5. GENE INTERACTIONS:

The phenomenon of two or more genes governing the development of a single character in such a way that they affect the expression of each other in various ways is known as gene interaction.

When one gene affects in any way the expression of another gene, the phenomenon is called epistatis. Thus all cases of gene interaction are examples of epistatis. But sometimes the term epistatis has been used to denote the masking effect of one gene on the expression of another gene.

There are several types of gene interaction. Some of the common gene interactions are as follows:

- 1. Typical dihybrid ratio for a single trait (9:3:3:1)
- 2. Duplicate gene action (15:1)
- 3. Complementary gene action (9:7)
- 4. Supplementary gene action (9:3:4)

- 5. Inhibitory gene action (13:3)
- 6. Masking gene action (12:3:1)
- 7. Polymeric gene action (9:6:1)
- 8. Additive gene action (1:4:6:4:1)

1) Typical dihybrid ratio for a single trait (9:3:3:1)

This type of gene interaction produces the typical di-hybrid ratio of 9:3:3:1 in F_2 for a single character. Evidently the concerned character is governed by two genes showing complete dominance.

In case of chickens or fowls, comb shape is governed by two genes. While one gene gives rise to rose comb, another gives rise to pea comb. Each of these two is dominant over single comb. However, when both are brought together, a new phenotype 'walnut' appears.

As worked out by Bateson and Punnett, when both dominant alleles are present 'walnut' phenotype appears and when both recessive alleles are present 'single' comb appears. 'Rose' and 'Pea' phenotypes appear due to the presence of different single dominant alleles. If pea (rrPP) and rose (RRpp) are crossed, F_1 birds showed 'walnut' comb as it has the dominant alleles of both the genes P and R.

Later on, when the F_1 walnut combed birds were inbred together, in F_2 generation there appeared walnut, rose, pea and single combed fowls. These types occurred in the proportions; 9/16 walnut, 3/16 rose, 3/16 pea and 1/16 single.



Fig. 55. Different shapes of combs in fowls

The mode of inheritance of the genes for 'rose' and 'pea' does not differ at all from the usual Mendelian scheme. The differences that distinguish this and similar cases from simple di-hybrid inheritance are that (i) the F_1 does not resemble with parents and (ii) apparently new or unusual characters (walnut) results from an interaction between two independently inherited genes, and the other (single comb) results from the interaction of their two recessive alleles. These peculiarities are not due to a new method of inheritance but simply to the fact or circumstance that both genes involved happen to express themselves in this case (fowl comb).



2) Duplicate gene action (15:1):

The two pairs of factors which have identical effect are known as duplicate factors. Or Characters showing duplicate factor or gene action are governed by two dominant factors. These dominant factors produce the same phenotype whether they are alone or in pairs. (Awned and awnless characters in rice plants)



			Gametes		
F_2	p ð	A ₁ A ₂			
: 	A ₁ A ₂	A ₁ A ₁ A ₂ A ₂ Awned	A ₁ A ₁ A ₂ a ₂ Awned	A ₁ a ₁ A ₂ A ₂ Awned	A ₁ a ₁ A ₂ a ₂ Awned
metes	A ₁ a ₂	A ₁ A ₁ A ₂ a ₂ Awned	A ₁ A ₁ a ₂ a ₂ Awned	A ₁ a ₁ A ₂ a ₂ Awned	A ₁ a ₁ a ₂ a ₂ Awned
	a ₁ A ₂	A ₁ a ₁ A ₂ A ₂ Awned	A ₁ a ₁ A ₂ a ₂ Awned	a ₁ a ₁ A ₂ A ₂ Awned	a ₁ a ₁ A ₂ a ₂ Awned
	a ₁ a ₂	A ₁ a ₁ A ₂ a ₂ Awned	A ₁ a ₁ a ₂ a ₂ Awned	a ₁ a ₁ A ₂ a ₂ Awned	a ₁ a ₁ a ₂ a ₂ Awned

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(Inheritance of Duplicate factors) Genotypes and phenotypes of F2 generation:

Genotype	Frequency	Phenotype	Frequency
$A_1A_1A_2A_2$	1		2.V=
$A_1A_1A_2a_2$	2		
A ₁ a ₁ A ₂ A ₂	2		
$A_1a_1A_2a_2$	4	Awned	15
$A_1A_2a_2a_2$	1		
$A_1 a_1 a_2 a_2$	2		
a1a1A2A2	1		
$a_1a_1A_2a_2$	2		
a1a1a2a2	1	Awnless	1

Thus, in duplicate gene action, the presence of a single dominant allele of any one of two genes governing the dominant phenotype e.g., awned type in rice, while the recessive phenotype e.g., awnless is produced only when both the genes are in the homozygous recessive condition.

