**FOREST TREE IMPROVEMENT   (2+1)**

**Class:- M.Sc (Forestry) and Ph.D (Forestry) Previous year**

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# Cell Division

Cell Division – 2 types - Direct cell division / Amitosis

- Indirect cell division - Mitosis / Equation division

- Meiosis / Reduction division.

1. Direct cell Division - Amitosis:

Cytoplasm – nucleus of a cell – divides – directly by constriction form two daughter cells.

Amitotic division – seen in – cells a lock district nuclei & CHS.

Eg: bacterial cells.

2. Indirect cell division – 2 types – Mitosis – does not involve Reduction in CHS no.

- Meiosis – Reduction in CHS no.

**Interphase:**

**1. Mitosis:**

Water flemming to red the term Mitosis – (1882) German biologist - Ist to study cell division.

Nucleus – of a dividing cell – indigo series of changes – Mitosis thus Mitosis regers only to Karyokinesis.

Occurs in all somatic cells of body.

Since equal division of nucleus followed by equal division of Cytoplasm – it is called equational division.

Suitable materials for study of Mitosis – root tips / shoot stips.

In Mitosis – 2 distinct successive process taken place.

1. Division of nucleus - Karyokinesis
2. Division of cytoplasm – Cytokinesis.

Karyokinesis / Division of nucleus:

This is a continuous of process

For the convenience of description – it is divided into several successive steps.

a) Anaphase b) Prophase

c) Telophase. D) Metaphase.

**Interphase:**

Known as DNA synthesis phase.

Convicts of 3 sub phase – G1 phase – Resting phase.

* S phase – DNA replication.
* G2 phase – resting phase replicatin.

**G1 phase:**

Pre DNA replication phase.

This is phase between telophase d.s phase.

Longert phase eg: Viciataba – 12 hours.

Protean of RNA mytherio takes phase.

**S phase:**

Next to G1 phase.

CHS & DNA replication takes phase.

Takes less time when compound to G1 phase. Eg: Vivia tala – 6 hours.

**G2 phase:**

Post – DNA replication phase.

Last stage of interphase.

Protean of RNA synthesis taken phase.

**Mitosis:**

Leads to separation of replicated DNA into 2 daughter nucleus without any recombination.

Thus the daughter nucleus have the same CHS comlin as that of parent nucleus.

**1. Prophase:**

* Its visible step in nuclear division.
* Series of changes takes place.
* The nuclear reticulam and nuclear - becomes clear - due to dehydration of nuclear sap.
* The chromatin network (woolen ball) dislocates - CHS becomes distinct. becomes shorter and thicher - due to increased condensation.
* By the middle of prophase the two chromatids of each CHS - becomes visible.
* In the beginning, the chromatids of the CHS-spirally coiled – (plecronemic coiling) but including takes place at the end of prophase.
* Each chromatids contain many deeply staining bodies - called chromonema.

At the late prophase,

* The chromatids become shorter and thicker.
* Nucleolus and nuclear membrane will disappear.

**2. Metaphase:**

* With the disappearance of nuclear membranes
* Metaphase - beging – with - appearance of spindle fibres.
* Spindle fibres - are responsible - for equal distributing of the CHS. two daughter cells.
* The movement of CHS to the middle and their orientation on the equatorial plate is termed metakinsis.
* In this stage - CHS can be easily counted and their size and shape can be determined.
* The spindle fibres - gets connected with the centromeres - called (chromosomal fibres).
* Other spindle fibres - that run between poles - without any interruption - called continuous fibres.
* The spindle attachment tegion – determines – the future shape of the CHS is rod /

J shaped / Ring shaped.

**3. Anaphase:**

* Then the centromere – of each CHS – divides – longitudinal plane and the two sister chromateids become completely free from each other.
* And migrate towards the opposite flotes.
* Centromere is the first position of the CHS – that brgins to move low order the poles.
* Here, the CHS gets more condensed – compared to metaphase CHS. And the spindle fibres that is attached with the centromere – contracts – towards the poles.

**4. Telophase:**

* Last visible stage of nuclear division.
* This stage begins when the sister chromatids of all the CHS of the cell – reaches the opposite pole.
* The CHS – begin to uncoil – become very long & Thin – appears like a coiled thin thread.
* Nucleolus reappears.
* Nuclear membarance – reorganized – around each group of CHS – in the poles.
* At the end of telophase – 2 daughter nuclei are completely organised from the 2 sets of daughter CHS.

**In terms of duration:**

Propose is the longest stage of cell division – Anaphase is the shortest.

Metaphase & Telophase are couriderally longer than Anaphase.

Metaphase is some what longer than telophase.

**Cytokinesis:**

* The division of extra nuclear protoplast – cytokinesis.
* This lappens either thro formation of cell plate in between the two newly formed daughter nucleus.
* This cell plate divides the protoplast into two resulting in two daughter cells. Enlarges in size.
* The two daughter cells – Thus contain.
* One nucleus each.
* Each nucleus having same no of CHS as that of the pacent cell.

**Genetics control of Mitosis:**

**Mitosis play – rote in the life of living organization.**

* During mitosis, the CHS split longitudinally and the Chromatics of there CHS – separate – into 2 equal groups and finally form 2 daughter nuclei.
* So, the same genetic constitution – is maintained – qualitatively as well as quantitatively in the CHS – of the 2 daughter nuclei.

**Mitosis – genetically controlled significance.**

1. After tusion of male and female gametes – zygote informed. So, Mitosis is responsible for development of zygote into adult organization.
2. Essential for normal growth & development of living organization. It gives shape to a specific organism.
3. Mitosis, in plto – leads to form of new parts – roots, leaves, stem braked. It helps in repairing of damaged parts.
4. Mitosis, leads to – production of identical progenies in veg. Propagated crops.
5. M – useful – in maintaining wraity of types – because – it leads to production of identical daughter cells & does not allow segregation and recombination to occur.
6. In animals, it helps in continuous replacement of old term's.

Eg. Blood cells.

**Meiosis:**

* Is the mechanism – where reduction in CHS no takes place. During cell division.
* Takes place before / after reproduction in the reproductive cells.
* Weisman –was the first to point out cells of CHS no (1887) in the reproductive cells. (Young anthesis)
* A diploid cell undergoes – 2 successive divisions – producing – 4 haploid cells.
* Acc to darlington (1956) – Meiosis – single CHS doubling taken place – followed by – 2 nuclear divisions.

i) Meiosis I ii) Meiosis II

**Premeiotic Interphace:**

* Stage prior to the entry of the cell to cell division.
* Consists of there phases G1 , S and G2 phase. – like Mitosis.
* Here, G2 phase is of very short duration.
* S phase occurs only once in the entire process of Meiosis 99.7% of the DNA in the nucleus is synthesized during S phase of remaining 0.3 % DNA synthesis – during zygotene stage.

## Meiosis - I

Reading in CHS no – half of the mother cell – so – reduction

Consists of 4 different phases.

1. Prophase
2. Metaphase
3. Anaphase
4. Telophase

After Interphase,

First prophase starts and Consists of 5 sub stages

**1) Leptotene:**

1. CHS – looks like – thin thread – interwoven – like a loose ball of wool.
2. CHS – scattered – through out the nucleus – in random.
3. RNA and protein synthesis takes place.
4. Chromomeres – visible – on the CHS – in the form of condensed regcons.

**2) Zygotene:**

1. Homologous CHS – begin to pair.
2. CHS – become shorter & thicker.
3. Synthesis of DNA (0.3 %)
4. Synaptonemal complex – develop & during this stage. (a protein frame work – found between paved CHS)

**3) Pachytene:**

1. CHS – look like bivalents – each bivalent – 2 chromatids thus each pain – has 4 chromotids - called as tetrads
2. Nucleolus is present – c is seen attached to CHS.
3. Formn of chiasma and crossing over takes place.

**4) Diplotene:**

1. Separation of homologous CHS – begins. It starts at centromere of moves gradually forwards the end.
2. The separating CHS – attached at some points – chiasmata these chiasmata are terminalzed lowards the end of biplotene.
3. CHS – become more condensed – become more shorter & thicker.
4. Nucleus decreases in size.

**5) Diakinesis:**

1. Starts after complete – terminalization of chiasmata is the event diplotene stage.
2. CHS – further condensed of very thick.
3. Bivalents are distributed throughout the cell.
4. Nucleolus of nuclear membrane – disappear (by the end of diakinesis)

# Metaphase I

1. The spindle fibre rgradually organizes.
2. Bivalents are arranged on the equalogical plate.
3. The untromere of each CHS – divides longitudinally.

## Anaphase - I

1. (As a result of longitudinal division, from each bivalent) one CHS move towards one pole of the other towards opposite pole. Eg; one homologous CHS – more towards one pole of other opposite pole.
2. The sister chromatids are seen attached to the centromere.
3. The homologous CHS reach the poles – at the end of this phase.

## Telophase - I

CHS – uncoil & regrouping of CHS occurs.

1. Nucleolus & Nuclear membrane reappear.
2. Two haploid daughter nuclei are formed.

## Meiosis - II

* The first nuclear division (Meiosis - I) results on reading of CHS no from diploid to haploid.
* The second nuclear division (Meiosis - II) is required to reduce the nuclear of chromatids per CHS.

**Meiosis – II differs from Mitosis in there aspects:**

1. The interphase prior to Meiosis – II is Very short. It does not have 'S' period – because – each CHS – already contains 2 chromatids.
2. The 2 chromatids in each CHS are not sister's thro out. ie., it may have some alternative segments due to recombination (Crossing over) between won sister chromstids.
3. In Meiosis II (ie., in Meiotic Meiosis ), division is with respect to haploid CHS No: Where in normal mitosis / is w.r.t diploid CHS No:

Except for this these aspects, Meiotic mitosis ie., Meiosis II is similar to normal

Mitosis. - contains all 4 stages – for Cytokinesis.

**Cytokinesis:**

Takes place after meiosis I of Meiosis II – separately sometimes it may even take place at the end of Meiosis –II

Eg. Maize after I & II

Trillium after Meiosis II only.

**Meiotic Control of Meiosis:**

* Believed – Meiosis – genetically controlled. Some of them are, ie; they are

controlled by genes.

**1. Synapsis of Exchange:**

Or pairing between homologous CHS – depend – on the presence of specific allele. When this allele is absent – synapsis is prevented between all homologous loi – no exchange occurs between homologous CHS – resulting in irregular distribution of CHS in Anaphases I.

Eg: In Drosophila's (Female) – Crossing over – does not occurs – because – the homo CHS – pair only in the Chromatic region near centromere.

This Leteochromatin region – devoid of active genes – exchange is prevented.

Wh

In female – pairing is normal.

**2. Centromere Behaviour:**

At metaphase II – centromeres of sister chromatids – lie close together when one of there faces one pole of spindle, the other one will auromatically faces the apposite fole.

In drosophila, in the presence of a particular allele, the sister centromeres spindle early at metaphase – II of orient to the spindle independently.

-So, both the centromeres orient to the same pole. However, this allele has no effect on

Meiosis I & Mitosis.

