Course Name: Basics of Crop Breeding and Plant Biotechnology

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Lecture-24: Allopolyploidy

Hello everybody. Welcome to SWAYAM NPTEL online course on Basics of Crop Breeding and Plant Biotechnology. We will be discussing the lecture under the heading of polyploidy especially, allopolyploidy. So, these are the things which will be covered over here. First of all, we will learn what is allopolyploidy, in our last lecture we have discussed about autopolyploidy. Then we will be discussing about the origin and production of allopolyploidy, then the morphological and cytological features of allopolyploids will be discussed, then the role of allopolyploidy in evolution will be discussed, thereafter, the application of allopolyploidy in crop improvement will be discussed and finally, we will be discussing the limitations of allopolyploidy.

So, first of all, let us see what are allopolyploids, how allopolyploidy is generated? So, allopolyploids are typically derived from hybridization between two or more distantly related species, and combination of divergent genomes. So, few things are important over here means, divergent genomes are combining together means, each genome is supposed to have a particular set of genes. Ok! Suppose a genome A is having 7 pairs of chromosomes.

So, in those 7 pairs different sets of genes might be available while, if we cross it with a distantly related species. Ok! Suppose a species B is being crossed, with that it is also having 7 pairs of chromosomes, and in B the gene content is mostly different. So, new sets of genes might be coming from there. So, in this way if all these genes come together means, 7 pairs means, these 7 chromosomes and these 7 chromosomes comes in

F_1 because, one set of chromosomes will be coming from each of this parent in F_1 in the hybrid. So, in this way initially from the divergent genomes the chromosome content come in the F_1, in the F_1 hybrid.

Thereafter due to chromosome duplication finally, the chromosome number is doubled and the allopolyploids are generated in the nature. So, later on we will be discussing it again and again. So, the merging genomes from different species, merging genomes from different species, they provide not only genome variation, but also novel opportunities to generate diversification, through their interactions that allow allopolyploidy to function as a potential source of new species. If you think about the genome which is coming from parent A and parent B in the newly formed allopolyploid then, within that allopolyploid several interactions might be taken place. Some genes coming from parent B might interact with some of the genes or proteins coming from parent A, and due to non-allelic interactions or due to epistatic interactions the some of the characters might be more pronounced.

So, in this way new variations are generated within the allopolyploid, within the allopolyploid compared to both of their parents. Then they are also known as hybrid polyploids, as hybridization is needed initially in between two distantly related species. So, they are known as hybrid polyploids or multispecies polyploids. Ok! Then an allopolyploid arises by combining genome of two diploid species also means, sometimes more than two genomes are involved, sometimes only two diploid species can merge together, their genomic content may merge together, and an allopolyploid can be formed. Then they have played greater role in crop evolution than autopolyploidy because, in autopolyploidy the genetic constituents from a particular individual will be coming from a particular genome, will be coming, it will be repeated while, in case of allopolyploid genetic constituents might be coming from two different species or more than that.

Now let us discuss, about the origin and production of allopolyploids. So, allopolyploids typically arise from the hybridization events between two distinct species, often from the same genus, that is the important point often from the same genus, or occasionally from different genera followed by chromosome doubling in the F_1 hybrid. So, from same genus also it may be arisen like different *Triticum* species might be crossed together to generate a tetraploid *Triticum* species, or sometimes from different genera means a cross might be taken place, between a *Brassica* species and a *Raphanus* species, those belongs to different genera. And once the cross is made and the chromosome doubling is done in F_1 hybrid, there from we can develop the allopolyploids we will see those examples later on. Then another thing, the unreduced gametes are formed by meiotic dysfunction at the meiosis I or at meiosis II here, a term is written unreduced gamete.

If you recall the meiosis process what we have discussed earlier during meiosis what happens? Two steps are there, meiosis I and meiosis II. In meiosis I what happens the homologous chromosome pairs in normal diploid cells, once the meiosis is started in meiosis I, the homologous chromosome pairs and each of this homolog are separated and move to a different pole. While in meiosis II, basically the chromatids available in each chromosome are separated. So, in this way from a particular cell if the chromosome number is 2n = 4, if this cell undergoes meiosis, there from 4 cells are produced having chromosome number n = 2, in each of them the chromosome number is half. So, here we are discussing about unreduced gamete, in unreduced gamete the chromosome number is not at all changed means either due to dysfunction in meiosis I or due to dysfunction at meiosis II.

