Pea (Pisum sativum L.) Growth Mutants

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ABSTRACT

This review is devoted to the Pisum sativum L. growth mutants. These mutants are presented by several groups of plants. The first group is characterized by short internodes (dwarf mutants le, na, lh, la, lh, ls) or by elongated internodes (slender mutant sln). The stem growth of mutants of both types (dwarf and slender) is controlled by hormones (GA and IAA) in the stem or in seeds. Mutants characterized by decreased apical bud growth and predominated axillary bud growth belong to another group. They exhibit a multi-branching phenotype. Based on grafting studies with these mutants, several genes have been identified that operate in the shoot and roots in order to moderate the level or transport of graft-transmissible signal involved in branching control (genes rms1, rms2, rms3, rms4, rms5, rms6, rms7). The level and transport of auxins, cytokinins and shoot-multiplication signal (SMS) take part in the regulation of stem branching. SMS can be surmised to be proteins, among them carotenoid cleavage dioxygenases. The third mutant group is defined as the foliage mutants (genes af, tl, tac, st) characterized by different total leaf weights and areas per plant: high positive correlations of root weight with leaf weight and stem weight also of root weight with leaf area are observed. The “chameleon” phenotype is controlled by two recessive genes af and tac, which characterized heterophyllia. The determinate habit mutation is controlled by a recessive allele of the deh gene and results in the reduction of reproductive node number. The recessive det mutant forms an apical raceme, stops growth of the main stem and also exhibits a determinant habit. The lupinoid phenotype is controlled by recessive det and fas genes and determines the apical multi-flower inflorescence which is analogous to a lupine inflorescence. These mutants are important for studying the regulation of plant growth and for progress in improving high productive pea varieties.

Keywords: branching, determinant phenotype, dwarfism, habit, leaf morphology, plant growth regulation, productivity, root-shoot interaction

Abbreviations: af, afila; BL, brassinolid; BS, brassinosteroid(s); CCD, carotenoid cleavage dioxygenase; cry, cripto; deh, determinate habit; det, determinate type; DSP, Dark Skin Perfection; fas, fasciata; GC-SIM, gas chromatograph-selection ion monitoring; GA, gibberellins, gibberellic acid; IAA, indole-3-acetic acid; MT, microtubulus; na, nana; NLEP, New Line Early Perfection; rms, ramosus; sln, slender; SMS, shoot-multiplication signals; st, stipule; tac, tendriled-acacia; tl, tendril; WT, wild type

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INTRODUCTION

The Pisum sativum L. species as a life form are referred to as lianoid herbaceous monoparic plants. The growth of the wild type (WT) plants during vegetation is practically unlimited. Under conditions of sufficient water supply their vegetation growth still continues after legume ripening, which decreases sufficiently possibility to use assimilates for seed formation. Excessive stem growth contributes to great plant lodging even before flower budding. Meanwhile a death of considerable leaf number and rotting of the lower stem part of most plants is registered as leading to a significant decline in efficiency of photosynthetic activity, in the reproductive process of the plants and resulting in low seed productivity (Gritton 1972).

First of all, it is necessary to draw an attention to receive of pea (Pisum sativum L.) mutant technology. Mendel obtained the le mutant by classical breeding experiments (Mendel 1866). Later investigators began to observe spontaneous mutants in wild cultivars or induce them by γ-irradiation or by chemical mutagens from usual cultivars (Kujala 1953; Sidorova 1968). For example, loci La and Cry were identified by de Haan (1927) and Rasmusson (1927). Combination la cry leads to the phenotype cryptodwarf in the presence of le (Rasmusson 1927). The recessive mutant na gives arises to phenotype nana and is characterized by extreme shortening of the internode and reduced yield (Wellensiek 1971). The recessive mutant lm gives rise to the micro phenotype (Rasmusson 1938; Lindqvist 1951). Usually authors claimed that these mutations affected some processes by genetic, morphological, physiological and biochemical analyses.

The gene nomenclature of dwarf internode length was established by Blixt (1977). As a rule, the first letter of the
gene name is in common with several of the established internode length loci (le, lm, la). Later, gene names were attributed according to the abilities of these genes to determine some morphological, physiological or biochemical features.

In the genome of this species recessive mutations have been outlined as affecting the organization of all growth processes, and determining specificity of adaptation to changed environmental conditions (Wehner and Gritton 1981; Goldman and Gritton 1992).

