

Center for Coffee Research and Education, CCRE
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The Origin and Environmental Conditions for Arabica Coffee
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1. Origin of Arabica Coffee (*Coffea arabica*) and the Center of Genetic Diversity of the Species

--The Birth of the Arabica

In a unique event, occurring during a long-ago night—or maybe during the day?—natural hybridization occurred between the two diploid species *Coffea canephora* and *Coffea eugenioides* to create the *Coffea arabica* species, an allotetraploid that would integrate both parental genomes.

This event took place between 10,000 and 20,000 years ago. All the plants and groups of Arabica coffee have been derived from this single individual (Scalabrin S., Toniutti L, *et al.* 2020), resulting in Arabica coffee being the least genetically diverse species in the world among the principal commercial crops.



Coffea eugenioides

X



Coffea canephora



Coffea arabica

Although it will be discussed later, it is worth noting the importance that *C. canephora* (Robusta) has had beyond its genetic contribution to the formation of *C. arabica* (Arabica). The serious damage caused by coffee rust in the Arabica coffee plantations in Asia between 1869 and 1900, particularly in Ceylon (now Sri Lanka), put the spotlight on Robusta coffee due to its resistance to and tolerance of this disease. The share of Robusta coffee in the worldwide production and consumption of coffee went from practically 0% then, to 40% today with a growing trend.

--Center of Genetic Diversity, Germplasm of the Center of Origin

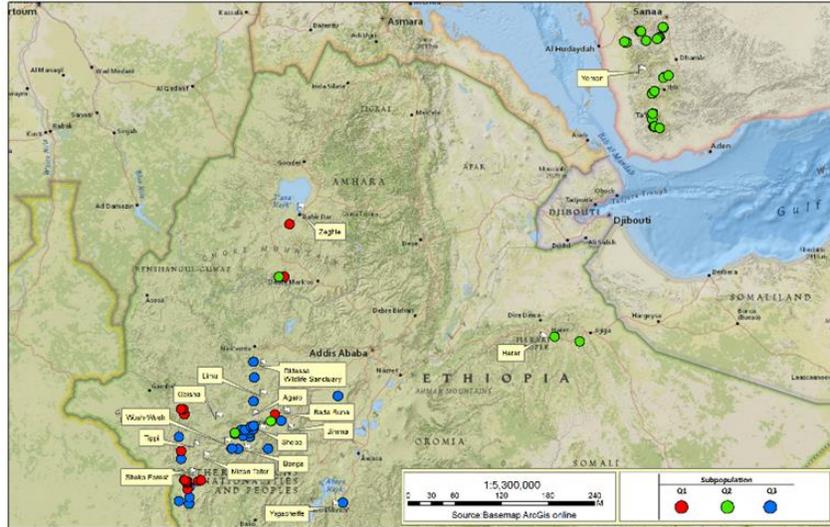
The center of origin and genetic diversity of Arabica coffee is recognized as corresponding to the current territories of southwest Ethiopia primarily, southern Sudan, and northern Kenya. Two important prospectings or collections of seeds from different coffee plantations were carried out in the southwest of Ethiopia by the FAO in 1964–1965 (FAO, 1968) and by the French Institute ORSTOM in 1966 (Guillaumet, J.L., Halle, F. 1978). These materials are found in different collections around the world, and one of them is the CATIE public collection in Costa Rica.

A group of investigators performed a genetic analysis based on the germplasm of these prospects present in the CATIE collection. The results allowed the establishment of the classification of three main groups (Scalabrin S., Toniutti L, *et al.* 2020).

The results revealed the genetic differentiation between two “wild” Ethiopian populations and the cultivated Harar-Yemen population. The structure of the three populations was well supported by the background geographic information in the reports on the FAO 1964–65 and ORSTOM 1966 surveys.

The investigators propose a structure for genetic diversity of the species based on three populations that include:

- primarily cultivated genotypes from Yemen, East Africa, and India in the Harar-Yemen population (G2, green circles);
- “wild” Ethiopian and local varieties in the Jimma-Bonga population (G1A, blue circles); and
- primarily “wild” Ethiopian genotypes in the Sheka population (G1B, red circles).



