

9. Polyploidy: Features and Applications

Mahebab

Division of Vegetable Crops,
ICAR-IIHR, Bengaluru.

Brunda N. B.

Division of Post Harvest Technology and
Agricultural Engineering ICAR-IIHR, Bengaluru.

Chandana S.

Division of Floriculture and Landscape Architecture,
ICAR-IIHR, Bengaluru.

Abstract:

Polyploidy and aneuploidy are significant genetic phenomena with profound implications in both natural evolution and agricultural breeding. Polyploids possess multiple sets of chromosomes, either from the same species (autopolyploids) or different species (allopolyploids), while aneuploids have an abnormal number of chromosomes resulting from the loss or addition of individual chromosomes.

This chapter explores the mechanisms, categorizations, characteristics, applications and limitations of both phenomena in plant biology. Polyploidy can arise through various mechanisms such as failure of chromosome separation during cell division, doubling of chromosomes in sex organs, fusion of gametes, abnormal meiosis and fertilization by multiple gametes. Autopolyploids and allopolyploids exhibit distinct cytological and morphological characteristics, impacting traits such as size, fertility, growth rate and resistance to environmental stresses.

Polyploidy has significant applications in agriculture, including the development of seedless fruits, high-yielding crops and disease-resistant varieties. Aneuploidy, on the other hand, results from the loss or addition of individual chromosomes and plays a crucial role in gene mapping, cross-species gene transfer, alien chromosome manipulation and identification of translocated chromosomes.

While aneuploids offer valuable tools for genetic research and breeding, they also present challenges in maintenance and viability, particularly in diploid species. Understanding the mechanisms and implications of polyploidy and aneuploidy provides valuable insights into plant evolution, genetic diversity and crop improvement strategies.

Keywords:

Polyploidy, chromosomes, gametes and aneuploids.

9.1 Introduction:

Euploidy is commonly referred to as polyploidy. In polyploid species, autopolyploids have identical genomes across the species, while allopolyploids have two or more distinct genomes. The somatic chromosome count in euploids can include three (triploid), four (tetraploid), five (pentaploid), six (hexaploid), seven (heptaploid), eight (octaploid) or more genomes. Autopolyploids are termed autotriploid, autotetraploid, autopentaploid, autohexaploid, autoheptaploid, autooctaploid and so forth, while allopolyploids are called allotetraploid, allopentaploid, allohexaploid, alloheptaploid, allooctaploid and so on.

Individuals with aneuploidy can have various chromosomal abnormalities. Nullisomics lack one complete pair of chromosomes ($2n-2$), while monosomics are missing just one chromosome ($2n-1$). Double monosomics have two missing chromosomes from different pairs ($2n - 1 - 1$). Trisomics have an extra chromosome ($2n + 1$), and double trisomics have two additional chromosomes, each from different pairs ($2n + 1 + 1$). Tetrasomics possess an extra pair of chromosomes ($2n + 2$). The terminology for describing these conditions can be complex, with breeders primarily focusing on monosomics, trisomics, and occasionally, nullisomics and tetrasomics. Euploids, on the other hand, have a chromosome number that is precisely a multiple of the basic or fundamental number of chromosomes.

Amphidiploids are allopolyploids with two copies of each genome, behaving diploid during meiosis. Except for minor differences, segmental allopolyploids consist of two or more genomes that are nearly identical to each other

9.2 Polyploidy Can Arise from Various Causes:

- **Failure of Chromosome Separation:** During cell division, chromosomes are supposed to separate properly. If this process fails and the cytoplasm does not cleave, a tetraploid cell with double the normal number of chromosomes is formed.
- **Doubling of Chromosomes in Sex Organs:** If the number of chromosomes in the somatic cells of a sex organ doubles, it results in a doubling of the number of chromosomes in the gametes produced by that organ.
- **Fusion of Gametes:** When a diploid gamete fuses with a haploid gamete, it produces a triploid organism. Similarly, the fusion of two diploid gametes can result in a tetraploid individual.
- **Abnormal Meiosis:** Occasionally, abnormal meiosis can lead to the formation of diploid gametes instead of haploid ones, contributing to polyploidy.
- **Fertilization by Multiple Gametes:** Polyploidy may also occur if an ovum or egg is fertilized by more than one male gamete, leading to an abnormal number of chromosomes in the resulting zygote

