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Concept of Gene Pool and Distant Hybridization in Vegetable Crops

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A B S T R A C T

Wide crossing or distant hybridization is an effective means of transferring desirable genes into cultivated species. It is more successful in closely related species, but as we move towards tertiary gene pool, it turns out to be very hard to move the quality of interest. The fundamental restricting variable is the cross-capacity hindrances between irrelevant species which generally makes trouble to create interspecific gene transfer. The main limiting factor is the cross-ability barriers between unrelated species which usually creates difficulty to produce interspecific hybrids. To re-establish the attribute of natural manageability and to battle the biotic and abiotic stress in developed vegetable yields, wide hybridization has been upheld a solid device in the hand of plant raisers as wild species are the rich pool of respectable characters, better quality and handling characteristics just as giving obstruction against biotic and abiotic stress. Wide hybridization comprises the efficient conventional breeding and modern molecular techniques as its compelling instrument in crop improvement.

Introduction

Thomas Fairchild studied the first report of distant hybridization in a cross of Carnation x Sweet willium in 1717. GeorgiKarpechenko created the intergeneric crosses hybrids of *Raphanus sativus* x *Brassica oleracea*, In June of 1922. Wilhelm Rimpau created the first fertile allopolyploid Wheat x Rye hybrid in 1888. In 1891, he published his findings. Distant hybridization - refers to crosses between two distinct species, genera, or higher-positioning taxa, which can break species limits, increment hereditary variety, and join the organic qualities of existing species (Pooja *et al., 2020)*. Intergeneric hybridization refers to crosses between two different genera, such as *Brassica oleracea* x *Diplotaxis (*Péron *et al.*, 1989*)*. Distant hybridisation is more likely practiced to transfer of desirable genes from secondary and tertiary gene pool to the cultivated species (primary gene pool) genome back round (Kaneko Yukio *et al., 2004)*.

Utilization of interspecific hybridisation for improvement of vegetable crops is limited only to a few crops because of the linkage drag, crossibility barriers, embryo abortion and cytological disruptions. Although several species have been shown to exhibit resistant and high-quality traits, interspecific gene transfer is not conceivable. Gene transformation techniques are a godsend for breeders when used in conjunction with proper *in-vivo* pollination and *in-vitro* embryo rescuing technology (Zhang *et al., 2016)*.

Gene pool concept

Gene pool is the group of all the genes, or genetic diversities present in any population or a crop species. Harlan and de Wet (1971) proposed the concept of gene pool (Fig-1) and classifying each crop species and its related species on the basis of gene pool concept. He classified all the crop species into 3 different gene pools, based on the genetic distance and crossibility nature.

Primary gene pool

The species in this group can be easily crossable with normal chromosomal pairing, proper segregation which facilitates easy transfer of desirable genes from wild species to the cultivated ones.

Secondary gene pool

The species in secondary gene pools are generally considered as different species of the crop. However, these species are closely related and can be crossable with the species of primary gene pools which produce some fertile hybrids. There are some reproductive barriers between the species of primary and secondary gene which leads some reproductive constraints like,

Hybrid breakdown

It's the post zygotic barrier. Those first hybrids are viable, but their offspring are feeble or sterile when they mate with another species or with either parent species.

Production of weak hybrids

Production of partially fertile hybrids

Improper chromosomal pairing

Recovery of desired phenotypes in subsequent generations may be difficult

Tertiary gene pools

Individuals from this genetic stock are all the more remotely identified with the individuals from the essential genetic stock. The going among essential and tertiary genetic stock can be conceivable however move of qualities from tertiary genetic supply to essential genetic supplies is undeniably challenging without utilization of some extreme measures such as;

Embryo rescue (*ex-vivo* pollination followed by *in-vitro* organ culture under controlled conditions)

Siliqua culture, Ovule culture and ovary culture

Inducing polyploidy (doubling of chromosomes)

Bridging crossing - Poysa reported in 1990 that using *L. chilense* as a bridge species to overcome the incompatibility of the cultivated tomato and *L. peruvianum (L. peruvianum* is crossed to *L. chilense*, and the progeny is crossed to *L. esculentu*), he was able to overcome the incompatibility of the cultivated tomato and *L. peruvianum*.

