoamerican gene pools of the host, suggesting a strong evolutionary relationship between host and pathogen populations (Vidigal Filho et al., 2020). This co-evolution has driven the diversification and clustering of resistance genes within the common bean genome, resulting in complex genetic architectures underlying disease resistance.

Resistance to anthracnose is typically controlled by single dominant genes, known as *Co loci*, many of which have been mapped across different chromosomes, with a high concentration in specific genomic regions. More than 20 anthracnose resistance genes have been identified to date, including *Co-4* and its alleles (*Co-4²*, *Co-4³*), which confer resistance to multiple pathogen races (Gonçalves-Vidigal et al., 2020). Similarly, resistance to angular leaf spot is often governed by major loci, designated as *Phg* genes (*Phg-1* to *Phg-5*), although quantitative resistance loci (QTLs) have also been reported (Nay et al., 2019).

Recent advances in genomics have demonstrated that resistance genes are not randomly distributed throughout the genome but are frequently organized into clusters enriched with genes encoding nucleotide-binding leucine-rich repeat (NB-LRR) proteins and receptor-like kinases (RLKs). Similar patterns of resistance gene clustering and association between loci controlling resistance to multiple pathogens have also been reported in Brazilian common bean germplasm (Coêlho, Gonçalves-Vidigal, Vidigal Filho, Franzon, & Martins, 2020; Paulino et al., 2022). These proteins play a central role in plant immunity by mediating pathogen recognition and activating defense responses. Furthermore, integrated genomic analyses of anthracnose resistance loci have shown that genomic regions surrounding resistance genes are densely populated with NB-LRR- and kinase-encoding genes, highlighting these regions as important hotspots of plant defense

(Vaz Bisneta & Gonçalves-Vidigal, 2020).

At the molecular level, plant immune responses are activated through two main mechanisms: PAMP-triggered immunity (PTI), mediated by pattern-recognition receptors such as RLKs, and effector-triggered immunity (ETI), mediated by intracellular NB-LRR proteins. These defense layers operate in a coordinated manner to provide robust resistance against pathogen infection. Gene expression studies further support the functional relevance of these resistance clusters, showing that candidate genes located near resistance loci are rapidly induced upon pathogen challenge, contributing to the activation of downstream defense pathways (Lovatto et al., 2023).

Importantly, studies have demonstrated that resistance to anthracnose and angular leaf spot can be co-inherited (Gonçalves-Vidigal et al., 2011). For instance, the *CoPv01^{CDRK}/PhgPv01^{CDRK}* locus identified in the California Dark Red Kidney (CDRK) cultivar confers resistance to both pathogens and has been fine-mapped to a narrow genomic region, providing strong evidence of co-localization and co-segregation of resistance genes (Gonçalves-Vidigal et al., 2020). These findings reinforce the concept that resistance to multiple diseases can be genetically linked and inherited together, offering valuable opportunities for breeding.

The cultivar Awauna UEM, developed by the Common Bean Breeding Program at Universidade Estadual de Maringá, represents a promising source of disease resistance. This cultivar carries the *Co-4²* allele, conferring broad resistance to *C. lindemuthianum*, as well as resistance to other important diseases. In contrast, IPR88 Uirapuru is widely adapted and high-yielding but susceptible to both anthracnose and angular leaf spots. The cross between these cultivars generated an F_{2:8} recombinant inbred line (RIL) population previously used for QTL mapping of yield-related traits.

Despite advances in identifying genomic regions associated with yield, disease resistance has not yet been investigated in this population. Given the increasing evidence that resistance genes are clustered and can co-segregate, analyzing the genetic relationship between resistance to anthracnose and angular leaf spot in this population is essential to elucidate its genetic architecture.

Therefore, the objective of this study was to analyze the co-segregation of resistance to race 73 of *Colletotrichum lindemuthianum* and race 63-39 of *Pseudocercospora griseola* in F_{2:8} recombinant inbred lines derived from the cross Awauna UEM × IPR88 Uirapuru. The results provide new insights into the genetic linkage between resistance loci, particularly the association between *Co-4²* and the angular leaf spot resistance locus (*PhgPv08^{AW}*), and contribute to the development of more efficient breeding strategies for durable and broad-spectrum disease resistance in common bean.