Mutants with dwarf growth are characterized by shortened internodes, which to some extent contribute to increased resistance to lodging of plants in the canopy. Recessive alleles le, na, and lkb have the greatest effect on internodes shortening, decreasing the stem length by 40-60% (Reid et al. 1983; Lawrence et al. 1992; Reid and Howell 1986).

The mutants characterized by decreased apical bud growth and predominant axillary bud growth belong to another group. They exhibit a multi-branching phenotype. Based on grafting studies with such mutants, several genes have been identified that operate in shoots and roots in order to moderate the level or transport of graft-transmissible signal involved in branching control (rms1, rms2, rms3, rms4, rms5, rms6, rms7) (Reid et al. 2006).

The modern stage of cultural evolution of pea is characterized by a great variability of mutations of leaf or foliage type (genes af, tl, tac, st) (Gritton 1972; Wehner and Gritton 1981).

The determinate habit mutations are controlled by recessive alleles of the del and deh genes (Popova 1972; Marx 1986).

At present one of the main directions in modern evolution of pea culture is in the introduction and recombination of genes changing the relation of growth processes with changes in the architecture of plants and a range of vegetative characteristics increasing productivity of the canopy. In this respect the leading role belongs to the growth mutants.

This review serves to acquaint readers with pea growth mutants, which were selected and studied for a long time by investigators. Besides, we would like to acquaint readers with the nature of these mutations and their behavior in the canopy.

A GROUP OF PEA MUTANTS WITH DIFFERENT STEM HEIGHT

These mutants are characterized by short internodes. The le, la, and na mutant alleles alter internode length in a similar way. They diminish epidermal cell length, but cell number is affected to a lesser extent. An opposite situation occurs in the outer cortical layer (Reid et al. 1983). The Na gene is complimentary to the Le gene. All dwarf pea mutants are subdivided into the following groups: sensitive and insensitive to gibberellin (GA) precursors (Reid and Howell 1995). The experiments with grafting of these mutants and with 13C, 3H GAs have shown that different steps of GA biosynthesis are blocked. It was shown that a recessive mutation in le blocks 3β-hydroxylation transforming GA30 to active GA1. As a result, GA20 metabolizes to non-active GA20 and dwarf plants develop (Ingram et al. 1984).

The lh and bs dwarf pea mutants were obtained from cv. ‘Torsdag’ by Sidorova (1968). The ‘Torsdag’ genotype (Lh Lh Lh Ls) accumulates endogenous GAs (Sidorova 1983; Reid and Potts 1986). The decreased level of gibberellin-like activity was apparent in extracts from either apical or basal portion of the shoots of lh and bs mutants (K-511). More sensitive studies (GC-SIM) are shown that these mutations block the gibberellin biosynthesis pathway prior to the production of biological active GAs (i.e. probably prior to ent-kaurene). (Reid and Potts 1986; Reid and Howell 1995). The lk dwarf mutant and lka and lkb semi-dwarf mutants obtained from cv. ‘Torsdag’ by Sidorova (1968) and Reid (1986) with an erectoid or semi-erectoid phenotype do not accumulate active GA1 (Lawrence et al. 1992). All of them were insensitive to (exogenously) applied GAs. Authors suggested that the lk, lka and lkb mutants are a pea plant category in which GA-reception and transduction GA signals leading to stem elongation are blocked. It was shown that an exogenous auxin, indole-3-acetic acid (IAA) (0.2 mM), also takes part in internode elongation (Yang et al. 1996). IAA induces a rapid increase in the growth rate of le mutants, but later their growth rate decreases. The effect of applied GA (35 μg/ml ethanol) is more prolonged. The studies which applied GA and IAA showed that the effects on internode growth of these hormones are additive. Moreover, it is supposed that low levels of endogenous IAA do not permit high endogenous GA to induce stem elongation of GA-insensitive mutant lkb. However, applied IAA (0.2 mM) elongates internodes in lkb semi-erectoid GA-insensitive mutant plants (Yang et al. 1996). These authors supposed that a low level of IAA depressed cell elongation although endogenous GA content remained high. It is possible that the effect of GA may be mediated by auxin.

Furthermore, according to Schutz et al. (2001) and Nemhauser and Chory (2004) these mutations may block brassinosteroid (BS) biosynthesis and depress internode elongation. Besides, it is shown that brassinolide (BL) (200 ng dissolved in 2 μl of ethanol) application to intact lk, lka and lk and lkb mutants changes microtubulus (MT) orientation of epidermal and cortical cells of lk and lkb plants showed more transverse growth, whereas lka plants showed a non-significant response in these cells. The growth rate of BL-treated lk and lkb plants elongated as WT (cv. ‘Torsdag’), whereas BL-treated lka mutant internodes did not elongate in comparison to WT. It is possible that the lka mutant has lost the BS-receptor (Knowles et al. 2004). It is interesting that BSs have been shown to affect MT orientation and alter mechanical properties of cell walls (Shibaoka 1996). Knowles et al. (2004) supposed that the BS response is linked to the regulation of MT orientation and of mechanical properties of cell walls.