Application of distant hybridization in crop improvement

Distant hybridisation used in vegetable crops for following purpose (Hajjar *et al., 2007)*, Step for the Pre-breeding

To create variability of crop species

To Transfer small chromosome segment from wild to cultivates species

To induce Disease resistance in cultivated species

Increase nutritional status of the crop

Mode of reproduction

Increase Yield

Transfer of sterile cytoplasm

Utilization of wild genetic stock for biotic and abiotic breeding

Development of new crop species

Improve Root nodulation

Induce Earliness

Problems associated with wide crosses

The major problems associated with wide crosses are

Cross Incompatibility

Hybrid In-viability

Hybrid Sterility

Hybrid Breakdown

Linkage drag

Restricted chromosome pairing.

Cross Incompatibility

Cross incompatibility is the inability of the functional pollen grains of one species or genus to fertilize another species or genus (Akaba *et al.,* 2009b*)*.

There are three main causes of cross incompatibility in crop species viz.

Pre –fertilization barriers or pre-syngamic barriers

These barriers somewhat resemblance with self-incompatibility

Lack of pollen germination in stigmatic surface

Slow growth of the pollen

Lack of stigma receptivity

Differences in flowering time

Post –fertilization barriers or post-syngamic barriers

Improper growth of pollen tube in the style and unable to reach the ovule

Inability of male gamete to fertilize the egg cell.

Lack of endosperm formation.

Embryo abortion and embryo starvation.

Abnormal fertilization.

Alteration in endosperm balance number (EBN).

Restricted chromosome pairing.

Examples

The cross between *Solanum khasianum* and *Solanum melongena* is not possible because of the pollens of *S. melongena* fails to reach the ovary of *S. khasianum.* The cross between *Solanum bulbocastanum* and *Solanum verrucosum* not possible because of failure of pollen tube growth of

S. verrucosum in the pistil of *S. bulbocastanum*. In the cross between *Lycopersicon peruvianum* and *Lycopersicon esculuntum*, *L. esculuntum* is prevented to use as male parent because the pollen tube growth of *L. esculentum* is checked in the style of *L. peruvianum*.

Such barriers in pistil are controlled by single dominant gene which can be controlled by incorporation of a recessive gene in the pollen.

In cucumber crosses between African group and *Cucumis* group classified into 3 types on the basis of pollen pistil interaction.

Bilateral congruity

Pollen tube growth is possible in both fore-ward and reciprocal crosses (Cross between African sp i.e., *C. africanus and C. dipsaceus* and *C. anguria*)

Bilateral incongruity

Failure of pollen postil interaction in both directions i.e., foreward and reciprocal crosses. (Cross between *C. metulifolius and C. melo*)

Unilateral incongruity

Failure of pollen pistil interaction in one direction but can successfully interact in other direction (most of the crosses of with *C. ficifolius, C. myriocarpus, C. prophetarum*)

Hybrid In-viability

This refers to the in-viability of the hybrid zygote or embryo. In some cases, zygote formation occurs, but further development of the zygote is restricted. In some other cases, after the completion of the first stages of development, the embryo gets aborted.

The causes for this are:

Unfavourable interactions between the chromosomes of the two species

Abnormal fertilization and embryo development

Failure of zygotic development

Unfavourable interaction of the endosperm with the embryo (embryonic breakdown)

Disharmony between cytoplasm and nuclear genes

Reciprocal crosses, application of growth hormones and embryo rescue are the techniques that can be used to overcome this problem.