Materials and Methods

Plant material

In total of 56 F_{2:8} recombinant inbred lines (RILs) derived from the cross between the common bean cultivars Awauna UEM (resistant) and IPR88 Uirapuru (susceptible) were used in this study. The parental lines were selected based on their contrasting reactions to anthracnose and angular leaf spot, making them suitable for genetic segregation and co-segregation analyses. The RIL population, previously developed by Reche et al. (2025), was obtained using the single-seed descent (SSD) method from the F₂ generation through successive selfing until the F_{2:8} generation, ensuring a high level of homozygosity. Seeds from each line were maintained under controlled storage conditions and sown individually in plastic trays containing a commercial substrate based on biostabilized pine bark. The plants were grown until trifoliate development in a greenhouse at the Núcleo de Pesquisa Aplicada à Agricultura (NUPAGRI) of the Universidade Estadual de Maringá (UEM) in Maringá, Paraná, Brazil.

Pathogen isolates and inoculation procedures

Two pathogen isolates were used for phenotypic evaluation: race 73 of *Colletotrichum lindemuthianum*, the causal agent of anthracnose (Figure 1), and race 63-39 of *Pseudocercospora griseola* (Figure 2), responsible for angular leaf spot. These isolates were selected due to their high virulence and relevance in common bean production systems. Inoculum preparation followed established protocols for each pathogen. For *C. lindemuthianum*, spore suspensions were obtained from infected plant tissues and adjusted to a concentration of 1.2×10^6 spores mL^{-1} using a hemocytometer (Pastor-Corrales, Otoya, Molina, & Singh, 1995).

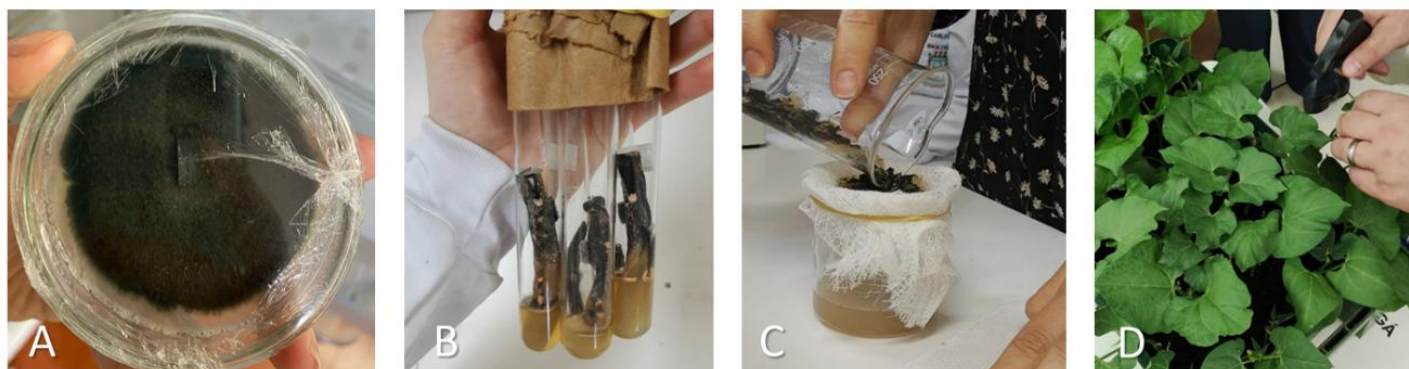


Figure 1. Sequential steps of *Colletotrichum lindemuthianum* culture repicaging and inoculation in common bean plants. (A) Fungal colony grown on culture medium in Petri dish; (B) transfer of mycelial plugs to test tubes containing culture medium for fungal multiplication; (C) preparation of the conidial suspension for inoculation; and (D) inoculation of common bean plants using a spray method.

For *P. griseola*, conidia obtained in Petri dishes were prepared and standardized to a suspension of 2.0×10^4 conidia mL^{-1} (Sanglard, Balbi, Barros, & Moreira, 2009). (Figure 2). Inoculations were performed at the V3 growth stage, when the first trifoliate leaf was fully expanded. Plants were uniformly sprayed with the respective inoculum suspensions until runoff using a manual sprayer.