A similar case of duplicate factor interaction governs the fruit shape in Bursa, endosperm colour in maize, nodulation in groundnut and certain characters in many other plants. First of all, the duplicate gene interaction was observed and explained by G.H. Shull in plant called shepherd's purse (*Capsella bursapastoris*.)

3) Complementary gene action (9:7):

In sweet pea (Lathyrus odoratus) two varieties of white flowering plants were seen. Each variety bred true and produced white flowers in successive generations. According to Bateson & Punnett, when two such white varieties of sweet pea were crossed, the offspring were found to have purple coloured flowers in F_1 but in F_2 generation 9 were purple and 7 white. This is again a modification of 9:3:3:1 ratio, where only one character i.e., flower colour is involved.

It is clear in the above example that for the production of the purple flower colour both complementary (C and P) genes are necessary to remain present. In the absence of either genes (C or P) the flowers are white.

Thus, it is clear that genes C and P interact and presence of both is essential for the purple colour in the flower. These types of genes in which one gene complements the action of the other gene, constitute complementary genes or factors. (Complementation between two non-allelic genes (C and P) are essential for production of a particular or special phenotype i.e., complementary factor)

Р	White	flowers Cpp	x	White flowe ccPP	ers
Game	tes C	Purj	ccPp	cP	
Game	p ô	CP, cp CP	Cp	cP	cp
	CP	CCPP Purple	CCPp Purple	CcPP Purple	CcPp Purple
Gametes	Ср	CCPp Purple	CCpp White	CcPp Purple	Ccpp White
	cP	CcPP Purple	CcPp Purple	ccPP White	ccPp White
	cp	CcPp Purple	Ccpp Whie	ccPp White	ccpp White

Phenotypic ratio : 9 Purple : 7 White

(Representing a Cross between two varieties of sweet pea)

Genotypes and Phenotypes of F₂ and breeding behaviour expected in F₂ of complementary factors:

Genotype ratio	Genotype Class	Phenotype class	Phenotype ratio
1 2 2 4	CCPP CCPp CcPP CcPp	Purple	9
1 2 1 2 1	CCpp Ccpp ccPP ccPp ccpp	White	7

Aleurone colour in maize is also controlled by complementary genes.

4) Supplementary gene action (9:3:4):

Here only one factor is sufficient to produce a phenotypic expression but addition of another factor causes the change in expression.

Or

Supplementary genes are two independent dominant genes interacting to produce a phenotypic expression different from that produced by either gene alone.

Or

In supplementary gene action, the dominant allele of one gene is essential for the development of the concerned phenotype, while the other gene modifies the expression of the first gene. For example, the development of grain colour in maize is governed by 2 dominant genes 'R' and 'P'.

The dominant allele 'R' is essential for red colour production; homozygous state of the recessive allele 'r' (rr) checks the production of red colour. The gene 'P' is unable to produce any colour on its own but it modifies the colour produced by the gene 'R' from red to purple. The recessive allele 'p' has no effect on grain colour.



⁽Cross between Purple and White grain colour in Maize.)

Frequency	Genotypes	Phenotypes
1	RRPP	
2	RRPp	Purple
2	RrPP	
4	RrPp	
1	RRpp	Red
2	Rrpp	
1	rrPP	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
2	rrPp	4 White
1	rrpp	

Showing genotypes and phenotypes of F₂ behaviour of supplementary factors in grain colour of maize:

Examples of supplementary factors have also been seen in other plants and animals too. For instance, it is clearly visible in skin colour of house mouse and guinea pigs. When black mice are crossed with ordinary albinos, the progeny are usually all agouti like the wild type. When these F_1 agouties are inbred, their progeny consists of 9/16 agouti, 3/16 black and 4/16 albino animals.

5) Inhibitory gene action (13:3):

In this type of modification two pairs of genes are involved and one of the non-allelic dominant gene inhibits the expression of the other non-allelic dominant gene.

Or

A gene which inhibits the expression of an active allele situated at different locus is called as inhibitory gene. Thus, in inhibitory gene action one dominant inhibitory gene prevents the expression of another dominant gene. Example of inhibitory gene is pigmentation in rice plants. In rice plants, the presence of gene 'P' is responsible for deep purple leaves. But if a gene 'I' is present then the expression of purple leaf colour is inhibited and the leaf becomes normal green. Thus, in a cross, between green (IIpp) and purple (iiPP), all the off springs in F_1 are green but in F_2 progeny, green and purple are obtained in ratio of 13:3. This modifies the typical 9:3:3:1 F_2 ratio in to a 13:3 ratio.



