On the complex nature of *unifoliata* locus and discovery of tightly linked gene causing multipistillate "umbelliferous" floral structure in pea (*Pisum sativum*)

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The *unifoliata* mutation of pea was first reported by Eriksson(1). Lamprecht (2) placed the gene *Uni* in linkage group (LG) III. The classical *unifoliata* mutation produces a single sessile leaflet of larger than usual size. Lamprecht (4) called it a "complex" mutation of homologous genes, also found in *Phaseolus vulgaris* and *Ph. multiflorus* (3). The epithet "complex" was given to this locus primarily because, besides converting a compound petiolate tendrilled leaf into simple, sessile and tendril-less, the *unifoliata* mutation also changes floral structure drastically. The flowers are, as usual, borne on a single peduncle in the leaf axil. However, each peduncle carries a large globule of dichotomously branched cluster of totally sterile flowers, each producing a small ovary. Many of these ovaries are incomplete in development, showing a clear transition from an open leafy structure to fully closed pistil. They are frequently without ovules, especially when the ovaries are underdeveloped and open. As many as 64 pistils were counted in a single globose cluster. A somewhat similar mutation was induced in *Tradescantia* and called "umbelliferous" (7). Such mutations were also called "clover type" (9) and symbol *Umb* was used to identify the genes producing such phenotype in recessive condition.

A mutation called "tendrilled acacia" (10, 11, 12) turned out to be a new allele of the gene *Uni* (5, 6). Sarala and Sharma (8) also showed *tac* (*uni*) to be linked with *Apu* and *St* on LG III. However, this mutation does not produce globular structure of sterile multipistillate flowers. The flowers are always borne singly; a few of these are open (not papillionaceous) and partially sterile. In totality, a *tac* plant can be called fertile. Another mutation with a different type of apical leaflet was reported by Sharma and Kumar (14). Thus, two fertile mutations (alleles) of the *uni* locus, *tac*^B and *tac*^S, are already known.

Another recessive unifoliate mutation has been induced in variety Large Podded G-20, which carries a single large sized leaflet on a short petiole. Its leaflet resembles the large terminal leaflet of tac^{B} mutation. The petiole is neither thickened at the base nor tapering towards the end as is characteristic of a normal compound leaf. The phenotype gives an impression as if this unifoliate structure represents only the terminal part of the leaf and the petiole in this case is the subterminal segment of leaf rachis in which a tac^{B} mutation occasionally produces tendrils (hence called tendrilled acacia) or remains without tendrils, and then the leaf has a long barren gap between the last pair of lateral leaflets and the large apical one.

On the basis of the above analysis it is concluded that this new mutation is another allele at the *Uni* locus and hence tentatively called "petiolate unifoliate" with gene symbol uni^{pet} awaiting experimental confirmation through mapping analysis. However, the uni^{pet} mutation being an allele of the *Uni* gene is supported by the fact that the uni^{pet} plants always produce globose sterile inflorescence of the so-called umbellate type as it happens in the well known *unifoliata* mutation of Lamprecht.

Another interesting fact was revealed by these mutation studies: several mutations with "umbelliferous" flowers were induced by fast neutrons, ethylene amine and diethyl sulphate without altering leaf structure, which remained tendrilled compound with the usual pairs of lateral leaflets. The "umbelliferous" inflorescence is known to accompany *unifoliata* mutations, and the *uni*^{pet} mutation isolated in the present study also produces "umbelliferous" inflorescence. However, because "umbelliferous" inflorescence can also be induced without affecting leaf morphology, it is clear that this floral trait is controlled by a genetic element other than the *Uni* locus as proposed by Lamprecht even without having a fertile mutation like tac^{B} and "umbelliferous" mutations with wild type leaves.

The mutation affecting floral structure is named, following the precedent in other plants, as *umbelliferous* and designated by gene symbol *Umb*, which in recessive condition produces globose "umbelliferous" floral structure.

PISUM GENETICS

The history of the *Uni* locus in *Pisum sativum* shows that it comprises two tightly linked genes—*Uni* and *Umb*—which are frequently mutated together as a result of a large deletion in the *uni-umb* region, spanning over the two independent functional units. The evidence available at present in support of this hypothesis is that both *uni* (*tac*) and *umb* mutations can be induced as individual events without mutually affecting their specific target organs, i.e., leaf and inflorescence, respectively.

It was proposed earlier (13) that the lateral and apical tendrils in *Pisum* differ in the genetic control during their differentiation. The *tac* alleles invariably eliminate the lateral tendrils (with leaky expression) and convert the apical tendril into a normal sized leaflet but have no influence on the lateral leaflets. The discovery of uni^{pet} mutation supports this hypothesis and also demonstrates that the uni mutation actually eliminates the lateral leaflets and tendrils while modifying the apical tendril into a normal leaflet. This results into placement of a nearly sessile leaflet on the main stem. The tac^{B} and tac^{S} alleles allow formation of lateral leaflets while retaining the subterminal part of the leaf rachis, occupied by the lateral tendrils in wild type, and simultaneously converts the terminal tendril into leaflet. Finally, the Lamprecht's *unifoliata* eliminates the leaf rachis completely, leaving behind a sessile leaflet which is actually the terminal tendril modified into leaflet and located right on the main stem.

Under the above scheme of gene expression and differential effect of the Uni alleles on various components of leaf, it would be appropriate to redesignate the old *unifoliata* mutation as uni^{L} (superscript L for Lamprecht).

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