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The story of coffee: legend and truth

A.J. Muñoz-Pajares [1,2,3,4,*], Vitor Várzea [2,5,6] and Maria do Céu Silva [2,5,6]

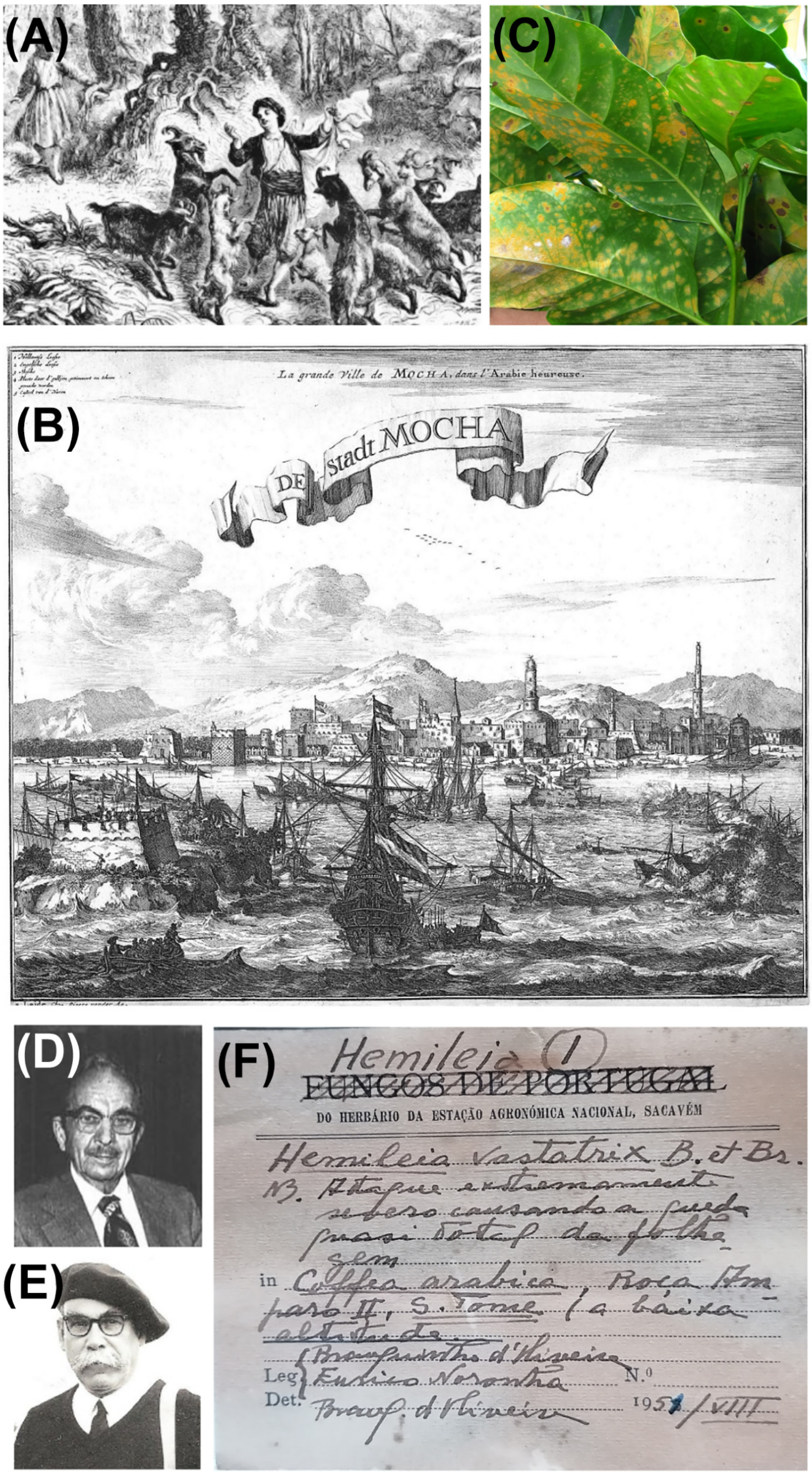
When we think about coffee, exotic tropical countries such as Colombia, Brazil, and Ethiopia first come to mind. However, the crucial contribution of Portugal and its scientists to each cup of coffee we drink remains either poorly known or overlooked.