Map of Ethiopia with the three wild genetic groups of Arabica coffee

The authors proposed naming the G2 population “the Harar-Yemen group,” as it includes the Ethiopian germplasm of the eastern region, the surroundings of the city of Harar, and all Yemeni varieties.

All accessions collected around Jimma on the sites of Agaro, Bonga, the Didessa Wildlife Sanctuary, Shebe, Gera, and Wush-Wush were assigned to the G1A population. Some accessions that were located naturally farther east through the Rift Valley in the Sidamo region (Yirga Cheffe) were also grouped into G1A. Therefore, this population includes germplasm dispersed across a vast region around Jimma, bordered to the north by the Didessa Wildlife Sanctuary, and to the south by Maji, Shebe, Bonga, Wush-Wush and the Bonga forest. They propose calling this population “Jimma-Bonga.”

The G1B population included all accessions from the Sheka forest, 91% of the accessions collected from Mizan-Teferi, and 92% of those collected from Teppi, around an area of tropical forest that is located approximately 200 km west of the city of Jimma. Therefore, they propose calling this population “Sheka.”

They also classified individuals within the three populations according to the category of plant material assigned by the FAO and ORSTOM reports. At the time of the prospecting, botanists classified 92% of the Harar-Yemen (Q2) population, 15% of the Jimma-Bonga (Q3) population, and no accession of the Sheka (Q1) population as “intensive planting.” Up to 63% of the Sheka population and 27% of the Jimma-Bonga population had been previously classified as accessions of coffee from the forest.

Studies conducted in Latin America and Cameroon showed the existence of incomplete resistance to rust in some plants of Ethiopian origin (Eskes, 1983; Gil *et al.*, 1990), and resistance to *Meloidogyne* spp. nematode populations in other studies (Anzueto *et al.*, 1991).

Geisha It also highlights the collection by the English on the Geisha mountain in southwestern Ethiopia, very likely in 1931. The seeds were collected in bulk from different trees, then exported

to the Kitale Center, Kenya, with the names Abisinia and Geisha. From Kenya, material was taken to the stations of Kawanda in Uganda in 1936, and Lyamungu in Tanzania. The first introduction the CATIE received (under code T-2722) was in July 1953, reported as a progeny of the VC-496 tree from Lyamungu. Seeds were then distributed to different Latin American countries, including Panama, where the exceptional quality of Geisha coffee was valued.

Rume Sudan There are materials that are equally important from other prospects, such as Thomas's (1942) in southeastern Sudan, which allowed the discovery of the Rume Sudan and Barbuk Sudan varieties.

--Genetic Resources Collected

The CATIE collection maintains approximately 800 wild accessions collected at their places of origin, such as ET-47, ET-61, Rume Sudan, and Wush-Wush, and "historical" varieties from East Africa, such as SL-28 and SL-34.



CATIE collection, Ethiopia-FAO section

Among the objectives of the collection is to use the genetic diversity present as a working basis for the genetic improvement program, and to supply genetic material intended for research or development programs.



General view of the CATIE coffee collection

--A Gift from an Asian Island to the World: the Timor Hybrid

The Timor Hybrid is a material derived from the natural crossing between Robusta coffee (*C. canephora*) and Arabica coffee, which received the genes of resistance to rust from the Robusta progenitor, which is called “introgression,” and which in biology means the movement of genes from one species to another as a result of an interspecific hybridization process, followed by recurring retrocrossings of the hybrids with the parents and vice versa. The introgression can be natural as in the case of the Timor Hybrid, or an “assisted introgression” performed by a person.

This material was identified around 1917 on the island of East Timor and labeled as a rust-resistant Arabica coffee. This population became commercially cultivated in Timor in the 1940s, replacing the susceptible local varieties. It is accepted that the Timor Hybrid population was mostly formed from a single plant existing in an Arabica coffee plantation. The subsequent populations were made up of more advanced progenies, probably with several retrocrossings with the traditional variety of Arabica coffee cultivated on that island (Bettencourt, A.J., 1973).

