within the juicy red flesh of the commercial strawberry lies a deep history that spans at least three continents and hundreds of thousands of years. The genetic heritage of this prized dessert fruit was crafted by nature, with its modern improvement driven by the indigenous Mapuche people of South America, a seafaring a French spy, and a plant-loving teenager that gathered fruits to present to a king. The many stories that punctuate the history of the modern strawberry relate to its contemporary cultivation and genetic potential for future production. The complete genetic storybook of the commercial strawberry has remained a secret to researchers, until now. Compared to other economically important plant species, commercial strawberry was slow to garner molecular attention, with only 58 small and mostly mis-annotated DNA sequences present in public databases in 2003. Bits and pieces were gathered through the next few years, with a genome of a simple diploid *Fragaria vesca* strawberry eventually published in 2011. At the time it represented the 12th plant genome sequenced, and the first to be sequenced and assembled using solely short-read technology. The commercial strawberry is octoploid, and some genome sequence has been reported by several groups that used a variety of short read technologies and genetic strategies to derive substantial, yet incomplete coverage and assembly. These avenues of progress set the table for the eventual publication of the octoploid strawberry sequence in February of 2019. The team obtained the 813.4 Mb cultivated commercial strawberry sequence from the California cultivar “Camarosa” and it reveals the reticulate roots of a curious species. The cultivated strawberry is known scientifically as *Fragaria × ananassa*, with the “×” reminding us that it is a hybrid borne of a human-facilitated, blind-date sexual connection between two distantly related New World species, *Fragaria virginiana* (from North America) and *Fragaria chiloensis* (from South America). The genomes of these two octoploid species contain the genetic artifacts of interspecies hybridization ferried forward likely because of the fitness of the resulting natural hybrid. The genetic evidence of connections across time and space reside in every single cell. This information has now been used to unravel strawberry’s complicated history, understand its current biology, and design molecular tools to speed future improvement.

**Unwinding the past**

While the modern strawberry’s chromosome collection is genomics complex, its fundamental genome is one of the simplest among crop plants. The strawberry of commerce is octoploid (2n = 8x = 56; seven chromosome sets and eight chromosomes per set, 56 total), meaning that each cell contains remnants of four separate ancestral diploid subgenomes that underlie strawberry’s form and function. Examination of the origins of these four subgenomic complements began early in the 20th century, with study of meiotic pairing, suggesting that an ancestor of the extant diploid species *F. vesca* was a contributor to the octoploid genome. Small hints of the identity of other subgenome donors came from genetic analyses and various reconstructions, along with some molecular and cytological data that provided critical clues. Several of these avenues suggested that an ancestor of *F. iinumae* was at least one of the other subgenome donors.

As pointed out by Edger et al., the genome is an allopolyploid, arising from multiple rounds of gametic nonreductions and cross pollination events.
resulting subgenomes continue to behave as separate blueprints interpreted simultaneously to define the assembly and function of a common complex structure. The multiple-blueprint problem has hampered simple genetic analyses, as if a locus was mapped in a diploid genome, it may reside in any, or all, of the subgenomes that comprise the modern octoploid strawberry. To make matters worse, strawberry is highly heterozygous, making it difficult to distinguish between homoeologous and paralogous gene copies.

The recently published “Camarosa” sequence strengthened the evidence identifying the other genomic constituents in commercial strawberry. The work agrees with earlier findings that F. iinumae and F. vesca are closest descendants to two of the four subgenome donors. But there is great diversity within F. vesca, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere. The authors were able to narrow down the subspecies to F. brachetata, a species that covers the northern hemisphere.
resistance genes have been characterized in strawberry, and they may represent new tools for molecular marker development that will allow breeders to coalesce multiple resistance genes into a single genetic background. Such advances would go a long way to increasing sustainable production of strawberry.

The genome also provides an anchor to tie in years of functional data obtained by transgenic or transient-expression analyses. The molecular basis for traits in strawberry have mostly been identified using these techniques, yet few of these published reports describe natural sources of genetic variation that can be exploited by breeders. Selection of eQTL-based markers may help translate an existing body of molecular work into widely applicable markers that can hasten variety improvement. In addition, an octoploid genome sequence offers an obvious advance towards defining gene editing targets that are specific to a desired single locus. The octoploid genome sequence is also a starting point to dissect functional aspects of variety-specific attributes, and enables new approaches such as capture-based sequencing.

Finally, the octoploid genome represents a crucial first step in developing the strawberry pan-genome—it will serve as the reference for the compendium of octoploid genomes that matter throughout the world. Cultivars and advanced selections from many breeding programs now can be examined with the meaningful molecular scrutiny of a subgenome location. The fine relationships between the wild octoploids and modern germplasm can be resolved, and potentially the wild accessions can provide a wealth of genetic resources to install new alleles for flavor, stress resilience and disease tolerance lost after centuries of intense annual selection.

Conclusions

The publication of complete octoploid strawberry sequence has accomplished what most high quality genomic resources do—they enable more questions to be asked in a meaningful way. In this case the information resolves a centuries-old question of subgenome composition, provides an understanding of how those subgenomes are organized and interact, and reveals a complete parts list for how to make a much appreciated and nutritious fruit. The sequence data can now be put into work in practical breeding application to improve strawberry and increase the economic and environmental viability of its production.

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