# Citrullus lanatus germplasm of southern Africa

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#### ABSTRACT

Citrullus lanatus germplasm from southern Africa is a rich source of diversity for cultivated watermelon. Wild, feral, and landrace populations of the species are found throughout the arid regions of southern Africa, where they serve as sources of water and food for humans and wildlife alike. Genetic resources from the region proved to be important sources of disease resistance for cultivated watermelon, contributing to the development of both Fusarium wilt- and anthracnose-resistant cultivars. Basic research, such as genomic mapping and the elucidation of drought tolerance, have also benefitted from the abundant genetic diversity. Currently, several ex situ collections in the region and the rest of the world house accessions originating from southern Africa. The USDA germplasm collection has been screened extensively for traits of interest in watermelon breeding, but full advantage has not been taken of some of the other collections. The C. lanatus germplasm from southern Africa is currently a largely underutilized source of diversity for watermelon improvement. Conservation of and access to ex situ collections should be given priority to ensure that this rich source of genetic variation is utilized to its full potential in both basic and applied research.

Keywords: tsamma, citroides, Fusarium wilt, anthracnose

### **INTRODUCTION**

In 2007, watermelon [*Citrullus lanatus* (Thunb.) Matsum. et Nakai] was responsible for approximately 7% of the total world vegetable tonnage (FAOSTAT, 2008). Recent classifications of the genus *Citrullus* recognize four diploid (2n + 2x = 22) species: *C. lanatus*, *C. ecirrhosus* Cogn., *C. colocynthis* (L.) Schrad., and *C. rehmii* De Winter (Robinson and Decker-Walters, 1997). *Citrullus lanatus* and *C. rehmii* are annuals, while *C. ecirrhosus* and *C. colocynthis* are perennials.

Interspecific crosses in *Citrullus* are possible to varying degrees (Robinson and Decker-Walters, 1997), but not unambiguous. For example, crosses between *C. lanatus* and *C. colocynthis* have been successful, but fruit set was low and directionality of the crosses influenced results (Sain et al., 2002). Cross directionality and the cultivars/accessions used also influenced pollen fertility of the resulting  $F_1$  hybrids, which was diminished compared to the parents (Khosoo, 1955; Singh, 1978; Boyhan, 1994; Sain and Joshi, 2003).

*C. lanatus* has botanically been further divided into *C. lanatus* var. *lanatus* and *C. lanatus* var. *citroides* (citron types) (Robinson and Decker-Walters, 1997), with the majority of the genetic diversity of the species found in the latter (Dane and Lang, 2004; Levi and Thomas, 2005; Dane and Liu, 2007). Diminished pollen fertility, low fruit set, and deviations from expected inheritance ratios have been observed in populations originating from *C. lanatus* intersubspecific crosses (Hawkins et al., 2001; Levi et al., 2004b; Prothro, 2010). However, infraspecific classification within *C. lanatus* is not clearcut and still somewhat controversial. Cross-compatibility and the resulting intersubspecific hybrids, as well as

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the existence of wild, feral, and landrace populations complicate classification. For the sake of this review the distinction within the species will be made simply between sweet (watermelon) and non-sweet (citron) types.

The path to domestication of watermelon is unclear, but it is thought that C. lanatus is native to southern Africa (Bates and Robinson, 1995). Both perennial C. colocynthis and wild citron have been suggested as the ancestors of watermelon (Esquinas-Alcazar and Gulick, 1983; Navot and Zamir, 1987; Robinson and Decker-Walters, 1997; Maynard, 2001; Wehner, 2008; Nimmakayala et al., 2010). A study of chloroplast diversity indicated that the genus showed two clades, one containing C. colocynthis and the other containing the three remaining species. These results are very similar to those obtained using isozymes, which showed two main branches in the genus, one for C. colocynthis and one for C. lanatus and C. ecirrhosus (Navot and Zamir, 1987). At the time of the isozyme study, C. rehmii had not yet been described (De Winter, 1990). Interestingly, the two studies also agree that C. colocynthis is more closely related to C. ecirrhosus than to C. lanatus. Since nearly all the isozyme alleles found in watermelon were also found in citron, the authors concluded that wild citrons were the progenitors of watermelons (Navot and Zamir, 1987). A more recent cpDNA study led Dane and Liu (2007) to suggest that watermelon and citron types evolved independently from perennial *C. ecirrhosus* from Namibia. Although these studies, 20 years apart, disagree about the details, they both agree that southern Africa is the center of origin of *C. lanatus*. However, studies on genome-wide nuclear DNA-based markers have shown that citron is more closely related to *C. colocynthis* than to watermelon (Levi et al., 2001a; Nimmakayala et al., 2010), leaving the true path to domestication of watermelon obscure.