The chromosome number is not reduced within the gametes. Ok! Then the chromosome doubling had occurred in somatic tissues means, it might occur the chromosome doubling might occur, in the somatic tissues due to an irregularity in the mitotic cell division. In the somatic tissue the mitosis is taken place while, in the reproductive tissue the meiosis is taken place. Earlier we have discussed about meiosis here, we are discussing about mitosis. Ok! Suppose we got F_1 plant, F_1 hybrid we have observed that F_1 plant is being grown, and the chromosome doubling had occurred in the somatic tissue, in this particular plant due to irregularities in the mitotic cell division.

And due to those irregularities, some allopolyploid sectors have been developed either in the apical meristem position, or in the axillary buds. So, in mitosis what happens it is taken place in the body cell, if chromosome number remain 2n = 4, after mitosis from one cell 2 cells are produced having chromosome number same 2n = 4. So, here they are talking about the chromosome doubling is taken place means, somehow the chromosome number has become 8 due to irregularities in the mitotic cell division in the apical meristemic region. So, in this way within that plant at a certain sector the allopolyploid branches might be developed. So, these sectors, those allopolyploid branches with double chromosome complement can be propagated through subsequent cell division or by through tissue culture, also we can amplify it, we can multiply it we can do rooting from that particular stem cutting and eventually, we can develop an allopolyploid individual within the hybrid organism because from the F_1 hybrid we have initiated this experiment.

So, in this way the allopolyploids are originated or they are produced. Let us take an example of *Raphanobrassica*. So, *Raphanobrassica* is an allopolyploid, it has been developed by crossing two different species even two different genus ok, one is *Brassica oleracea* and another one is *Raphanus sativus*. So, initially this is a man-made allopolyploid, human have created this particular allopolyploid. So, initial concept was that the scientist tried to get the root of *Raphanus sativus*.

So, *Raphanus sativus* has a robust root and that is edible while, the scientist tried to get the advantage of the leafy vegetable part of Brassica species. So, they attempted the cross between these two species over there in *Brassica oleracea* the n = 9 while, in *Raphanus sativus* also n = 9. So, once the cross was made between these two crops. So, the F_1 was obtained, in F_1 the chromosome from *Brassica oleracea* came, as well as the chromosome from *Raphanus sativus* came. So, in this way two different genomes came together and thereafter, due to chromosome doubling finally, the *Raphanobrassica* have been originated.

So, whatever the features of *Raphanobrassica*, whatever was predicted earlier before making this cross and getting the actual product the result was not up to the mark. Ultimately, whatever obtained that was this crop, was having the root system like *Brassica* and leaf system like the *Raphanus* one. So, that was just the opposite of the expectation, but anyway it is an allopolyploid developed by the human beings. So, once that F_1 was developed it was almost completely sterile in nature, because two sets of genome was there during meiosis, during gamete formation the chromosomal pairing was not proper, but a few number of seeds were developed. Few seeds developed might be due to, the improper chromosome, improper meiosis or improper mitosis and eventually, the *Raphanobrassica* have been formed as an allotetraploid.

So, the production of allopolyploid involves two steps, first one is the production of F_1 distant hybrid by crossing either two different species to distinctly related species or to different genera thereafter, we have to do the chromosome doubling. Now coming to the evolution of bread wheat, in bread wheat the common bread wheat is hexaploid in nature, and in common bread wheat basically three different genomes have come together. One genome has come from *Triticum monococcum* that is having chromosome number n = 7 here, basically 2n = 14 in *Triticum monococcum* its genome is capital A capital A type while, in nature it has been crossed with *Aegilops speltoides* another plant where 2n = 14 and n = 7 its genome type is capital B capital B. So, in nature the crossing has been made between these two crops *Triticum monococcum* and *Aegilops speltoides* and finally, the F_1 was developed that was having the genome content A and B means 7 chromosomes came from here, and 7 chromosomes came from here in the F1. Thereafter, spontaneous chromosome doubling occurred in the nature and an amphidiploid has been developed having the genome content capital A capital A capital B capital B capital A capital A belongs to the genomic part, which is coming from *Triticum monococcum* and capital B capital B is the genomic part coming from *Aegilops speltoides*.

So, it is amphidiploid if you recall, what is diploid in diploid single set of chromosomes is available in two copies. So, here different sets of chromosomes are there, but all of the chromosomes are available in two copies. So, they are behaving like a diploid. So, it is known as amphidiploid here n = 14 and 2n = 28. So, in this way the tetraploid emmer wheat has been developed.

