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Re-Creating *Coffea arabica*: The Perspective

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Researchers predict the possible extinction[1] of Arabica coffee (*Coffea arabica* L.) in the wild by about 2080 on the basis of climate changes that include the rising temperatures, decreasing rainfall, increased incidence of pests and diseases and declining growth and productivity of the plants. Climatic changes may also lead to the unsuitability of the present producing areas to grow Arabica coffee that is also predicted by many studies[2,3,4,7]. Another important aspect of these predictions is the narrow genetic base of the commercial coffee plant varieties and even the limited genetic variability in the wild Arabica[5,63]. However, the two old coffee varieties, *Typica* and *Bourbon* have shown a large capability of adaptation in the various climatic zones (now termed as Bean Belt) into which they were introduced by the Colonial powers[6]. Most of the modern varieties in cultivation are derived from these original varieties through breeding efforts that increased their adaptation in the growing areas as reflected in increasing yield over many years. In the light of these facts the predicted extinction appears to be more alarmist than real. There are a few other points of paradox also in the various research papers. Many papers speak of increasing temperatures that started in the 1960s[4,7]. But we have seen increased production and price declines leading to price crises that led to the breakdown of International Coffee Agreement in 1989. In spite of these paradoxes, climate change is real and it is likely to have an impact on the coffee plant and its productivity. If we anticipate the worst, then it is possible that wild Arabica coffee may become extinct as predicted and adaptation of coffee plant in the producing areas may also become poor. Thus, plans have to be made for sustaining the coffee supply chain and its many dependents. In this paper, a perspective on re-creating *Coffea arabica* is presented to mitigate the possible extinction of this species and continuation of cultivation of coffee in the current growing areas also in the future.

Why should we re-create Arabica?

From the foregoing introduction, we understand that there are two possible contexts which prompt the need to create alternatives to Arabica coffee plant. The first is possible extinction of *Coffea arabica* and the second is reduced adaptation of existing varieties of this

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species in the many producing areas of the world reducing the yields. Apart from these two contexts, coffee production, processing and marketing (the supply chain) supports the livelihoods of millions of people and re-creating an equivalent of Arabica coffee is very important for sustaining that context also.

The first context leads to a loss of the original genes and variability of *C. arabica* present in the genetic resources in the centre of origin and diversity (Ethiopia)[8,9,10,11,12] that have not been utilized in breeding or cultivation, so far. It is estimated that only a small fraction of the genetic variability of this species is utilized[1]. Even so, the utility of many other germplasm collected in Ethiopia appears to be limited in the light of their lower adaptation in coffee producing areas of the world as reflected in their survival and/or productivity or even quality[13]. The original Ethiopian Arabicas like Cioccie, Agaro, Geisha, Yirgalem etc. have fallen susceptible to the leaf rust disease in the Indian coffee growing areas and did not become popular with the growers. Thus, the Ethiopian Arabica germplasm may be important in the context of the coffee industry of Ethiopia and its neighboring countries and may not be as important as it is projected to be for the many other coffee producing countries. The many hybrids created in breeding efforts have proven to be adequate not only to increase productivity, but also to improve quality through various agronomic and processing practices[13,14]. In this context, creating new interspecific hybrids and integrating them in Arabica coffee breeding may prove itself to be important in increasing the genetic plasticity of Arabica and consequent adaptability in the various producing areas[15,16]. Some of these interspecific hybrids may even become possible replacements for the existing varieties of Arabica coffee in the future.

A point to be remembered is that the extinction of only wild *C. arabica* is predicted and it can be surviving in the many habitats into which it was introduced. Thus, Ethiopia should cooperate with all coffee growing countries in the efforts to conserve as much of the their original Arabica germplasm as possible in the gene banks maintained in different countries within the provisions of the Rio Summit on mutually agreed terms[17,72].