This barrier is known as post syngamic barrier

Example

Tomato

Cross between *S. esculentum* and *S. peruvianum* complex is failure due to embryo breakdown (*Chetelat et al., 2016).*

Brinjal

Crosses between *S. melongena* and *S. khasianum* is failure due to collapse of embryo after fertilization (somatoplastic sterility - by Brink and Cooper)

Okra

The cross between *A. esculentus and A. moschatus or A. ficulneus* is failure due to post syngamic barrier.

Cucumber

Post syngamic barrier between *C. sativus* and *C. melo* doesn't allow the seeds to germination.

Pumpkin

Post syngamic barrier also seen in the crosses between *C. moschata*x, *C. maxima* and *C. moschata* x *C. pepo*.

French bean

Failure of crosses between *P. vulgaris* and *P. acutifolius* is due to embryo abortion – inability of interspecific hybrids to develop (Morris *et al.*, 1999).

Hybrid Sterility

This refers to the inability of a hybrid to produce fertile offspring. This is more predominant in the case of intergeneric crosses. The major reason behind hybrid sterility is the lack of structural homology among the chromosomes of the two species.

This may lead to meiotic abnormalities like chromosome scattering, chromosome extension, lagging of chromosome in the anaphase, formation of Anaphase bridge, development of chromosome rings and chains, and irregular and unequal anaphase separations.

These irregularities may lead to aberrations in chromosome structure.

Lack of homology between chromosomes may also lead to incomplete pairing of chromosomes.

Sterility caused by structural differences between the chromosomes of two species can be overcome by amphi-diploidization using colchicine.

Hybrid Breakdown

Hybrid breakdown is a major constraint in interspecific crosses. When F1 hybrid of an interspecific crosses are vigorous and fertile but there F2 progeny is weak and sterile it is known as hybrid breakdown. So, hybrid breakdown obstructs the progress of interspecific gene transfer. This may be because of the structural difference of chromosomes or problems in gene combinations.

Linkage drag

Large amounts of donor chromosome remain even after many backcrosses, Undesirable due to other donor genes that negatively affect agronomic performance.

Techniques to make wide crosses successful:

Selection of Plants

The most viable parents' available ought to be chosen for the crosses.

Reciprocal Crosses

Reciprocal cross may be attempted when unidirectional combination fails.

Example

The crosses between *S. melongena* and *S. khasianum* is only possible if, *S. melongena* is used as female parent.

In case of chilli, *C. annuum* and *C. chinensis*is only possible if *C. annuum* is used as female parent (Nee *et al., 2006)*.

The crosses between *Solanum verrucosum* and diploid potato is self-sterile while reciprocal is self-fertile.

Table.1 Gene pool of different vegetable crops

Sl. No.	Crop Name	Primary gene pool	Secondary gene pool	Tertiary gene pool	References
1	Tomato	*S. Lycopersicon* *S. pimpinellifolium* *S. cheesmani*	*S. parviflorum* *S. chmielewskii* *S. hirsutum*	*S. peruvianum* *S. chilense*	
2	Brinjal	*S. incanum* *S. insanum*	*S. anguivi* *S. dasyphyllum* *S. pyrocanthus* *S. tomentosum*	*S. torvum* *S. sisymbrifolium* *S. elaeagnifolium* *S. khasianum*	
3	Chilli	*C. annuum* *C. frutescence* *C. chinensis*	*C. baccatumvarbaccatum* *C. baccatumvar pendulum*	*C. pubescence* *C. chacoense* *C. exemium* *C. cardenasii*	Ibiza et al., 2012, Yoon et al., 2004.
4	Crucifers	*Brassica oleracea*	*B. juncea* *B. carinata* *B. rapa*	*Eruca sp.* *Sinapsis sp.*	Choudhary *et al.*, 2000, Kaneko *et al.*, 2014, Zhang *et al.*, 2006.
5	Cucumber	*Cucumis sativus. var. sativus* *C.s var. hardwickii*	*C. hystrix* *African cucumber*	*Cucumis melo L.* *Cucurbita Sp.*	
6	Pea	*Pisum Sativum* *P. elatius* *P. pumilio,* *P. abyssinicum*	*P. humile* *P. formosum* *P. fulvum*	*Vavilovia formosa*	*Sinjushin et al., 2022*
7	Common bean	*Domesticated cultivated species*	*P. coccineus, P. polyanthus, P. costaricensis*	*P. acutifolius, P. parvifolius*	*Gepts et al., 2005*
8	Cow Pea	*Four cultigroups, land races, andsubsp. tenuis, denkindtiana, stenophylla*	Subsp.*pubescence*	*V. vexillata,V.radiata*	*Freytag et al., 2002, Pandey et al., 2016*
9	Cluster bean	*Cultivars, land races C. tetragonoloba*	*C. dentate, C. senegalensis, C. serrata*	*none*	*Freytag et al., 2002*
10.	Azuki bean	*V. angularis var. angularis,* *V. angularis var. nipponensis,* *V. hirtella,* *V. minima,* *V. nakashimae,* *V. nepalensis,*	*V.umbellata*		*Freytag et al., 2002, Singh et al., 2007*