So, different types of wheats are there, I have discussed about the monoploid wheat, sorry, the diploid wheat, this is the diploid wheat, this is the tetraploid wheat emmer wheat, and in nature the tetraploid wheat it has been crossed with another plant species that is *Aegilops squarrosa*. They were also 2n was 14, the diploid chromosome number was 14, and its genome content was D type means different sets of genomes was there, capital D capital D. So, once the cross was made between these two then F_1 was having capital A capital B and capital D genomes, three sets of genomes came together spontaneous chromosome doubling occurred in nature and finally, the hexaploid wheat have been generated, that also behave like an amphidiploid, it also behaves like an amphidiploid. So, in hexaploid wheat, three different genomes are there capital AA capital BB and capital DD and here 2n = 42, and we should write it in this way 2n = 6x = 42, basically, x means basic chromosome number means, three sets of chromosomes have come from three different crop plants one is *Triticum monococcum,* one is *Aegilops speltoides,* and third one is *Aegilops squarrosa* and all sets are available in two copies. So, 6x chromosome is available over there.

So, in this way 2n = 6x = 42 chromosome is available in hexaploid wheat. Now we will discuss about the evolution of amphidiploid *Brassica* species. In *Brassica* also three progenitors are there, one is *Brassica nigra* where, 2n = 16, one is *Brassica oleracea* where 2n = 18, and another one is *Brassica campestris* here, 2n = 20. So, this three *Brassica* species played a major role in the evolution of other different *Brassica* species. So, once in nature the cross was made between *Brassica nigra* and *Brassica oleracea* then within the gamete 8 chromosomes came from here and 9 chromosomes came from here.

And finally, the *Brassica carinata* has been developed having the chromosome number n = 17 and eventually, the chromosome doubling taken place and Abyssinian mustard have been developed in nature. While when the cross was made between *Brassica oleracea* and *Brassica campestris* then here from within the gamete 9 chromosome came here from within the gamete 10 chromosome came, and after fusion of their gametes the *Brassica napus* have been developed as F_1. And eventually the chromosome number have been doubled, and their n =19 and 2n = 38, in this way the *Brassica napus* that is rutabaga or oil rape has been produced in nature. While *Brassica juncea* that is known as the Indian mustard or leaf mustard it has been originated by crossing between the *Brassica nigra* and *Brassica campestris*. Here from 8 chromosome came and here from 10 chromosome came, and due to their fusion in F_1 finally, 18 chromosome was developed eventually the chromosome has been duplicated amplified chromosome number has been doubled and the *Brassica juncea* the leaf mustard or Indian mustard have been generated.

So, this triangle was proposed by Nagaharu, and this is also known as U triangle. Now let us discuss the evolution of cotton. Cultivated tetraploid cotton species are available, some of them are known as American cotton, some of them are known as Indian cotton. Ok! So, let us discuss the evolution of cultivated tetraploid species of *Gossypium barbadense*, ok, that is known as American cotton. So, it was developed by crossing between the *Gossypium herbaceum* having chromosome number n = 13 that is 2n = 26 and the *Gossypium raimondii* here also chromosome number was 2n = 26.

So, their F_1 was formed in nature it was sterile somehow, the chromosome doubling took place in the nature and finally, the *Gossypium barbadense* the allotetraploid American cotton has been formed. Here the genome content is capital A capital A capital D capital D, capital A capital A genome has come from *Gossypium herbaceum* and capital D capital D genome has come from *Gossypium raimondii*. In case of *Gossypium hirsutum*, there also it was developed by crossing between two different cotton species one was the old-world diploid cotton having the genome content capital A capital A having the genome content capital A capital A while the capital D capital D genome came from *Gossypium thurberi*. The F_1 was sterile like the earlier one, and finally, the *Gossypium hirsutum* developed having the genome capital A capital A capital D capital D. Now let us discuss about another important manmade hexaploid.

It is a manmade allopolyploid species here basically one *Triticum* species and *Secale cereale* that is rye was crossed for some specific reason. In rye it has been found, that rye used to show relatively more cold tolerance than the wheat while, the baking properties is good in *Triticum turgidum*. So, to combine these characteristics this approach was taken by a group of scientists and they have crossed between *Triticum turgidum* and *Secale cereale*. So, from *Triticum turgidum* it is a tetraploid wheat, it is a tetraploid wheat. From/in this tetraploid species two different genomes are already there, capital A capital A and capital B capital B. Capital A capital B genome has come from two different species earlier through nature and thereafter, purposefully it was crossed with rye having the genome of capital R capital R. Ok!