Several of the Timor Hybrid plants were later used for hybridizations with Caturra, Villa Sarchí and Catuaí to create commercial, rust-resistant varieties, and in this way achieve the “assisted introgression” of the resistance genes originally from Robusta coffee on the island of Timor.

--The Stages of Genetic Improvement of Arabica Coffee

Bertrand (2017) proposes a graphic diagram to explain the four stages of genetic improvement of Arabica coffee, which we have modified by adding the germplasm of the center of origin, as a Stage 0, considering that several wild accessions have been used as progenitors for the creation of F1 hybrids.

- **Stage 0:** Germplasm of the center of origin (mentioned above)
- **Stage 1:** Historic populations of mass selection in Asia, Africa, and Latin America SL-28 in Kenya; Java in Cameroon, Kent and S-288 in India; N-39 in Tanzania; Geisha in East Africa; Bourbon and Typica in Latin America, Blue Mountain (Typica) in Jamaica.

- **Stage 2:** Varieties of the “Green Revolution” by pedigree selection, 1960–1980, Caturra and Catuaí.
- **Stage 3:** Introgressed varieties Use of the introgression of genes from Robusta through the Timor Hybrid for rust resistance, 1960–2010 Catimores, Sarchimores, Colombia and Castillo varieties, Cavimores, other retrocrossings.
- **Stage 4:** F1 hybrid varieties. Use of wild accessions for crossings with commercial varieties such as Sarchimor, Catuai, and Caturra to create F1 Hybrids, with the purpose of integrating vigor, resistance to rust and other pests, better adaptation, and cup quality.

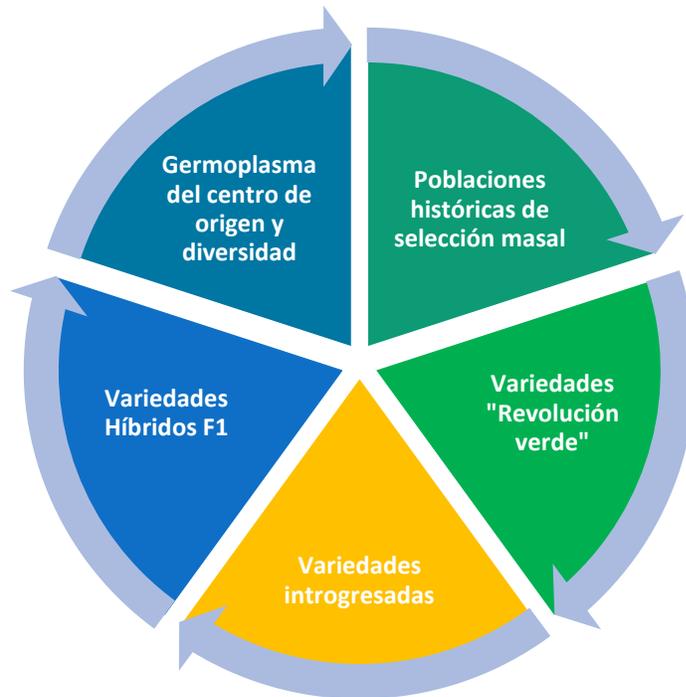


Diagram of the main stages of genetic improvement of Arabica coffee.

We recommend adding a discussion on the development of rust-resistant varieties (introgressed). The introduction of rust-resistant offspring to Mesoamerica was carried out since the 80s through the Programa Cooperativo Regional para el Desarrollo Tecnológico y Modernización de la Caficultura (Regional Cooperative Program for the Technological Development and Modernization of Coffee Cultivation), PROMECAFE, (Echeverri and Fernández, 1989), and through bilateral agreements between the Centro Internacional das Ferrugens do Cafeeiro (International Center for Coffee Rust) (CIFC) of Portugal and institutions in Mexico and El Salvador, followed by local selection processes over several generations, by studying their adaptation and production, and then proceeding to release certain varieties in the 1990s. Despite the imminent rust threat, most countries continued to cultivate traditional and improved traditional varieties to renew old coffee plantations. The use of resistant varieties in general remained low-scale in most Latin American countries, with the exception of Colombia and Honduras, which promoted renewal programs with resistant varieties.

