

Polypoidy in plant evolution

Multiple sets of chromosomes

Humans, like nearly all animals, have two sets of chromosomes, one from each parent. We are diploid organisms, arising from the fusion of a haploid sperm and a haploid egg. Polyploid organisms, in contrast, have three or more sets of chromosomes. Such duplicate sets of chromosomes are more than are required for the plant to function, but they can bring advantages. Polyploids have larger cells to accommodate their extra DNA and therefore the plants are often larger than their diploid parents. The regulation and expression of genes in polyploids, often in new combinations, also contributes to greater variety.

Polyploidy has occurred independently many times in plant evolution, and is an important mechanism in the production of new species. Recent genomic studies have revealed ancient whole genome duplications in plants. This implies that most, if not all, 'diploid' plants are actually paleopolyploids (ancient polyploids). Therefore it might be more accurate to think of most plants as polyploids with some having undergone additional rounds of polyploidy more recently. Some estimates suggest that between 30 and 80% of living plant species are polyploid.

Their importance to agriculture and therefore the economic value of polyploids cannot be understated. The four most widely-cultivated crop plants in the world (wheat, rice, soybeans and maize) are all polyploids. In fact, 15 of the 21 most important crops, as measured by area of cultivation, are polyploids.

Crops	Ploidy	No. of sets of chromosomes
Apple, banana, citrus, ginger, seedless watermelon	Triploid	3
Apple, durum wheat, cotton, potato, cabbage, leek, tobacco, peanut	Tetraploid	4
Bread wheat, triticale, oat, kiwifruit	Hexaploid	6
Strawberry, sugar-cane	Octaploid	8



David Monniaux, Wikimedia Commons.



Damien Boileau, Wikimedia Commons.



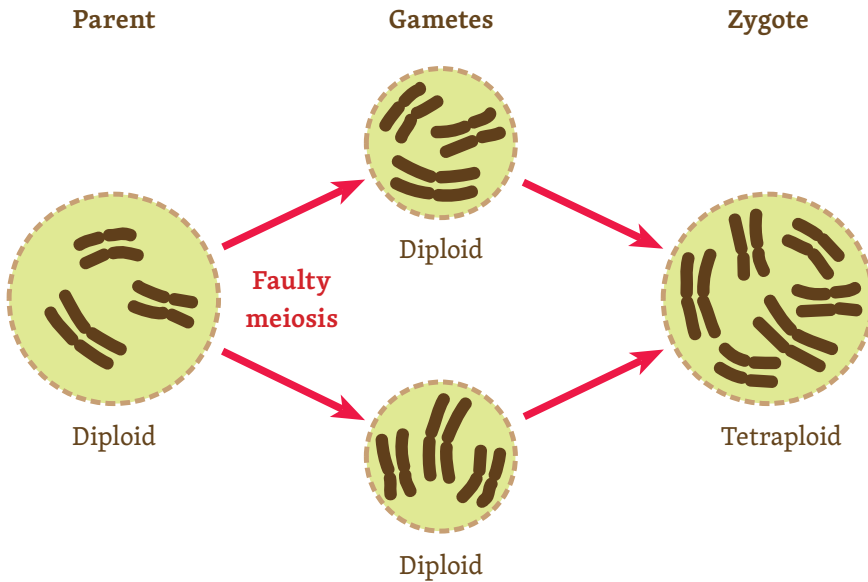
iStock photo.



iStock photo.

Wheat, rice, soya and maize, the four most widely-cultivated crop plants, are all polyploid.

IMAGE AFTER: Wikimedia Commons.



One of the ways in which polyploidy can arise in plants.

How polyploids are formed

There are two sorts of polyploid plants: *autopolyploids* and *allopolyploids*.

Autopolyploids have multiple sets of chromosomes from the same species. They can result from the fusion of gametes formed after an error in meiosis (see diagram above). They can also be formed by spontaneous doubling of the chromosomes. Both processes can occur naturally. Autopolyploids, such as bananas, are often infertile so such species have to be propagated from vegetative tissue.

Allopolyploids have sets of chromosomes derived from different species. For example, the common brassicas *Brassica oleracea*, *B. rapa* and *B. nigra* hybridise to form three allotetraploids: *B. napus*, *B. juncea* and *B. carinata*. The relationships between these plants are often represented in a diagram:

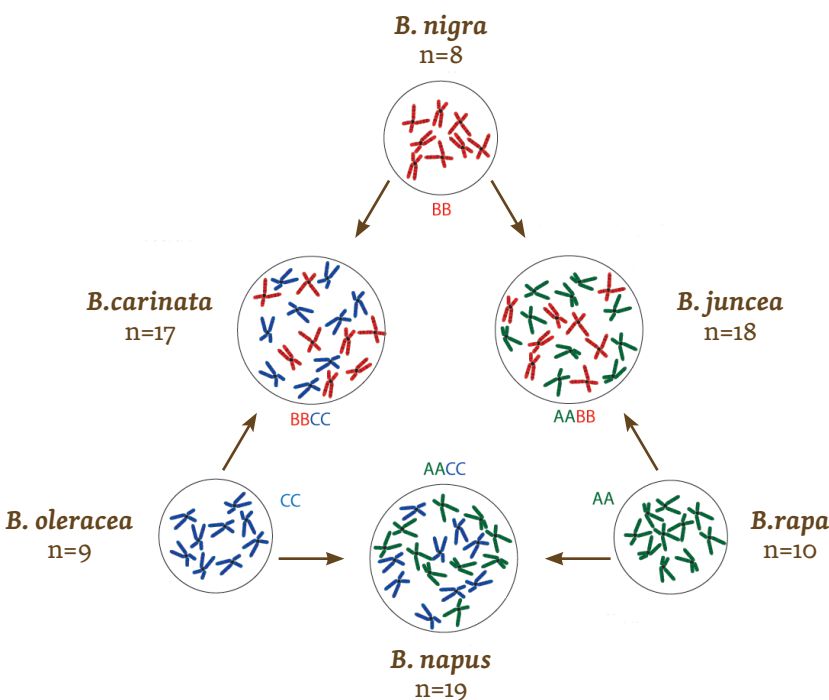


IMAGE AFTER: Wikimedia Commons.



Markus Hagenlocher, Wikimedia Commons.

Triticale, a cereal crop, has six sets of chromosomes: four from wheat and two from rye.

The 'Triangle of U', showing the relationships between three common brassicas and hybrid allotetraploid species.

- B. nigra* = Black mustard
- B. juncea* = Indian mustard
- B. rapa* = Field mustard (turnip)
- B. napus* = Oilseed rape
- B. oleracea* = Wild cabbage
- B. carinata* = Ethiopian mustard

Nicotiana – a model plant

Nicotiana is a plant genus which contains of 75 species, including tobacco (*N. tabacum*) and its wild relatives. The main centre of diversity for the genus is South America although species of the genus are native to Australia, Africa and North/Central America. Although *N. tabacum* is only a single species it receives a disproportionately large amount of attention from scientists. This is because *N. tabacum* has become a *model organism* for genetic studies. Model organisms are studied to understand particular biological phenomena, with the expectation that discoveries made will provide an insight into the workings of other organisms. In 1986 it was the first flowering plant to have its entire chloroplast genome sequenced (the nuclear genome is currently being sequenced). Tobacco is also the most widely-cultivated non-food crop in the world.



Ken Hammond, US Department of Agriculture / Wikimedia Commons



Left: Willie Greeninge checks his tobacco plants at his farm in Chatham, Virginia, USA. Right: Botanical illustration of the flowers and seeds of *Nicotiana tabacum*.

Nicotiana polyploids

About half of the species of *Nicotiana* are diploid and half are polyploid. All of the polyploids are *allotetraploids* (polyploids with chromosomes from two species). They have *four* sets of chromosomes: two sets from their maternal parent and two from their paternal parent. They can therefore be thought of as polyploid hybrids containing twice as much DNA as is required for a functional organism.

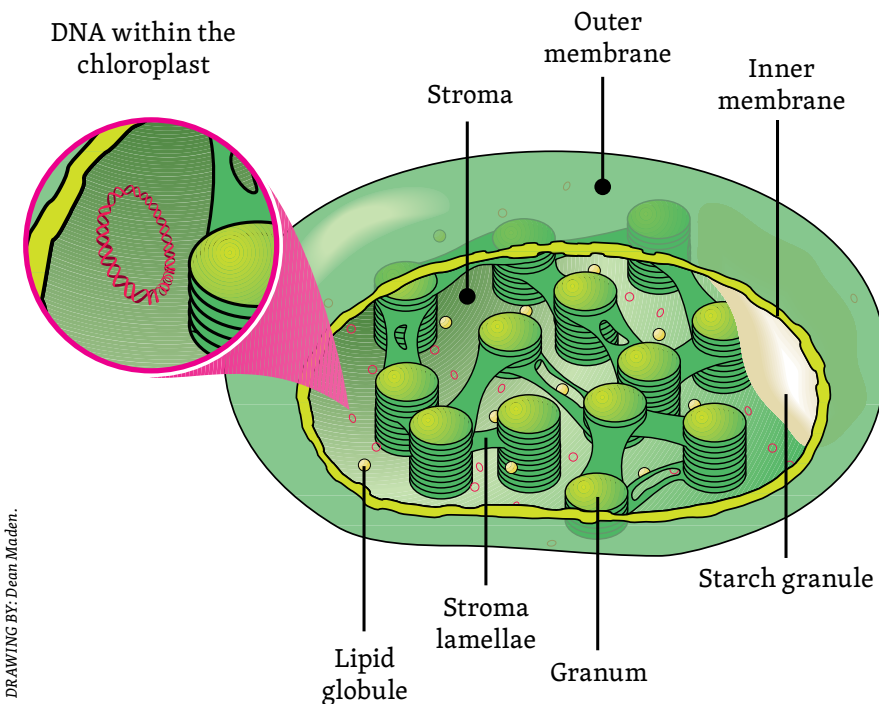
The allotetraploids in *Nicotiana* range from relatively recently-formed species (thousands of years old) to ancient species (millions of years old). The base (diploid) chromosome number in *Nicotiana* is $n=12$ and therefore most allotetraploids are $n=24$.