Table.2 Achievements of interspecific hybridisation

Crop	Varieties	Interspecific hybridisation	Character transferred
Potato	KufriKuber	*(Solanum curtilobum x S. tuberosum) x S. andigenum*	High tuber yield
tomato	Pusa Red Plum	*S. lycopersicon x S. pimpinellifolium*	Rich in Ascorbic acid
	Hissar Anmol	*S. lycopersicon x S. hirsutum f.sp. glabratum*	Tomato Leaf Curl Resistant
Okra	Pusa A 4	*Abelmoschusesculentus x A. manihot ssp. manihot*	YVMV resistance
	Punjab -7	*Abelmoschus esculentus (Pusa Sawani) x A. Manihot ssp. manihot*	YVMV resistance
	Punjab Padmini	*Abelmoschus esculentus (Rashmi) x A. manihot ssp. manihot*	YVMV resistance
	ParbhaniKranti	*Abelmoschus esculentus (Pusa Sawani) x A. manihot*	YVMV resistance
	ArkaAnamika	*Abelmoschus esculentus x A. tetraphyllys*	YVMV and Fruit Borer Resistant
	ArkaAbhay	*Abelmoschus esculentus x A. tetraphyllys*	YVMV and Fruit Borer Resistant
Amaranthus	Pusa Kiran	*A. tricolor x A. tristis*	
Cucumber	*Cucumishystivus*	*Cucumis hystrix x C. sativus*	Downey mildew, Nematode, Gummy stem blight

Table.3 Achievements through inter generic Crosses

New crop	Parents	Special characters
Raphanobrassica	Radish x Cabbage	1st intergeneric cross Fodder crop
Hakuran	Cabbage x Chinese Cabbage (developed by embryo culture)	Leafy vegetable, resistant to bacterial soft rot, drought, and Heat
Caulicob	Cabbage x Cauliflower	
Nabicol	Kale x Turnip	
Swede	Turnip x Cabbage	Cruciferous root vegetable
Solanopersicon	*Solanum tuberosum x Lycopersicon esculentum*	
Nicotiopersicon	*N. tabacum x L. esculentum*	

Table.4 Disease and Pest Resistance sources

Sl. No	Crop	Character transferred	From wild species
1	Tomato	Fusarium wilt, almost all insects	*Solanum hirsutum*
		Tomato leaf curl	*Solanum chilense*
		Nematode	*S. peruvianum*
2	Brinjal	Bacterial Wilt	*S. stenotomum*
		Shoot and fruit borer	*S. incanum*
		Epilachna beetle	*S. nigrum, S. tutvom*
3	Potato	Late blight, Early blight, Potato virus-x	*S. demissum*
		Nematode	*S. vernei*
4	Okra	YVMV resistance	*Abelmoschus caillei*
		Fruit and shoot borrer	*A.manihot*
5	Onion	Purple blotch, Thrips	*Allium fistulosum*
6	French bean	Rust	*P. flavescens*
7	Cucumber	Green mottle mosaic virus	*Cucumis hardwickii*
		Fruit fly	*C.trigonus*