The narrow genetic base of the main varieties of Arabica coffee cultivated in Latin America is widely known because of the history of its origin and introduction (Bertrand, *et al.* 1999). We specifically refer to the Typica and Bourbon varieties, and then to the varieties derived from them via natural mutation, cross-pollination, and hybridizations: Caturra, Pacas, Villa Sarchí, Catuaí, Pacamara, and others.

None of these varieties is resistant to the primary races of rust, which was already known and was evident since the disease arrived on the Latin American continent, when low-intensity attacks and some epidemic stages were observed in certain territories. However, the susceptibility of these varieties would be clearly evident decades later, extensively in most coffee-growing countries in Latin America, compared to the epidemic behavior of rust as of 2012 (Avelino, *et al.* 2015).



The impact of rust on susceptible coffee plants

The primary impact of the rust epidemic was made evident by the decrease in Arabica coffee production in Latin American countries, combined with the following factors:

- predominance of the cultivation of susceptible varieties;
- climatic conditions adverse to the crop and favorable to the disease;
- low international coffee prices; and consequently,
- little investment in maintenance of the plantations.

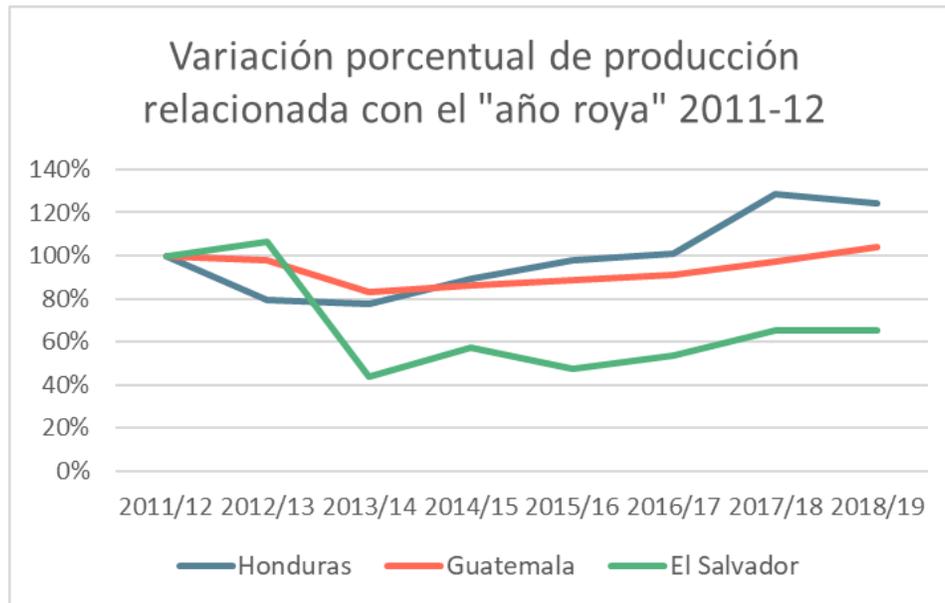
The first country affected by the recent rust epidemic was Colombia in 2008–2011, despite the fact that it already had resistant varieties in a majority of the area. At that time, climatic conditions influenced by the La Niña climate event prevailed in that country.

A few years later, starting in 2012, the Mesoamerican and Caribbean countries followed, under warmer weather conditions, less rainfall, and irregular periods of rainfall distribution (Avelino *et al.* 2015).

The chart shows the variations in percentage of production in Honduras, Guatemala, and El Salvador related to 2011–12 before being the impact of rust.

The cumulative production losses of these three countries for the 5 years following the epidemic were 7.5 million 60-kilo sacks of gold coffee (9.8 million 46-kilo sacks). These decreases in

production would correspond to 840 million USD, which individually have had a strong impact on producers' incomes and their families' standard of living.



Percentage variation of production in Honduras, Guatemala, and El Salvador vs 2011–12

Source: ICO, <http://www.ico.org/>

Honduras was the country that showed a faster recovery after the rust epidemic. The majority of its area was already cultivated with resistant varieties, following the guidelines of a national renewal and reactivation policy for its coffee cultivation.