The second context is reduced adaptability of the various varieties under cultivation in the areas of their cultivation on account of climate change[2,3,4,7]. Climate change is a hot subject debated on many platforms and there are a number of studies that documented the climate change related behavioral changes in pests and diseases of coffee[18,19,20]. Even though this subject has come to be very prominent in the recent past, evolutionary biologists recognized that environment change is an all time phenomenon[21] that led to the extinction of major groups of organisms in the evolutionary past. Even the emergence of Arabica coffee was linked to such events of Pleistocene[22,23]. Thus, this element has to be factored into any breeding program that is designed for creating materials which are expected to be useful for long periods of time. Even the predicted climate changes are expected to render some of the current growing areas unsuitable but make some other areas suitable for growing coffee. Thus, the many cultivated varieties of coffee developed in the past century are not totally useless.

Many studies in this context are focused on Meso-America and Latin America, but did not touch up on emerging new producer-consumers like China[68,69]. These studies indicated that the areas suitable for cultivating Arabica coffee and even Robusta coffee may get reduced by 80% by the year 2050 on the basis of changed behavior of pollinating bees that is conditioned by the changes in climate. However, these studies indicate a reduced species richness of bees and not their total absence in the areas currently suitable for coffee. Thus, if the new materials are resilient to climatic changes, the available pollinators may still find them attractive. So, the materials to be created should have a wide-ranging adaptability across the environments in which coffee is currently grown, but the parents for such a breeding effort should come from the areas with high temperature and low rainfall and frequent droughts. These efforts may be supplemented and augmented by adding new tetraploid (amphidiploid) germplasm that can be created through interspecific hybridization of diploid species native to the areas of current and future suitability for Arabica coffee cultivation.

Another important aspect of coffee genetics is the gene conversion in the interspecific hybrids of diploid species and possibly in the various tetraploid Arabicoid hybrids[70,71]. This is implicated in the evolution of quality[13] in Arabica coffee and also in the possible loss of resistance[50] in the cultivated Arabica coffee hybrids. There is considerable evidence that quality is not negatively affected in these hybrids as discussed later in this paper. But, there is no evidence for the recovery of resistance that was lost. Hence, search for new sources of resistance is an eternal quest. In coffee, this is mainly focused on genes imparting resistance to leaf rust. This is very important, because leaf rust infestation leads to defoliation that predisposes the plants to other diseases and particularly, the deadly pest white stem borer[50].

How do we re-create Arabica?

The idea of re-creating Arabica coffee was floated first by the World Coffee Research that proposed the re-creation of this species by hybridizing the putative evolutionary parent species *C. eugenioides* and *C. canephora* involving many plants of these species carrying as much genetic diversity as possible[5]. Underlying this proposal was the idea that original Arabica coffee plant was born in a single hybridization event between single individuals of the two progenitor species. This effort is expected to create an equivalent of *C. arabica* with much more genetic diversity and thus more resilient to climatic changes. Thus, efforts to re-create Arabica should be based on the sound knowledge of genetics and evolution of this species. Two important points were made in the context of possible extinction of Arabica coffee and its re-creation. First is to evolve pest and disease resistant coffee varieties whose cultivation will be benign to the environment with much lower use of agrochemicals. However, there is no further elaboration on how this is to be achieved for a changing climate. The second point made is that knowledge of genetics is available for only two of the more than 100 species of *Coffea*. These two points bring out the perceived large gap in our knowledge and the filling of this gap may lead to greater sustainability of cultivating coffee in the future and even the survival of Arabica coffee through climatic changes. This paper makes an attempt to put together, the knowledge on genetics of the various species of *Coffea* and the possible ways of creating new germplasm that will help not only breeding new strains of Arabica but also creating possible new equivalents of this species that may survive the climate changes.

While extensive knowledge of genetics of the commercially important species *C. arabica* and *C. canephora* is available, considerable knowledge of the genetics of several other species of *Coffea* is also available and can be used to generate a plan of action for the re-creation of a novel equivalent of Arabica coffee plant. Most of this knowledge is generated through conventional genetic approaches and this paper also envisages that conventional methods be used in creating Arabica coffee anew.

