



The complexity of anthracnose in bean: relevant aspects of genetic and genomic resistance

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ABSTRACT

The complexity of anthracnose and the bean population structure present ongoing challenges in genetic research. Anthracnose, a devastating disease affecting common bean, is challenging due to the genetic variability of the pathogen, *Colletotrichum lindemuthianum*. The identification of disease resistance genes is challenging due to the polygenic nature of disease resistance. However, remarkable advances in genetic research are shaping the current landscape. Genomic research and the use of molecular markers have played a key role in the search for resistance to anthracnose. Advanced genomic association techniques and their application in the study of anthracnose resistance are discussed. These advances are accelerating the process of genetic improvement, driving the development of more resistant and productive bean cultivars, and contributing to global food security. This work emphasizes the importance of genetic research in the search for lasting solutions to anthracnose, facilitating the identification of new sources of resistance and an understanding of the complex genetic interactions involved and offering valuable *insights* for plant breeding and sustainable bean production worldwide.

RESUMO

A complexidade da antracnose e a estrutura populacional dos feijões apresentam desafios contínuos na pesquisa genética. A antracnose, uma doença devastadora que afeta o feijão comum, é desafiadora devido à variabilidade genética do patógeno, *Colletotrichum lindemuthianum*. A identificação de genes de resistência a doença é desafiadora devido à natureza poligênica dessa característica. No entanto, avanços notáveis na pesquisa genética estão moldando o cenário atual. A pesquisa genômica e o uso de marcadores moleculares, desempenharam um papel fundamental na busca por resistência à antracnose. Técnicas avançadas de associação genômica e sua aplicação no estudo da resistência à antracnose são discutidas. Esses avanços estão acelerando o processo de melhoramento genético, impulsionando o desenvolvimento de cultivares de feijão mais resistentes e produtivas, e contribuindo para a segurança alimentar global. Este trabalho enfatiza a importância da pesquisa genética na busca por soluções duradouras para a antracnose, permitindo a identificação de novas fontes de resistência e uma compreensão das complexas interações genéticas envolvidas, oferecendo *insights* valiosos para o melhoramento genético de plantas e a produção sustentável de feijões em todo o mundo.

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Introduction

Phaseolus vulgaris L., popularly known as common bean, is the main species cultivated in Brazil (Abebe & Alemayehu 2022) and one of the most important legumes for human consumption worldwide; it is the basis of traditional foods (Rawal & Navarro 2019) and represents one of the least expensive sources of protein in Brazil and most developing countries in Africa, Asia, and Latin America (Rahate et al., 2021).

Anthrachnose, a disease caused by the fungus *Colletotrichum lindemuthianum*, is one of the main causes of productivity losses in bean plantations, causes lesions at all stages of cultivation (Canale et al., 2020), and, if left unchecked, can lead to losses of up to 100% in production (Coêlho et al., 2016). Among these methodologies, the use of genetically resistant cultivars is crucial for controlling anthracnose; however, even with this approach and management practices, such as seed treatment, fungicide application, crop rotation and the use of certified seeds, the crop is susceptible to the disease in the presence of several breeds of the pathogen (Padder et al., 2017).

Most cultivars are susceptible due to pathogenic variability, making disease control challenging, and more than 298 races of *C. lindemuthianum* have been identified worldwide (Sharma et al., 2008; Nunes et al., 2021). The mapping of genomic regions that confer resistance is a crucial biotechnological tool, allowing the anticipation of selection through molecular markers (Mores et al., 2021); however, to effectively use this tool, a deeper knowledge of the genome of the crop in question is required (Miedaner, 2016).

This article provides a literature review of books and articles published in national and international journals and presents a comprehensive overview of advances in research on anthracnose in common bean, highlighting the importance of identifying resistance genes and discussing advanced genomic association techniques. This information is valuable to researchers and professionals in the field of agriculture and provides a solid foundation for future research and development of more resistant bean varieties.

Origin and domestication of common bean

The common bean is among the oldest crops in the world (Gepts, 1998), and in Brazil, its cultivation has a history dating back more than 2000 years, with evidence of seeds found in caves dating back to this period (Rocha, 2011), and the transition from its wild form to the cultivated variety is believed to have occurred approximately 10,000 years ago (Gepts & Debouck, 1991). Schmutz et al. (2014) noted that common bean has a unique common ancestor, likely originating in the region that now corresponds to Mexico. Early studies based on isoenzymes (Singh et al., 1991), seed proteins (Gepts & Bliss, 1986), morphological traits (Durán et al., 2005) and DNA markers (Blair et al., 2003) demonstrated the existence of two geographically different centres of origin: Mesoamerican and Andean.