Figure 2. Sequential procedure for subculturing *Pseudocercospora griseola* under in vitro conditions. (A) Fungal colony grown on culture medium in Petri dish; (B) aseptic transfer of fungal structures using a sterile inoculation needle under flame sterilization; (C) inoculation of fungal material onto fresh culture medium for colony maintenance and multiplication; and (D) excision of actively growing mycelial fragments for subsequent subcultures or experimental use.

Immediately after inoculation, plants were transferred to a humid chamber and maintained under controlled conditions ($20 \pm 2^\circ\text{C}$ and relative humidity $>95\%$) for 72 h to promote infection. Subsequently, plants were returned to greenhouse conditions for

symptom development.

Disease evaluation

Disease severity was assessed visually 7–10 days after inoculation, depending on the pathogen, using a standardized 1–9 scale. Scores ranging from 1 to 3 were classified as resistant (R), indicating no symptoms or limited lesion development, whereas scores from 4 to 9 were classified as susceptible (S), indicating moderate to severe disease symptoms. Each RIL and parental line was evaluated with multiple plants to ensure consistency of phenotypic classification. The final classification for each line was determined based on the predominant response observed among replicates (Pastor-Corrales et al., 1995; Inglis, Hagedorn, & Rand, 1988).

Statistical analysis

The segregation ratios for resistance and susceptibility were analyzed using the chi-square (χ^2) goodness-of-fit test to verify adherence to the expected Mendelian ratio of 1:1 (resistant:susceptible), which is characteristic of monogenic inheritance in recombinant inbred line (RIL) populations. Statistical analyses were performed using the R software environment (R Core Team, 2026).

The chi-square statistics were calculated according to the following model:

$$\chi^2 = \sum \frac{(O_i - E_i)^2}{E_i}$$

where O_i corresponds to the observed frequency and E_i to the expected frequency of resistant and susceptible lines. The expected segregation ratio adopted was 1:1, considering a single major locus controlling resistance. The significance of deviations between observed and expected frequencies was assessed at the 5% probability level ($P \leq 0.05$).

Additionally, co-segregation between resistance to anthracnose and angular leaf spot was evaluated by comparing the phenotypic classification of each RIL for both diseases. Recombinant lines were identified based on discordant resistance responses, allowing the estimation of genetic linkage between the resistance loci.

Results and Discussion

Phenotypic evaluation of the parental lines and the 56 F_{2:8} recombinant inbred lines (RILs) derived from the cross Awauna UEM × IPR88 Uirapuru confirmed clear and consistent contrasting responses to both pathogens evaluated. The cultivar Awauna UEM exhibited complete resistance to race 73 of *Colletotrichum lindemuthianum* and race 63-39 of *Pseudocercospora griseola*, showing no visible symptoms or only minor lesions corresponding to resistance scores. In contrast, IPR88 Uirapuru displayed complete susceptibility to both pathogens, with severe disease symptoms characterized by extensive lesion development and high severity scores.

The F_{2:8} population exhibited clear segregation for resistance and susceptibility to both diseases. Segregation data (Table 1) indicated that resistance to anthracnose followed a 1:1 ratio (27 resistant:29 susceptible), which did not significantly deviate from the expected Mendelian ratio ($\chi^2 = 0.071$; $P = 0.78$). This result is consistent with the presence of a single dominant gene controlling resistance, corresponding to the *Co-4²* allele inherited from Awauna UEM.

Table 1. Phenotypic reaction of 56 F_{2:8} recombinant inbred lines from the common bean cross Awauna UEM × IPR88 Uirapuru following inoculation with race 73 of *Colletotrichum lindemuthianum* and race 63-39 of *Pseudocercospora griseola*.

Parents	Generation	Observed segregation (1RR:1SS) ¹	Expected segregation (1RR:1SS)	<i>P</i> -value	
Raça 73 do <i>C. lindemuthianum</i>					
Awauna UEM	R	10:0			
IPR88 Uirapuru	S	0:10			
Awauna UEM x IPR88 Uirapuru	F _{2:8}	27:29	28:28	0.071	0.78
Race 63-39 of <i>P. griseola</i>					
Awauna UEM	R	10:0			
IPR88 Uirapuru	S	0:10			
Awauna UEM x IPR88 Uirapuru	F _{2:8}	25:31	28:28	0.64	0,42

¹Chi-square (χ^2) *P*-values > 0.05 indicate no significant deviation between observed and expected values; RR: resistant; SS: susceptible.