Despite the uncertainty about the exact path to domestication of watermelon, there is no doubt that the *C. lanatus* germplasm from southern Africa is an invaluable source of genetic diversity for the crop. This review will focus on the in situ distribution and ex situ collections of southern African *C. lanatus* germplasm, as well as its utilization in watermelon improvement.

### DISTRIBUTION AND USES OF CITRULLUS LANATUS IN SOUTHERN AFRICA

*C. lanatus* is found throughout southern Africa but is more common in the drier arid and semiarid regions of Botswana, Namibia, South Africa, and Zimbabwe (Fig. 1) where rainfall is below 650 mm annually (Kottek et al., 2006; Mujaju et al., 2010; Mienkie Welman, pers. comm.). For the purpose of this review the term "southern Africa" will refer to Angola, Botswana,



Fig. 1. Köppen–Geiger climate map of southern Africa (modified by Taylor Ladd from Kottek et al. (2006)) indicating the main climates as equatorial, arid, or warm temperature. *C. lanatus* germplasm is most common in the arid regions.

Lesotho, Madagascar, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe. Natural populations usually germinate in the hot months of December or January, depending on rainfall, reaching maturity in late autumn (April–May), and then lasting through the winter months (van Wyk and Gericke, 2000). In southern Africa, the species is found in many forms, including commercial cultivars, landraces, feral, and wild populations (Maggs-Kölling et al., 2000).

Locally, it is common to classify the species according to origin and local uses. The local sweet watermelon landraces are closely related to commercial watermelon (Maggs-Kölling et al., 2000), while citron types are classified as either tsamma—the wild, bland, non-bitter form used as a water source and animal feed; makataan—the large-fruited cultigen used for preserves, pickles, and jams; or bitterboela (karkoer)—the wild, bitter form (Meeuse, 1962; Mienkie Welman, pers. comm.). Non-bitter types are cultivated for both animal feed (cow-melons), and human consumption (edible seeds, flesh, and leaves). The citron fruit and leaves are usually consumed cooked for human consumption, although the flesh can be eaten fresh (Mujaju et al., 2010).

The tsamma is famous as a source of water in the Kalahari Desert for both humans and animals (Knight, 1995; van Wyk and Gericke, 2000). It is probably most famously described by David Livingstone (1872) as "the most surprising plant in the Desert". It is particularly associated with the San people, who are traditional hunter-gatherers in the region. In order to have a reliable water source when traveling across the Kalahari Desert, fruit is collected in a bag made from animal sinew and carried along on the journey (van Wyk and Gericke, 2000). For human consumption one end of the fruit is cut off and the inside turned into a pulp which can be eaten. The fruit can be stored for many months after picking (van Wyk and Gericke, 2000; Mujaju et al., 2010), while the seeds can be roasted and ground into a meal. This meal is also sometimes mixed with saliva and used as a type of "skin-cream" by local women (van Wyk and Gericke, 2000).

The tsamma fruit are also an essential source of water for wildlife in the region. The fruit ripen during the cold, dry months when other water sources are scarce. Rodents are often the first to eat through the hard rind (Fig. 2), which then exposes the flesh to larger animals (Knight, 1995). The fruit are consumed by a wide variety of animals including carnivores, like hyenas, and ungulates, like gemsbok (Knight, 1995).