**3. Spindle shape:**

* Governed by a specific allele.
* Pressure of abnormal alleles – changes the shape of spindle – Meiosis
* A normal allele – cause the meiotic spindle – to have convergent end.

With such spindle – the CHS move to the poles in groups of are included in the telophase nuclei. But in the presence of abnormal alleles – divergent spindle leads to spread of CHS during Anaphase – hence some are left out in telophase nuclei.

1. **Spindle Orientation:**

Similar in both Meiosis I & Meiosis II – have 4 nuclease formed if in opposite – it will form cluster of 4 nuclei / cells.

**Significance of Meiosis:**

* Role – in living organization.
* Helps in – maintaining the CHS no courtant in a species. Meiosis results in production of gametes with haploid CHS no. Contain of Female & Male – leads to formn of Zygote – receives ½ CHS no from Female thus the original somatic CHS no is restored.
* Meiosis – facilitates – Segregation of independent assortment of CHS & genes.
* Recombination of genes – results in –Creation of Variability. - C is essential for evolution of new crop plants.
* In sexually reproduction crops – Meiosis – helps – for continuity of generation.

**Comparison of Mitosis / Meiosis:**

##### Similarities

1. Involves nuclear division
2. Involves spindle formation
3. Genetically controlled
4. Different successive phases
5. Involves cytokinesis at the end forming 2 daughter nuclei.

#### Dissimilarities

|  |  |  |
| --- | --- | --- |
| **SL. No.** | **Mitosis** | **Meiosis** |
| 1. | One nuclear division | Two |
| 2. | Production of 2 daughter nuclei | 4 daughter nucleus . |
| 3. | CHS no is the same (2n) | CHS no. reduced to half (n) |
| 4. | Daughter cells – identical – in structure of CHS composition | Different from mother cell in CHS no of composition |
| 5. | Occurs in somatic cells. | Reproductive issues. |
| 6. | Total DNA of nucleus replicates during sphase | 99.7 % of DNA replicates during sphase of remaining 0.3 % during zygotene stage. |
| 7. | No parieing between homologous CHS | Homologous CHS pair during pachytene. |
| 8. | Segregation of Recombination do not occurs – this by maintain purity | Crossing over taken place during pachytene – variability |
| 9. | CHS – are in the form of dyad at metaphase | Tetrad at metaphase. |
| 10. | One member of sister chromatids move to opposite pole during Anaphase. | One member of homologous CHS move to opposite pole during Anaphase I. |

**33. POLYPLOIDS AND ANEUPLOIDS- INDUCTION OF CHROMOSOME VARIATION IN TREE SPECIES**

Most plants and animals possess two sets of chromosomes in their somatic cells and are therefore called diploids (di = two, ploid = fold).

**Haploids**

Individuals with one set of chromsomes in their somatic cells are called haploids or monoploids. Haploidy in flowering plants was first recorded by Blakeslee (1937) in Datura stramonium. Since, then, haploids have been recorded in various other species.

Table 13-1. Haploids

|  |  |
| --- | --- |
| Name of species | Somatic chromosome number in haploid |
| Triticum monococcum | 7 |
| Zea mays | 10 |
| Brassica caompestris | 10 |
| Oryza sativa | 12 |

Haploids usually arise from eggs which have the reduced number of chromosomes but which have not been fertilised by the male gametes. One in every 1,000 seedlings of maize was found to be a haploid, developed from the unfertilised egg(i.e., by female parthenogenesis).

Polyembryony in plants is a possible source of haploids. Polyembryonic condition is sometimes due to the occurrence of more than one embryo sac within a ovule. Out of the four haploid megaspores derived by meiotic divisions from a single megaspore another cell, more than one way develop into embryo sacs. For instance, in rice, two seedlings arose from a single seed. One of them was a diploid and arose from a fertilised egg. The other was a haploid and arose by parthenogenesis from another egg. Besides the diploid embryo produced from the fertilised egg, haploid embryos may occasionally be produced from nuclei of the embryo sac other than the egg. Production of embryos from synergids without fetilisation is more common than production of embryos from antipodals. For instance, out of about 30,000 seeds of Gossypium hirsutum, 20 were found to give rise to twin embryos of which four were haploids.

Haploids can be obtained by anther and pollen culture using tissue culture techniques and also by wide species crosses.

Haploids are generally smaller in size than the diploids. Their guard cells are also smaller than those of the diploids. They are highly stertile because none of the chromosomes of a true haploid has a homologue. Each chromosome moves on to the equator as an univalent and passes to either pole at random. Gametes with less than the haploid number of chromosomes are formed and these are frequently inviable. A few gametes may, however, be formed as a result of all the chromosomes going to the same pole. If one egg with a haploid set is fertilized by one sperm which has also the same haploid set of chromosomes, a diploid which is homozygous for all its genes will be obtained.

Haploids may be classified into mono-haploids and poly-haploids. Mono-haploids are haploids which arise from true diploids and whose chromosomes are therefore non-homologous to one another, e.g., haploid of Zea mays. Poly-haploids are haploids which arise from polyploids, e.g., haploid of Triticum aestivum with one representative of each chromosome of the A,B and D genomes.

**Genome**

True diploids, as mentioned earlier, are those plants and animals which possesss only two sets of homologous chromosomes in their somatic cells.

The complete set of chromosomes found in the gamete of a true diploid is called a genome. For instance, Pennisetum glaucum is a true diploid which has 14 chromosomes in its somatic cells, composed of two sets of seven chromosomes each. A gamete of this plant will therefore contain one set of seven chromosomes, I, II, III, IV, V, VI and VII. This set of seven chromosomes found in the gametic is called a genome and if this is represented as A, the genomic constitution of the plant is AA.

**Basic number**

The number of chromosomes constituting a genome is called the basic number. It is the number of chromosomes found in the gamete of a true diploid.

Various species of a genus often have somatic numbers of chromosomes that are multiplies of the basic number. For instance, the species of Solanum have the following numbers of chromosomes in their somatic cells.

Table 13-2. Chromosome number of Solanum

|  |  |
| --- | --- |
| Species | Somatic number of chromosomes |
| S. chacoense | 24 |
| S.rybinii | 24 |
| S.torvum | 24 |
| S.wendlandii | 24 |
| S.xanthocarpum | 24 |
| S.medians | 36 |
| S.acaule | 48 |
| S.tuberosum | 48 |
| S.curtilobum | 60 |
| S.edinense | 60 |
| S.demissum | 72 |
| S.nigrum | 72 |

Species of Solanum which have a chromosome number of 24 are true diploids and species which have somatic numbers higher than 24, but which are multiples of 12, are called polyploids.

**Polyploids**

A polyploid (poly = many; ploid = fold) or an euploid is an individual whose somatic cells possess more than two sets of chromosomes and whose somatic number of chromosomes is an exact multiple of the monoploid (or haploid or basic) number.

The level of polyploidy is based on the number of times the somatic numbers are multiples of the basic numbers (x).

**Polyploidy in Solanum**

|  |  |  |  |
| --- | --- | --- | --- |
| Name of species | Somatic number(2n) | Multiples of basic numbers (x = 12) | Level of ploidy |
| S. chacoense | 24 | 2x | Diploid |
| S. medians | 36 | 3x | Triploid |
| S. tuberosum | 48 | 4x | Tetraploid |
| S. curtilobum | 60 | 5x | Pentaploid |
| S. demissum | 72 | 6x | Hexaploid |

**Classification of polyploids**

|  |  |  |  |
| --- | --- | --- | --- |
| Polyploids | | | |
| Based on origin | | Based on genome | |
| Natural | Induced | Autopoly-ploids | Allopoly-ploids |

**Natural polyploids**

Polyploids arise in nature most commonly by failure of meiosis that result in the formation of unreduced gametes. They may also be formed from somatic cells in which a failure of mitosis has resulted in doubling of the chromosome complement. Gametes produced by flowers on such polyploid shoots have the same number of chromosomes as that in the somatic cells of the original plant and will, on fertilisation, give rise to polyploids.

The cultivated banana and tobacco are examples of natural polyploids.

**Induced polyploids**

When it was observed that polyploids, in general, were larger and more vigorous than the diploids, interest in the induction of polyploids increased. One of the earliest methods of obtaining polyploids was by temperatures for short periods. Doubling in maize was induced by this method. Shoots that arise near the union of stock and scion in grafts, and shoots that arise from decapitated plants were also observed to be polyploids. Besides heat treatment, cold treatment and irradiation with X-ray and gamma rays also induce polyploidy. Polyploids were induced in tomato by cutting off the tops of growing plants and by treating the shoots with indole acetic acid to stimulate callus formation. A number of chemicals like acenapththene, chloral hydrate, nitrous oxide,8-hydroxy quinoline, ethyl mercury chloride, hexachloride, cyclohexane and sulphanilamide also induce polyploidy. None of the above methods, however could be considered successful form an experimental point of view. But with the independent and almost simultaneous discovery in 1937 by Blakeslee and by Nebel that the alkaloid colchicum autumnale of family Liliaceae, was very effective in doubling the chromosome number, an easy and effective methods for production of polyploids became available to the plant breeders.

Colchicine brings about doubling of chromosomes by acting on the spindle mechanism. During normal mitosis, each chromosome divides longitudinally into two chromatids, each of which goes to one pole. Colchicine treated cells undergo a peculiar mitosis called cilchicine mitosis (c-mitosis). The chromosomes behave normally till the end of prophase. The nuclear membrane then disappears but no spindle is formed. The two chromatids of each chromosome separate at the centromere but do not go to the poles. A nuclear membrane is formed around the whole group of chromosomes resulting in the formation of a single nucleus with 4x chromosomes instead of two daughter nuclei, each with 2x chromosomes.

Colchicine may be applied as aqueous solutions or as pastes mixed with lanolin. It can be applied to shoot apices of young seedlings, as for instance, in watermelon where one drop of 0.2 to 0.4% aqueous colchine is applied to growing tips daily for two successive days. Or, young seedlings can be immersed in a solution of colchicine, as for example, in beet where seedlings with coleoptiles and roots a few millimetres long are immersed in a thin layer of 0.1% aqueous colchicine for three hours at 27oC. colcemid is a synthetic equivalent of colchicine available for ploidy induction.

Cell, tissue and protoplast cultures also induce polyploidy.

Triploid sugar beet, triploid seedless watermelon, autotetraploid rye and Triticale are examples of induced polyploids.

**Autopolyploids**

Autopolyploid is a polyploid arising through multiplication of a single genome. In other words, it is a polyploid of a single species and all its sets of chromosome are identical or very closely similar to each other. If **A** refers to a basic set of chromosomes (i.e., a ganome), an autotriploid may be denoted as **AAA** and an autotetraploid as **AAAA**.

Some of the crop plants that are believed to be autopolyploids are listed below:

Table 13-4. Autopolyploid crops

|  |  |  |
| --- | --- | --- |
| Name | Somatic chromosome number | Level of ploidy |
| Banana | 33 | 3 x |
| Alfalfa | 32 | 4 x |
| Groundnut | 40 | 4 x |
| Coffee | 44 | 4 x |
| Potato | 48 | 4 x |
| Sweet potato | 90 | 6 x |

The characteristics of autopolyploids are as follows:

Polyploids have larger cells than diploids. Their pollen grains and guard cells of the stomata are larger in size than those of the diploids. This larger cell size contributes to larger plant size and higher yields. Polyploids have generallly larger, thicker and darker green leaves, and bigger flowers, fruits and seeds than the diploids. In tomato, the vitamin content in increased by polyploidy. In tobacco, the nicotine content increases and in beet, the sugar content increases.