9.3 Mechanism of Polyploidy:

Plants can spontaneously become polyploid through a variety of cytological pathways, as Ramsey and Schemske (1998) reported. Meiotic nuclear restitution is one such procedure that produces gametes with a somatic nuclear condition ($2n$) when gametes are generated

without a chromosomal number reduction. This condition is caused in part by abnormalities in spindle formation, spindle function and cytokinesis during meiosis. Polyploid organisms arise from the subsequent fusing of reduced and non-reduced gametes. For example, as seen in the F1 progenies of open-pollinated diploid apples, autotetraploids can develop in diploid populations through the union of two unreduced 2n gametes. Similarly, 90% of F2 progenies originating from interspecific crosses between ornamental plants *Digitalis ambigua* and *Digitalis purpurea* were shown to have spontaneous allotetraploids. Another example is the fusion of reduced (2x) and unreduced (4x) gametes to create autohexaploid *Beta vulgaris* (sugar beet) and alfalfa from cultured autotetraploid types.

Chromosomal doubling during mitosis serves as a crucial mechanism for the development of polyploids. This phenomenon has been observed in both meristematic and non-meristematic tissues of various plant species, such as tomatoes and beans. In plant breeding, polyploids can be intentionally generated by disrupting mitosis. Techniques for inducing polyploidy include subjecting plants to high temperatures or using chemical agents like colchicine or dinitroanilines, which inhibit mitosis. Furthermore, polyspermy—in which one egg is fertilized by numerous male nuclei—is a rare mode of polyploid development that has been reported in certain orchids by Ramsey and Schemske (1998).

Categorization: based on origin: Induced and Natural, Autopolyploids and allopolyploids based on genome

Natural polyploids: In nature, polyploids are created when meiosis fails and results in the production of gametes that are not reduced. They could potentially originate from somatic cells whose chromosomal complement has doubled due to a mitotic failure. Natural polyploids include tobacco and cultivated bananas.

9.4 Types of Polyploidies:

Table 9.1: Types of Polyploid

Types of polyploid	Definition	Representation
Polyploidy	A condition when there are more than two genomes	-
1. Autopolyploidy	The same genome is being duplicated	-
Autotriploidy	Three identical copies of the same genome	3x
Autotetraploidy	Four identical copies of the same genome	4x
Autopentaploidy	Five identical copies of the same genome	5x
Autohexaploidy	Six identical copies of the same genome	6x

Types of polyploid	Definition	Representation
2. Allopolyploidy	A condition in which the whole genomes of two or more species mix.	-
Allotetraploidy	Two different genomes, each in two copies	$2x_1 + 2x_2$
Allotetraploidy	Three different genomes, each in two copies	$2x_1 + 2x_2 + 2x_3$
Allotetraploidy	Four different genomes, each in two copies	$2x_1 + 2x_2 + 2x_3 + 2x_4$

9.4.1 Autopolyploidy:

A variety of chromosomal doubling processes can result in autopolyploidy, which includes triploidy, tetraploidy and greater degrees of ploidy. Among these techniques are:

- **Spontaneous Doubling:** Occasional chromosome doubling may occur in somatic tissues and low frequencies of unreduced gametes can also be produced.
- **Physical Agents:** Treatments such as heat or cold exposure, as well as X-ray or gamma-ray irradiation, can induce polyploidy at low frequencies. For instance, cold treatment led to tetraploid branch formation in *Datura*, while exposing maize plants or ears to temperatures of 38-45°C during zygote division resulted in 2-5% tetraploid progeny. Heat treatment has also been successful in inducing polyploidy in barley, wheat, rye and other crop species.
- **In Vitro Regeneration:** Polyploidy commonly occurs in cells cultured in vitro, with some plants regenerated from callus and suspension cultures exhibiting polyploidy. Various ploidy levels have been observed in plants regenerated from callus cultures of *Nicotiana*, *Datura*, rice and other species.
- **Colchicine Treatment:** Colchicine treatment is the most effective and widely used method for inducing chromosome doubling. Colchicine, a compound with the chemical formula $C_{22}H_{25}O_6N$, inhibits spindle formation, preventing sister chromatids from moving to opposite poles during cell division. Consequently, the resulting restitution nucleus contains all chromatids, leading to chromosome number doubling.
- **Other Chemical Agents:** Some chemicals, such as 8-hydroxyquinoline and nitrous oxide, also have polyploidizing effects, although they are less effective than colchicine and are not commonly used.