The large-fruited cooking melon (makataan) is widely cultivated in the region and can be cooked as a kind of porridge to be eaten with corn meal (the local staple), while the cooked leaves are eaten as a vegetable (see van Wyk and Gericke, 2000, for picture). However, it is best known as the source of preserves and a popular jam ("waatlemoenstukkekonfeit") that is made from the thick rind of these fruit. These large-fruited landraces seem to be more homogeneous across regions, and a common ancestry in southern Africa has been suggested (Maggs-Kölling et al., 2000).

The bitter inedible form, "bitterboela", is found throughout the region and can only be identified by tasting the flesh (Livingstone, 1872). The fruits are considered poisonous, but are sometimes consumed by animals, and are used for medicinal purposes, such as a purgative (Mienkie Welman, pers. comm.).

### GERMPLASM COLLECTIONS

As a center of origin for cultivated watermelon, southern Africa is an important source of *C. lanatus* germplasm diversity for the crop. Cultivated watermelon has a very narrow genetic base (Levi et al., 2001b, 2004a), making the availability of this germplasm source that much more important. It is not considered a threatened species in the region and historically there has been little conservation effort. However, as a neglected crop, the Southern African Development Community (SADC) Plant Genetic Resources Centre (SPGRC) and National Plant Resources Centre Regional Network have recently identified it as a priority for conservation (Munyenyembe, 2009; Mujaju et al., 2010).

The C. lanatus collection at SPGRC includes 179 accessions, including 93, 42, and 29 from Botswana, Namibia and South Africa, respectively (Table 1) (Barnabas Kapange, personal communication; Munyenyembe, 2009; SPGRC, 2011). Other data available for the accessions include altitude, longitude, and latitude (presumably of collection sites). However, this collection does not distribute germplasm, and accessions can only be obtained from the individual National Plant Genetic Resource Centers in the different SADC countries (Barnabas Kapange, personal communication). However, the collection is useful to researchers because it gives an indication of the accessions held at the different national collections. It is important to note though that it should not be seen as a complete list of accessions held in southern Africa or as an indication of the availability of such accessions.

The National Botanical Research Institute (NBRI), National Plant Genetic Resources Centre (Namibia) and the Zambia Agriculture Research Institute (ZARI) maintain 89 and 75 entries, respectively (Sonja Loots, personal communication; Mwila et al., 2008). Little information could be obtained about the origin, description and availability of the entries in the ZARI collection, but it is likely to include local varieties/landraces (Mwila et al., 2008). The NBRI collection contains mainly wild accessions collected between 1990 and 2001. Detailed collection site information is available, and information on many local uses such as "cooked with porridge", "seeds roasted, eaten" or "hyena water source" are available (Sonja Loots, pers. comm.). It is likely that there is considerably overlap between the NBRI accessions and the accessions of Namibian origin in the SPGRC collection, but the extent of the overlap could not be readily determined.

The United States Department of Agriculture—Agricultural Research Service (USDA-ARS) germplasm collection (Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, USDA-ARS, Griffin, GA) contains more than 1,800 entries, of which approximately 280 originate from southern Africa, mainly from Zimbabwe (Table 1). The entries in the collection are classified as *C. lanatus* var. *lanatus* or *C. lanatus* var. *citroides*, and a few entries are classified as only *C. lanatus*. The available information for the entries includes disease resistance and



Fig. 2. Wild *C. lanatus* in South Africa (31°22'S, 19°07'E, elevation 720 m) in April 2010. The dry surrounding vegetation, as well as damage from animals, probably porcupines, are visible.