In each genus, there is an optimum level of polyploidy beyond which growth may be depressed with increasing number of chromosomes. In most genera, this optimum appears to be achieved at the triploid or the tetraploid level but in some genera, octoploids or even higher polyploids are vigorous.

The growth rate of autopolyploids is generally slower than that of the diploids. Flowering is often delayed in polyploids.

Autopolyploids are generally lower in fertility than the diploids.

**Allopolyploids**

Allopolyploids are polyploids containing genetically different chromosome sets from two or more species. they usually arise form hybrids between more or less distantly related species. Stebbins calls them as `**true allopolyploids**' or `**genomic allopolyploids**' (in contrast to `segmental allopolyploids') and defines them as polyploids derived from hybridisation between two or more distantly related species whose chromosomes are so different that they are unable to pair in the diploid hybrid. If the two sets of chromosomes (i.e., genomes) in the two parents of the hybrid are represented by **AA** and **BB** respectively, the two sets of chromosomes of the diploid hybrid can be represented by **AB**. This diploid hybrid is completely sterile because the chromosomes are not homologous to one another and there is no regular pairing at meiosis. When the chromosome number is doubled, the tetraploid will have a genomic constitution represented by **AABB**. It does not have four homologous sets of chromosomes like an autotetraploid but has two non-homologous sets, each represented twice. Each chromosoe from the set **A** of the tetraploid will have a homologous partner from the second set of **A** and similarly each chromosome from the set **B** will have a homologous partner from the second set of **B**. it does not form quadrivalents, trivalents and univalents like an autotetraploid but forms only bivalents like a true diploid. Disjunction of the bivlanets is normal and the tetraploid is often fully fertile. An allotetraploid is called **amphidiploid** because it behaves like a diploid, even though it is a tetraploid.

A classical example of an intergeneric amphidiploid is Raphanobrassica produced by Karpechenko (1928) by crossing the radish, Raphanus sativus (2n = 18) with the cabbage, Brassica aleracea (2n = 18). The hybrid showed 18 chromosomes, of which 9 were from radish and 9 from cabbage and was sterile. At meiosis the chromosomes did not pair but distributed themselves at random in the first division. A few seeds were however produced by chance in the F1 plants and examination of the plants raised from these seeds showed that they contained 36 chromosomes instead of 18 as in the hybrid. These plants were therefore tetraploids. At meiosis, pairing was regular and the plants were fertile. Raphanobrassica is thus an allotetraploid derived by doubling of the chromosomes in the gametes of the diploid hybrid, unreduced female gametes being fertilised by unreduced male gametes. Unfortunately is combined the uneconomic features of both parents, viz., the roots of cabbage and the leaves of radish.

Some of the crop plants that are believed to be allopolyploids are listed below:

Table 13-5. Allopolyploid crops

|  |  |  |
| --- | --- | --- |
| Name | Somatic chromosome number | Level of ploidy |
| Gossypium hirsutum | 52 | 4 x |
| Gossypium barbadense | 52 | 4 x |
| Nicotiana tabacum | 48 | 4 x |
| Triticum aestivum | 42 | 6 x |
| Saccharum officinarum | 80 | 8 x |

**Polyploids in the Plant Kingdom**

Evolution polyploids is much more widespread in the plant kingdom than among animals. Polyploid is rare in fungi, but is recorded in some group of algae and bryophytes. High degree of polyploidy is found among pteridophytes, such as Psilotum, Equisetum, Lycopodium, Selaginella, Isoetes, Ophioglossum and Osmund. The highest recorded polyploidy on ferns is in Ophioglossum reticulatum, which shows 630 bivalents at meiosis (2n = 1260).

Polyploidy in gymnosperms is rare. The only gymnosperm genus in which polyploidy seems to have played a major evolutionary role is the peculiar desert genus Ephedra, eight of its species being tetraploids.

The prevalence of polyploidy in angiosperms varies greatly from family to family and even from genus within the same family. According to Stebbins (1971), 30 to 35 per cent of all species of flowering plants have gametic chromosome numbers that are multiples of the basic number of the genus and are hence **"straight polyploids”**. Grant (1971) working on the assumption that species with numbers higher than n = 13 are polyploids estimated that 47 per cent of all angiosperm species are polyploids (4 per cent of dicytoledons and 58 per cent of monocotyledons). Among angiosperm families, higher frequencies of polyploids occur in Ranunculaceae, Polygonaceae, Crassulaceae, Rosaceae, Malvaceae, Araliaceae, Graminae and Iridiaceae.

The percentage of polyploid species in the total angiosperm flora increases with latitude. In Eurasia and the Artic, the frequency of polyploids goes up from 37 per cent in Sicily and the Artic, to 57 per cent in Sweden and Finland, 71 per cent in Iceland and 86 per cent in Pearyland (latitude 82 - 84o). polyploids are better adapted to cold and other extreme conditions.

Among angiosperms, perennial herbs have the highest percentage of polyploids while annuals and woody plants show significantly lower percentage (Muntzing, 1936; Stebbins 1938). Grant (1971) listed the conditions that favour successful speciation by allopolyploids as 1) a long life cycle usually combined with some method of vegetative reproduction, 2) the existence of primary speciation combined with chromosomal rearrangement and 3) frequent spontaneous interspecific hybridization.

Polyploidy a highly variable role in the evolution of plant genera. On the one hand, in genera in which most of the species are diploids, but a small numbers are tetraploids, the role of polyploidy is rather minimal. On the other hand, in genera in which all the species are polyploids, the diploids have become extinct. Polyploids, especially higher polyploids would not be sensitive to loss or gain of one or even several chromosomes. The vast majority of plant polyploids seem to carry complete genomes with no chromosomes missing or in excess. One of the mostremarkable polyploid complexes that have been studied is the North American genus Claytoniana (Portulacaceae). This includes diploids with 2n = 12, 14 and 16 and polyploids with 2n = 17 through 37, 40, 42, 44, 46, 48, 50, 72, 81, 85, 86, 87, 91, 93, 94, 96, 98, 102, 103, 104, 105,110, 121, 173,177 and 191 (Singh et al., 1988).

**Role of polyploidy in evolution of species**

Polyploidy has played a very important part in the evolution of many of our cultivated species. a few examples to illustrate the role of allopolyploidy in the origin of species are given below:

**Polyploidy in wheat**

The species of Triticum can be grouped, according to the number of chromosomes, into the diploid (Einkorn) group (2n = 14), the tetraplid (Emmer) group (2n = 28) and the hexaploid (Vulgare) group (2n = 42).

Table 13-6. The species of Triticum

|  |  |
| --- | --- |
| Species | Somatic number (2n) |
| T. boeoticum (=aegilopoides), Wild einkorn | 14 |
| T. monococcum, Cultivated einkorn | 14 |
| T. dicoccoides, Wild emmer | 28 |
| T.timopheevi | 28 |
| T.ducoccum, Cultivated emmer | 28 |
| T. durum, Macaroni Wheat | 28 |
| T. turgidum | 28 |
| T. turanicum (-orientale) | 28 |
| T. polonicum | 28 |
| T. carthlicum (=persicum) | 28 |
| T.aestivum s. sp. Spelta | 42 |
| Macha | 42 |
| Vavilovi | 42 |
| Compactum, Club wheat | 42 |
| Sphaerococcum, Indian dwarf wheat | 42 |
| Vulgare, Common bread wheat | 42 |

It is believed that the teraploid group arose as an amphidiploid from the hybrid between the diploid wheat (with genomes **AA**) and an unknown species (with genomes **BB**). The hexaploid group is believed to have originated from a hybrid between a tetraploid wheat (genomes, **AABB**) and Aegilops speices (2n = 14; genomes **DD**) by doubling of the hybrid. Kihara in Japan and McFadden and Sears in the U.S.A. have succeeded in synthesising a hexaploid wheat by crossing the emmer wheat (T. dicoccoides) with Aegilops squarrosa (2n = 14) and then doubling the chromosomes of the hybrid. The synthesized species resembled the common bread wheat and, when crossed with it, gave fertile offspring with regular meiosis.

McFadden and Sears (1946) were successful in crossing tetraploid wheat (2n = 4X = 28) with Aegilops squarrosa (2n = 14) and showed that when the triploid product was treated with colchicine, the synthetic hexaploid so formed resembled hexaploid wheat. Sarkar and Stebbins (1956), after studying the pattern of variation in Triticum and Aegilops, considered Aegilops speltoides as the most likely donor of the **B** genome.

The probable origin of the hexaploid wheat may be summarised as follows:

|  |  |  |  |
| --- | --- | --- | --- |
| T. boeoticum (or T. monococcum) | | Ae. Speltoides | |
| 2n = 14 (**AA**) |  | X | 2n= 14 (**BB**) |
|  |  | F1  2n = 14 (**AB**) |  |
|  |  | Amphidiploid  2n = 28 (**AABB**) | X Ae. Squarrosa  2n = 14 (**DD**) |
|  |  |  | F1  2n = 21 (**ABD**)  hexaploid wheat  2n = 42 (**AABBDD**) |

**Polyploidy in cotton**

The species in Gossypium have either 26 or 52 chromosomes in their somatic cells and can be classified under diploids or tetraploids as follow:

Table 13-7. the species of Gossypium

|  |  |
| --- | --- |
| Species | Distribution |
| DIPLOIDS 2n = 26 | |
| G. arboreum (cultivated) | Asia |
| G. herbaceum (cultivated) | Asia |
| G. anomalum | Africa & Arabia |
| G. triphyllum | Africa & Arabia |
| G. stocksii | Africa & Arabia |
| G. areysianum | Africa & Arabia |
| G. somalense | Africa & Arabia |
| G. sturtii | Australia |
| G. robinsonii | Australia |
| G. aridum | America |
| G. armourianum | America |
| G. harknesii | America |
| G. klotzschianum | America |
| G. trilobum | America |
| G. gossypioides | America |
| G. thurberi | America |
| G. raimondii | America |
| TETRAPLOIDS 2n = 52 | |
| G. barbadense (cultivated) | America |
| G. hirsutum (cultivated) | America |
| G. tomentosum | America |

All the Old World species have 26 large chromosomes in their somatic cells. The New World species with the exception of G. barbadense, G. hirsutum and G. tomentosum also have a somatic number of 26 chromosomes but their chromosomes are smaller than those of the Old World species. the two cultivated New World species G. barbadense and G. hirsutum and one wild species endemic in Hawaii, G. tomentosum have 52 chromosomes in their somatic cells, of which 26 are large and 26 are small. Skovsted (1937) therefore postulated that the tetraploid New World cottons arose by amphidiploidy from a hybrid between an Old World and a New World species. Proof for the hypothesis was obtained in 1940 when Harland and Beasley independently synthesized an amphidiploid by treatment of the sterile hybrid G. arboreum x G. thuberi. Though the synthesized tetraploid was partially male sterile, giving hybrids that were highly fertile and in whose pollen mother cells, the chromosomes were generally found to pair as bivalents.