The commercially most important *C. arabica* is the only tetraploid (2n=4x=44) species of the genus *Coffea* while almost all other species including *C. canephora* (Robusta) are diploid (2n=2x=22)[24,25,26]. Also, *C. arabica* is the only self-compatible species and all diploids are self-incompatible. There is a large body of information on the origin of Arabica coffee through interspecific hybridization of *C. eugenioides* and *C. canephora* or closely related sub-species of these two[22,27,28]. Other studies suggest that *C. liberica* or *C. congensis* could have been involved in this event[29,30]. All studies agree that *C. eugenioides* is the possible female progenitor. The other species are considered possible male progenitor. One study proposed that *C. arabica* is a compilospecies that might have inherited genes from several closely related species[6].

Knowledge of reproductive relationship of *C. arabica* with other species of *Coffea* is important as this was exploited in the various breeding efforts. As already mentioned *C. arabica* is the only self-compatible species producing seed up on self-pollination. This self-compatibility is an outcome of the interspecific hybridization and subsequent doubling of chromosomes that involves faithful and complete duplication of all genes carried on the chromosomes of the contributing diploid species, including those governing the self-incompatibility. Such a phenomenon was really observed in an amphiploid of the diploid *Coffea* species *C. liberica* and *C. eugenioides* in India[10,31,60]. This amphiploid was named as *Ligenioides*, combining the specific epithets of the two parent species[32]. This amphiploid is self-compatible, crosses well with several varieties of *C. arabica* to give rise to fertile hybrids that manifest genetic segregations characteristic of Arabica coffee[61] and is considered a source of new genes for breeding new varieties of Arabica coffee. Similar neutralization of self-incompatibility was reported in other plant systems also[65,66].

Even though Arabica is self-compatible, floral structure of this species is the same as in the diploid species of *Coffea*. This conservation of floral structure was accompanied by another important feature generally found in the diploid species of *Coffea*, i.e. the ability to cross with related species to produce fertile or moderately fertile hybrids that was exploited to introduce new genes into *C. arabica*. In the breeding efforts of the past one century disease resistance genes were introduced into *C. arabica* through the natural interspecific hybrids like S.26, S.333 (carrying S_H3 gene of *C. liberica*) and Hibrido de Timor (carrying the $S_H6,7,8,9$ of *C. canephora*)[54]. Crossing of *C. arabica* with the diploid species *C. canephora*, *C. congensis*, *C. excelsa*, *C. liberica*, *C. eugenioides* and *C. racemosa* to produce moderately fertile hybrids that can form a bridge to further transfer the genes of diploid species to Arabica by appropriate breeding methods was documented in coffee literature[50]. These diploid species are known to be carrying the genes for resistance to important adversaries like leaf rust, coffee berry disease, nematodes, stem borers, leaf miners, berry borers, drought and possibly others[64]. Thus, using these genetic resources in developing improved Arabica varieties is indispensable. These species come from diverse ecosystems of the mainland of Africa and their hybrids are expected to manifest adaptability to a wide range of environments and the possible changes of climate. This capability of Arabica to assimilate genes from many related species is the basis of the proposition that it could be a compilospecies.

As mentioned above, the diploid species of *Coffea* cross naturally[33] to produce moderately fertile hybrds and this aspect is very important for re-creating *C. arabica*. There are studies that determined the crossing relationships among diploid species[31,34,35] and between diploids and the tetraploid Arabica[36,37]. On the basis of these studies, coffee gene pool was divided into three major sections in the context of breeding Arabica[38]. The different genotypes of Arabica and the Arabicoid interspecific hybrids, which are all tetraploid, readily cross with Arabica and their genes can be transferred to *C. arabica* by simple crossing and selection in the progenies and constitute the primary gene pool. The many species capable of crossing with Arabica to give rise to moderately fertile hybrids constitute the secondary gene pool that contributed genes for all earlier coffee breeding exercises. The third group of species does not directly cross with Arabica, but can cross with the species of the secondary gene pool to produce hybrids that can be used as bridge genotypes to transfer genes to Arabica. This comprises the tertiary gene pool. In fact, the whole gene pool of the genus *Coffea* was considered a vast genetic continuum on account of the free flow of genes between the apparently different species[67]. From this discourse, it can be seen that genes from all diploid species of *Coffea* can be transferred to *C. arabica*. However, the transfer of genes to *C. arabica* from the secondary and tertiary gene pools demands special knowledge and skills of genetics.