A. Cytological and Morphological Characteristics of Autopolyploids:

The morphological characteristics of polyploids exhibit some variation among different species. The general characteristics are outlined below.

- Compared to diploids, polyploid cells are bigger in size.
- In comparison to diploids, polyploids have fewer stomata per unit area and larger guard cells.

- Generally speaking, polyploid pollen grains are bigger than those of equivalent diploids.
- In general, polyploids flower later and grow more slowly.
- Compared to diploids, polyploids typically have fewer, bigger and thicker leaves as well as larger flowers and fruits.
- Polyploids typically have lower fertility because of genotypic imbalance and anomalies during meiosis.
- Autopolyploidy frequently results in increased vegetative growth and general vigor. However, polyploids can occasionally be weaker and smaller.
- The roots are longer and more robust.
- Compared to diploids, flowers, pollens, and seeds are larger.
- Growth rate is slower and maturity duration is longer compared to diploids.
- Compared to diploids the water content is higher in polyploid.

B. Applications of Autopolyploidy:

- Triploids: Triploid strains arise from the mating of diploid and tetraploid strains. With rare exceptions, they are almost always extremely sterile. Watermelons with no seeds can be produced with this function. They might be more active than the typical diploids in some species, such as sugarbeets. In Japan, watermelons without seeds are cultivated commercially. Tetraploid (4x, used as female) and diploid (x, used as male) lines are crossed to make them. Almost all of the seeds produced by triploid plants are tiny, white, primitive structures similar to cucumber seeds; they do not generate real seeds. However, a few typical-sized seeds—which are usually empty—may appear. Pollination is necessary for optimal fruit setting. In order to achieve this, 1 diploid: 5 triploid plants are the ratio in which diploid lines are planted.
- Tetraploid sugarbeets (*B. vulgaris*) provide lower yields than diploids due to smaller roots, whereas triploid sugarbeets (*B. vulgaris*) produce larger roots and more sugar per unit area. It seems that sugarbeets are best at having a ploidy of 3x. Japan and Europe have been commercial producers of triploid sugarbeet cultivars. Because the beet blossom is tiny, triploid sugarbeet is difficult to produce seeds from. There are two methods available for producing triploid seed: identifying two plants as male and four as female, or two plants as male and four as female. By alternating 4x and 2x lines in a 3:1 ratio, commercial triploid sugarbeet seed is created. Sugarbeet triploids have the potential to yield 10–15% more than diploids.
- Autotetraploids have been developed in forage crops like berseem, alfalfa and rye; vegetables like radish, turnip and cabbage and fruits like grapes. Tetraploid varieties of rye are grown in Sweden and Germany. They have larger seeds and higher proteins than diploids.

9.4.2 Allopolyploidy:

Allopolyploids, which possess genomes from two or more species, are common in several crop plants. Creating allopolyploids has been a focus, primarily aiming to develop new species. Some successes include the emergence of Triticale as a viable crop species in certain regions, along with promising results from other allopolyploids like Raphanobrassica and certain forage grasses.

Genera containing allopolyploid species often include both crop and non-crop varieties, with crops existing as either allopolyploid or diploid species.

Artificially synthesized allopolyploids serve two main purposes: studying the origins of naturally occurring allopolyploids and exploring the potential for creating new species. Examples include:

- **Raphanobrassica:** This was an early attempt at synthesizing an allopolyploid, combining radish (*Raphanus sativus*) and cabbage (*Brassica oleracea*) by Russian geneticist Karpechenko in 1928. The goal was to create a fertile hybrid with radish roots and cabbage leaves, but instead, a fertile amphidiploid ($4n = 36$) was obtained, featuring cabbage roots and radish leaves, rendering it impractical.
- **Tobacco (*N. digluta*):** Clausen and Goodspeed produced a new hexaploid tobacco species (*Nicotiana*) by crossing *Nicotiana tabacum* ($2n = 48$) with *N. glutinosa* ($2n = 24$). The resulting F1 hybrid was sterile ($2n = 36$), but fertility was restored by chromosome doubling using colchicine treatment, resulting in the creation of *N. digluta*.
- **Triticale:** This novel crop species arose from a cross between wheat (*Triticum aestivum*) and rye (*Secale cereale*, $n = 7$). Some triticales originated from crosses between tetraploid wheat (*Triticum turgidum*) and rye, while others resulted from crosses between hexaploid wheat (*T. aestivum*) and rye.