It is, however, not clear how a species now confined to the Old World could have hybridized with a species confined to the New World. Hutchinson and Stephens suggest that the cultivated Asiatic cottons were carried by an early civilization to the New World and that natural hybridization of the cultivated crop with a neighbouring wild American species gave rise to the first amphidiploid. They postulate that the tetraploid New World cottons have originated by amphidiploidy from a hybrid between the cultivated Asiatic species G. arboreum and the wild South American species G. raimondii.

The probable origin of the tetraploid New World cottons is as follows:

|  |  |  |
| --- | --- | --- |
| G. arboreum  2n = 26 (**AA**) | X | G. raimondii  2n = 26 (**DD**) |
|  | F1  2n = 26 (**AD**) |  |
|  | Tetraploid cotton  2n = 52 (**AADD**) |  |

**Polyploidy in tobacco**

Nicotiana tabacum (2n = 48) is believed to be an allotetraploid derived from the hybrid between N. sylvestris (2n = 24) and N. tomentosiformis (2n = 24) due to the following reasons:

When N. sylvestris is crossed with N. tabacum, the hybrid has 12 chromosomes from the former and 24 chromosomes from the latter. This hybrid forms 12 bivalents and 12 univalents at meiosis. Evidently, the 12 chromosomes from N. sylvestris pair with 12 chromosomes from N. tabacum to form 12 bivalents. The other 12 chromosomes from N. tabacum remain as univalents. Out of the 24 chromosomes of N. tabacum, 12 are thus homologous with the 12 chromosomes (i.e., the genome **A**) of N. sylvestris.

During meiosis in the F1 of a cross between N. tomentosiformis and N. tabacum,12 bivalents and 12 univalents are seen. The 12 chromosomes of the former pair with 12 chromosomes of the latter, leaving the other 12 chromosomes of N. tabacum, as univalents. Out of the 24 chromosomes of N. tabacum, 12 are thus homologous with the 12 chromosomes (i.e., genome **B**) of N. tomentosiformis.

In the F1 of a cross between N. sylvestris and N. tomentosiformis, there are 24 univalents showing that the chromosome complement (i.e., genome **A**) of N. sylvestris is not homologous with the chromosome complement (i.e., genome **B**) of N. tomentosiformis.

In N. tabacum pairing at meiosis results in the regular formation of 24 bivalents. This shows that the 48 chromosomes of N. tabacum are composed of 12 pairs from N. sylvestris and 12 pairs from N. tomentosiformis.

An allopolyploid aritifically produced from the hybrid between N. sylvestris and N. tomentosiformis has a phenotype very similar to that of N. tabacum. Although female sterile, it is male fertile and crosses readily with naturally occurring N. tabacum giving fertile hybrids.

**Polyploidy in mustard**

Brassica juncea is another example of a crop plant originating through polyploidy.

The hybrid between B. juncea (2n = 36) and B. campestris (2n = 20) has 28 chromosomes of which 18 are from the former and 10 from the latter. At meiosis, it shows 10 bivalents and 8 univalents. Evidently the 10 chromosomes of B. campestris pair with 10 chromosomes of B. juncea, leaving the other 8 chromosomes of B. juncea as univalents.

The hybrid between B. juncea and B. nigra (2n = 16) has 26 chromosomes. At meiosis it shows 8 bivalents and 10 univalents. The 8 bivalents are formed by the association of the 8 chromosomes of B. nigra with 8 chromosomes of B. juncea. The other 10 chromosomes of B. juncea constitute the 10 univalents. This shows that B. juncea is a natural amphidiploid (**AABB**) combining the basic sets of B. campestris (**AA**) and B. nigra (**BB**).

Ramanujam and Srinivasachar synthesized B. juncea from a cross between B. campestris and B. nigra. The F1 of a cross between these two species had 18 chromosomes in its somatic cells. It was highly sterile. One of the buds of this plant was treated with colchicine. There was good seed-set and progenies raised from the seeds were fertile. They closely resembled the naturally existing B. juncea and crossed readily with it.

The probable origin of B. juncea can be summarised as follows:

|  |  |  |
| --- | --- | --- |
| B. campestris  2n = 20 (**AA**) | X | B. nigra  2n = 16 (**BB**) |
|  | F1  2n = 18 (**AB**) |  |
|  | B. juncea  2n = 36 (**AABB**) |  |

**Aneuploids**

An aneuploid is an organism whose somatic chromosome number is not an exact multiple of the monoploid number. Thus, a **nullisomic** is an individual in which both members of one pair of chromosomes are missing from the normal complement of the somatic cells (2n - 2). A **monosomic** lacks one chromosome of the normal complement of the somatic cells (2n - 1). A **trisomic** is an individual with one chromosoem more than the normal complement of the somatic cells (2n + 1). A **tetrasomic** is an organism with one pair of chromosomes more than the normal complement of the somatic cells (2n + 2).

In a diploid, the two members of a pair of homologous chromosomes regularly segregate during meiosis and gametes, each with a haploid set of chromosomes, are formed. The occasional failure of the homologous chromosomes to segregate at meiosis, a phenomenon known as non-disjunction, results in the formation of gametes with one or more chromosomes less than or more than the haploid set. Such gametes on fertilisation give rise to aneuploids. Aneuploids are also seen among the progeny of crossed in which one, or both, of the parents is polyploid.

Aneuploids are usually less vigorous than their diploid progenitors presumably because of physiological disturbances that are associated with unbalanced numbers of chromosomes. In general, aneuploids are viable only in species with polyploid ancestry. Another characteristic of aneuploids is their high sterility resulting from irregular meiosis.

**Monosomics**

A monosomic is an individual that lacks one chromosome of the normal complement of somatic cells (2n - 1).

The characteristics of a monosomic are similar to those of a deficiency. If the lost chromosome is one that is not absolutely essential for the organism, it may survive but if the lost chromosome is one that is very important, it may not live. Bridges discovered Drosophila flies with only one dot-like fourth chromosome. Hapla IV flies have high mortality and reduced fertility. XO flies have been found but they are sterile. Haplo II and Haplo III types have not been found in Drosophila.

Loss of one chromosome in normal diploid plants may result in lethality. Thus, for example, monosomics are inviable in Datura stramonium. Polyploid plants, however, have been found to tolerate the loss of one chromosome. Twenty- four different monosomics, each lacking a single different chromosome of the normal complement, have been isolated in Nicotiana tabacum which is a tetraploid with 2n = 48. These 24 monosomics are morphologically distinct from each other and from the disomic (i.e., the normal plant with 4 bivalents at meiosis). In hexaploid wheat (2n = 42), 21 different monosomics have been isolated by Sears.

Monosomics produce two kinds of gametes, one kind with n chromosomes and the other kind with n - 1 chromosomes. When selfed, monosomics, therefore, produce normal (i.e., disomic), monosomic and nullisomic offspring.

**Nullisomics**

A nullisomic is an individual that lacks both members of one specific pair of chromosomes (2n - 2).

Nullisomics are inviable in some species like Nicotiana tabacum, but in other species like Triticum aestivum, they are viable. In the Chinese Spring variety of wheat, Sears established 21 nullisomic lines (2n = 40), each lacking a single pair of chromosomes of the normal complement of the somatic cells. Different nullisomics are morphologically different from one another and from the normal Chinese Spring. They are reduced in size and vigour and are highly sterile. One selfing, they produce only nullisomics as their gametes contain only n - 1 (i.e., 20) chromosomes each.

**Trisomics**

A trisomic is an individual with one chromosome more than the normal complement of the somatic cells ( 2n + 1 ).

In general, an extra chromosome does not produce so striking an effect as a missing one. In wheat, trisomics ( 2n = 43) occur but they are nearly indistinguishable from normal plants (i.e, disomes with 2n = 42). Blakeslee has isolated 12 different trisomics in Datura stramonium (2n = 24), each having in triplicate a single different chromosome of the normal set. These trisomics differ morphologically from one another and from the diploid form. Bridges discovered Drosophila flies with three dot-like chromosomes (Triplo IV) or three X chromosomes. Triplo II and Triplo III flies are inviable.

Although trisomics give rise to two kinds of gametes, one kind with n chromosomes and the other kind with n + 1 chromosomes, they tend to be somewhat more stable genetically than monosomics.

**Tetrasomics**

A tetrasomic is an individual with two chromosomes more than the normal complement of the somatic cell (2n + 2).

In a normal tetrasomic, two units of the same chromosome will be found besides the normal diploid number. If two different chromosomes (say chromosome No.1 and chromosome No.2) are present besides the normal diploid number, it is called a double trisomic (2n + 1 + 1). During meiosis a quadrivalent is formed besides the bivalents in a tetrasomic, while two trivalents and two bivalents are formed in a double trisomic.

Tetrasomics produce gametes with n + 1 chromosome and when crossed with normal diploids (2n), they produce high frequency of trisomics.

Nullisomic analysis helps to identify genes with specific chromosomes in a polyploid species or to substitute chromosomes containing a specific gene or genes from other varieties or related species to a polyploid species.

**34. PRINCIPLES OF TREE CYTOLOGY AND GENETICS**

## All organisms, including those below the stage of chromosome development, characterized by two qualities, namely, replication or genetic constancy, and mutation or genetic change. Because of mutation, organisms are represented in nature by populations of genotypes. From the onset of life there is an interaction of heredity and environment, and the environmental conditions under which organisms live are subject to change. Because different populations contain individuals that are more or less well adapted to specific environments, the genetic composition of populations becomes altered as a result of natural selection. If the environmental stresses are more severe than the genetic possibilities of a population or species, the population or species will disappear and be replaced by others.

The genetic composition of a population of higher organisms changes because of mutation and recombination. In mutation, the genes or molecules of heredity are changed in various ways and often in their normal order on the chromosome. The chromosomes form linkage groups which limit the possibilities for recombination but, because of crossing-over, linkage groups are broken thereby increasing potential recombination during sexual reproduction.

During the differentiation of cells, the hereditary material becomes concentrated on the chromosomes in the nucleus, while the physiological and developmental activities become centered in the cytoplasm (Figure 1). This does not imply physiological inactivity on the part of the nucleus, nor lack of hereditary information in the cytoplasm; indeed, the genes of the chromosomes are the source of biochemical instructions to the cytoplasm, and in the cytoplasm there are "plasmagenes" or "plastogenes" that act as independent hereditary units.

### 

### Cytology of forest trees

This chapter deals with forest trees and their cytogenetic behavior. It will be evident from the introductory discussion that the past history of a species or genus is of basic importance for its present genetic constitution, its population structure, its polymorphy and its distribution. There are also fundamental differences between species, genera and families in their cytological characters. The differences of chromosome behavior are related to

1. the basic chromosome number;  
2. chromosome size and structure; and  
3. degree of polyploidy.

These problems have been discussed in considerable detail by Gustafsson (1960*a*), with reference to the pioneer research work on tree cytology carried out by K. and H. J. Sax in the early 1930s.