Coffee is the staple drink for millions of people who cannot imagine life without it. Coffee plants belong to the genus *Coffea* which includes over 100 species, but only two, *C. arabica L.* (Arabica) and *C. canephora* Pierre ex A. Froehner (Robusta), are commercially used for the production of coffee as a beverage. Coffee produced by *C. arabica* has lower caffeine content and less bitterness, and is considered to be of higher quality. Despite producing a lower-quality coffee, *C. canephora* plants show higher genetic diversity and are more resistant to adverse conditions such as high temperatures, drought, and pathogen challenge. The *C. arabica* plant is native to the highlands of East Africa and can be traced back to the ancient coffee forests (late 13th or early 14th century) on the Ethiopian plateau. Nevertheless, we do not know its exact origins, or when or how the consumption of coffee was discovered. One legend claims that the first person who discovered the effects of caffeine was Kaldi, a goat herder from Abyssinia (nowadays Ethiopia). Kaldi realized that his goats became frenetic after eating the red berries of certain shrubs. Curious about that effect, he tried some of the fruits and suddenly felt full of energy (Figure 1A). The young goat herder shared his discovery with a local Sufi monk who, according to some versions of the story, also felt immediately invigorated after trying the fruits. According to other versions, the monk rejected Kaldi's berries and threw them into a fire. A few minutes later, a delicious smell came from the ember, and the monk recovered the roasted beans, ground them up, and put the resulting powder into boiling water. The taste of this beverage delighted the monk. According to both versions, the monk was able to stay awake during the religious services of that night much more easily than usual. Soon the use of a beverage prepared by boiling coffee's red berries in water was generalized in Sufi monasteries [1]. Coffee seeds spread along trade and pilgrimage routes in the early 15th century to Yemen and further across the Arabian Peninsula, where the first plants were grown for local consumption. That is why, despite its African origin, the species was named *arabica*.

By the 16th century, coffee was a popular beverage in Egypt, Persia, Syria, and Turkey. Coffee houses emerged across the Middle East, East Africa, and eventually across Europe after initial controversies. Muslim religious authorities (briefly) banned coffee consumption, arguing similarities between the effects of coffee and alcohol consumption. Several Christian authorities also called coffee 'the Satan's Drink', and condemned or banned coffee consumption in Europe. According to another legend, this changed when Pope Clement VIII gave his papal approval to coffee consumption in Europe because, being 'so delicious, it would be a pity to let the infidels have its exclusive use. We shall fool Satan by baptizing it, and making it a truly Christian beverage'. For centuries, coffee was exported in roasted or baked form, and only the Yemenis could grow it (Figure 1B). According to Indian tradition, the pilgrim Baba Budan introduced coffee cultivation into southern India after bringing seven raw beans from the port of Mocha (Yemen) while coming back from pilgrimage. In 1616 a coffee plant was successfully transported from Mocha to Holland (The Netherlands) and by 1850 European powers had established plantations in many areas under their control to keep authority over the highly profitable coffee trade (www.gutenberg.org/cache/epub/28500/pg28500-images.html) (Figure 2).

In 1861, somewhere close to Lake Victoria (Eastern Africa), a British explorer reported unhealthy wild coffee plants showing leaves with yellow-orange colored round spots, and coffee leaf rust (CLR) was discovered (Figure 1C). In 1869, the disease (nicknamed 'devastating Emily' by local farmers) was dramatically affecting coffee production in Sri Lanka (formerly Ceylon). The analysis of infected coffee leaves resulted in the identification of a fungus named *Hemileia vastatrix* as the causal agent of CLR. In Sri Lanka, CLR reduced coffee production by 75%, leading most farmers to cultivate other crops (mainly tea) instead of coffee. Between 1890 and 1900, CLR completely collapsed Sri Lanka's coffee industry, impacting its economy and society (Figure 1D), and expanded to most of the coffee-growing countries in Asia. Between 1920 and 1950, the fungus also infected plantations in the African continent. CLR was first detected in Brazil in 1971 and dispersed progressively across the coffee plantations of other Latin American countries. It was reported for the first time in Hawaii in 2020. Nowadays, CLR is present in all coffee-growing regions [2–5] (Figure 2).