Similarly, resistance to angular leaf spot also segregated in a 1:1 ratio (25 resistant: 31 susceptible), with no significant deviation from expected values ($\chi^2 = 0.64$; *P* = 0.42). This segregation pattern supports the hypothesis that resistance to *P. griseola* in this population is also controlled by a major gene. The consistency of segregation ratios for both diseases reinforces the genetic simplicity of resistance inheritance in this cross.

Co-segregation analysis (Table 2) provided further insights into the genetic relationship between resistance to anthracnose and angular leaf spot. Among the 56 RILs evaluated, 50 lines exhibited identical phenotypic responses to both pathogens, being either resistant to both diseases or susceptible to both. In contrast, only six lines showed discordant reactions, indicating recombination between resistance loci.

The low frequency of recombinant lines suggests strong genetic linkage between the loci controlling resistance to *C. lindemuthianum* and *P. griseola*. This high level of phenotypic concordance indicates that these resistance loci are likely located in close proximity within the genome and tend to be inherited together. The presence of a limited number of recombinants further supports the hypothesis of tight linkage, while also indicating that recombination, although rare, does occur within this genomic region.

Overall, the results demonstrate a clear pattern of monogenic inheritance for both traits and provide strong evidence for co-segregation between resistance to anthracnose and angular leaf spot in this population.

The segregation patterns observed in this study clearly indicate that resistance to anthracnose race 73 is controlled by a single dominant gene, consistent with the *Co-4²* allele previously described in common bean. Similarly, the 1:1 segregation ratio observed for angular leaf spot supports the hypothesis that resistance to *Pseudocercospora griseola* is also governed by a major locus in this population.

A key finding of this study is the strong co-segregation between resistance to anthracnose and angular leaf spot, which provides robust evidence for tight genetic linkage between the *Co-4²* gene and the angular leaf spot resistance locus identified here as *PhgPv08^{AW}*, derived from the cultivar Awauna UEM. The low frequency of recombinant lines further supports the hypothesis that these loci are physically linked and likely inherited as a single genetic unit in most individuals.

Table 2. Phenotypic response of resistant and susceptible plants in F_{2:8} recombinant inbred lines derived from the cross Awauna UEM × IPR88 Uirapuru.

Inbred lines	Race 73 of <i>C. lindemuthianum</i>	Race 63-39 of <i>P. griseola</i>
1	R ¹	R
2	S	S
4	S	S
6	R	R
7	S	S
8	S	S
9	S	S
10	S	S
11	R	S
12	R	S
15	R	S
16	S	S
18	S	S
19	S	S
21	S	S
24	S	S
25	S	S
27	S	S
28	S	S
30	R	R
31	R	R
32	S	S
36	R	R
37	R	R
38	R	R
39	R	R
41	R	R
42	S	R
43	R	R
44	R	R
45	R	R
46	R	R
47	R	R
50	R	R
51	R	S
53	R	R
54	S	S
56	S	S
57	S	S
58	S	S
59	S	R
60	R	R
61	S	S
62	S	S
64	R	R
65	R	R
66	S	S
67	R	R
68	S	S
70	S	S
71	R	R
72	R	R
74	R	R
77	S	S
78	S	S
79	S	S

¹R: resistant; S: susceptible

This pattern is consistent with previous studies demonstrating that resistance loci to different pathogens are frequently clustered within the same genomic regions in *Phaseolus vulgaris* (Valentini et al., 2017; Gonçalves-Vidigal et al., 2020). In particular, chromosome Pv08 has been widely recognized as a hotspot for disease resistance genes, including *Co-4* alleles and multiple QTLs associated with resistance to diverse pathogens (Miklas et al., 2000; Vaz Bisneta & Gonçalves-Vidigal, 2020; Oblessuc, Francisco, & Melotto, 2015; Oblessuc, Bridges, & Melotto, 2022). The co-localization of *Co-4²* and *P PhgPv08^{AW}* observed in this study reinforces the concept that resistance to anthracnose and angular leaf spot can be genetically associated within the same chromosomal region.