In contrast to dwarf mutants, a slender mutant (sin gene) is known (Ross et al. 1995). The seedlings and young plants of this type differ by the appearance of a slender or hyper-elongated phenotype which is related to large quantities of GA20. GA20 metabolizes in excess to GA1 during seed germination (Reid and Howell 1995). When the influx of GA20 from seeds diminishes, there is a transition by the plant to normal growth. The SLN gene of pea encodes a gibberellin-2-oxidase (Martin et al. 1999), a step of GA metabolism in normal pea plants. In a double mutant, the le gene is epistatic to the sin gene.

concluding this part of the review it should be stressed that stem elongation of intact plants is dependent on the GA and BS levels in stem internodes, hormone reception and transduction of hormonal signals. In addition, the existence of cross-talk between pathways in plants indicates a role of these signaling cascades in the relay of hormonal signals into the nucleus (Kulaeva and Prokopceva 2004).

A GROUP OF PEA MUTANTS WITH DECREASED APICAL DOMINANCE

These mutants are characterized by decreased apical bud growth and predominant axillary bud growth. As expected, high endogenous levels of IAA in apical buds maintain apical dominance. Plant decapitation alters IAA and cytokinin content. The recessive rms mutations of the RAMOSUS (RMS) gene cause shoot branching in P. sativum plants. These mutations cause increased branching at basal and aerial nodes especially after plant decapitation (Blixt 1974; Beveridge et al. 1996; Beveridge 2006). The rms mutant plants differ from WT plants by increased lateral axillary bud release and their growth. Shoots of isogenic lines of ramosus2 mutants (rms2) produce lateral branching below node 3 and above node 7. Apical dominance is restored by grafting to RMS2 (WT) stocks. Mutant rms2 stocks do not promote affect apical dominance in WT shoots in reciprocal
foliage types was similar to normal (WT) except for the roots of grafting studies show that a mobile signal was produced by and lateral growth in comparison with WT plants. However, (Beveridge 2006). Such signals (SMSs) might act as inhibitors of shoot branching transmissible signal (STS). Such shoot-multiplication sig-}

1950s (Kujala 1953; Soloviova 1958). In the isolation for the first time as spontaneous mutants in the acacia-like (White 1917). The tendrils are substituted with leaflets, and leaves become stipules in proximal position and one or several pairs of TYPES independent mechanisms.

Moreover, grafting studies show that non-allelic rms3 and rms4 mutations also cause the release of axillary buds and lateral growth in comparison with WT plants. However, grafting studies show that a mobile signal was produced by the roots of RMS (WT) plants. IAA levels are not dimin-ished in apical and nodal parts of rms4 and rms3 plants in comparison with WT plants (Beveridge et al. 1996; Beveridge 2006). It was proposed that the interaction of auxins and cytokinins might regulate branching in plants (e.g. Bangert et al. 2000; Kotova et al. 2004). The graft-transmissible signal may fulfill cytokinin export from the roots of decapitated pea plants. It is known that the cytokinin (zea-}

It should be commented that pea plant branching is con-trolled by several shoot-root signals: phytohormones, CCD and other non-identified factors.

THE MUTANTS WITH DIFFERENT FOLIAGE TYPES

The conventional pea leaf contains a pair of well-developed stipules in proximal position and one or several pairs of leaflets along the central leaf axis. The leaf axis extends to moderately developed tendrils. In the af mutant leaflets are transformed into tendrils. Such af forms with tendrils were isolated for the first time as spontaneous mutants in the 1950s (Kujala 1953; Soloviova 1958). In the tl mutants, tendrils are substituted with leaflets, and leaves become acacia-like (White 1917). The st gene reduces the large stipule to a small, strap-shaped one (Pellet and Sverdruk 1923). Transformation of one leaf component to another indicates that these mutations are homeotic. This suggestion was later supported by electron microscopic evidence (Gritton et al. 1973).