The Mesoamerican centre includes small-seed genotypes with type "S" phaseolin and represents genotypes from the northern region of Mexico to Colombia (Coelho et al., 2007). The beans from the Andean centre have, for the most part, an indeterminate growth habit, with large rounded seeds and a wide range of colours; their phaseolin proteins are predominantly "T" type, although types "A", "C" and "H" may also be present (Schmutz et al., 2014). However, Bitocchi et al. (2013) demonstrated the existence of relict cultivars in the northern regions of Peru and Ecuador that have the phaseolin type "I" protein, which has not been found in any of the other centres of origin.

These domestication events were followed by local adaptations, resulting in the development of local breeds with distinct characteristics (Mamidi et al., 2011). The domestication process triggered significant morphological changes, including increased seed and leaf size, changes in growth habits and responses to photoperiod, and variations in integument colour and patterns that distinguish different culturally adapted classes (Schmutz et al., 2014). According to Ron et al. (2015), beans have spread to various regions of the world and have been domesticated according to local market demands.

General aspects of common bean cultivation

The bean plant is an autogamous annual cycle plant with a cross-fertilization rate of approximately 5%, which allows the formation of new colours, shapes, chemical constituents and genetic combinations (Burle et al., 2010). It has a diploid chromosome number of $2n = 2x = 22$ (Singh et al., 1991) and a relatively small genome of approximately 587 Mbp (Schmutz et al., 2014).

The bean belongs to the Fabaceae family and the genus *Phaseolus* L., which is considered monophyletic (Freytag & Debouck et al., 2003; Delgado-Salinas et al. 2006), and encompasses approximately 92 species that are widely distributed worldwide; however, five species have particular economic relevance: *P. vulgaris*, *P. lanatus*, *P. coccineus*, *P. acutifolius*, and *P. polyanthus* (World Flora Online [WFO] 2023; Schmutz et al., 2014).

Bean kernels come in a variety of shapes and exhibit a wide variety of colours. Different types of bean species are cultivated and are popularly known in some commercial groups as carioca, black, roxinho, rosinha, manteiga, manteigão and jalo beans (Siega et al., 2022). In addition, beans are composed of 1 to 20% dietary fibre, 60 to 65% carbohydrates, and 1 to 3% lipids and contain the minerals Ca, Fe, Cu, Zn, K, P and Mg along with vitamins, especially those of the B complex, such as riboflavin, niacin and folate (Lajolo et al., 1996).

The common bean is an herbaceous plant with different growth patterns and is classified into four types by the *International Center for Tropical Agriculture* (CIAT): Type I - determinate growth, shrubby and erect; Type II - indeterminate growth, shrubby and erect with few branches on the stem; Type III - indeterminate growth, prostrate or semiprostrate bearing, and open and well-developed branches; and Type IV - indeterminate growth, climbing

size, stem dominating the upper part, and poorly developed lateral branches (Oliveira et al., 2018).

According to Quintela (2000), common bean has nine vegetative phases: V₀—when the seed begins germination; V₁—emergence; V₂—the first primary leaves open completely; V₃—the first open trifoliate leaf appears; V₄—the third trifoliate leaf opens and branch production begins; and V₅ to V₉—the reproductive phase with the preflowering stage until physiological maturation, when the seeds begin to dry, acquiring the specific colour of the cultivar.

Socioeconomic importance of common bean

Common bean is considered the most important species of *Phaseolus* cultivated worldwide (Efstathiadou et al., 2021) and is an agricultural product of importance because of its nutritional, agronomic and socioeconomic value.

From a nutritional point of view, the grain has numerous health benefits, including antioxidant, antidiabetic, anti-inflammatory, and anticancer properties (Ganesan & Xu, 2017); is rich in polyphenols (Mullins et al., 2021); has a low glycaemic index; and is rich in soluble and insoluble fibre, which can aid in weight management (Messina, 2014). These properties are important because they provide opportunities for the development of cultivars that cater to different nutritional needs and consumption preferences.