A. Role of Allopolyploidy in Evolution:

About one-third of the Angiosperms are thought to be polyploid, with allopolyploids making up the great majority. The pairing of the diploid and allopolyploid species' chromosomes serves as the primary basis for identifying the parental diploid species. The similarity between the chromosomes of two species is seen when some of the diploid species' chromosomes couple with those of an allopolyploid species. The allopolyploid species may have one or more parental species, according to this homology. We will quickly go over the potential evolutionary history of some significant allopolyploid crop species, including Brassica, cotton, tobacco, and wheat. Evolution of Amphidiploid Brassica Species: The well-known U's Triangle, which N. U. postulated in 1935, is used to explain the formation of amphidiploid Brassica species. An amphidiploid from the cross *B. nigra* ($n = 8$) x *B. campestris* ($n = 10$) is *B. juncea* ($n = 18$), an amphidiploid from the cross *B. oleracea* ($n = 9$) x *B. campestris* ($n = 10$) and an amphidiploid from the cross *B. nigra* ($n = 8$) x *B. oleracea* ($n = 9$) is *B. napus* ($n = 19$). The above-mentioned approach produces synthetic allopolyploids that are similar to natural amphidiploids, cross with them readily and yield reasonably viable hybrids between the two.

B. Application of Allopolyploidy:

- **Tracing Crop Origins:** Allopolyploidy is key in tracing the origins of natural allopolyploids. Studying chromosome pairing between allopolyploids and diploid species aids in this process. Affinity in pairing suggests the involvement of diploid species in polyploid evolution, while lack of pairing rules it out.

- **Creation of New Species:** Allopolyploidy can result in new crop species, exemplified by triticale—a hybrid of wheat and rye. Triticale inherits desirable traits from both parents, with primary and secondary triticales being distinct types, the latter superior in many aspects. Cultivated strawberries and loganberries also arose from interspecies crosses.
- **Interspecific Gene Transfer:** When desired traits aren't present within a species, they can be transferred from related species through interspecific gene transfer, achieved via alien addition or substitution. While this method is effective for disease resistance, it may also introduce undesirable traits. For instance, mosaic resistance was transferred from *N. glutinosa* to *N. tabacum* in tobacco.
- **Bridging Crosses:** In cases where direct species crosses are hindered by F1 sterility, bridging crosses are employed. An amphidiploid is first created between the species, then crossed with the recipient species. This approach is used to transfer genes from wild species, especially in tobacco and cotton. Additionally, allopolyploids offer advantages such as easier conservation of heterotic effects and restoration of fertility in interspecific hybrids through artificial chromosome doubling.

C. Significance of Polyploidy:

- Polyploidy serves as a significant source of genetic variation, facilitating the evolution of new varieties, species and even genera.
- It often results in advantageous traits such as increased size and hardness, a phenomenon known as hybrid vigor.
- Triploid plants have been instrumental in producing seedless varieties of watermelons, tomatoes, grapes and other crops.
- Allopolyploidy has been utilized to develop disease-resistant and high-yielding crop species like hybrid wheat and hybrid paddy.
- Polyploidy is commonly employed in the production of fodder plants due to the larger leaves, flowers and fruits of polyploid varieties compared to diploid ones.
- Polyploid plants exhibit greater morphological, genetic and physiological advancements compared to diploid counterparts, enabling them to confront ecological challenges more effectively.

D. Industrial Application of Polyploidy:

Chromosome doubling in plants has significant industrial applications, primarily due to its impact on various physiological properties. One notable effect is the increase in both primary and secondary metabolism. This increase, which can be as high as 100% in some cases, has been extensively utilized in the breeding of narcotic plants like Cannabis, Datura, and Atropa. Additionally, in vitro systems for secondary metabolite production that exploit polyploidy have been developed.

For example, the production of the antimalarial sesquiterpene artemisinin was enhanced sixfold by inducing tetraploids of the wild diploid *Artemisia annua* L. Furthermore, significant improvements have been achieved in the commercial synthesis of sex hormones and corticosteroids through the artificial induction of tetraploids from diploid *Dioscorea*.