***Basic chromosome number***

In gymnosperms the basic numbers (x) are 7 (*Ephedra*), 8 and 9 (several genera of *Cycadaceae*), 10 (*Sciadopitys*), 11, 12 and 13 (numerous genera); they may also reach higher values such as 19 and 20 (*Podocarpus*) and 22 (*Pseudolarix*). The last-mentioned numbers are no doubt secondary, that is, derived, and may in several cases have resulted from some sort of chromosome breakage or translocation.

The angiosperm tree genera belong to several different families of the natural system. The chromosome differences are consequently complex and varied. The basic numbers range from 6 and 7 (*Cassia*), through 8 (*Carpinus*), 9 (*Hevea*), 10 (*Cornus*), 11 (*Corylus* and *Eucalyptus*), 12 (*Quercus*), 13 (*Acer* and *Ficus*), 14 (*Alnus* and *Betula*) to 19 (*Populus*), 21 (*Platanus*), 23 (*Fraxinus*) and 41 (*Tilia*).

Gymnosperm and angiosperm genera also differ in average chromosome size. This does not mean that the small-chromosomed angiosperms have fewer genes than the large-chromosomed gymnosperms; it signifies only that the extragenic material of the gymnosperm chromosomes has undergone extraordinary development. Selective factors can apparently increase or decrease chromosome size, according to the type of environment or, to follow the Danish botanist Raunkiaer, to the life form of the species. See, for instance, Babcock (1947), Stebbins (1950) and Gustafsson (1951, 1960*a*).

Stebbins has pointed out that many woody angiosperms possess smaller chromosomes than do the related herbaceous species. This difference may depend on the fact that the angiosperm wood contains fiber cells from small-sized cambia initials or, according to Stebbins, on the true or false presumption that woody plants in general require a genetic system with a maximum amount of genie recombination, such a system being favored by many and small chromosomes. The principal gymnosperms, the *Coniferales* lack wood fibers and possess cambial initials about equal in size. They have, as discussed above, a fairly high but, when compared with the angiosperms, still distinctly low basic chromosome number with large-sized chromosomes. Presumably, Stebbins says, the reduction in chromosome size appeared early in the evolution of woody angiosperms.

There is an interesting connection between chromosome size and radiosensitivity demonstrated in recent years by the research of Sparrow and his coworkers. Sparrow and Miksche (1981) showed a good positive correlation between growth inhibition by ionizing radiation and the size of the interphase nuclei in shoot meristems. The effect of chromosome size on radiosensitivity in forest tree species was verified by Gustafsson and Simak (1968), and Wettstein *et al.* (1969) who compared radiation effects on species of *Populus*, *Pinus*, and *Picea*. Members of the *Pinaceae* have large nuclei when compared to angiosperms and the nuclear volume of the pines is approximately five times that of the oaks (*Quercus* spp.) although both genera have a somatic number of 2n = 24. This might explain the greater radiosensitivity in the *Pinaceae*.

Since Gustafsson and Simak (1968) reported the high sensitivity of pine and spruce to radiation, considerable information has accumulated. Pedigo (1980, 1982) and Platt (1983) have described the effects on *Pinus* *taeda*, Sparrow *et al.* (1963) on *Pinus* *strobus*, Mergen and Stairs (1982) on *Pinus* *rigida*, and Brandenburg *et al.* (1962) on *Pinus monophylla.*

Of considerable interest are the effects of low-level chronic radiation on pine trees. Pinus rigida trees have been killed after an exposure of five years to  -rays at the rate of not more than 8 r per day during eight months of each year. Quercus trees exposed to the same conditions survived this chronic gamma radiation, probably because of their smaller nuclear volume. However, the R1 progeny from both genera was much more variable than the control, reflecting genetic effects that had occurred in the chronically irradiated trees. This suggests that an appreciable number of genetic and physiological changes can occur in trees as a result of cumulative low-level chronic radiation.

*Polyploidy*

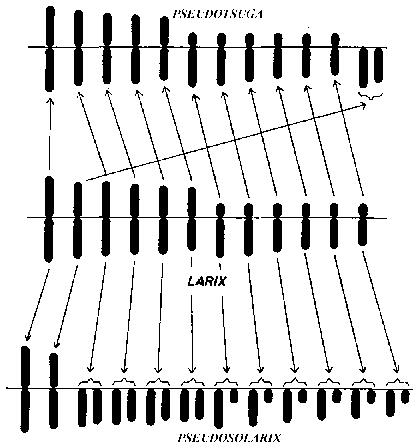
Only few genera of gymnosperms contain polyploid species. Examples are *Ephedra, Gnetum*, and *Welwitschia*. *Juniperus chinensis* tetraploid and *Sequoia sempervirens* is a naturally occurring hexaploid species. Although polyploidy does not play a significant part in the variation pattern of the *Pinaceae*, polyploid plants are occasionally found in nurseries and in nature. Aneuploid and mixoploid conditions were found in dwarf *Picea* *abies* seedlings (Kiellander, 1950; Illies, 1959) and a twin seedling of *Abies* *firma* was found to be tetraploid (Kanezawa, 1949). There are isolated reports of natural polyploidy in *Larix*. Christiansen (1950) located a mature tetraploid *Larix decidua*, and Chiba and Watanabe (1962) found among 2-year-old transplants of *Larix leptolepis* 8 polyploid seedlings - 2 had diploid roots, while the remaining 8 were all tetraploid. A single tree that arose from a cross between *Larix decidua* and *L. occidentalis* was triploid (Larsen and Westergaard, 1938). Spontaneous polyploid or mixoploid trees have been reported in four species of pine. Zinnai (1953) located 5 tetraploid *Pinus* *densiflora* seedlings; in *Pinus elliottii* mixoploid seedlings with 2n, 3n, and 4n chromosome complements were described by Mergen (1960); the presence of polyploidy in *Pinus sylvestris* in Sweden was reported by Johnsson (1959); and Nishimura (1980) described a tetraploid seedling of *Pinus thunbergii* that arose from a all-embryonic seed.

Gymnosperm species have been made polyploid by colchicine treatment (Merger, 1959). Polyploidy was successfully induced in all species attempted, and the overall changes in the seedlings or trees were similar. In general, the needles were shortened and thickened, the number of cells was reduced, branching was coarser, flowering was suppressed, and dwarfing of the trees was common. With most species tetraploids are not considered desirable, but they are of use as an intermediate step in the production of triploids.

Efforts to bypass the tetraploid sporophyte stage have been made by treating microsporangiate strobili of *Larix leptolepis* (Illies, 1956) and *Pinus nigra* and *Pinus mugo* (Mergen, 1959) during microsporogenesis. Diploid pollen grains were produced but no results from the progeny of this type of pollen are available. This method is promising, however, and will undoubtedly receive further attention. Further information about polyploidy in gymnosperms is given by Gustafsson (1960*a*), Mehra (1960) and Mergen (1963).

Natural polyploidy often arises after hybridization between different species or populations with the taxonomic status of species, and the subsequent doubling of the chromosome number, owing to the formation of unreduced gametes (a condition known as amphiploidy or allopolyploidy). Such a type of polyploidy is common among angiosperm crop plants (*Nicotiana, Gossypium, Triticum, Brassica*) and also among wild species (*Galeopsis Rubus, Poa*) and new combinations can be produced artificially, an example being *Triticale* which is a new "genus" combining *Triticum* and *Secale*. In numerous other instances, polyploidy is intraspecific in origin (the term used being autopolyploidy). Limits between allo- and autopolyploidy are fluid (Müntzing, 1938). The genus *Dactylis* is interesting in this respect since the naturally occurring tetraploids are often considered to be interspecific polyploids, although the corresponding diploids are no doubt closely related (Müntzing, 1956).

**FIGURE 2 - Karyotype evolution: chromosome changes during evolution illustrated by the karyotypes (idiograms) of Pseudotsuga, Larix and Pseudolarix.**



An interesting case was reported by Wright (1969a) in white ash, *Fraxinus* *americana*, which is divided into three "ecotypes," one northern (2n = 46), one intermediate (containing polyploidy) and one southern (with 2n = 46, 92, 138). The pumpkin ash, *Fraxinus* *tomentosa* is a rare hexaploid species (2n = 138), probably derived from a cross between a diploid green ash and a tetraploid white ash (Wright, 1959b). In *Fraxinus*, according to these analyses, both autopolyploidy and amphiploidy occur.

The most outstanding feature of intraspecific polyploid races consists of changes in developmental rhythm and ecological behavior, as first illustrated by Müntzing, (1938) and further elaborated by Stebbins (1950, 1956) and Müntzing, (1956, 1959). The general "gigas" appearance, the increase in vegetative growth, the alteration of incompatibility reactions and the changes in ecological requirements enable autopolyploids to extend the cultivation area of the diploids. Such polyploids are also useful in forest tree breeding, an idea put forward by Nilsson-Ehle in his early studies on the reaction and potentialities of the autotriploid giant aspen, *Populus* *tremula*. In gymnosperms, and in numerous hardwoods, allopolyploids may be even more suitable than autopolyploids for direct use in practice.

*Disploidy and secondary polyploidy*

The term disploidy (Chiarugi, 1932) signifies that different basic numbers, phylogenetically connected, occur in a genus. The term is not common in the literature but is quite useful. In tree genera disploidy is not infrequent. In the genera *Cycas* and *Microcycas*, for example, there occur the basic numbers 11, 12 and 13, which are probably derived from each other. In *Podocarpus*, with basic numbers of 11, 12, 19 and 20, some sort of chromosome breakage, leading to disploidy, probably occurs. According to Barlow (1959), the Australian genus *Casuarina* shows x = 8, 9, 10, 11, 12, 13, and so on. Even more interesting from an evolutionist's point of view is the genus *Pseudolarix*, related to *Larix*, where it seems possible to define the probable phylogenetic changes by means of chromosome analysis (Figure 2). *Pseudolarix* *amabilis* with x = 22 has two pairs of chromosomes with submedian or median centromeres and 20 pairs with almost terminal centromeres. In *Larix* all chromosomes have median, submedian or subterminal centromeres. It is feasible that *Pseudolarix* originated from *Larix* by means of chromosome breakage at the centromere regions of 10 chromosomes of the haploid set, whereas two chromosomes have remained unchanged (cf. Mergen, 1961).

According to Barner and Christiansen (1962), *Pseudotsuga* *taxifolia* has 13 pairs of chromosomes, the 2 shortest of which are telocentric, that is, they possess terminal or almost terminal centromeres. If these 2 chromosomes are regarded as being derived from a single long chromosome with a median or submedian centromere, the idiogram is quite similar to that of *Larix*. There are, in addition, other generic peculiarities which point to a fairly close phylogenetic relationship of these 2 genera.

When the idiograms of gymnosperm species and genera have been worked out in more detail, a series of conclusions relating to the connection of chromosome alterations and phylogeny will be possible.