From the foregoing discussion it is clear that interspecific hybrids between different diploid species of *Coffea* can be produced with relative ease. These interspecific hybrids are fairly or moderately fertile, depending on the genetic relationship between the parent species. It is possible to double the chromosomes of these allodiploids by colchicine treatment that is expected to improve their fertility. In the efforts to re-create *C. arabica*, it is proposed to produce as many of such tetraploid interspecific hybrids involving as many species as possible and allow them to interbreed. This is proposed on the basis of the possible scenario of events that led to the emergence of *C. arabica* in the Pleistocene[6,23]. Interbreeding of these tetraploid interspecific hybrids may produce very diverse progenies from which Arabica-like plants can be selected and perpetuated and represent the re-created *C. arabica*.

At this point of time, it is important to understand the possible events of Pleistocene that might have promoted the emergence of *C. arabica*. The origin of *C. arabica* was considered to have taken place in the Pleistocene period of the Quaternary[22], a time when agriculture has not yet begun. Thus, any hybridization events were spontaneous and survival of the hybrid species was solely through positive Natural Selection. Early thinking on the origin of *C. arabica* suggested that *C. eugenioides*[10,29,30,34,35,39,40,41] could be the female progenitor of Arabica as already mentioned. The male progenitor was variously thought to be *C. canephora*[34,39,40,41], *C. congensis*[30,40], *C. liberica*[10,26,41] *C. dewevrei*[10,42,43], *C. racemosa*[44] or *C. kapakata*[45] by different investigators on the basis of certain characters observed in *C. arabica* and chromosome behavior at meiosis in the hybrids. If these perceptions were considered to be true, we have to visualize a scenario of these species coexisting in a population that might have got separated from the centre of origin and diversity of *Coffea* in a remote area (probably, present equatorial Africa) and found itself in a hostile and inhospitable climate. This could have been a consequence of one of the glaciation events of Pleistocene. That probably triggered a new evolutionary trend through inter species hybridization and spontaneous tetraploidization[6,23]. Even in this case, assuming a single hybridization event between single plants of any two species severely restricts the diversity that a species needs to survive so many millennia of time in an environment that has been undergoing change constantly[21]. Our present knowledge of the family Rubiaceae and the species *C. arabica* indicates that the family probably originated in the Eocene period[46] and *C. arabica* in the Pleistocene (late Pleistocene or early Holocene?)[22]. This means that the species has survived, at the least, 12000 years or more up to about 2.5 million years. This survival demands that the organism should carry adequate genetic diversity and plasticity to adapt to the contemporary and changing climatic conditions. Its solo existence in Ethiopian highlands and Boma Plateau of Sudan, its wide adaptation in the various locations of introduction and its capability to accept genes from the related species suggest that it could be a compilospecies[6,23]. This means that re-creating it should involve more than two species.

Considering the climate of Quaternary that is also called the Ice Age[47], large areas of the earth were covered by glaciers in the Pleistocene, the first epoch of the Quaternary. These ice sheets started melting with increasing temperatures towards the later part of that epoch and the glaciation events were linked to the origin of Arabica coffee during this period[22]. Considering its wild existence in the upper montane forests of Ethiopia, a plausible assumption is that the nascent allotetraploids were adapted to a climate that was the colder even at that time. Thus, if we wish to re-create Arabica from the same progenitor species, we should also have a similar climate for its adaptation. This scenario appears to be a very difficult one to create. Over the several millennia of Quaternary, some of the other species of *Coffea* that could have also participated in the origin of *C. arabica* found adaptation in much harsher climates. Some of these species were found to be crossable with *C. arabica* and were used in its improvement. There is also considerable understanding of the crossability relationships among the species of *Coffea*. There were reports of spontaneous hybridization between species giving birth to Arabicoids with introgressed genes from some of these species and even a case of allopolyploidy. All these natural hybrids and the allopolyploid were used in improving Arabica for disease and pest resistance[48,49,50]. An important point is that all of them were created in the contemporary climate of the recent past and all of them closely resemble Arabica in their morphology. Thus, thoughts on re-creating Arabica may have to be re-oriented to include the many species of the diploid gene pool that manifest considerable resistance to the many adversaries of Arabica coffee in the current climate. This leads to the creation of a gene pyramid[62] that helps the new arrival to resist the adversaries for a considerably long time.