#### Table 1

Germplasm collections containing *C. lanatus* accessions from southern Africa by country of origin and collection, where NBRI: National Botanical Research Institute—National Plant Genetic Resources Centre (Namibia); SPGRC: SADC Plant Genetic Resources Centre, Lusaka, Zambia; ZARI: Zambia Agriculture Research Institute (Zambia); DEU: Genebank, Institute of Plant Genetics and Crop Plant Research, Gatersleben (Germany); ITA: Istituto del Germoplasma, Consiglio Nazionale delle Richerche, Bari (Italy); MSB: Millennium Seed Bank Project—Royal Botanic Gardens (United Kingdom); VIR: N.I. Vavilov Research Institute of Plant Industry. (Russian Federation); UKR: Institute of the Southern Vegetable and Melon Growing (Ukraine), USDA: USDA, ARS Southern Regional PI Station (United States)

Country of	of Local Collections			International Collections						
Origin	NBRI <sup>1</sup>	SPGRC <sup>2</sup>	ZARI <sup>3</sup>	DEU <sup>4</sup>	$ITA^4$	MSB <sup>5</sup>	$VIR^4$	UKR <sup>4</sup>	USDA <sup>6</sup>	
Angola							1	1		
Botswana		93				5	58	4	16	
Lesotho										
Madagascar							2			
Malawi		1								
Mozambique		6					2			
Namibia	89	42				1		2		
South Africa		29		8	1	3	24	3	58	
Swaziland		7						4		
Zambia		1	75					64		
Zimbabwe				1			3	138		
Total	89	179	75	9	1	9	90	7	283	

<sup>1</sup>Sonja Loots, pers. comm.. <sup>2</sup>Barnabas Kapange, pers. comm.; Munyenyembe, 2009; SPGRC, 2011. <sup>3</sup>Mwila et al., 2008. <sup>4</sup>ECPGR Cucurbits Database, 2011. <sup>5</sup>Michiel van Slageren, pers. comm. <sup>6</sup>USDA-ARS, 2011.

morphological observations. Pictures of seed are also available for many entries and a core collection based on morphological data has been assembled (Bob Jarret, pers. comm.).

According to the European Cooperative Programme for Plant Genetic Resources (ECPGR) database (ECPGR Cucurbits Database, 2011), the N.I. Vavilov Research Institute of Plant Industry (VIR; http://www. vir.nw.ru) (Russian Federation) contains a large number of accessions originating from southern Africa (Table 1). The VIR database lists 90 such accessions, including 58 from Botswana and 24 from South Africa (Table 1). The majority of the accessions are wild or represent landraces (http://www.vir.nw.ru; Irina Gashkova, personal communication), and little information other than the year accessions entered the collection is available. The accessions from Botswana were added to the collection in the 1980s, while most of the rest of the collection was acquired earlier. Classifications such as C. lanatus subsp. vulgaris, C. lanatus subsp. capensis and C. lanatus subsp. cordophanus are still common in this database. However, work is currently underway to improve descriptions and passport data of accessions appearing in the ECPGR Cucurbits Database (Díez et al., 2011) and it is hoped that more detailed information will become available in the not too distant future.

Availability of accessions held at these sites for use

in research or plant improvement has been difficult to assess. The accessions held at the USDA collection are generally publicly available, but the availability of accessions at the other relatively large collections such as NBRI and VIR is unclear. Seed of at least some of accessions held at VIR is available for distribution (Irina Gashkova, pers. comm.), but customs limitations render the logistics of actually obtaining seed impractical for most researchers outside of Russia. Together with the lack of detailed passport information and descriptors, it makes using some of the collections to their full potential difficult. However, these challenges are faced by many crop germplasm collections, and with the recent efforts of SPGRC and the ECPGR Cucurbits Database this will no doubt improve in the future.