After this rust epidemic period began, the impact of the disease was evident on most farms, where strong defoliation, falling fruit, and fruits that did not complete their maturation were observed. The recovery of the farm was a slow process because the impact continued over the following years in variable periods depending on the producers' investment capacity and the climate.

Field observations indicated that the greatest impacts on susceptible varieties corresponded to aging plantations of the Typica and Bourbon varieties, with little or no fertilization. Caturra and Catuaí plantations with little management were also affected significantly, although relatively less than the aforementioned.

It is important to indicate that a new race of rust can attack a certain resistant variety in a region or country, making this variety susceptible to the new race.

The case of the Lempira variety was recently discovered in Honduras, where, through observations and studies conducted by IHCAFE, the presence of a new race of rust affecting Lempira plantations was confirmed (Avelino and Anzueto, 2020).

The genetic load of resistant varieties is variable and generally not well known at the end of the selection processes. Susceptibility to a new race of rust may be due to having fewer resistance genes.

It is acknowledged that the vertical or complete resistance corresponding to most of the resistant varieties (derived from the Timor Hybrid) is a resistance that is not long-lasting, and that these resistant varieties would gradually be affected by new races of rust, but they would still be expected to present some levels of partial resistance or tolerance.

It is difficult to predict when new races of rust will overcome vertical resistance, and in which varieties first, but this situation should not limit the use of these varieties that have other important characteristics, such as vegetative vigor and high productivity, and some of them also have excellent cup quality.

2. The Arabica Coffee Climate and Ecological Conditions

--Overview

Climate affects the coffee plant and the soil directly and indirectly, mainly through rain, wind, temperature, relative humidity, and hours of light.

Temperature is the primary climatic factor that defines a region's suitability for the commercial cultivation of coffee, in other words, where it could thrive. For Arabica coffee, the ideal range of suitability is an average annual temperature between 19 and 22 degrees centigrade (°C), and a normal range of suitability is between 18 and 23°C. Regions that have annual average temperatures below 18°C and above 23°C are considered as not suitable.

In Central America, the driest coffee-producing regions get approximately 1200–1400 millimeters of rainfall in normal years. Years with deficient rainfall and very long periods of midsummer heat have a negative effect on coffee production. These conditions are usually accompanied by higher temperatures, with a marked negative impact on plant development and production.

In recent years, environmental changes have occurred, characterized by increased temperatures, variability in rainfall, and longer drought periods, which have a negative effect on production.

Coffee crops grow well with a minimum of 1200–1300 mm of adequately distributed annual rainfall. However, the water requirement of coffee varies, depending on the different stages of vegetative development. Hence, for example, during and after harvesting, the coffee plants require less humidity, so the lack of rainfall will not have a negative effect on their development.

--Development of the Plant

A period of one and one-half months to two months of water stress is necessary after the differentiation of the flower buds for an abundant flowering to take place. Toward the end of this period of moderate water stress, with the stimulus of a rainfall of 8–10 mm, the flowers will open between 8 and 15 days after the rain. After flowering, the conditions of temperature and availability of rainwater will affect the bonding of the flower, and development of the fruit and bean.

High environmental temperatures and lack of water at certain times during fruit and bean growth can affect their normal development.

If the lack of water continues after flower buds start forming, and, in addition, there are maximum daily temperatures too high for the coffee plant, around 32°C or more for several consecutive days, then flower abortion can occur, and in extreme situations, the flower atrophy known as “star flower” can occur, where the flower does not develop normally, and is then unable to form and produce fruit

The first critical stage is between the 45th and 80th days, with the risk of a “purge” of green fruit and affecting the size of the bean of the first blooms.

The second critical stage occurs approximately between 80 and 120 days after flowering, which is when the bean is “filled” and the fruits have high demand for carbohydrates. Under conditions of high temperatures and/or water deficit in the aforementioned stage, transporting carbohydrates to the fruits would be restricted, causing the formation of “black beans,” and in the most extreme cases, the abortion of milky beans, which the Brazilians call “black heart.”