An important aspect of the crop is its wide capacity for edaphoclimatic adaptation, which allows its cultivation throughout the year in almost all Brazilian states and at different times and harvest periods (Gomes et al., 2020), and it can be cultivated both by large, highly technified producers and by small farmers who depend mainly on family labour (Siega et al., 2022).

According to the *Food and Agriculture Organization* (FAO), in 2021, almost 27.8 million tons of beans were produced in a planted area of 35.9 thousand hectares. Brazil is the second largest producer of beans in the world, with a production of 2.8 million tons (t), second only to that of India (6.1 million t). For the 2022/23 season (three harvests), the estimated average production volume in Brazil was 3.04 million tons, 1.7% higher than that of the previous harvest (Companhia Nacional de Abastecimento [CONAB], 2023); the main producing states were Paraná (728.1 thousand tons), Minas Gerais (556.7 thousand tons) and Mato Grosso (307.1 thousand tons).

According to data from CONAB (2023), the average productivity achieved in the 2022/23 harvest was 1,129 kg/ha, 7.9% higher than the average productivity in the 2021/22 cycle; however, most of the beans produced in Brazil are used for domestic consumption (93.7%) (CONAB 2023), and even though Brazil is a major world producer, imports are still necessary to satisfy national demands and control the internal regulatory stock.

In this context, considering an initial stock of 208.3 thousand tons, a consumption of 2.85 million tons, exports of 165 thousand tons and imports of 100 thousand tons, the result is

a remaining stock of approximately 333.9 thousand tons that plays a key role in maintaining the domestic supply at normal levels (CONAB 2023).

Anthracnose in common kidney bean

Anthracnose, caused by *Colletotrichum lindemuthianum* (Wendland et al., 2018), is one of the main fungal diseases affecting common bean. According to O'Connell et al. (2012), the main symptoms of the disease include necrosis that can affect the entire aerial part of the plant (a characteristic symptom); elongated lesions with a reddish or dark brown colour on the leaves, usually more common on the underside; depressed and circular lesions on the pods, with a darker brown border; and discoloration and the formation of dark lesions in the seed integument or in the cotyledons (Wendland et al., 2018). The symptoms of anthracnose are crucial for the identification of the pathogen, and it is essential to observe the characteristics of the lesions caused by this disease to determine appropriate management measures.

The ability to transmit the disease through seeds and through rainwater droplets or irrigation (Ferreira & Junior, 2023), combined with its occurrence during the three growing seasons, can result in productivity losses of up to 100%, especially under favourable environmental conditions (Rey et al., 2005), causing great economic losses.

The use of resistant cultivars is one of the most effective approaches for controlling anthracnose (Wendland et al., 2018). According to Nunes et al. (2021), genetic resistance not only reduces the impacts of the disease but also reduces the need for pesticides, thus reducing environmental damage and production costs.

However, the large pathogenic variability and wide distribution of pathotypes prove to be major challenges for the development of resistant cultivars. The fungus *C. lindemuthianum* exhibits remarkable variability and is capable of generating new breeds that can overcome the genetic resistance present in commercial cultivars (Pastor-Corrales et al., 1993). According to Nunes et al. (2021), 298 breeds of *C. lindemuthianum* have been described in 29 countries in the Americas, Europe, Asia, and Africa from 1991 to 2020. In Brazil, 89 breeds have been characterized, distributed across 15 common bean-producing states. Paraná, the largest producer of common beans, has the greatest variability, with 62 breeds identified (Xavier et al., 2021).

Genetic resistance to anthracnose

Currently, several research centres are focused on breeding efforts aiming to develop anthracnose-resistant common bean varieties. This approach is considered the most effective at mitigating the negative impacts caused by *C. lindemuthianum* on the quality and productivity of bean crops (Ferreira & Junior, 2023).

Several genes and alleles responsible for resistance, such as Pv01, Pv02, Pv03, Pv04, Pv07, Pv08, and Pv11, have been identified and mapped into specific binding groups (Nunes

et al., 2021). The identification of genomic regions, genes, and alleles for resistance to anthracnose caused by *C. lindemuthianum* has been a significant area of research. Kelly and Young (1996) introduced a unified naming system, using the symbol "Co" followed by numbers or letters, for fungal resistance genes. This standardized system facilitates the characterization of pathogen races, the mapping of resistance genes, and the implementation of gene pyramiding strategies to achieve long-lasting resistance.