## GERMPLASM UTILIZATION

Germplasm from southern Africa has been extensively used in watermelon breeding, mainly to improve disease resistance. The accessions in the USDA germplasm collection have been extensively screened for resistance to a wide range of diseases. Sources of resistance to many important diseases have been identified, often in citron types, but also in watermelon (Table 2). In pioneering work on the use of exotic germplasm for disease resistance, Orton (1907) used a citron from

#### Table 2

Disease resistance identified in *C. lanatus* germplasm from southern Africa. Diseases represented are AR–1: anthracnose races 1 and 3; AR–2: anthracnose race 2; BFB: bacterial fruit blotch; FW–1: Fusarium wilt races 0 and 1; FW–2: Fusarium wilt race 2; GSB: gummy stem blight; PM–2W: powdery mildew race 2W; PRSV–W: papaya ringspot virus – watermelon strain; RKN: root knot nematodes; SB: seed blight; SqVYV: squash vein yellowing virus; WMV: watermelon mosaic virus; ZYMV: zucchini yellow mosaic virus

Accession Number	Origin	Infraspecific Classification <sup>1</sup>	Resistance	Source
Africa 8	South Africa	NA	AR-1	Layton, 1937; Parris, 1949
Africa 9	South Africa	NA	AR-1	Layton, 1937; Parris, 1949
Africa 13	South Africa	NA	AR-1	Layton, 1937; Parris, 1949
PI 225557	Zimbabwe	CLL	PM-2W	Tetteh et al., 2010
PI 244017	South Africa	CLC	PRSV–W	Strange et al., 2002
PI 244018	South Africa	CLC	PRSV–W, ZYMV, WMV	Gillaspie and Wright, 1993; Provvidenti and Hampton, 1992; Strange et al., 2002
PI 244019	South Africa	CLC	GSB, PRSV–W, WMV	Gillaspie and Wright, 1993; Gusmini et al., 2005; Strange et al., 2002
PI 248774	Namibia	CLC	AR-1	Levi et al., 2001a; USDA-ARS, 2011
PI 255137	South Africa	CLC	PRSV–W, WMV	Gillaspie and Wright, 1993; Strange et al., 2002
PI 270562	South Africa	CLC	AR-1	Levi et al., 2001a; USDA-ARS, 2011
PI 270563	South Africa	CLC	AR-1	Levi et al., 2001a; USDA-ARS, 2011
PI 271769	South Africa	CLC	FW-2	Dane et al., 1998
PI 271770	South Africa	CLC	RKN	Boyhan et al., 2003
PI 271771	South Africa	CLC	GSB	Gusmini et al., 2005
PI 271775	South Africa	CLC	AR-1	Sowell, 1975; Sowell et al., 1980
PI 271778	South Africa	NA	AR–2, GSB	Sowell, 1975; Sowell and Pointer, 1962b; Winstead et al., 1959
PI 271779	South Africa	CLC	AR-1, AR-2	Levi et al., 2001a; Winstead et al., 1959
PI 295843	South Africa	CLC	BFB	Rhodes et al., 1991
PI 295845	South Africa	CLL	RKN	Boyhan et al., 2003
PI 296332	South Africa	CLL	GSB	Gusmini et al., 2005
PI 296341	South Africa	CLL	FW-0,1,2	Martyn and Netzer, 1991; Netzer and Martyn, 1989
PI 299378	South Africa	CLC	BFB, FW2	Boyhan et al., 2003; Rhodes et al., °1991
PI 299379	South Africa	CLC	AR-1, AR-2	Levi et al., 2001a; USDA–ARS, 2011; Winstead et al., 1959
PI 299563	South Africa	CLL	Melon Aphid	MacCarter and Habech, 1973
PI 459074	Botswana	CLL	PM-2W	Davis et al., 2007
PI 482246	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482252	Zimbabwe	CLC	WMV	GRIN USDA-ARS, 2011
PI 482255	Zimbabwe	CLL	PM-2W	Davis et al., 2007
PI 482259	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482261	Zimbabwe	CLC	ZYMV	Provvidenti, 1991
PI 482266	Zimbabwe	CLL	SqVYV	Kousik et al., 2009
PI 482271	Zimbabwe	CLL	RKN	Boyhan et al., 2003
PI 482273	Zimbabwe	CLC	FW-2	Boyhan et al., 2003
PI 482276	Zimbabwe	CLC	GSB, ZYMV	Guner, 2004; Gusmini et al., 2005
PI 482277	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482282	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482283	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482286	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482288	Zimbabwe	CLL	PM-2W	Tetteh et al., 2010
PI 482298	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482299	Zimbabwe	CLC	FW2, PRSV–W, ZYMV, PM–2W	Boyhan et al., 2003; Provvidenti, 1991; Strange et al., 2002; Tetteh et al., 2010