To prevent the dramatic socioeconomic impact of the coffee industry collapse in other countries (particularly in South America), the Governments of the USA and Portugal created the Coffee Rust Research Center (Centro de Investigação das Ferrugens do Cafeeiro, CIFC) in 1955 (Figure 1E). The CIFC was established in Lisbon because continental Portugal was



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not a coffee growing country (thus minimizing risks associated with accidental release of the fungus), but several Portuguese colonies (e.g., Angola, East Timor, São Tomé, and Principe) were coffee producers (thus maximizing connections between research and plantations). Since its foundation, the CIFC has played a central role creating an International Research Network of over 40 coffee-growing countries on CLR, aiming to assist these countries in developing varieties resistant to this disease.

CIFC researchers developed protocols to inoculate coffee leaves with *H. vastatrix* isolates from different origins (Figure 1F) and to monitor the result of the infection. They found that some plants were naturally resistant to particular fungus isolates that were able to infect other plants. That is, different plants may vary in the symptoms they show when infected using the same fungus. Similarly, different fungi also may show differences in their abilities to infect the same plant. The work carried out at CIFC led to the characterization of more than 55 rust races and about 50 coffee physiological groups of resistance (27 of them were used as coffee differentials of rust races), as well as nine 'resistance factors' (named S_H1–S_H9). To date, the genetic basis has been described only for S_{H3} [5].

In 1927, a vigorous plant apparently not affected by rust was found in Ermera (East Timor) among plants of *C. arabica* var. Typica that had been devastated by CLR. This plant showed a phenotype intermediate between *C. arabica* and *C. canephora*, and was considered a natural hybrid between these two species, being designated Timor Hybrid ('Híbrido de Timor', HDT). From 1957, seeds from its derivatives were submitted to the CIFC for resistance characterization. Some of these plants were found to be resistant to all the rust races known at that time, but showed extremely low fruit production.

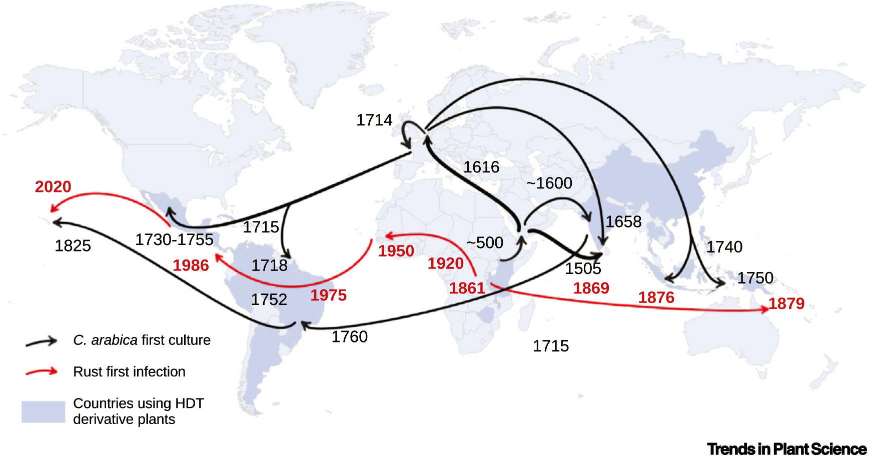

Figure 2. A simplified representation of the propagation of coffee plants (black) and coffee leaf rust (red). The main coffee-growing regions where Timor hybrid (HDT) derivatives have been cultivated are represented in blue. For further details see www.gutenberg.org/cache/epub/28500/pg28500-images.html.

However, pollen from these HDT derivatives was successfully used to perform controlled crosses with different *C. arabica* varieties to yield fruit-productive progeny with rust resistance. After several generations, this breeding scheme produced resistant plants that were provided free of charge to all the coffee-growing countries (Figure 2). As a result, almost 99% of the current rust-resistant Arabica coffee varieties worldwide derive from the landmark CIFC studies based on the HDT [5].

Unfortunately, over the past 20 years some of these varieties have become susceptible in some growing countries due to the emergence of more virulent *H. vastatrix* races able to overcome the SH factors [6]. This loss of resistance has been attributed (among other factors) to mutation and other natural processes of variability in the fungus genome, and erosion of the genetic background of resistance in the selection process associated with poor monitoring of the virulence of local rust races [5–7]. Pathogen ability to overcome HDT S_H factors is confirmed by the fact that rust samples recently received from East Timor (where the majority of coffee plantations are HDT derivatives of the original plant) correspond to the most virulent characterized so far at the CIFC.