*Nucleus and cytoplasm*

In the introduction it was pointed out that in the cytoplasm there are constituents which can also be considered self-replicating and, in a sense, independent of the nuclear genes. This fact lies behind the terms genome (the sum of nuclear genes, Winkler, 1920) and plasmon (the sum of the hereditary factors of the cytoplasm, Wettstein, 1926) as well as the less clear term plastom (the hereditary factors of the plastics, Renner, 1934, Michaelis, 1957/58, and Gustafsson and Wettstein, 1957/58). Of general interest is the plasmatic basis of male sterility in hermaphroditic species, such as maize, sugar cane, sugar beet, onion and *Dactylis*, which makes this plasmatic factor an important tool in breeding for hybrid vigor or heterosis. The situation is similar where there is differentiation into different sexes and cytoplasmic factors influence the formation of female or male sex organs (examples being *Aquilegia, Godetia, Bryonia Satureja, Cirsium* and *Streptocarpus*). In this connection, the classic studies of Correns (1908, 1916) are of great importance. The conifers are generally monoecious but in many species, such as *Pinus sylvestris*, individuals are found which are predominantly male or female. A systematic selection for dioecy may be quite useful in breeding for heterosis or hybrid vigor and the use of male-sterile individuals in crossing work. By contrast, the change from monoecy or dioecy (for instance in *Salix* or *Populus*) to hermaphroditism may be advantageous for the production of inbred lines. Such changes have been effected in hemp (Sisov, 1937; Sengbusch, 1952), with changes from dioecy to monoecy or hermaphroditism.

In the last few years there have been indications that plasmatic inheritance can be introduced into a species *via* induced mutations in nuclear genes (Figure 3). With regard to some chlorophyll lethals, for instance, nuclear mutations induce irreversible changes in the plastics or plastogenes. If the nuclear genes are then removed, the plastic breakdown persists and is transmitted plasmatically through the mother plant to the offspring (Wettstein, 1961, and unpubl., Gustafsson 1960b). It would be highly desirable if plasmatically and genically conditioned male sterility or dioecy could also be induced or isolated in tree species.

With regard to disease resistance, some data obtained by Langner (1952) indicate the occurrence of a cytoplasmic background of susceptibility to needle-cast in crossings between *Larix decidua* and *L. leptolepis*.

### Genecology of tree species

*Species and population structure*

The species is in one sense the fundamental unit of evolution. However, the definition of a species depends on the viewpoints of the observer and experimenter. In 1922 Turesson tried to make a sharp division within and between species or groups of species founded not on morphological but on biological characters. He distinguished between:

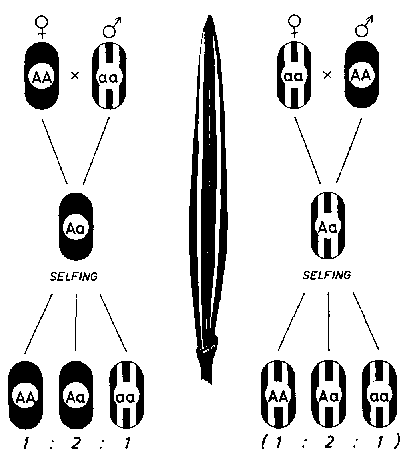
1. ecotypes, which are interfertile subunits;

2. ecospecies, which can form hybrids although with a decreased hybrid fertility and a reduced viability of the hybrid offspring;

3. coenospecies, consisting of one or more ecospecies which may exchange genes among themselves but cannot recombine with other groups of species.

Turesson's concepts were later especially advocated by Clausen, Keck and Hiesey in their outstanding studies on the Californian flora (see Clausen, 1951). However, the concepts have not met with general acceptance. For the purposes of this report it is sufficient to consider that in general a species is heterogenous and polymorphic, that it is divided into populations adapted or in the process of adaptation to various climates, sites and niches. Whether or not the populations within a species are morphologically different from one another is then of secondary importance; likewise, whether the populations form more or less sharply delimited ecotypes or constitute clines with gradual changes in physiological and morphological characters (Huxley, 1938; Langlet, 1959a, b) is also of secondary importance for this discussion.

**FIGURE 3. - Gene dependent plastom mutation: cytoplasmatic changes, in this case plastid aberrations, conditioned by gene mutations.**



The degree of heterogeneity and the intensity of gene recombination depend largely on the type of fertilization, that is, self- or cross-fertilization, or, even, on the disappearance of fertilization in parthenogenetic and vegetatively propagating species. The occurrence of natural selfing is fully established in a number of tree species including conifers. Such is the case in the uniform *Picea* *omorika*, according to Langner (1959). However, even then crosses occur, often with pronounced segregation in later generations. In small populations or isolates, selfing may set in with consequent increase in homozygosity and general decrease of viability of the homozygous variants, due to inbreeding effects. In hermaphrodite or monoecious tree species the degree of natural selfing may vary from year to year, depending on the amount of flowering and spread of the pollen within the stand (for details of the distance of pollen flight, see Andersson, 1955). This fact must be seriously considered when natural regeneration is applied in silviculture. It has been pointed out that in species which are usually cross-fertilizing like *Picea abies, Pinus sylvestris,* and *Pinus monticola*, self-fertilization may occur quite readily and some fully self-compatible variants are encountered (Sylvén, 1910; Plym Forshell, 1953; Barnes *et al.*, 1962; Eklundt Ehrenberg, 1963). Self-fertile biotypes arise spontaneously or in experiments under the action of mutagenic agents, by loss-mutation or destruction of the incompatibility genes and alleles.

However, in numerous plant species, including conifers and angiosperm tree species, there exist a series of transitions between full self-incompatibility to pronounced selfing ability. Nevertheless, the species are for ecological, historical or migrational reasons divided into populations which intercross in nature and are more or less adapted to their special habitats and as constituents of natural plant communities, with competition and co-operation of the individual biotypes both between and within species.

A most interesting analysis concerns the effects of self-fertilization *contra* cross-fertilization in 4 trees of *Pinus monticola* (Barnes *et al*., 1962), 2 of which were self-fertile, and 2 partially self-sterile. Pollen of the individual trees was mixed and the mixture used for fertilization. The proportion of outcrossed and selfed seed varied, depending on the genotypes of the mother tree and of the pollen parent. In some instances, self-pollen was as effective as foreign pollen; in most cases, however, it was less effective.

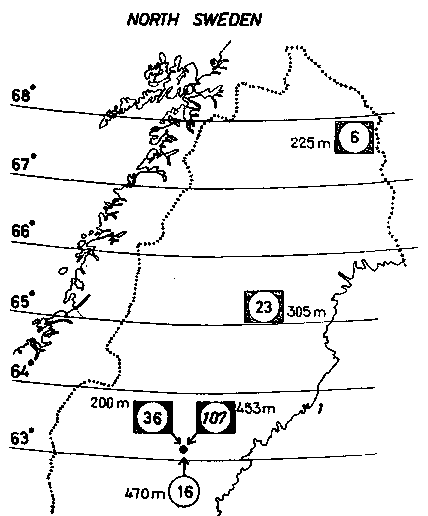
In apomictic species, strongly heterozygous hybrids may breed true and spread widely in nature, owing to their ability to undergo asexual seed formation or vegetative modes of propagation. Such species are rather rare among the economically valuable forest trees, although apomixis has been found to occur in *Alnus, Euonymus, Sorbus* and other genera, and many species, like the aspens, poplars and willows, do propagate vegetatively.

*Tree populations and their adaptation*

It is often considered that natural populations are in general well-adapted to environmental conditions. In a recent paper by Duffield (1962, page 9) for instance, the following sentence is found: "As a breeding procedure, therefore, induction of mutations is simply gambling against extremely high odds, *for in organisms as well-adapted as most forest trees*, virtually any change is likely to be for the worse" (the italics are the present writer's). On the contrary, a tree population often fails to acquire a complete adaptation to its habitat. This holds true for flowering ability as in *Picea abies* which flowers irregularly over large parts of its area of distribution, or for seed setting which either does not occur at all or is hampered in various ways, as in the case of *Pinus sylvestris* and *Picea* *abies* at high altitudes and latitudes (Simak and Gustafsson, 1954). However, the survival and growth of the vegetative phase may often be imperfect as can be seen in the inadequate frost and cold hardiness of local populations under severe conditions. For Scandinavian populations of *Pinus* *sylvestris* (Figure 4) this was fully realized by Wibeck (1933), and then worked out in more detail by Eiche (1962 and unpubl.); see also Gustafsson (1962). It must not be forgotten that a natural environment is always changing and that local tree populations have to undergo successive processes of adaptation which also lead to genetic changes of the potential variability. In addition, historical contingencies such as the original heterozygosity, the mode of migration from less to more severe conditions, irregular attacks or catastrophes due to insects, fungi, rodents, fires, and so on, may greatly influence the constitution of the local population.

Calculated per time unit and perhaps also per generation, forest trees show slow adaptation to changing environmental conditions. This is even more delayed by poor flowering conditions or failure to set seed. (In certain districts of Sweden, for example, a good seed set of *Pinus* *sylvestris* occurs once in 30 or 40 years.) Generally, in northern populations of pines and spruces, the juvenile stage, up to 15 or 20 years, is most sensitive to an extreme type of climate. Having passed this stage, the stand as well as the individual biotypes can be considered vegetatively adapted. Depending therefore on the climatic conditions following field germination or planting, the local populations are more or less adapted to the conditions of a given locality, involving long-lasting consequences for the generations to come.

**FIGURE 4. - Adaptation of pine populations: indigenous populations of Pinus sylvestris in Sweden are often less adapted to the local climate than introduced (in this case more northern) populations.**



|  |  |  |  |
| --- | --- | --- | --- |
| **Prov.** | **Survival %** | **Undamaged shoot %** | **Height cm** |
| 6 | 80 | 77 | 58 |
| 23 | 57 | 55 | 67 |
| 36 | 19 | 12 | 42 |
| *107* | *45* | *34* | *58* |

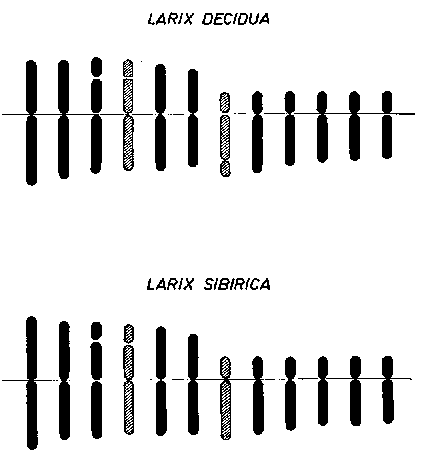
Tree populations are, in general, imperfectly adapted to many forms of human intervention, such as methods of thinning and they are - as wild species - not adequately selected to serve man's needs in timber quality, pulp production or chemical composition. This state of affairs makes forest tree breeding even more urgent, with the object of eventually bringing about an intensified domestication of tree species.