Fig.1 Gene Pool, Harlan and de Wet (1971)

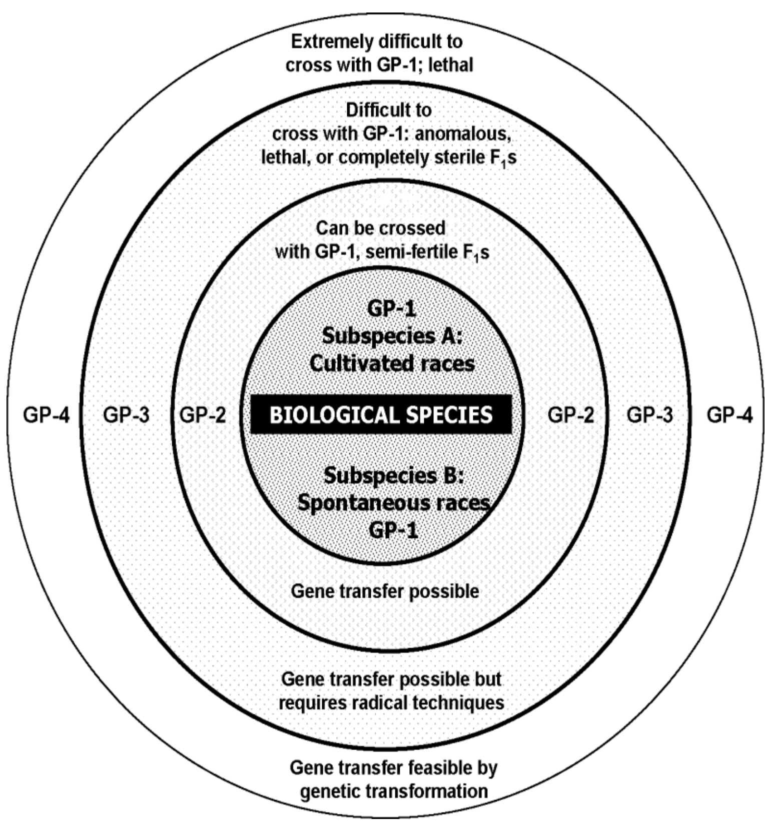
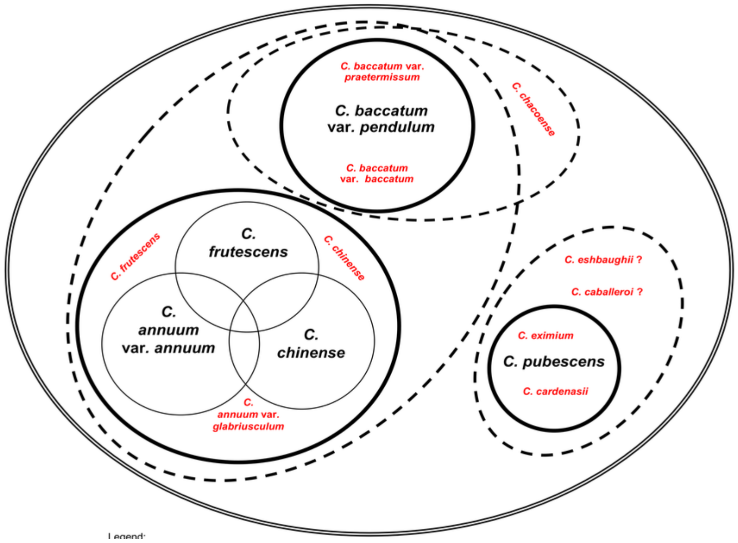


Fig.2 Source - *OECD, 2006.* Gene pool of Chilli.



Red letters- Wild species, Black letters – Cultivated species.