Currently, the most common strategy to control CLR is by application of massive antifungal treatments. Due to the economic cost and environmental impact associated with this strategy, several alternative approaches are being developed to control CLR, but most of them show poor performance when tested in field conditions [8]. Modern genomic approaches can provide a new opportunity to explore plants' natural resistance by allowing the in-depth characterization of its genomic basis. Several authors are using genomics to identify candidate genes to CLR resistance in HDT derivatives [9] as well as in other related species [10]. The fact that the S_H3 (the most durable resistance factor [11]) originated after an introgression with *C. liberica* highlights both the importance of characterizing resistance genes also in wild coffee relatives and the critical consequences of losing such species, as 75% of them are currently threatened [12]. The description of new sources of resistance may help to control rust expansions by gene pyramiding – that is, the accumulation of multiple resistance genes in a single variety – as it is more difficult for the pathogen to overcome multiple resistance genes [13].

The HDT plant and its derivatives have played a key role in breeding programs and coffee production worldwide, but many open questions remain regarding its natural resistance. In fact, HDT-derived varieties also show very high resistance to other pathogens such as the fungus *Colletotrichum kahawae*, the nematode *Meloidogyne exigua*, and the bacterium *Pseudomonas syringae* pv. *garcae.* The application of genomics to HDT derivatives,

Figure 1. (A) The legendary discovery of the coffee drink by Kaldi and his goats, attributed to 'a modern French artist' (www.gutenberg.org/cache/epub/28500/pg28500-images.html). (B) Roasted coffee beans were exported worldwide from the port of Mocha (Yemen) for two centuries, this city becoming an important trade center as shown in this 1680 drawing of the city of Mocha ('De stadt Mocha' *KB Den Haag, KW shelfmark, foliation*). (C) Coffee leaf rust (CLR) symptoms and signs: chlorotic spots and uredosporic sori on the lower leaves surface. The infected leaves drop, resulting in a reduction in the rate of photosynthesis, affecting coffee yield and even plant growth and survival. (D) Professor Frederick Lovejoy Wellman (1897–1994), an American plant pathologist who described the social impact of coffee leaf rust in Sri Lanka as follows: 'plantations were abandoned, laborers were left to go back to savagery and disease, political turmoil followed; there were world shaking economic losses, families were destroyed, and men killed each other as well as committing suicide' [14]. Picture credits: Frederick Lovejoy Wellman, 1897–1994, E. Echandi, The American Phytopathological Society, doi.org/10.1094/Phyto-84-1385. (E) Professor António Branquinho D'Oliveira (1904–1983), founder and director of the Coffee Rust Research Center (CIFC) between 1955 and 1973. Since its foundation, the CIFC has been assisting the coffee-growing countries in solving the CLR problem by characterizing the regional variability of the pathogen and supporting national breeding programs to develop resistant varieties, offering opportunities for environmentally and economically sustainable coffee production. Furthermore, the CIFC has contributed considerably to the training of pathologists and breeders from many coffee-growing countries. (F) Voucher register of the first isolate of *Hemileia vastatrix* received by the CIFC. Today, the CIFC has valuable collections of several hundred coffee plants and isolates of *H. vastatrix* from different geographic origins. These collections, unique in the world, are a key resource for supporting breeding programs to develop resistant varieties to CLR in different coffee-growing countries.

wild coffee species, and natural hybrids may ensure the sustainable and ecological production of coffee, the second most popular drink after water.

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Declaration of interests

No interests are declared.

[1]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal
[2]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
[3]Departamento de Genética, Universidad de Granada, Campus Fuentenueva, 18071 Granada, Spain
[4]Research Unit Modeling Nature, Universidad de Granada, Granada, Spain
[5]CIFC – Centro de Investigação das Ferrugens do Cafeeiro, Instituto Superior de Agronomia, Universidade de Lisboa, Quinta do Marquês, 2784-505 Oeiras, Portugal
[6]LEAF – Linking Landscape, Environment, Agriculture and Food, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisboa, Portugal

*Correspondence:
ajesusmp@ugr.es (A.J. Muñoz-Pajares).

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