Both the tobacco plant, *N. tabacum*, and its wild relative *N. clevelandii* ('Cleveland's tobacco') are allotetraploids.

Bi-parental vs maternal inheritance

The cell nucleus contains the chromosomes that house the nuclear genes. Nuclear genes undergo recombination (re-shuffling at meiosis) and are bi-parentally inherited (that is, one set of chromosomes is inherited from each parent).

Chloroplasts are cellular organelles that perform photosynthesis. They have their own genome, a small circular chromosome which resembles a bacterial genome. In contrast to the nuclear genome, the chloroplast genome is non-recombining and in almost all flowering plants it is inherited as a unit from 'mother' to offspring. This difference in inheritance pattern between nuclear and chloroplast genomes will be used in the following exercise to determine the 'parents' of two allotetraploid species of *Nicotiana*.



Structure of a chloroplast, showing the location of the DNA.

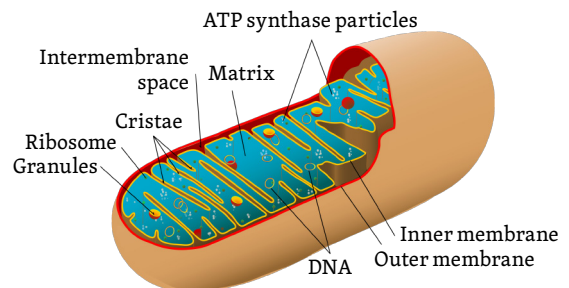
DRAWING BY: Dean Madden.

Mitochondrial Eve

Mitochondria, the organelles that perform respiration, are also maternally inherited. They have been used by researchers to trace the maternal lineage in various animal groups.

The 'Mitochondrial Eve' story was popularised by Richard Dawkins in his book 'River out of Eden'. In that case, mitochondrial evolution was used to pinpoint the maternal ancestor of all living humans.

River out of Eden: A Darwinian view of life by Richard Dawkins (2001) Phoenix. ISBN: 978 1857994056.



Structure of a mitochondrion, showing the location of the DNA.

DRAWING BY: Mariana Ruiz Villarreal, Wikimedia Commons.

Who's the daddy?

In the following exercise, you will first be given a tree diagram generated using DNA sequence data from one of the nuclear genes from the two allotetraploids, *N. tabacum* and *N. clevelandii*, and several related haploid species that could be 'parents' of these two polyploids.

By looking at which species are grouped together on the tree, you will be able to see which species the 'parents' are. What you won't be able to tell is which species is the 'mother' and which is the 'father'. In other words, you won't know which set of chromosomes came from the pollen and which from the ovules.

Because the chloroplast genome is transferred in the 'maternal' line only, however (that is, only in the ovules) if you compare DNA sequences from the plants' chloroplast genomes, you should be able to see which species was the 'female' donor. The second part of the exercise therefore is to perform an analysis using DNA sequences from the chloroplast genome. Once you know who the 'mummy' is, a process of deduction will reveal the identity of the 'daddy'!

PART 1: Analysing the nuclear DNA

Glutamine synthetase is an enzyme involved in nitrogen metabolism. It is encoded by a single nuclear gene, and all the species under investigation have a copy of it. Part of the DNA sequence of this gene (a fragment about 900 base-pairs long) was used to construct the tree diagram on the following page. *Symonanthus aromaticus* is an Australian relative of *Nicotiana*.

Questions

Examine the tree diagram on the following page.

- Which species has been used as an outgroup?
- Which species are haploid?
- Which species are allotetraploid?
- Describe in general terms how the species are grouped on the tree.
- Why do *N. tabacum* and *N. clevelandii* occur twice on the tree?
- Which species appear to have crossed to form
 - N. clevelandii* and
 - N. tabacum*?

Hint: similar gene sequences will be placed closer together on the tree.

A tree based on nuclear DNA sequences of part of the glutamine synthetase gene.