--Cupping Quality

Higher temperatures can also cause forced maturity of the fruits, which will look like they reached complete maturity, but the beans would be partially immature to a greater or lesser degree, which can affect the expression of cup quality with variable assessments of roughness.

In the quality monitoring carried out by ANACAFÉ (Guatemala) in the 2014–15 harvest, a greater frequency of coffee samples with a rough or slightly rough cupping quality was detected, even in batches harvested at the optimal maturity point and with well-conducted wet fruit-to-bean and drying processes. In the case of the Chiquimula and Zacapa departments, the rate of rough cupping defect was 37% (Neighborhoods, 2015). Based on data from the weather station in Olopa, Chiquimula, the average temperature for 2014–15 was observed to be the highest in the 5 years analyzed, and there was also less rain in 2014–15. It was concluded that the increase in the rough cupping percentage was significantly influenced by the predominant climatic conditions of high temperature and less rainfall.

In recent years, the phenolic or astringent cupping problem that could be attributed to forced maturity has also been mentioned. This can be brought on under conditions of high fruit load, insufficient fertilization, and high temperatures during the maturity phase. A phenolic or astringent taste is typical of immature coffee beans where there is an excess of phenolic compounds, especially certain types of chlorogenic acids that normally disappear or are reduced during a normal maturity.

--Behavior of Diseases and Pests

Coffee producers have observed variations in climate behavior with increases in environmental temperature, as well as in the quantity and distribution of rainfall, which, in addition to affecting production, fosters the increase of some diseases and pests. As an example, although the factors responsible for the coffee rust epidemic of the years 2011–12 in Central America are not fully understood, there are strong indications that it would be a combination of economic and climatic conditions, such as those responsible for the phytosanitary crisis, since in 2012 there were higher temperatures and changes in the distribution of rainfall that could have enabled the rust epidemic. The progression of this disease in coffee plants is associated with the combination of climatic

conditions, the coffee plant, and rust. The climatic factors favorable for the disease are temperatures between 20°C and 25°C and moisture in the leaves for the germination of fungus spores or seeds. This is brought on by frequent rainy conditions, nighttime dew, and very shady environments.

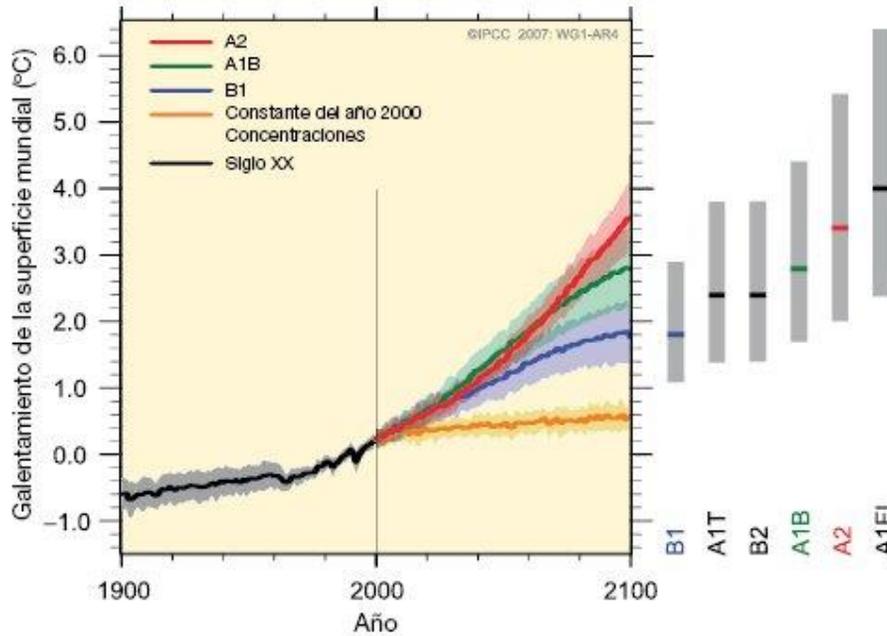
--Changes in Areas Suitable for Arabica Coffee

Intergovernmental Panel on Climate Change (IPCC): according to the IPCC, human influence on the climate system is clear. The warming observed from 1850–1900 to 1986–2005 is 0.61°C (IPCC, 2014).