Why should we include the other species that were known to produce beans that give a poor quality beverage? What are the genetic implications for quality and adaptation?

In the context of these questions, I would like to address the matter of adaptation first. The events of Pleistocene that led to the first appearance of *C. arabica* and its survival until now would have included resistance to the contemporary pests and diseases in all likelihood as this determines the fitness to survive[51]. That resistance has seen the species through the so many centuries that it has been existing before its discovery by man and his manipulations to produce it on a commercial scale. The pests and diseases that infest the various varieties of Arabica coffee, now-a-days is attributed to the lower genetic diversity in the gene pool of cultivated Arabica initially[52] and this observation got extended to the wild forms also in a recent study of the germplasm collections maintained in Costa Rica as mentioned in an internet story[5]. One limitation of this germplasm study could be that the explorers who collected these materials depended primarily on the morphological characters and the genetic diversity of collections may be very low in the modern context of molecular biology. Sampling of the early collections also would have been random. Thus, this could be a profound reflection of the Founder effect. Also, it is possible that the disease and pest organisms evolved into forms that can overcome the innate resistance of all original Arabicas. Some of the modern hybrids carrying the introgressed genes from diploid species are manifesting resistance to some of the disease and pest adversaries and promise to be of value in cultivation[52,53,54]. Considering these facts, it may be pragmatic to think of re-creating *C. arabica* by involving different diploid species carrying resistance to nematodes, leaf miners, stem borers and the diseases like leaf rust, berry disease and bacterial blight. A basic concept for creating novel allotetraploid germplasm to be used in Arabica coffee breeding was posted on the internet[15]. In the present scenario of pest and disease infestation[55,56], re-creating *C. arabica* from such diverse allotetraploids makes better sense than the suggested path of hybridizing only *C. canephora* and *C. eugenioides*.

The question of coffee quality has been debated for many decades. The intrinsic elements that condition the taste and flavour of the consumed beverage are described as fair average quality and can be realized in most of the coffee produced anywhere in the world. Our concern in the context of possible extinction of the coffee plant should be in preserving the coffee plants that can produce beans with this basic quality standard. The early period coffee tasters were of the belief that the best quality is realized from the Arabica coffee plants whose breeding history does not involve any diploid species. But then, dealing with adversaries like coffee leaf rust, coffee berry disease and stem borers and leaf miners made it necessary to involve the diploid species like *C. canephora* (Robusta), *C. liberica*, *C. racemosa* and others in evolving Arabica coffee varieties with resistance to them. Beverage quality of these varieties was considered inferior to that of pure Arabicas for a considerable time. Even so, consumers all over the world accepted the quality of beverage derived from the beans of these varieties[13,57,58]. However, literature of the more recent times indicates that some of these hybrids are not simply good but better in quality over the conventional Arabica in beverage quality[59]. All these facts suggest that basic beverage quality does not suffer because of introducing genes from other *Coffea* species into *C. arabica*. On the other hand, it seems to improve. A natural allotetraploid derived by spontaneous doubling of chromosomes in a hybrid of *C. liberica* and *C. eugenioides* also produced beverage of good quality indicating that tetraploidy may be at the root of Arabica's quality. Genetic basis of such beverage quality characters was well explained in literature[13]. These aspects have to be seriously considered when we propose to re-create Arabica.

On the whole, re-creating Arabica coffee is important but requires to internalize many aspects as narrated above to evolve a new species (shall we call it *C. arabica*?) that can effectively replace the old *C. arabica* and survive for, at least, another 15000 years or more to sustain the lives of all those who depend on the coffee supply chain.

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