Accession Number	Origin	Infraspecific Classification <sup>1</sup>	Resistance	Source
PI 482302	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482303	Zimbabwe	CLC	RKN	Thies and Levi, 2007
PI 482307	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482308	Zimbabwe	CLC	FW-2, ZYMV	Boyhan et al., 2003; Provvidenti, 1991
PI 482309	Zimbabwe	CLC	RKN	Boyhan et al., 2003
PI 482311	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482315	Zimbabwe	CLC	PRSV–W	Strange et al., 2002
PI 482318	Zimbabwe	NA	PM-2W, PRSV-W	Strange et al., 2002; Tetteh et al., 2010
PI 482319	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482321	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482322	Zimbabwe	CLC	PM-2W, PRSV-W,	Provvidenti, 1991; Strange et al., 2002;
			ZYMV	Tetteh et al., 2010
PI 482326	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482338	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482341	Zimbabwe	CLL	PM-2W	Tetteh et al., 2010
PI 482342	Zimbabwe	CLC	PRSV–W	Strange et al., 2002
PI 482361	Zimbabwe	CLC	PM-2W	Tetteh et al., 2010
PI 482362	Zimbabwe	CLL	PM-2W	Davis et al., 2007
PI 482377	Zimbabwe	CLL	PM-2W	Tetteh et al., 2010
PI 482379	Zimbabwe	CLC	GSB, PRSV-W	Gusmini et al., 2005; Strange et al., 2002
PI 485580	Botswana	CLC	ZYMV	Guner, 2004
PI 485583	Botswana	CLC	PRSV–W	Strange et al., 2002
PI 494815	Zambia	CLL	RKN	Boyhan et al., 1994
PI 500303	Zambia	CLC	PM-2W	Tetteh et al., 2010
PI 500312	Zambia	CLL	PM-2W	Tetteh et al., 2010
PI 500315	Zambia	CLL	AR-2	Boyhan et al., 1994
PI 500329	Zambia	CLL	AR-2, RKN, PM-2W	Boyhan et al., 1994; Tetteh et al., 2010
PI 500331	Zambia	CLC	PM-2W	Tetteh et al., 2010
PI 500332	Zambia	CLC	PM-2W	Tetteh et al., 2010
PI 500334	Zambia	CLC	GSB	Boyhan et al., 1994
PI 500335	Zambia	CLC	GSB	Boyhan et al., 1994
PI 500354	Zambia	CLC	Broad mites, PM-2W	Kousik et al., 2007; Tetteh et al., 2010
PI 505590	Zambia	CLL	GSB	Boyhan et al., 1994
PI 505592	Zambia	CLL	AR-2	Boyhan et al., 1994
PI 505593	Zambia	CLL	AR-2	Boyhan et al., 1994
PI 526233	Zimbabwe	CLL	GSB	Gusmini et al., 2005
PI 596662	South Africa	CLC	ZYMV	Guner, 2004
PI 596696	South Africa	CLC	PM-2W	Tetteh et al., 2010

Table 2, continued

<sup>1</sup> Infraspecific Classification: CLC-*Citrullus lanatus* var. *citroides*; CLL-*C. lanatus* var. *lanatus*; NA-not available.