The nomenclature proposed by these authors for *C. lindemuthianum* resistance genes was adopted by the Genetics Committee of the *Bean Improvement Cooperative* (BIC) (Nunes et al., 2021). Thus, 14 genes and 11 alleles identified in common bean accessions in the two gene pools were officially named according to this organization: Co-1 and the Co-12, Co-13, Co-14 and Co-15 alleles (Melotto & Kelly, 2000; Gonçalves-Vidigal & Kelly, 2006); Co-2 (Mastenbroek, 1960); Co-3 and its allelic series Co-32, Co-33, Co-34 and Co-35 (Bannerot, 1965; Fouilloux, 1979; Young et al., 1998; Geffroy et al., 1999; Gonçalves-Vidigal et al., 2013); Co-4 and the Co-42 and Co-43 alleles (Fouilloux, 1976; Young et al., 1998; Alzate-Marin et al., 2007); Co-5 and Co-52 (Fouilloux, 1976; Vallejo & Kelly, 2009); Co-6 (Schwartz et al., 1982); Co-8 (Alzate-Marin et al., 1997); Co-11 (Gonçalves-Vidigal et al., 2007); Co-12 (Gonçalves-Vidigal et al., 2008); Co-13 (Gonçalves-Vidigal et al., 2009); Co-14 (Gonçalves-Vidigal et al., 2012); Co-15 (Sousa et al., 2015); Co-16 (Coimbra-Gonçalves et al., 2016); and Co-17 (Trabanco et al., 2015).

According to a survey carried out by Xavier (2021), other genes that confer resistance to anthracnose in common bean have been identified, although they have not yet been officially approved by BIC: Co-x, Co-w, Co-y, Co-u, and Co-z (Geffroy et al., 1999; Geffroy et al., 2008); Co-Pa (Castro et al., 2017); Co-Perla (Paulino et al., 2019); Co-AC (Nanami et al., 2017; Gilio et al., 2020); CoPvo1CDRK (CDRK) (Gonçalves-Vidigal et al., 2020); and the Co-1HY allele (Chen et al., 2017).

Genetic mapping and genome-wide association

Genetic mapping is a crucial tool for understanding genetic inheritance, gene segregation, and the physical relationships among genes. In addition, it plays a key role in the selection of parents for breeding programs, the identification of desirable traits in plants, gene cloning, and research into gene editing technologies (Vieira et al., 2018).

The construction of a genetic map involves several steps, from identifying genetic markers to determining the order and distance between them (Zhang et al., 2019). In this context, molecular markers and genomic association analyses are essential tools for the genetic improvement of plants, enabling the development of more productive and resistant cultivars (Vianello et al., 2023).

Genome-wide association studies (GWASs) play an important role in identifying polymorphisms related to specific phenotypic traits (Bastos et al., 2023). To effectively utilize GWASs across a diverse panel of samples, it is crucial that markers are widely distributed across the genome (Tsunoda et al., 2019).

With advances in bioinformatics, the GWAS methodology has undergone constant modifications, enabling the analysis of complex genetic bases (Nicholls et al., 2020). Among the models used, the *general linear model* (GLM) is commonly used to identify unique *loci* (Novembre, 2014). However, the *mixed linear model* (MLM) has stood out as the most popular, as it incorporates both population structure and genetic relationships to control for false-positives (Conomos et al., 2018).

MLM-based enhancements such as the *compressed mixed linear model* (CMLM) (Zhang et al., 2010), the *efficient and parallel computing for mixed-model association edited* (ECMLM) (Li et al., 2014), and the *factored spectrally transformed linear mixed models* (FaST-LMM) (Lippert et al., 2011) have been developed to enhance the computational models used in GWASs. The SUPER model, proposed by Wang et al. (2014), further extended the FaST-LMM, increasing its statistical power.

All of these models, including the *Efficient Mixed-Model Association Expedited* (EMMAX) (Kang et al., 2010) and the *Genome-wide Efficient Mixed-Model Association* (GEMMA) (Zhou & Stephens, 2012), conduct genomic association analysis in a one-dimensional approach, making it necessary to apply corrections to reduce the rate of false positives (Wang et al., 2016).