			Gan	netes		
\mathbf{F}_2	000	IP	Ip	iP	ip	
	IP	IIPP Green	IIPp Green	liPP Green	liPp Green	Phenotypes : 13 Green
Gametes	Ip	IIPp Green	IIpp Green	liPp Green	lipp Green	3 Purple
	iP	liPP Green	liPp Green	iiPP Purple	iiPp Purple	
	ip	liPp Green	lipp Green	iiPp Purple	iipp Green	

It is now well understood that pigmentation in rice plant is governed by two non-allelic genes. 'P' gene produces purple colour while its recessive 'p' green colours. Another dominant gene 'I' which produces green colour in rice plants, inhibits or prevents the colour production by 'P' when both 'I' and 'P' are present together.

The recessive alleles 'I' is ineffective and does not affect the colour production in any way in rice plants. Other examples of inhibitory gene action are the development of feather colour in fowls, seed colour in maize etc. Bateson and Punnett for the first time made the discovery of Inhibitory gene in fowls.

Genotypes	Genotypic ratios	Phenotype	Phenotypic ratio
IIPP	1		
IIPp	2		93.02
LIPP	2	Green	13
liPp	4		
IIpp	1		
lipp	2		
iipp	1		
iiPP	1	26.2 . 05	200.0
iiPp	2	Purple	3

Genotypes and phenotypes of F₂ generation:

6) Masking gene action (12:3:1): also known as epistatic gene action.

The term "epistatis" was first used by Bateson (1909). It is the interaction between non-allelic genes in which one gene suppresses the expression of other gene. A gene that hides or masks the expression of another non-allelic gene is called as epistatic factor and the gene that is hidden or suppressed is said to be hypostatic.

This phenomenon of masking one gene by another non-allelic gene is known as epistatis and is similar to dominance, except that it occurs between nonallelomorphic genes, instead of comprising allelomorphic genes. Such a gene interaction has been also named as masking gene action.

In Cucurbita pepo, there are 3 types of fruit colour- (i) White (ii) Yellow and (iii) Green. White is found dominant over yellow as well as green colour. When yellow is crossed with green, yellow is found to be dominant. Here, the character (colour of fruit) is governed by 2 pair of genes-

White x green \rightarrow White dominant

Yellow x green \rightarrow Yellow dominant

Here white is dominant factor and yellow is hypostatic factor.

White x Yellow \rightarrow White dominant.

If white dominant is represented by 'W' and its recessive by 'Y', both non-allelic factors or genes may be represented as follows-



			fing	Sel		
	Genotypes	wy	wY	Wy	WY	5
	WWYY-1 WWYy-2	WwYy White	WwYY White	WWYy White	WWYY White	WY
	Wwyy-2 WwYY-2	Wwyy White	WwYy White	WWyy White	WWYy White	Wy
12 White	WWyy-1 WwYy-4	wwYy Yellow	wwYy Yellow	WwYy White	WwYY White	wY
3 Yellow	wwYY-1 wwYy-2	wwyy Green	wwYy Yellow	Wwyy White	WwYy White	wy
1 Green	wwyy-1	and the course				

(Showing genotypes & phenotypes of F2 generation)

7) Polymeric gene action (9:6:1):

When two genes govern any character separately, their effect is equal but when both the genes are present together, there phenotypic effect is increased or raised as if the effects of the two genes were additive or cummulative. It is notable in this case that both the genes show complete dominance. "Additive or cummulative effect of genes present at different loci is called polymerism."

In wheat three types of pericarp colour is found:

(i) Deep red (ii) Light red and (iii) Colourless. When a cross is made between plants having deep red (AABB) and colourless (aabb) pericarp, the F_1 (AaBb) has deep red pericarp due to the additive effect of both the genes A and B.

In F_2 generation, on an average, 9/16 plants will have dominant alleles of both the genes A and B; as a result these plants will produce deep red per-carp. 6/16 plants will have light red pericarp since they have either A or B, but not both. The rest 1/16 plant will be homozygous recessive for both the genes and will be therefore, colourless.



Phenotypic ratio : 9 Deep red : 6 Light red : 1 Colourless pericarp

Genotypes and phenotypes of the F₂ generation:

Genotypes	Frequency	Phenotypes	Frequency
AABB	1		
AABb	2	Deep red	9
AaBB	2	0.0000000000000	
AaBb	4		
AAbb	1	05.8.98	
Aabb	2	Light red	6
aaBB	2	8.0.0	
aaBb	1		
aabb	1	Colourless	1

Thus, polymerism interaction modifies the typical 9:3:3:1 ratio in to 9:6:1 ratio. Other examples of polymerism interaction are also known, e.g., fruit shape in summer squash etc.