: Primary gene pool

: Secondary gene pool

: Tertiary gene pool

Fig.3 Gene pool of Brinjal

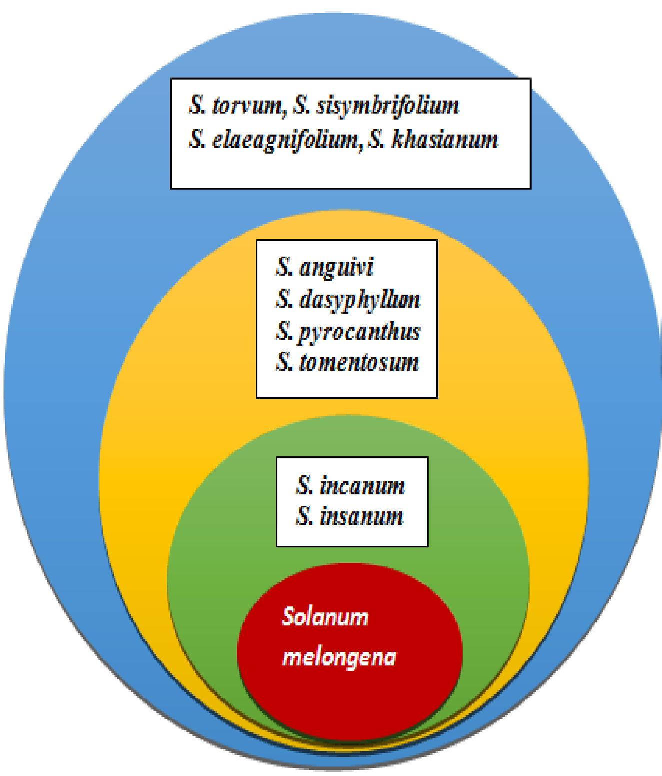
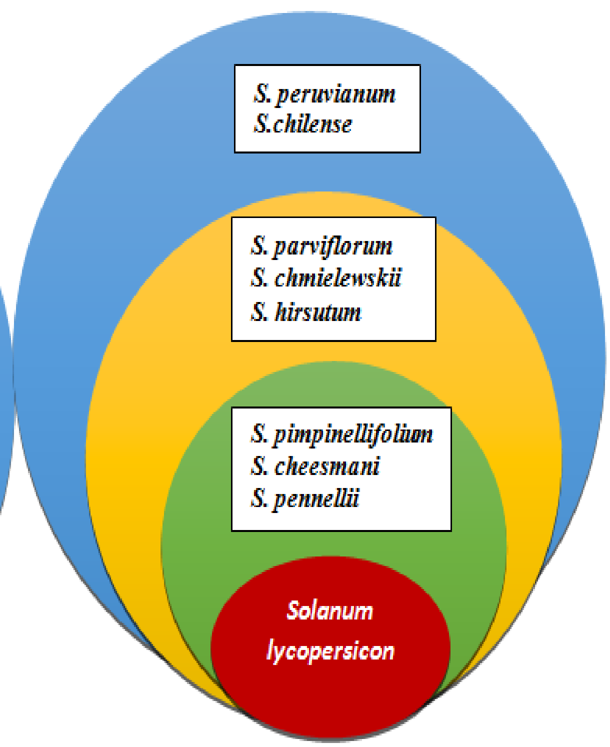
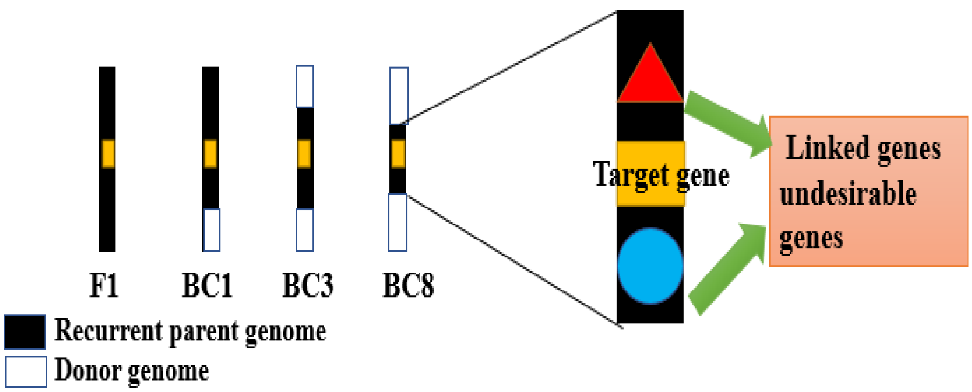