*Genotypic composition of cross-fertilizing populations*

It is of fundamental importance in plant breeding to analyze the genotypic composition of a population: how the genes are distributed on the chromosomes, their effects in the heterozygous and homozygous condition, their free or limited recombination. Studies on *Drosophila* by Mather (1943, 1960), Dobzhansky (1951) and their co-workers, have provided a fairly good picture of population behavior and constitution, under natural as well as experimental conditions, and under severe and mild selection pressures. The extreme heterozygosity of natural populations, involving breakage and rearrangements of chromosome segments, is an established fact; likewise, the abundance of mutations in the heterozygous state, which act as lethals and semilethals when homozygous and decrease viability, is well proved. Many such mutations increase viability above "normal" when heterozygous, an example being the chlorophyll lethals Gustafsson (1954). Eiche (1955) has shown that such chlorophyll lethals are common in natural populations of forest trees. In any case, there is a complex balance between all types of genes and mutations, heterozygous as well as homozygous. Owing to linkage phenomena the potential variability is restricted in the early stages of selection, but is released when crossing-over and recombination of genes in nearby chromosome segments have taken place.

Unfortunately, not much is known about the occurrence of spontaneous inversions or translocations in tree species. Sugihara (1940) has shown that translocations occur in local populations of *Cephalotaxus* *drupacea*, since quadrivalents and hexavalents are said to occur during meiosis of biotypes of this species. Small inversions may be present in every species without having been noticed in the few studies on meiosis so far made. A careful analysis of the idiograms of related species, for instance in *Larix* (Figure 6) or *Pinus* among conifers, would reveal whether species differentiation takes place not only by gene mutation but also by minute and gross chromosome rearrangements. It is evident from hybridization work that far-reaching crosses can be made in numerous species and genera of conifers. This fact can be utilized for the production of hybrid vigor (Righter, 1946, 1960; Hyun, 1960). In nature, species hybridization is often associated with a good deal of species introgression (Anderson, 1949; Stebbins, 1960); that is, genes are transferred from one species to another by hybridization and later back-crossing of the hybrid to one or the other of the parent species. Such introgression has been reported also for species of *Alnus, Quercus* and *Pinus*.

**FIGURE 5. - Idiograms of larch species: related species often have different karyotypes (idiograms) as is shown by these idiograms of Larix decidua and L. sibirica.**



The harmonious development of many tree populations is intimately associated with symbiotic phenomena, for instance with the occurrence of mycorrhiza. This leads to the mutual interaction and continuous adaptation of entirely different groups of organisms. Moreover, as shown by numerous workers, a stand of trees often or regularly forms an enormous "convivium" resulting from a far-reaching root symbiosis with transport of nutrients, hormones, exudates, water and other materials from one individual to another. The biological consequences of such mutual biotic influences have so far not been considered from a genetic or biometric point of view.

### Genetic structure of tree species as a basis for breeding

*Quantitative inheritance and its genetic background*

In the preceding paragraphs the complex constitution of cross-fertilizing plant species has been emphasized. The populations react to natural and artificial selection in the manner of polygenic systems consisting of numerous genes, most of which have slight individual effects, at least in the heterozygous state, and form the genetic basis of quantitative characters. The theory of quantitative inheritance has been developed by Mather in numerous papers (Mather, 1960). As early as 1915 Nilsson-Ehle pointed to the existence of such complex hereditary systems and wrote: "It is evident from the rather comprehensive analyses made in different countries that the characters important in practice, provided they are quantitative, must in general be conceived as being made up of several and sometimes numerous genetic factors, which obey the Mendelian laws... All hereditary properties, not only external morphological characters of little importance in the breeding program, but also physiological or biological characters, such as winter hardiness, genetic resistance to disease, earliness, lodging resistance, germination capacity, and so on, clearly segregate after crossings and form new combinations. In general, quantitative properties act in this way, examples being size properties and protein content in wheat. In no investigation has the author found characters of practical importance with another behavior... The segregation may be more or less complex - which according to the theory presented here depends on the number and action of the different genetic factors - but there is no doubt that different properties act basically alike. The composition of characters of practical importance as depending on a great number of genetic factors is of the greatest importance for the principles and methods of plant breeding" (*op. cit*., page 57, translated).

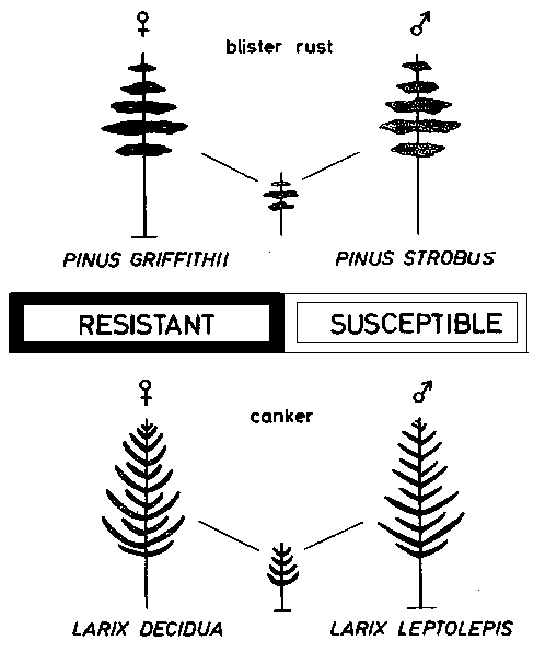
However, when Nilsson-Ehle, East, Fisher, Mather, and others stress the importance of genes with small effects, it must not be forgotten that cultivated plants also deviate from their wild ancestors in several drastically and abruptly changed characters (Schwanitz, 1957). Mutations with major effects have continually contributed to the process of domestication. Around these major changes recombination and further mutation is at work, fitting large and slight changes together into a balanced whole, where numerous genes influence the same quantitative character. In cross-fertilizing species, deleterious genes and mutations also exert slight modifying effects in the heterozygous state. The reason why single gene changes are so difficult to analyze in studies on the quantitative inheritance of forest trees is simple enough: the design of experiments and methods of measurements are often imprecise and inadequate, and environmental effects conceal slight genetic effects.

*Disease resistance and major gene effects*

The genetics of disease resistance in forest trees has become important in recent years. In a review published in 1962, Heimburger stated the problem in the following way: "The genetic background of resistance in the host can be polygenic or governed by a smaller number of major genes, although in most cases resistance to disease in plants has been found to be based on a combination of polygenes and major genes. Major genes governing resistance to disease constitute the basis for most of the spectacular advances in breeding for disease in agriculture and horticulture." On the other hand Heimburger subsequently stated: "It must be kept in mind, however, that most cultivated plants have been produced by selection and breeding mostly on the basis of polygenes and that many new and useful characters, such as disease resistance, can be materially enhanced in this manner if no other closely related material with superior resistance are available" (*op. cit*., page 358). The data on disease resistance in forest trees are vague and contradictory. This is mainly because the inheritance of resistance has largely been studied in species crossings, where the hybrid condition complicated the physiological action of the genes for resistance derived from quite different sources. That species hybrids between resistant biotypes will often turn out to be susceptible is perhaps to be expected. Heimburger himself cites hybrids between *Pinus griffithii* and *Pinus strobus*, where the "inhibiting mechanism broke down, the infection spread rapidly from the needles to the stem and heavy mortality of the seedlings was the result" (*op. cit.*, page 360). On the other hand, cases are known where one species makes the species hybrid almost entirely resistant, an example being the cross between the canker-resistant *Larix leptolepis* and *Larix decidua* (Figure 6).

There are abundant data available from work on agricultural and horticultural plants to show that major genes are involved in resistance. Knight (1946) lists 33 crop plants in which major gene resistance to 84 pests and diseases has been demonstrated. Recent work by Briggs, Flor, Favret and others has shown that there are numerous genes producing resistance within a species, and that these genes are often not distributed at random over the genome of the host plant but tend to be grouped in genetical segments, concentrated on a few chromosomes. Briggs was the first to suggest such a phenomenon in bunt disease in wheat. The genetics of resistance to mildew in barley (Figure 7) is possibly the most striking example (Favret, 1960a, b). Eighteen different factors for resistance to mildew are distributed over 14 loci; 17 lie on chromosome 5 and one on chromosome 4. Thirteen loci form a large "isophenic segment" of 45 to 50 cross-over units. This isophenic segment can be divided into four sections according to the nature of the alleles for resistance. Some loci contain only one allele for resistance, others are built up on a series of 2 to 5 alleles. Three loci are closely linked forming a genie complex in a short segment with a length of about one cross-over unit. Most genes for resistance are dominant or semidominant, although recessive factors also occur.

**FIGURE 6. - Disease resistance in species hybrids, in this case of conifers, may be "recessive" (upper figure) or "dominant" (lower figure).**

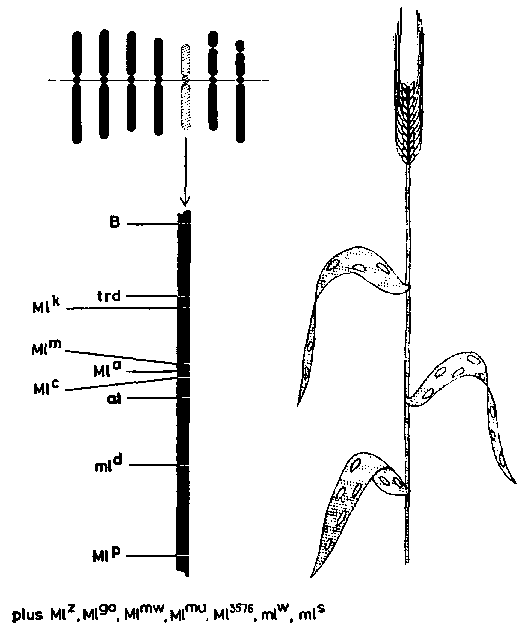


It is certainly suggestive that this complex system of resistance has been found in several carefully studied species. This may argue for a similar condition also in conifers and broadleaved trees. Although many genes are involved each of them has in general a "major" effect. Therefore, inheritance is not "polygenic" in the sense of Heimburger, following Mather, in showing small additive effects, but is "multi-factorial" in the sense of Nilsson-Ehle, perhaps based on a series of small duplications, as suggested by Favret in his mutation work, many factors for resistance being dominant or semidominant. In addition, it must be emphasized that disease *resistance* and field *tolerance* of a disease may involve different phenomena.

*The concept of heritability*

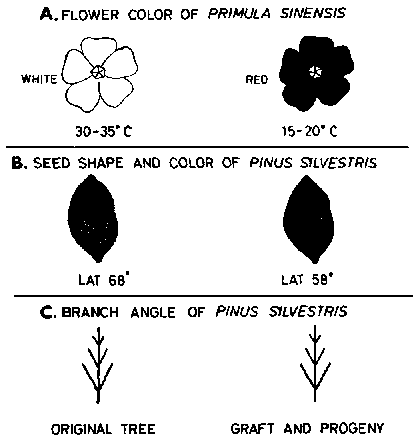
In studies on quantitative characters in trees, such as volume production, height or diameter increment, stem form and wood properties, the experiments should be designed to differentiate between genetic and environmental influences and to estimate the extent to which a certain phenotype is determined by heredity and by the environment. In animal breeding the long generation time and the high cost of progeny testing make these problems as important as in tree breeding and the concept of heritability (h²) (*cf*. Lush, 1948) has been devised for that part of the total phenotypic variance (VP) due to genetic factors with additive effects (VA.). Originally the term heritability referred only to the correlation between parents and offspring but in tree breeding heritability is often used in two senses following the ideas presented by Lush (1948). In the broad sense, heritability refers to the functioning of the whole genotype and is used in contrast to environmental variance. The narrow definition of heritability includes only the average effects of the genes, carried from parents to offspring in meiosis (chromosome segregation) and subsequent fertilization (chromosome recombination). "This narrow meaning of heritability is used when the main emphasis is on expressing what fraction of the phenotypic difference between parents may reasonably be expected to be recovered in the offspring" (Lush *op. cit*.). See also Toda, 1957; Zobel, 1961; and Eklundh Ehrenberg, 1963.