8) Additive gene action (1:4:6:4:1):

In additive gene action, each positive allele of the two genes governing a trait produces equal and identical effect on the character. The effects of all the positive alleles present in an individual at the two loci are additive. As a result, the 9:3:3:1 dihybrid F_2 ratio is partitioned into the 1:4:6:4:1 ratio. This gene action is the basis for the multiple factor hypothesis of Nilsson-Ehle. Therefore, the genes showing additive gene action are called multiple factors or more commonly, polygenes. Each polygene has two alleles. One allele of each polygene produces a positive effect in the character governed by the gene; this is called positive allele. The other allele of each gene has no effect on the character, and is known as negative allele. The positive alleles are, as a convention, denoted by capital letters, while negative alleles are given the respective small letters as symbols. However, this notation does not indicate a dominance of the positive alleles over the negative ones.

For example, seed colour in tetraploid wheat is governed by two polygenes R_1 and R_2 . The positive alleles of these two genes, *viz.*, R_1 and R_2 , produce colour. Their negative alleles, namely, r_1 and r_2 , do not produce any colour. Each R_1 and R_2 allele produces a small amount of colour. The effects produced by all the R_1 and R_2 alleles are additive. Therefore, the total intensity of colour produced depends on the total number of positive alleles of the two genes present. Thus, $R_1R_1R_2R_2$ produces dark red colour, $R_1R_1R_2r_2$ generates medium dark red, $R_1r_1R_2r_2$, etc. Yield medium red and so on. When a variety having dark red ($R_1R_1R_2R_2$) seeds is crossed with a variety having white seeds $(r_1r_1r_2r_2)$, F1 $(R_1r_1R_2r_2)$ has medium red seeds, this is because F₁ seeds only two positive alleles (one R₁ and one R₂). In the F₂ generation one zygote out of sixteen will have four positive alleles $(R_1R_1R_2R_2)$. the seeds will be identical to one of the parents, and will have dark red colour. In four (out of 16) seeds, three positive alleles will be present $(R_1r_1R_2R_2 \text{ and } R_1R_1R_2r_2)$. These seeds will be lighter in colour than the seeds of the dark red colour parent but darker than the F₁ seeds; they will be medium- dark red in colour. Six (out of 16) seeds will have only two positive alleles each $(R_1r_1R_2r_2, R_1R_1r_2r_2, r_1r_1R_2R_2)$. They will be identical to the F1 seeds and medium red in colour. In four (out of 16) other seeds $(R_1r_1r_2r_2, and r_1r_1R_2r_2)$, only one positive allele will be present. The colour of these seeds will be light red. In the remaining one seed (out of 16), there will be no positive allele $(r_1r_1r_2r_2)$. This seed will be white in colour.



\$ S	R_1R_2	R 1 r 2	r 1 R 2	r 1 r 2
D.D.	$R_1R_1R_2R_2$	$R_1R_1R_2r_2$	$R_1r_1R_2R_2$	$R_1r_1R_2r_2$
N 1 N 2	Dark red	Medium dark red	Medium dark red	medium red
Dama	$R_1R_1R_2r_2$	$R_1R_1r_2r_2$	$R_1r_1R_2r_2$	$R_1r_1r_2r_2$
K 112	Medium Dark red	Medium red	Medium red	Light red
r: Do	$R_1r_1R_2R_2$	$R_1r_1R_2r_2$	$r_1r_1R_2R_2$	$r_1r_1R_2r_2$
11 K 2	Medium dark red	Medium red	medium red	light red
r ₁ r ₂	$R_1r_1R_2r_2$	$R_1r_1r_2r_2$	$r_1r_1R_2r_2$	$\mathbf{r}_1\mathbf{r}_1\mathbf{r}_2\mathbf{r}_2$
1112	Medium red	Light red	light red	white

Thus the multiple factor hypothesis or the additive gene action is able to fully explain the 1:4:6:4:1 ratio for seed colour in F2 generation of wheat and oat crosses. Additive gene action is involved in the expression of quantitative traits. Qualitative traits show a continuous variation. As a result, they can not be classified into two or more separate classes. These characters are governed by polygenes. Genes with small cumulative effects governing a single trait are known as polygenes. In contrast, genes having a large effect on the characters they govern are called oligogenes or major genes. Oligogenes generally govern qualitative traits with discrete variation. They permit classification of individuals into few discrete classes for the characters they govern. All the other cases of gene interaction described in this chapter are due to oligogenes.

Genotypic and phenotypic frequencies produced by the segregation of two genes, R1 and R2, with cumulative effect on seed colour in wheat

genotype	frequency	Number of dominant alleles	Phenotype	frequency
R1R1R2R2	1	4	Dark red	1
R1r1R2R2	2	3	Medium dark red	4
R1R1R2r2	2	3	Medium dark red	
R1r1R2r2	4	2	Medium red	
R1R1r2r2	1	2	Medium red	6
r1r1R2R2	1	2	Medium red	
R1r1r2r2	2	1	Light red	4
r1r1R2r2	2	1	Light red	
r1r1r2r2	1	0	white	1