Africa to develop 'Conqueror', the first Fusarium wilt (*Fusarium oxysporum* f. sp. *niveum* (E.F. Sm.) Snyd. & Hans.) resistant watermelon cultivar (Orton, 1907; Parris, 1949; Bruton et al., 2007; Wehner, 2008). Although 'Conqueror' was not very successful, it was used to develop other resistant cultivars such as 'Iowa Belle' and 'Iowa King', which had better fruit quality (Wehner, 2008). Porter (1928) also identified selections of "forage melons" from Africa as resistant to Fusarium wilt, but their exact origin is unclear, as is the extent to which they were used in watermelon breeding. More

recently, plant introduction (PI) 296341 from South Africa has been shown to be resistant to races 0, 1, and 2 of Fusarium wilt (Table 2) (Netzer and Martyn, 1989; Martyn and Netzer, 1991). Although the majority of diploid (seeded) watermelon cultivars grown in the US are now resistant to race 1, researchers have continued to search for additional sources of resistance to race 2. To that end, Boyhan et al. (2003) and Dane et al. (1998) have identified new race 2-resistant accessions, including PI 271769, PI 299378, PI 482273, PI 482299, and PI 482308 from southern Africa.

In addition to Fusarium wilt, anthracnose (caused by Colletotrichum orbiculare (Berk. & Mont.) Arx) also received a lot of attention by early watermelon breeders. In the early 1900s, Duke Layton at the USDA received three edible and two inedible anthracnose-resistant sources from South Africa (Parris, 1949). The edible types would later be called Africa 8, Africa 9, and Africa 13 (Parris, 1949) and are the source of the dominant resistance to anthracnose races 1 and 3, later named Ar-1 (Layton, 1937; Guner and Wehner, 2004). Africa 8 has been used extensively to develop anthracnose-resistant cultivars and is part of the pedigree of cultivars like 'Crimson Sweet', 'Charleston Gray', and 'Jubilee' (Wehner, 2002). Other sources of resistance to anthracnose races 1 and 3 that originated from southern Africa are PI 248774, PI 270562, PI 270563, and PI 271775 (Table 2) (Levi et al., 2001a; USDA-ARS, 2011). Resistance to anthracnose race 2, controlled by the Ar-2gene, has been identified in PI 271775, PI 271778, PI 271779, and PI 299379 (Winstead et al., 1959; Guner and Wehner, 2004), and additional sources were identified in PI 500315, PI 500329, PI 505592, and PI 505593 by Boyhan et al. (1994).

Virus resistance seems to be common in citron germplasm from the region, and various sources have been identified (Table 2). Resistance to watermelon mosaic virus (WMV) was observed in PI 244018, PI 244019, PI 255137, and PI 482252 (Gillaspie and Wright, 1993; Levi et al., 2001a; USDA-ARS, 2011), and in fact, the first three also have resistance to another potyvirus, papaya ringspot virus-watermelon strain (PRSV-W) (Provvidenti and Hampton, 1992; Strange et al., 2002). Other sources of PRSV-W resistance from southern Africa are PI 244017, PI 482318, PI 482342, PI 482299, PI 482315, PI 482322, PI 482379, and PI 485583 (Strange et al., 2002). Recessive resistance (zym-FL) to the Florida strain of zucchini yellow mosaic virus (ZYMV-FL) was identified in PI 482322, PI 482299, PI 482261, and PI 482308 (Provvidenti, 1991), with additional sources found in PI 244018, PI 482276, PI 485580, and PI 596662 (Guner, 2004; Provvidenti and Hampton, 1992).

Gummy stem blight (GSB), a fungal disease caused by *Didymella bryoniae* (Fuckel) Rehm, is a serious limiting disease in the southeastern US, and resistance to this disease in cultivated watermelon has proven elusive. Resistance to GSB has been described in PI 271778, PI 244019, PI 271771, PI 482276, PI 482379, PI 500334, PI 500335, PI 296332, PI 505590, and PI 526233 (Table 2) (Sowell and Pointer, 1962; Sowell, 1975; Boyhan et al., 1994; Gusmini et al., 2005). PI 271778 was used as the male parent in a cross with 'Jubilee' to produce 'AU-Jubilant' (Norton et al., 1986). Resistance in PI 271778 was thought to be a single recessive gene *db*, but 'AU-Jubilant' was less resistant than PI 271778, suggesting that more genes are involved (Norton, 1979; Gusmini, 2005). Currently there are no commercial watermelon cultivars with high levels of resistance to GSB.