Efforts have also been made to enhance the production of botanical insecticides like pyrethrin by inducing chromosome doubling in plants like *Chrysanthemum cinerariifolium*. Moreover, plants such as *Carum cari*, *Ocimum kilmandscharicum* and *Mentha arvensis* have shown increased production of terpenes following artificial chromosome doubling. The enhanced production of secondary metabolites, including alkaloids and terpenes, in polyploids may also confer resistance to pests and pathogens. Studies comparing diploid and tetraploid forms of plants like *Glycine tabacina* and *Trifolium pratense* have shown increased resistance to leaf rust, insects and nematodes in tetraploids compared to diploids.

E. Limitations of Polyploidy:

- **Limited Applicability:** Single-species polyploidy has restricted use and is primarily applicable to crops that reproduce asexually, like banana, potato, sugarcane, and grapes.
- **Maintenance Challenges:** Maintaining monoploids and triploids is impractical for sexually reproducing crop species.
- **Expression of Undesirable Traits:** In bispecies or multispecies polyploids, traits are contributed by each parental species, sometimes leading to the expression of undesirable characteristics, as seen in *Raphanobrassica*.
- **Additional Drawbacks:** Induced polyploids often exhibit drawbacks such as reduced fertility, genetic instability, slow growth, and delayed maturity.
- **Limited Potential for New Species:** The likelihood of developing new species through allopolyploidy is exceedingly low.

9.4.3 Aneuploidy:

The two types of aneuploids that are most frequently employed in genetic research are trisomics (found in diploid species like maize, bajra, tomato, rye, pea, spinach, etc.) and monosomics (found in polyploid species like tobacco, wheat, and oats). Nullisomics only holds true in a few numbers of extremely polyploid species, such as oats and wheat and not even in tobacco. In general, aneuploids are not as active as their diploid ancestors. An further trait of aneuploids is their high sterility, which results in erratic meiosis

Table 9.2: Various types of aneuploidy

Types of aneuploidies	Definition	Representation
Hypoploidy	deletion of one or two chromosomes from diploid.	
Monosomics	one chromosome lost from one pair or from two distinct chromosomes pair	$2n-1$ or $2n-1-1$
Nullisomics	one chromosomal pair lost	$2n-2$
Hyperploidy	chromosomal addition to one or two distinct pairs of chromosomes	

Types of aneuploidies	Definition	Representation
Trisomics	one chromosome being added to either one pair or two separate pairs of chromosomes.	$2n+1$ or $2n+1+1$
Tetrasomics	two chromosomes are added to one pair or two separate pairs of chromosomes	$2n+2$ or $2n+2+2$

A individual who is monosomic is one who is missing one chromosome from the typical complement of somatic cells ($2n - 1$). The creature might survive if the missing chromosome is not vital to its survival, but it might not make it if the lost chromosome is crucial. In plants that are normally diploid, the loss of one chromosome may be fatal. For instance, in *Datura* sp., monosomics are not feasible. It has been discovered that polyploid plants may withstand the loss of a single chromosome. *Nicotiana tabacum* is a tetraploid with $2n = 48$. Twenty-four distinct monosomics, each lacking a single different chromosome of the usual complement, have been identified. In haploid wheat ($2n = 42$), these 24 monosomics are morphologically dissimilar from one another, 21 different monosomics have been isolated. Two different types of gametes—one with n chromosomes and the other with $n - 1$ chromosome—are produced by monosomic. Therefore, when selfed, monosomics give rise to nullisomic, monosomic and regular (i.e., disomic) progeny.

An individual who is nullisomic is one who does not have both copies of a particular pair of chromosomes ($2n-2$). uncertain species, such as *Nicotiana tabacum*, nellisomics are inviable; however, un other species, such as *Triticum aestivum*, they are viable. Sears identified 21 nullisomic lines ($2n = 40$) in the Chinese Spring wheat variety, each of which lacked a single pair of chromosomes from the somatic cell's usual complement. Morphologically, distinct nullisomics differ from one another and from the typical Chinese Spring. They are extremely sterile and have lost most of their vigour and growth. They only make nullisomics when they self because each of their gametes has $n - 1$ (or 20) chromosomes.