Non-isogenic lines of mutant (cultivars) and conven-tional foliage types (WT) have been compared (Gritton 1972). However, it is difficult to reveal the effect of foliage type from the effect of the background genotype on growth and productivity. To eliminate the effects of genetic background investigators used near-isogenic lines of different foliage types. The af, tl and st genes were incorporated singly and in all combinations into cultivars ‘A45’, ‘Al-sweet’, ‘Sprite’, ‘New Season’, ‘New Line Early Perfec-tion’ (NLEP), and ‘Dark Skin Perfection’ (DSP). Near-isogenic lines of the several foliage types were produced using at least 6 backcrosses. It was shown that their productivity was dependent on foliage type. The productivity of all foliage types was similar to normal (WT) except for the af of Tl Tl st st and af of tl tl st st types, which had reduced productivity (Wehner and Gritton 1981). These differences of the patterns are accounted for by variation in stipule size.

In the period preceding flowering, the loss of the leaflets in the af of mutant plants was partly compensated by the overgrowth of the stipules (Kof et al. 2004). In the st mutants such a phenomenon is not possible.

It should be stressed that the replacement of leaflets with tendrils transforms leaf morphology and changes the whole plant architecture in af forms. Thus, due to inter-twined tendrils, the af of pea stand is resistant to lodging and it reduces lodging significantly (Goldman and Gritton 1992; Kof et al. 2003, 2004). Wind and rain usually result in lodging by harvest time. This slow harvesting machinery and may reduce the yield and quality of shelled peas. Tendrils sup-port the plants and reduce lodging; reduced lodging may result in greater yield (Wehner and Gritton 1981; Kof et al. 1993).

Related to this, the af mutant is most in demand in breeding of this culture and more than 80% of modern pea cultivars are leafless. There is a risk of mutant reversion to the WT in field studies. However, the frequency of remuta-tions and reversion to WT are 0.001%. That is why such reversion of mutants to WT are not important especially in indus-trial studies (Kondykov et al. 2002).

In spite of lower assimilating area and chlorophyll content per plant at the period preceding flowering, the af mutants and WT plants did not differ in their final biomass and grain yield (Kof et al. 2001, 2004). The WT and af and tl mutants of pea did not noticeably differ in the chlorophyll content in light-harvesting complexes and chlorophyll a/b ratio. More than that, the Fv/Fm ratio, where Fv = Fm – Fo, was equal to 0.76-0.79 in all leaf units of WT and mutant lines under study (Kof et al. 2004; unpublished data). These data indicate the similar efficiency of the primary charge separation in photosynthetic system 2 and the similar ef-ficiency of photosynthetic utilization of solar energy.

However, the af plants have a reduced leaf apparatus which decreases excess foliage areas in comparison to WT and tl plants. This decrease increases light penetration into the canopy (Harvey 1978; Wehner and Gritton 1981). More-over, the comparative study of three foliage types of near-isogenic lines (WT, af, tl) in four genetic backgrounds (Al-sweet, New Season, NLEP, DSP) revealed such peculiarities. Replacement of leaflets with tendrils in af plants decreased the area shaded by a plant. This area was measured by the distance from the stem to the distal (uppermost) point of leaflets for WT and tl plants or stipules for af forms. This distance was taken for radius of the circle (r) to calculate the areas shaded by a plant. This area was measured by the distance from the stem to the distal (uppermost) point of leaflets for WT and tl plants or stipules for af forms. This distance was taken for radius of the circle (r) to calculate the areas shaded by a plant.

Thus these mutant lines differ considerably depending on the vertical distribution of solar radiation in the canopy (Gritton 1972; Wehner and Gritton 1981). High light transmittance of the af canopy promotes the expansion of the actinic photosynthetic leaf apparatus and increases the photosassimilating capacity of the plants whose leaflets are substituted with tendrils, especially in later developmen-tal phases.

There is still an open question: How are assimilates syn-thesized in the leaves distributed between growing plant or-gans, roots in particular? This question was decided by using near-isogenic lines. These lines have been bred by the incorporation of the af and tl genes in cv. NLEP (Wehner and Gritton 1981). The relative rates of shoot and root weight growth presume that plants develop their leaf aparatus early, in what we may conditionally call the juvenile period of growth in plants with five to seven leaves (true leaves, different from primary embryonic leaves). During this period, in spite of differences between genotypes in leaf morphology and area, they did not differ in shoot (leaves plus stem) weight indices. It means that the expenditures for root development were also similar. Only starting from leaf
9, the leaf weight in the \( af \) line lagged behind the corresponding indices in the WT and \( tl \) lines with their well-developed leaflets. The rate of root biomass accumulation was directly related to the accumulation of shoot biomass, primary that of leaves. This rate was at a minimum in \( af \) plants and considerably higher in the WT and \( tl \) plants, developing leaflets (Fig. 1). A correlation analysis demonstrated a close, direct link between leaf and root biomass in the pre-floral period of development (Kof et al. 2006). However the decrease in leaf area does not always diminish the size of the root system. Thus, in dwarf mutants, a higher root weight/shoot weight ratio is characteristic of the resulting dwarf plants with reduced leaf surface and extended roots. Such a morphological pattern of pea mutants was employed for breeding short-stature cultivars with enhanced root nodulation capacity (Sidorova et al. 2004). The restricted leaf growth in mesophytic plants is known to result from ecological stresses, such as drought (Pustovoitova et al. 2003), while in some of hemicerophytes adapted to drought, the well-developed roots penetrate deeply in the soil and provide water for shoot growth (Slavnyi 1989).