Other diseases and pests for which resistance has been found in southern African germplasm (Table 2) are squash vein yellowing virus (Kousik et al., 2009), powdery mildew race 2W (*Podosphaera xanthii* (Castagne) Braun & Shishkoff) (Tetteh et al., 2010), root-knot nematodes (Boyhan et al., 2003; Thies and Levi, 2007), bacterial fruit blotch (Rhodes et al., 1991), broad mites (Kousik et al., 2007), and melon aphids (MacCarter and Habech, 1973).

Several accessions showing resistance to a number of diseases (Table 2) are, most notably, PI 244018, PI 244019, PI 482299, PI 482322, and PI 500329. It is important to note that resistance is more common in an accession that has been botanically classified as *C. lanatus* var. *citroides* (Table 2), although it is unclear whether this is a true representation of the distribution of resistance, or is due to sampling bias. Nevertheless, it is an important point to note due to the fertility issues and deviations from expected inheritance ratios observed in populations originating from *C. lanatus* intersubspecific crosses (Hawkins et al., 2001; Levi et al., 2004b; Prothro, 2010).

In addition to disease resistance, the southern African germplasm is a potential source of drought resistance. This was recognized more than 100 years ago when a botanist from the Cape colony (current South Africa) sent tsamma germplasm to Arizona and California for testing under dry, hot conditions (Kennedy, 1900). It was reported that the plants grew well under drought conditions and were readily eaten by livestock (except pigs), but it is unclear whether these were ever used in breeding programs. Recent research on drought tolerance in wild C. lanatus from Botswana (No101117-1) has shown that not only do these plants use their root system for water storage, but the plants also extend their root systems in response to drought (Larcher, 1995; Yoshimura et al., 2008). In domesticated watermelon cultivars, root growth is suppressed at the onset of drought, but in the wild accession, vigorous root growth follows the onset of drought (Yoshimura et al., 2008). The mechanisms involved in this drought tolerance are a continuing and exciting research field contributing to our understanding of abiotic stresses in plants (Kawasaki et al., 2000; Akashi et al., 2005; Takahara et al., 2005; Kohzuma et al., 2009; Kajikawa et al., 2010). In addition, genes for cool temperature resistance (Ctr) from PI 482261 (Provvidenti, 1992) and seedling leaf variegation (slv) in PI 482261 (Provvidenti, 1994) have also been described.

C. lanatus germplasm from southern Africa has also been used extensively to construct genetic maps and, to a lesser extent, to find quantitative trait loci (QTL) associated with important horticultural traits. A wild citron from southern Africa, designated SA-1, was used to construct linkage maps of watermelon and to map QTL linked to rind characteristics, red flesh color, and flesh sugar content (Hashizume et al., 1996, 2003). The Fusarium wilt-resistant PI 296341 from South Africa, as well as Griffin 14113 from Namibia, have also been used as parents in developing mapping populations (Hawkins et al., 2001; Levi et al., 2002, 2004b; Zhang et al., 2004). PI 296341 was also used to identify NBS-LRR gene anolgues in watermelon (Harris et al., 2009). PI 244019 was the male parent of an intersubspecific population used to produce a single nucleotide polymorphism (SNP) genetic map for C. lanatus. OTL associated with several traits, including fruit size, sugar content, seed size, and flower type were identified in this population (Prothro, 2010).

While the USDA-ARS germplasm collection has been used extensively, some other collections such as VIR and those from the SADC countries seem to be severely underutilized, at least in a search of published scientific literature. The accessions held at these collections are yet untapped sources of genetic variation that are essential for the continued improvement of cultivated watermelon worldwide.

As one of the centers of origin of C. *lanatus*, southern Africa is an invaluable source of diversity for the species. Like many domesticated crops, cultivated watermelon has a narrow genetic base, making it prone to biotic and abiotic stresses. The germplasm from southern Africa has proved to be a rich source of resistance/ tolerance to these stresses, underlining the importance of conservation of germplasm from this region.

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