An individual who possesses one extra chromosome ($n+1$) beyond the typical complement of somatic cells is said to be trisomic. Generally speaking, the effects of an extra chromosome are not as noticeable as those of a missing one. Trisomics ($2n = 43$) do exist in wheat, however they are essentially the same as disomes ($2n = 42$), which are typical plants. In *Datura* sp. ($2n = 24$), Blakeslee has identified 12 distinct trisomics, each of which possesses one unique chromosome from the usual set-in triplicate. There are morphological differences between these trisomics and the diploid form. Trisomics tend to be considerably more stable genetically than monosomics, despite producing two types of gametes: one with n chromosomes and the other with $n + 1$ chromosomes.

An individual with two chromosomes extra than the typical complement of the somatic cell is said to be tetrasomic ($2n + 1$). In addition to the typical diploid number, two units of the same chromosome will be present in a normal tetrasomic. A double trisomic ($2n + 1 + 1$) is characterized by the presence of two distinct chromosomes (for example, chromosomes No. 1 and No. 2) in addition to the standard diploid number.

In a tetrasomic, a quadrivalent forms in addition to the bivalents during meiosis, whereas in a double trisomic, two trivalents and two bivalents form. When normal diploids ($2n$) are crossed with tetrasomic gametes ($n + 1$ chromosome), a high frequency of trisomics is produced.

A. Source and Method of Production:

- **Spontaneous Generation:** Rarely do aneuploids occur spontaneously. In the beginning, aneuploidy happened spontaneously in test populations. During meiosis, irregularities result in the production of $n + 1$ and $n - 1$ gametes. In *Datura*, for example, it is estimated that 0.4 percent of pollen grains are likely $n + 1$, resulting in progeny that after fertilization have $2n + 1$ and $2n - 1$ chromosomal counts.
- **Autotriploid Plants:** One of the main sources of aneuploids is triploid plants. A range of aneuploid progeny are produced when triploids have uneven chromosomal distribution after their first meiotic division.
- **Asynaptic and Desynaptic Plants:** During meiosis's first metaphase, a portion or all of the chromosomes appear as univalent in plants that display asynapsis or desynapsis. These plants produce progeny that have a comparatively significant amount of aneuploidy.
- **Translocation Heterozygotes:** One $n + 1$ and one $n - 1$ gamete is formed when the translocation heterozygote with a 3:1 chromosomal disjunction breaks into a ring or chain of four chromosomes. As a result, the offspring of translocation heterozygotes exhibit variable frequency of aneuploids.
- **Tetrasomic Plants:** At considerable frequency, $n + 1$ gametes are produced by tetrasomic ($2n + 2$) plants. An increased frequency of trisomics is produced when they are crossed with typical disomic ($2n$) plants. Where possible, tetrasomics can be saved to create trisomics.
- **Double Trisomy:** When two different chromosomes are triplicated in a diploid organism, a double trisomy occurs, resulting in the chromosomal formula $2n + 1 + 1$.

B. Application of Aneuploidy in Plant Breeding:

Gene Mapping: Aneuploids serve as valuable tools in gene mapping, particularly monosomics and nullisomics. Monosomics are employed in wheat, cotton, tobacco, oats, and other crops to pinpoint genes on specific chromosomes. In nullisomics, the loss of a chromosome pair impacts the expression of certain traits, associating altered characteristics with the absent chromosomes.

Hence, nullisomic series aid in locating genes across chromosomes. However, monosomics are preferred for such analyses over nullisomics due to their superior vigor and fertility.

Cross-Species Gene Transfer: Monosomics play a role in transferring chromosomes containing desirable genes between species.

Alien Chromosome Manipulation: Aneuploids are instrumental in creating alien addition and substitution lines in various crop species.

Identification of Translocated Chromosomes: Primary trisomics facilitate the identification of chromosomes involved in translocations.

C. Limitation of Aneupoidy:

- Monosomics are not viable in diploid species: They can only survive in polyploid species such as tetraploids or hexaploids.
- Viability in Highly Polyploid Species: Nullisomics are not viable in diploid species: they can only survive in highly polyploid species like hexaploids.
- Survival of Trisomics: Trisomics can survive in diploid species.
- Challenges in Maintenance: Maintaining nullisomics and monosomics poses difficulties.

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