Fig.4 Gene pool of Tomato



Cultivated species, Primary gene pool, Secondary gene pool, Tertiary gene pool

Fig.5 Linkage drag schematic representation.



Manipulation of Ploidy level

Diploidization of single genomes to make them combined will be useful to make the cross fertile

Example

In potato there is a wide range of variation in ploidy level. By doubling ploidy level, *Solanum chacoense*, it can be crossable with *S. tuberesum (*Chandel *et al.*, 2015*)*.

Solanum melongena may not be crossable with *Solanum indicum*. But the cytoplasmic effects can be altered by changing the ploidy level of one of the parents. *S. melongena* as tetraploid has been crossable with *S. indicum* in both the direction.

Bridge Crosses

When two parents are unable to produce fertile hybrid, a third parent which is compatible with both the parents can be used for bridge crosses and thus produce viable offspring.

Examples

Solanum bulbocastanum (have valuable characters) is not crossable with *S. tuberosum*. So, *S. pinnatisectum* used as bridging species (now *S. phureja*, 2x and *S. acaule*, 4x also used as bridging sp to transfer late blight resistance to the cultivated species). Resistance to potato virus Y transferred from nontuberous sp *S. etuberosum* by using *S. verrucosum* and *S. pinnatisectum* as bridging sp.

Use of Pollen Mixture

Unfavourable interaction among pollen and pistil on account of wide crosses can be defeated somewhat by using pollen mixture.

Example

Cross between *Capsicum metulifolius* and *C. africanus* can be possible by application of Mentor pollen which improves the seed set.

Manipulation of Pistil

Decapitation of the style will sometimes prove helpful in overcoming incompatibility.

Use of Growth Regulators

Pollen tube development can be sped up by utilizing growth regulators like IAA, NAA, 2,4-D and Gibberellic acid. Application of gibberellic acid (75 ppm) one or two day before or after pollination promotes pollen tube growth and ovary development. Application of 1000 ppm GA3 increases the frequency of embryos.

Example

Application of NAA and potassium gibberelate applied to pedicle of pollinated flower of *Phaseolus vulgaris* and *P. aculifolius* improves seed set

Protoplast Fusion

Somatic fusion, also known as protoplast fusion, is a sort of genetic manipulation in plants in which 2 distinct species of plants are fused together to generate a new hybrid plant possessing the features of both. 1997, T. Cardi, Produced the of novel CMS *Brassica oleracea* by protoplast fusion of 'Anand' cytoplasm from *B. rapa*,"

Embryo Rescue

Hybrid zygotes formed by wide crosses may fail to develop in some of cases. The zygotes are taken out and grown in in vitro medium to overcome this problem (*Debbarama e al., 2013)*.

Example

Cucumber species *Cucumis hystivus* is developed by embryo culture of species *C. hystrix* and *C. sativus (*Ondrej *et al., 2006).*

Interspecific hybridisation is an important approach in vegetable crops for interspecific/intergeneric gene transfer. The main limiting factor is the cross-ability barrier, Linkage drag and there is need to find out the actual barrier in various cross combination and to overcome these barriers. In other case even if a species has a desirable character and is also crossable with the cultivated varieties, concerned efforts have not been made to advance the crosses to the final stage; thus, the interspecific gene transfer remains incomplete. All the desirable genes particularly resistant genes are not fully explored in the wild or semi wild species and there is need to make enough screening of all possible accessions of allied species and cataloguing of the species so that we can transfer desirable genes by utilizing proper technology for advancement of cultivates species.

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