Over here the chromosome number was n = 14 and here chromosome number was n = 7. So, once the cross was made the F_1 hybrid was developed, it was mostly sterile in nature and F_1 was having n = 21 because, A B R; 3 different genome came together in F_1. So, the pairing was missing during meiosis, during gamete formation. So, most of the F_1 was sterile and thereafter, chromosome number was doubled by applying colchicine, a particular chemical that is used mostly for chromosome doubling, we have discussed earlier. So, applying colchicine the chromosome doubling occurred and finally, A A B B R R genome was developed, and the Triticale a manmade cereal was developed, it is hexaploid in nature, it is allohexaploid because two eventually basically three different genomes are coming together over here.

And once this hexaploid Triticale was formed, it was eventually fertile in nature, because it was behaving like a amphidiploid and it is behavior was different from both of their parents, its seeds are mostly shiny in nature, and they are basically silvery in color mostly and they are hardy in nature compared to the *Triticum turgidum* as well as *Secale cereale*. Now let us discuss the morphological and cytological features of allopolyploids. First it is very difficult to predict the precise combination of characters that would appear in this species. As we have started our discussion with *Raphanobrassica*, there the attempt of the scientist was to get the root like *Raphanus sativus* and leaf like *Brassica* species, but whatever they got it was just reverse. So, it is very difficult to predict that what should be the final outcome of this combination of this genetic combination.

Next one the natural distribution of allopolyploids is usually different from those of ancestral diploid species, because new sets of genes coming together and a lot of intergenic interactions are taken place, inter allelic interactions are taken place and the epistasis is observed and finally, their growth behavior their growing conditions might vary. So, their natural distribution is also different from the originator species. Next one the evolution of allopolyploidy in nature has been favored by the new ecological areas for the establishment of allopolyploids means, it has been popularized in new areas. Like if you think, about the cotton development means, once the tetraploid cotton has been generated, some of them have been suitable in Indian condition, some of them have been suitable in American condition, but their initial progenitors the diploid cotton might be from a different place. Then many of the allopolyploids reproduce through apomixis that is, the important term in apomixis basically seed will be developed without fertilization. Ok!

So, which enable them to produce seed without fertilization, which helps them in maintaining the genetic stability and favorable traits are also maintained. Means, once the seeds will be formed, then definitely new permutation combinations within the available chromosomes will be taken place within the homologous chromosome will be taken place, but if a plant is maintained through apomixis its genetic content will not be disturbed, it will be maintained generation after generation, because no perfect meiosis is taken place for pollen grains or egg cell formation. So, those things are skipped and the genetic content remains same generation after generation through apomixis. Now interaction between the cytoplasmic factors like mitochondria and chloroplasts and the nuclear genome in allopolyploids impact their traits, that is a very important fact because from two different genome the chromosomes are coming together in F_1. So, among those two genomes one genome will be used as a female parent, and one genome will be used as a male parent. Ok!

So, the genome which will be used as a female parent therefrom, mitochondria, chloroplast most of the maternal inheritance related things will be coming. So, that might have some interaction with the nuclear genome also, and it may affect those things in the allopolyploids in trait development, in different metabolism as well as in gene regulation. This interaction affects the energy production, gene expression, cellular process contributing to the diversity and adaptation of the allopolyploid species. So, it has been found that those allopolyploids are diverse compared to the original species and they are more adaptive in nature. So, these are the few facts that allopolyploids are known as amphidiploids when they possess two sets of chromosomes from each parent species resulting in a balanced chromosome number.

Once the chromosome numbers, once the chromosomes which are coming in F_1 will be doubled, then it will behave like an amphidiploid we have mentioned earlier. And this type of polyploid arises from the hybridization of two distinct species, followed by chromosome doubling. An amphidiploid exhibits stable fertility, once the amphidiploid is formed means, each chromosome will be having its pair and it will be showing stable fertility, and they often display characteristics of both parental species. May be in F_1 condition once single set of chromosomes are there, we may not see the parental features, but once the amphidiploid is formed, we may see both parental features. Now let us discuss what might happen in an amphidiploid means, once the gametes will be produced in those amphidiploids what type of gametes might be there?

So, let us assume that two divergent plants have been crossed to develop an amphidiploid, they are highly divergent in nature. Ok! Suppose from one plant this chromosome has come, and from another plant this chromosome has come. So, they have completely different sets of genes, most of the genes are not means, they cannot pair properly. Ok! Suppose one is *Triticum* species one is *Secale* species. So, over there is no chance, there is no chance of pairing among themselves.