The “chameleon” phenotype is controlled by recessive genes, \( af \) and \( tac \) (tendrilled acacia) (Zelenov 1991). The mutant “tendrilled acacia” forms apical leaves and a lateral pair of tendrils (Sharma and Kumar 1981). A distinctive feature of the “chameleon” phenotype is the presence of heterophyllous layers: lower composite leaves have 2-3 leaves and a tendril, the leaves of the middle layer are presented by tendrils and in the zone of fruit-bearing the composite leaf is presented by multiple-branched tendrils whose leaves are irregularly located on their distal parts. Expression of the trait of heterophyllous layers is dependent to a great extent on the genetic surrounding and conditions of vegetation. The degree of leaflet development is dependent on genetic background, light intensity and light day length. A biomass yield of the chameleon phenotype is 20-30% higher than that is in WT. However, a dry seed yield is less (smaller) than that in WT. The chameleon plants are a combination of WT and \( af \) and \( tac \) peculiarities. The “chameleon” phenotype has great physiological indices of productivity and increased biological potential of productivity. Cv. ‘Spartak’ (chameleon phenotype) is now studied in the Russian State Agronomic Stations from 2006.

**MUTANTS WITH DETERMINATE PHENOTYPES**

Mutants with a determinate phenotype are controlled by a recessive allele of the \( det \) gene (Popova 1972; Marx 1986; Sweicik 1987; Shevchenko 1989). The determinate type was obtained from cv. “Svoboda 10” by chemical mutagenesis by Popova (1972) and Sweicik (1987). Its action is in blocking the apical growth of the stem after formation of two apical bifurcated inflorescences. As a result a strictly limited number of productive internodes is formed in plants (Fig. 2). Two groups of genotypes are distinguished: in one of them a maximum of two productive internodes are formed, while in the others – from two to five internodes are formed depending on growth conditions. A reduced number of productive internodes enables a shortened generative period and uniform ripening of compactly located beans.

The “lupinoid” phenotype is controlled by recessive alleles of the \( det \) (determinant type) and \( fas \) (fasciata) genes (Uvarov 1993). The \( fas \) mutant was obtained by Uvarov (1993) as spontaneous mutant. A combination of these mutant genes determines the development of multi-flowered apical inflorescence consisting of 10-15 alternately located flowers on a short (5-15 mm) anthophore (Fig. 3). The inflorescence type is analogous to that of lupinus (Lupinus lupinus). The compact location of beans contributes to uniform ripening. Lupinoids have a great potential of seed productivity. However, an imbalance between high potential and real productivity is observed in the forms with this type of determinate, explained by increased abortion of flowers, beans (legumes) and seeds. One of the main reasons of this is high lodging of lupinoids determined by unstable construction of the plant. An algorithm of this problem-solving provides an introgressive hybridization to dwarf stem and tendrilled leaf genes (Zadorin and Yakovlev 1998; Kondikov et al. 2002). There is increasing phenotypic variation as

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**Fig. 1 Three pea foliage types. Normal (WT) has \( AfAfTlTL \) genotype (left), \( af \)(middle), \( tl \)(right).**

**Fig. 2 A mutant with determinate phenotype (\( det \) gene).**
most of the growth mutants display negative pleiotropia in seed and general productivity their use has a perspective for solving individual problems of plant genetics. Production of a corresponding genetic environment with the help of gene-modifiers is necessary in order to decrease their depressive characteristics. The search of economically valuable mutants and directed recombinant genesis at this stage remains the most efficient means of breeding peas. Taking into account genetic peculiarities of the pea growth mutants as well as the fact that they influence significantly the organization of growth processes, hormonal balance and specificity of adaptation of plants, they are of interest for researchers in the field of genetics, physiology and general biology.

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