Five integrative reasons for concern provide a framework for summarizing key risks in the various sectors and regions. Indicated for the first time in the Third IPCC Assessment Report, the reasons for concern show the consequences of warming, as well as adaptation limits for people, economies, and ecosystems. All temperatures are expressed as a change in the mean global temperature in relation to the (“recent”) 1986–2005 period:

- i. Unique and threatened systems: The number of such systems at risk of serious consequences is greater in the event of additional heating of about 1°C.
- ii. Extreme weather events: The risks linked to climate change derived from extreme episodes, such as heat waves, extreme precipitation, and coastal floods.
- iii. Distribution of impacts: The risks are distributed unevenly and are generally greater for the disadvantaged people and communities of the countries, regardless of their level of development.
- iv. Global aggregate impacts: The risks of aggregate impacts at the global level are moderate for additional warming, between 1 and 2°C, reflecting both the impacts on the biodiversity of the Earth as well as on the overall global economy (medium confidence level). The risk of widespread loss of biodiversity with the related destruction of ecosystem goods and services is high in the event of an additional warming of about 3°C (high confidence level). Aggregate economic damage is accelerated by the increase in temperature (limited evidence, high agreement level), but there are few quantitative estimates completed for additional warming of about 3°C or more.
- v. Large-scale, singular events: With an increase in warming, some physical systems or ecosystems can become at risk of abrupt and irreversible changes. The risks associated with these critical points become moderate with additional warming of between 0 and 1°C. The risks increase disproportionately as warming rises between 1 and 2°C and exceeds 3°C.

In the following graph, the solid lines represent the mean global warming temperatures obtained with multiple models (with respect to 1980–1999) for scenarios A2, A1B and B1 shown as a continuation of the simulations of the 20th century.



For the next two decades, a warm-up of about 0.2°C per decade is projected for a range of emission scenarios. Even if the concentrations of all greenhouse gases and aerosols had remained constant at the levels of the year 2000, a subsequent warming of approximately 0.1°C per decade could be expected.

If greenhouse gas emissions are maintained at the current rate or at a higher rate, they would cause greater warming and trigger many changes in the global climate system during the 21st century, which would most likely surpass those observed during the 20th century

--Centro Internacional de Agricultura Tropical (International Center for Tropical Agriculture, CIAT):

Various studies, including those of the CIAT, have shown that climate change will affect climatic suitability for Arabica coffee (*Coffea arabica*) within the current production regions (Ovalle-Rivera *et al.*, 2018). Increases in temperature and changes in precipitation patterns will decrease yield, reduce quality, and increase the pressure of pests and diseases.

CIAT: More recently, the CIAT developed a gradient for the impact of climate change on coffee production. The gradient is a specific evaluation of coffee from the results of the projected climate impact for this crop, which shows the most likely degree of adaptation effort necessary in potential future climate scenarios.

This is the first worldwide study of the impact of climate change on the suitability of growing Arabica coffee, modeling the global distribution of Arabica coffee under changes in climatic suitability for the 2050s, as projected by 21 models of global circulation. The results suggest a decrease in the areas suitable for Arabica coffee in Mesoamerica at lower altitudes. At the global level, they predict decreases in climatic suitability at lower altitudes and high latitudes, which can change production among the main regions that produce Arabica coffee (Bunn *et al.*, 2019).