So, if two genomes have little similarity, then in F_1 this will be the scenario and once the amphidiploid will be formed, once the amphidiploid will be formed then, the scenario will be, the scenario will be like this in the amphidiploid. So, over here each of this chromosome will be having its pair, and this pair of chromosomes will not try to make any pairing with this set of chromosomes, right, while, this pair of chromosomes will not try to make any pairing with this set of chromosomes. So, basically each pair can separate properly during gamete formation, proper bivalents are formed that is paired chromosome at metaphase I. And over here the outcome is high fertility, and stable genetics and cytology is also observed means stability is observed there the fertility is fine, seed production is fine, but if within the two genomes, what have been crossed earlier some similarity is available. So, let us discuss this part once again suppose, from one parent this chromosome has come while, from another parent this chromosome has come. Ok!

Over here B and D genes are available while from previous parent we had A and B gene. So, now the chromosome doubling has been taken place in F_1, after chromosome doubling these things will be available. So, now let us see, what might happen during gamete formation. So, during gamete formation different scenarios might be there. So, this type of situation may raise, because if you see within these two species the B gene is available means, some genetic part is available in both the parents.

So, this type of situation may be arise the B gene coming from parent 1 and parent 2 they may try to be closer. Ok! While definitely A gene which is coming from parent 1 only, they will stay closer, and in this way the proper bivalent formation might not be taken place. So, some homology between the genomes, if it is available then, when there is a partial similarity chromosome might pair imperfectly leading to formation of quadrivalence. In this way quadrivalence like set of 4 chromosomes might occur during meiosis, and what is the outcome the reduced fertility, and specific issues in reproduction is observed due to imbalance chromosome segregation. The level of similarity between the genomes determines the regularity of chromosome pairing during meiosis. Ok!

So, if similarity is more, then the irregularity will be more during gamete formation in meiosis, ok, which will turn influence fertility, and genetic stability in the amphidiploid organism. So, allopolyploidy is the powerful tool in crop improvement offering avenues to enhance genetic diversity, develop resilient and high yielding varieties and improve the overall quality of crops, crucial for global food security and agriculture. It is although sorry, although we have attempted to develop *Raphanobrassica* the attempt was not up to the mark, but the Triticale was a success story. So, in this way using allopolyploids or using the concept of allopolyploidy the scientist can attempt different polyploid crop development for the improving the global food security and most allopolyploid. So, self-compatibility that can favor rapid reproduction while some of their parents are self-incompatible.

So, these are the role of allopolyploidy in evolution. First allopolyploids have been more successful as crop species than autopolyploids because, if you take the example of wheat, wheat is highly famous. If you see the example of cotton, that is highly famous the allopolyploids are there while, in case of autopolyploidy not too much crop is famous across the world. Some of them are mostly because banana, potato those are autopolyploids. Anyway, the allopolyploids are more successful as crop species. Then they have contributed to great extent in the evolution of plants means, if you see the natural evolution in most of the in different crops you can see their evolutionary perspectives the involvement of allopolyploidy.

Then about one third of the angiosperms are polyploid, and one third among them are allopolyploids in nature. They can be a driving force in species development, and enhances genetic diversity by merging genome from different species into a single organism, that thing have been discussed earlier. Then allopolyploidy can confer adaptive advantages, allowing organism to thrive in diverse environment. The allopolyploids can be grown in a new region, in a new area also compared to the parents from which it has been developed. So, in diverse environment they can accommodate themselves easily.

Then allopolyploids often exhibit hybrid vigor, displaying superior traits compared to their parental species. These are the natural allopolyploids, what we have discussed some of them we have discussed so far like wheat, *Nicotiana tabacum*, *Gossypium hirsutum*, then amphidiploid *Brassica* species, different *Brassica* species are there, oat those are natural allopolyploids. While artificially or manmade allopolyploids are there, like *Raphanobrassica* and Triticale. So, these are the application of allopolyploidy in crop improvement. First utilization as bridging species allopolyploid could be utilized as bridging species, by taking the genome from two different species the F_1 could be generated and eventually, by chromosome doubling we can develop the allopolyploids.

Then creation of new species could be done through this approach, then widening the base of existing polyploids, then polyploid is one of the source of variation means, if large number of genomes are there, a lot of genic interactions will be there and if mutation is taken place more variations could be generated. Then allopolyploid is one of the effective mechanisms for maintaining hybrid vigor. These are the limitations of allopolyploidy first of all, the effect of allopolyploidy cannot be predicted as we have seen in *Raphanobrassica*. So, it cannot be predicted from earlier. The newly synthesized allopolyploids have many defects like low fertility, then cytogenetic and genetic instability those type of problem might be arise in allopolyploids.

But in most of the cases if the chromosome doubling is done, if they become amphidiploids within a couple of generations these problems could be resolved. Then synthetic allopolyploids have to be improved through extensive breeding at polyploidy level. Only small proportions are promising so far what have been found by different researchers. So, these are the references of today's lecture. Thank you.