Regarding the polygenic phenotypic traits, other models are described, the so-called GWAS for multi-locus (ML-GWAS). In this field, the models MLMM (*Multi-Locus Mixed-Model*) (Segura et al., 2012), mrMLM (*Multiple-Locus Random-SNP Mixed Linear Model*) (Wang et al., 2016), FarmCPU (*Fixed and random model Circulating Probability Unification*) (Liu et al., 2016), LASSO (*Least Absolute Shrinkage and Selection Operator*) (Xu et al., 2020), pLARmEB (*Polygenic and Low-Rank Approximation Mixed Model for Genome-Wide Association Studies*) (Zhang et al., 2017), ISIS-EM-BLASSO (*Iterative Stepwise Surrogate Empirical Bayes LASSO*), FASTmrMLM (*Fast Multi-Locus Mixed-Model*) (Tamba et al. 2017), FASTmrEMMA (*Fast Multi-Locus Random-SNP-Effect Efficient Mixed Model for Genome-Wide Association Studies*) (Wen et al., 2018), pKWmEB (*Polygenic Kernel-Wide Association Study with epistasis*) (Ren et al., 2018) e, BLINK (*Bayesian Information and Linkage with Background Information*) (Huang et al., 2019) they are commonly used because they have greater statistical power and accuracy in the detection of QTNs (*Quantitative Trait Nucleotides*).

According to Guan et al. (2019), these models play an important role in minimizing errors in genomic association studies, ensuring that the identified associations are statistically significant and not influenced by population factors. They represent valuable tools in the

search for genetic markers related to traits of interest in plants, including those of relevance to genetic improvement.

Due to the great genetic diversity of common bean, which is characterized by two distinct gene pools, and considering that many phenotypic variations are associated with this population structure, the use of the FarmCPU model is promising for studying the genetic architecture of these traits (Diniz et al., 2019). This model can offer valuable *insights* into how genetic diversity affects common bean traits in different contexts, contributing to crop breeding.

Supplemental Table 1 highlights the key anthracnose resistance genes approved and identified in common bean cultivars through genome-wide association analysis, including information on markers, breeds, and corresponding references.

Final thoughts

It is important to recognize that anthracnose is a complex disease influenced by the diversity of the pathogen and the genetic structure of bean populations, so the identification of resistance genes is a challenging task, mainly due to the genetic variability of the pathogen. Genome-binding techniques provide a powerful approach for elucidating the genetic architecture of anthracnose resistance and play a significant role in providing a solid foundation for future research and the development of more resistant bean varieties. Advances in research related to anthracnose in common bean are remarkable and have led to scientific advances of great value to researchers and professionals in the field of agriculture.

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Supplementary Table 1.

*Genes and alleles that confer resistance to anthracnose in common bean cultivars (*Phaseolus vulgaris* L.), with information on molecular markers, breeds and bibliographic references.*

PV	Source of resistance	Genes/Loci	Marker Type*	Mark Name	Race	References
Pv01	GWAS ⁴	ANT1.1	SSR	PvM56	4	PERSEGUINI et al. 2016
		ANT1.2	SSR	BMc271		
		ANT1.4	SSR	PvM123		
		ANT1.5	SSR	PvM15		
		ANT1.6	SNP	scaffold00024_916410		
	GWAS ⁸¹	ANT1.3	SRR	NSSR8	81	WU et al. 2019
Pv02	GWAS ⁴	ANT2.1	SSR	PvM153	4	PERSEGUINI et al. 2016
		ANT2.2	SSR	PvM93	Field	FRITSCHÉ-NETO et al. 2019
	GWAS ^F	ANT2.3	SNP	BARCPV_1.0_Ch02_23542475		
			SNP	BARCPV_1.0_Ch02_23644618		
	GWAS ⁸¹	ANT2.4	SSR	NSSR24	81	WU et al. 2019
GWAS ^{39,55}	ANT2.5	SNP	ss715648451	39, 55	ZUIDERVEEN et al. 2016	
Pv03	GWAS ¹⁵⁴⁵	ANT3.1	SNP	S03_13038972	1545	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
		ANT3.2	SSR	IAC167	81	PERSEGUINI et al. 2016
	GWAS ⁴	ANT3.3	SSR	PvM126		
			SSR	PVEST236		
		ANT3.4	SSR	PvM124		
		ANT3.5	SNP	scaffold00045_345513		
	ANT3.6	SSR	PvM95			
Pv04	GWAS ²	ANT4.1	SNP	S04_58467	2	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
			SNP	S04_63495		
			SNP	S04_93389		
	GWAS ⁷	ANT4.2	SNP	ss715642306	7	ZUIDERVEEN et al. 2016
	GWAS ¹⁰⁹	ANT4.3	SNP	ss715649432	109	
	GWAS ⁹	ANT4.5	SNP	S04_1736070	9	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
SNP			S04_1743258			
SNP			S04_1743544			
GWAS ⁸¹	ANT4.4	SSR	NSSR234	81	WU et al. 2019	