References

1. Anzueto, F., Eskes, A.B., Sarah, J.L., Decazy, B., 1991. Recherche de la resistance á Meloidogyne sp. Dans une collection de Coffea arabica. In: 14 Coloquio Científico Internacional sobre el café. San Francisco, EE. UU., 14-19 de julio, 1991. Vevey, Suiza, ASIC. p. 534-543.
2. Avelino J., Cristancho M; Georgiou S; Imbach, P, Aguilar L., Bornemann G, Läderach P, Anzueto F, Hruska A, & Morales C. 2015. The coffee rust crises in Colombia and Central America (2008–2013): Impacts, plausible causes and proposed solutions. This article is published with open access at Pringerlink.com.
3. Avelino, J., Anzueto, F. 2020. Coffee Rust Epidemics in Central America: Chronicle of a Resistance Breakdown Following the Great Epidemics of 2012 and 2013. In: Emerging Plant Diseases and Global Food Security, Section II: Ecology, Epidemiology, and Population Biology of Emerging Plant Diseases. J. B. Ristaino and A. Records, eds. The American Phytopathological Society. ISBN : 978-0-89054-638-3.
4. Bertrand, B., Aguilar, G., Santacreo, R., Anzueto, F., 1999. El mejoramiento genético en América Central. In: Bertrand, B., Rapidel, B. (Eds.), Desafíos de la caficultura en Centroamérica. IICA, San José, pp. 407-456.
5. Bertrand, B. 2017. El Mejoramiento Genético de Coffea arabica en Centroamérica. Presentación, 37 láminas, color.
6. Bettencourt, A.J., 1973. Considerações sobre o Híbrido de Timor. In: Campinas, I.A.C. (Ed.).
7. Bunn, C; Lundy, M; Castro-Llanos, F. 2019. Climate Change Impacts on Coffee Production in Mexico and Central America. International Center for Tropical Agriculture (CIAT), Cali, Colombia. 24p. <https://hdl.handle.net/10568/104019>
8. Echeverri, J., Fernández C., 1989. The PROMECAFE program for Central America. In: Coffee rust: epidemiology, resistance and management. Ed. by A.C. Kussalappa and A.B. Eskes. Boca Ratón, Florida, U.S. ISBN 0-8493-6899-5. 337 p.
9. Eskes, A.B. 1983. Incomplete resistance to coffee leaf rust (Hemileia vastatrix). Tesis de doctorado. Universidad de Agricultura, Wageningen, Países Bajos. 140 p.
10. FAO, 1968. FAO Coffee mission to Ethiopia 1964-1965. Informe de recolección. Roma, Italia, FAO. 200 p.
11. Gil, S.L., Berry, D., Bieysse, D. 1990. Recherche sur la résistance incomplète á Hemileia vastatrix Berk et Br. Dans un groupe de génotypes de Coffea arabica L. d'origine éthiopienne. Café-Cacao-Thé 34(2) : 105-133.
12. Guillaumet, J.L., Halle, F. 1978. Echantillonnage du materiel récolté en Ethiopie. Bulletin I.F.C.C. 14: 13-18.
13. IPCC, 2014: Cambio climático 2014: Impactos, adaptación y vulnerabilidad. Resúmenes, preguntas frecuentes y recuadros multicapítulos. (Climate Change 2014: Impacts, Adaptation, and Vulnerability. Summaries, FAQs, and Multichapter-Boxes.) Contribution of Working Group II to the Fifth Evaluation Report of the Intergovernmental Group of Experts on Climate Change (Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White [eds.]) World Meteorological Organization, Geneva (Switzerland), 200 pages.
14. Ovalle-Rivera O, Läderach P, Bunn C, Obersteiner M, Schroth G. (2015). Projected Shifts in Coffea arabica Suitability among Major Global Producing Regions Due to Climate Change. PLoS ONE 10(4): e0124155.

15. Scalabrin S, Toniutti L, Di Gaspero G, Scaglione D, Magris G, Vidotto M, Pinosio S, Cattonaro F, Magni F, Jurman I, Cerutti M, Suggi Liverani F, Navarini L, Del Terra L, Pellegrino G, Ruosi MR, Vitulo N, Valle G, Pallavicini A, Graziosi G, Klein PE, Bentley N, Murray S, Solano W, Hakimi AA, Schilling T, Montagnon C, Morgante M & Bertrand B. 2020. A single polyploidization event at the origin of the tetraploid genome of *Coffea arabica* is responsible for the extremely low genetic variation in wild and cultivated germplasm. *Scientific Reports* (2020) 10:4642 <https://doi.org/10.1038/s41598-020-61216-71>.
16. Thomas, A.S. 1942. The wild Arabica coffee on the Boma Plateau of Anglo-Egyptian Sudan. *Empire Journal of Experimental Agriculture* 10: 207-212.