At the molecular level, the *Co-4* locus is part of a complex genomic region enriched in genes encoding receptor-like kinases (RLKs) and nucleotide-binding leucine-rich repeat (NB-LRR) proteins, which are central components of plant immune systems. RLKs function as pattern-recognition receptors (PRRs), mediating PAMP-triggered immunity (PTI), while NB-LRR proteins are responsible for effector-triggered immunity (ETI). This dual-layered immune system enables rapid and robust responses to pathogen infection.

Integrated genomic analyses have demonstrated that resistance loci are frequently embedded within clusters of RLK and NB-LRR genes, forming genomic hotspots of defense-related functions (Vaz Bisneta & Gonçalves-Vidigal, 2020). The high density of these genes within resistance clusters suggests coordinated regulation and functional interaction, contributing to enhanced resistance efficiency. Functional studies further indicate that *CoK-4* proteins share structural and functional similarities with *FERONIA-like* kinases, supporting their role in both developmental processes and immune signaling (Oblessuc et al., 2015; Azevedo, Gonçalves-Vidigal, Oblessuc, & Melotto, 2018).

Recent expression analyses provide additional support for the functional relevance of these resistance clusters. Candidate genes such as *Phvul.001G245300* (LRR-kinase) and *Phvul.001G246300* (ABA receptor PYL) show strong induction upon pathogen challenge, indicating activation of signaling pathways associated with plant defense. Moreover, the upregulation of pathogenesis-related genes (e.g., PR1 and PR2) suggests activation of salicylic acid-mediated systemic acquired resistance, highlighting the integration of local and systemic defense responses (Lovatto et al., 2023).

The co-segregation of *Co-4²* with *PhgPv08^{AW}* can therefore be interpreted as a consequence of this genomic organization, in which functionally related resistance genes are physically clustered and co-inherited. Importantly, this association does not appear to involve the previously described *Phg-2* locus, which is also located on Pv08 but positioned distally and reported to exhibit weaker linkage with *Co loci*. Instead, the evidence supports the existence of a distinct angular leaf spot resistance locus (*PhgPv08^{AW}*) closely linked to *Co-4²* (Souza et al., 2023).

From a breeding perspective, this genetic configuration represents a highly advantageous characteristic, as the use of linked resistance loci has been considered a promising strategy to enhance marker-assisted selection and accelerate the development of cultivars with durable resistance, particularly under conditions of high pathogen variability (Paulino et al., 2022; Gonçalves et al., 2023). Furthermore, the co-segregation of resistance to two important diseases allows the simultaneous selection of both traits, substantially improving the efficiency of breeding programs. This genetic association also facilitates gene pyramiding strategies and contributes to the development of cultivars with broad-spectrum resistance, thereby reducing dependence on chemical control and promoting more sustainable agricultural systems (Lovatto et al., 2023).

However, the presence of recombinant lines indicates that linkage between *Co-4²* and *PhgPv08^{AW}* is not absolute. Recombination events, although infrequent, may lead to the dissociation of resistance traits, emphasizing the importance of developing tightly linked molecular markers for reliable selection. High-resolution mapping, genome-wide association studies (GWAS), and functional genomics approaches will be essential to precisely delimit these loci and validate candidate genes.

Conclusions

Overall, the results of this study provide strong evidence that resistance to anthracnose and angular leaf spot in the Awauna UEM × IPR88 Uirapuru population is controlled by tightly linked loci that co-segregate and likely form part of a resistance gene cluster on chromosome Pv08. This genomic architecture reflects evolutionary pressures imposed by pathogen diversity and represents a highly effective strategy for coordinated immune responses. The integration of genetic, genomic, and functional data offers a powerful framework for advancing common bean breeding toward durable and broad-spectrum disease resistance.

Conflict of interest

The authors declare that there is no conflict of interest with this article.

Data availability statement

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

Declaration of use of AI Technologies

We hereby declare that no artificial intelligence (AI) technologies were used in the preparation of this manuscript. All research, data analysis, and manuscript preparation were conducted manually and without the assistance of AI tools or technologies

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