	ANT4.8	SSR	NSSR65		
GWAS ⁴	ANT4.6	SNP	scaffold00090_802505	4	PERSEGUINI et al. 2016
	ANT4.7	SNP	scaffold00060_874577		
			ss715649771		
			ss715649774		
			ss715649776		
			ss715649777		
			ss715648681		
			ss715640024		
			ss715640025		
			ss715642306		
			ss715649433		
GWAS ⁶⁵		SNP	ss715649434	65	COSTA et al. 2021
			ss715649437		
			ss715646910		
			ss715646889		
			ss715646891		
			ss715646891		
			ss715646892		
			ss715646892		
			ss715646893		
			ss715646893		
			ss715646247		
		SNP	S05_706152		
		SNP	S05_713832		
GWAS ¹⁵⁴⁵	ANT5.1	SNP	S05_739138	1545	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
		SNP	S05_747744		
Pv05		SNP	S05_755558		
GWAS ⁸¹	ANT5.2	SSR	NSSR73	81	WU et al. 2019
GWAS ⁶⁵		SNP	ss715650069	65	COSTA et al. 2021
		SSR	PvM07		
GWAS ⁴	ANT5.3	SNP	scaffold00062_295319	4	PERSEGUINI et al. 2016
GWAS ⁸¹	ANT6.1	SSR	NSSR117	81	WU et al. 2019
Pv06					
GWAS ⁴	ANT6.2	SSR	PvM14		
	ANT6.2	SNP	scaffold00128_112577	4	PERSEGUINI et al. 2016

			SNP	scaffold00128_197955		
		ANT6.3	SNP	scaffold00001_2118513		
			SNP	scaffold00001_1947432		
	GWAS ²	ANT6.4	SNP	S06_28545207	2	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
Pv07	GWAS ⁴	ANT7.1	SNP	scaffold00021_89379	4	PERSEGUINI et al. 2016
			SNP	scaffold00021_767280		
		ANT7.2	SNP	scaffold00088_364454		
		ANTT.3	SNP	scaffold00094_563857		
		ANT7.4	SNP	scaffold00098_217812		
Pv08	GWAS ⁴	ANT8.1	SNP	scaffold00105_48480	4	PERSEGUINI et al. 2016
			SNP	scaffold00097_323110		
		ANT8.2	SNP	scaffold00097_164240		
			SNP	scaffold00034_860044		
		ANT8.3	SSR	PvM68		
		ANT8.4	SSR	IAC254		
Pv09	Cornell 49242	CoPv09c ^C	SSR	BM202	453	CAMPA et al. 2014
			InDel	IND_09_28.0580		
			InDel	IND_09_29.1822		
			SSR	ATA217		
Pv10	GWAS ⁷	ANT10.1	SNP	ss715648754	7	ZUIDERVEEN et al. 2016
	GWAS ⁶⁵		SNP	ss715639777	65	COSTA et al. 2021
	GWAS ⁸¹	ANT10.2	SSR	NSSR265	81	WU et al. 2019
Pv11	GWAS ⁷	ANT11.2	SNP	ss715645476	7	ZUIDERVEEN et al. 2016
	GWAS ⁸¹	ANT11.1	SSR	NSSR271	81	WU et al. 2019
		ANT11.6	SSR	NSSR281		
	GWAS ⁴	ANT11.3	SNP	scaffold00009_1366067	4	PERSEGUINI et al. 2016
	GWAS ²	ANT11.4	SNP	scaffold00009_825782	2	VAZ BISNETA & GONÇALVES-VIDIGAL 2020
			SSR	IAC127		
			SNP	S11_46403555		
		SNP	S11_46403801			
ANT11.7		SNP	S11_46519783			
	SNP	S11_46529024				
	SNP	S11_46531625				
GWAS ⁶⁵		SNP	ss715648093	65	COSTA et al. 2021	

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