**FIGURE 7. - Resistance to a fungus disease, in this case barley mildew, is often conditioned by many genes, dominant or recessive, which lie in specific segments of chromosomes, called isophenic segments.**

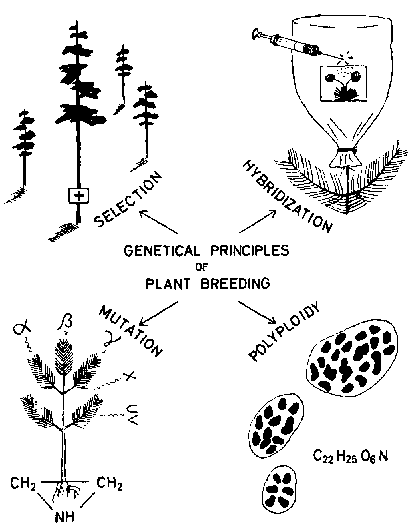


Heritability in the broad sense is a restatement of Johannsen's contrast of genotype and phenotype. The concept is beautifully illustrated by the experiments on flower color and temperature in *Primula* *sinensis* described by Erwin Baur (1919) in his classical textbook on genetics (Figure 8). In those forest trees in which vegetative propagation is a common procedure, clonal analysis easily reveals the genotypic component of variation. This is an important principle in the selection of plus trees because numerous factors, such as soil properties, water balance, stand density, irregular thinning, and so on, may result in a plus development of genetically inferior trees or a minus development of genetically superior trees. However, stem form, branching habit, and especially branch angle, are often highly fixed genetically. The seed properties of *Pinus sylvestris* demonstrate in an elegant manner the relative influence of heredity and environment (Simak and Gustafsson, 1954). Characters such as seed color and seed size depend for their expression on the ripeness of the seed and are easily influenced by environmental changes. By contrast the characters affecting seed shape, that is, the ratio of length to breadth, surface structure and wing shape, are less changed by environment. The morphological details of seed which are specific to the individual biotypes, for example, a curved or tapering tip or a strongly marked asymmetrical hilum, are highly fixed and independent of changes in climate or soil. These highly fixed characters permit precise control of pine material used in grafting and seed orchards.

**FIGURE 8. - Genotype response in different environments. A. Shows the phenotypic response of a Primula genotype to slight changes in temperature. B. Illustrates how the seed shape of Pinus genotype is largely independent of climatic conditions, whereas seed color is greatly changed by environment. C. Shows that the branch angle of Pinus sylvestris has high "heritability", in both the broad and the narrow sense.**



**FIGURE 9. - Genetic principles of plant breeding.**



Wood properties have in the last few years attracted great interest (Zobel, 1961; Ericson, 1960, 1961; Well wood and Smith, 1962). In some species, the correlation of specific gravity between selected plus trees and their clones in clonal tests is rather pronounced. The higher the basic density of a clone of *Pinus sylvestris* the higher is its pulp yield and the tearing strength of its pulp. Well-wood and Smith (*op. cit.*) have shown that in *Pseudotsuga taxifolia* and *Tsuga heterophylla*, there is no connection between the external features of a plus tree and its internal wood properties. In breeding for increased pulp yield in these species, the wood properties must be analyzed separately.

Heritability in the narrow sense is, with certain restrictions, a useful concept. If the experiments are correctly designed, mathematical analysis will indicate the size of the genetic component of variance at least in the offspring of crosses within populations. The important problem is to remove the nonspecific environmental influences. If the plus trees used in breeding are carefully selected, biotypes with minus hereditary characters will automatically be excluded from seed production. This is a negative but important procedure. However, the positive aspect of selection will be emphasized if the plus trees are carefully selected, tested in clone tests and crossed with suitable partners. It is encouraging to note that provenance tests, using mixtures of seed, have revealed a distinct connection between the phenotypic status of the parent stands and their offspring; Petrini (1959) described such a situation in a 50-year-old provenance test of *Pinus* *sylvestris*. In her studies on plus trees versus minus trees, Eklundh Ehrenberg (1963) has shown that the progeny of selected plus trees are superior in growth and development to the progeny of minus trees.

However, the object of tree breeding is to exploit not only general but also specific effects of combination. The formation of seed orchards containing 30, 40 or more clones derived from plus trees in a given region is an act of safety that can be recommended for forest areas with severe and varied site and climatic conditions. On the other hand, in more productive regions with favorable climatic conditions the number of clones might be reduced and, as experience accumulates, more emphasis can be put on specific combining ability. In seed orchards formed to exploit hybrid vigor by species and provenance crosses, the number of different clones may after careful progeny tests be reduced still further. This is especially the case when natural regeneration is not practiced and future generations of forests will be planted. Mathematical calculations of the relation of parent trees to offspring (that is, heritability in the narrow sense) will often fail if specific combining effects are not considered.

*Genetic principles of plant breeding*

It is necessary now to summarize the genetic factors involved in plant breeding, all of which are also acting in nature (Figure 9). These are:

1. selection;

2. hybridization;

(*a*) F1 heterosis or hybrid vigor in crosses between species, populations and individuals,

(*b*) F2 to Fn recombination and transgression,

© back-crossing of F1 to Fn individuals to one or other parent;

3. spontaneous or induced mutation due to molecular instability, ionizing radiations or chemical mutagens;

4. natural or artificial polyploidy, resulting in allo- and autopolyploidy.

Numerous devices are available for developing the long-term work of breeding. These include vegetative propagation, the use of male sterility, production of inbred or homozygous lines and their subsequent mass propagation by grafting. X-ray analysis depicts embryo and endosperm development. Mass infection to reveal genetic resistance to disease can be done in glasshouses. Climatic control of various kinds can be used to study genotype-phenotype relationships and the physiological and ecological conditions leading to early and profuse flowering. Correlations of characters in parent and offspring at an early stage simplify the correct selection of parent trees for crossing work. The necessity of mathematical analysis must be stressed. Numerous other scientific and technical methods, many not yet available, can be expected to accelerate research and speed the practical application of results.

### Domestication of tree species

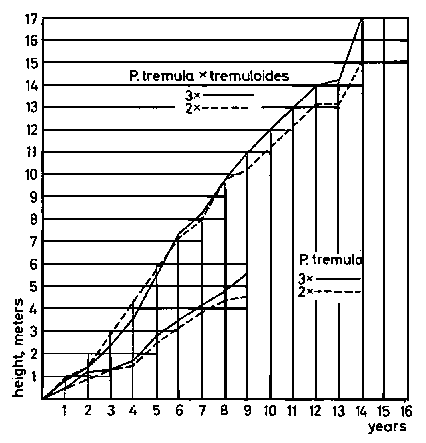
A fascinating aspect of modern biology is the general applicability and validity of genetic principles in many individual species and genera. This makes possible the transfer of results obtained from bacteria, fungi, or flies to populations of trees or to man. The application of these results may be limited by the size of the organism or the length of its reproductive cycle. There is something fatalistic in the geneticist's view of life, that hereditary material consisting of fixed units with a high degree of constancy is transferred unchanged from generation to generation, although with the possibility of mutation. However, genetic material does not exist in a vacuum and through mutation and recombination, genotypes have been selected and molded for thousands or millions of years in varying environments. In other words, a genotype without an environment is a meaningless concept.

This interaction of genotype and environment is seen in the practice of silviculture. The economic value of a stand may be increased through thinning, pruning, and other forms of management, but no forester can produce a plus stand from one which is failing because of unsuitable provenance. It is impossible to apply breeding and genetics to forest trees without due consideration of many other disciplines of forestry. In this respect there may be a difference between forestry and agriculture.

In agricultural and horticultural crops, distinct changes have occurred during their development from the original wild state. These differences involve morphological changes, physiological changes leading to increased production, and variations in the underlying karyotype. Karyotype changes involve the number and structure of chromosomes and the arrangement of genes in the chromosomes. A typical example is provided by comparing the wild diploid species of *Triticum* and *Aegilops* with the hexaploid commercial species *Triticum aestivum*. Even within diploid crop plants the modernization has been remarkable. Contrast, for example, the hybrid maize of the corn belt of the United States of America with the primitive maize discovered in the caves of New Mexico and South America (Mangsladorf, 1958). In addition, some species such as the lupine have quite recently become used as crop plants. Alkaloid-free cultivars were developed with great skill by Sengbusch in the late 1920s, and the lupine have since been steadily improved by further mutation and recombination.

A similar process of domestication has begun in some forest trees, initiated by Nilsson Ehle's discovery of the fast-growing triploid aspens (Nilsson-Ehle, 1936). Using crosses between tetraploids and diploids, it is now possible to produce great quantities of triploids. Further improvement has been obtained by Johnsson (1953 and unpubl.) who has shown (*cf*. Gustafsson, 1960b) that hybrids between *Populus tremula* and *Populus tremuloides* are more productive in Sweden than the native Populus tremula (Figure 10). By introducing tetraploid *Populus tremula* into the crossing program Johnsson was able further to increase yield and, at the same time, transfer resistance, or at least tolerance, to *Valsa nivea* from the tetraploid to the hybrid. On the other hand, numerous cultivars of *Populus* are highly bred clones at the diploid level, also involving various species crosses. However, it appears that poplar breeding has often been casual, and in the future careful planning of the crosses will lead to even better results.

**FIGURE 10. - Height growth of species hybrids and triploids in Populus - illustrating the combination of two breeding methods.**



In conifers, as in broadleaved trees and agricultural crops, domestication will cause far-reaching changes in population structure. Hybrids are easy to produce in some tree genera, particularly *Pinus* and *Larix*. Many combine hybrid vigor with disease resistance or tolerance. Nothing is known about triploid hybrids in *Pinus* but possibly some will be of value in the future. At the intraspecific level, population crosses are likely to be of more immediate practical importance. For example, the central European, Polish or west Russian provenances of *Picea abies* transferred to Scandinavia are often more productive than the native Scandinavian populations. Seed and seedlings of these provenances have been imported in large quantities and selected plus trees of native and foreign origin are already established in seed orchards in Sweden (Andersson and Andersson, 1962). Wide out-crosses have been made in experimental clonal seed orchards and these will fundamentally change the population structure when used as F1 seed. The stands may be highly heterogenous but will be highly productive. Further plus tree selection may be made in these stands.

The rate of domestication in forest trees will naturally be slower than that of annual or biennial crops and will vary according to the species and characters under selection. The end product must vary with the needs of utilization and the ecological conditions of the growing site. Populations delivered by plant breeders into practice have to be completely adapted to the climates and sites for which they are planned. This implies the full conformity of the sum of the genotypes in the population and their environment, and this fundamental principle thus provides the beginning and end of this chapter.