

(+1) and (-1) deviations in development of floral meristems in *Trientalis europaea* L.

Oleg N. Tikhodeyev, Maria A. Neustroeva & Marina Y. Tikhodeyeva

Summary: We have found that both (+1) and (-1) local deviations occur in *Trientalis europaea* floral meristems in good accordance with Poisson distribution. The meristems with low initial multiplicity of the organs primordia (M_5 and M_6) are shown to be predisposed to (+1) deviations. In contrary, in meristems with higher initial multiplicity (M_7 and M_8), (-1) deviations are preferred. We propose that stochastic misbalances in *T. europaea* floral meristem size play the key role in this phenotypic plasticity.

Zusammenfassung: Wir konnten herausfinden, dass beide, (+1) und (-1) Abweichungen, in guter Übereinstimmung mit der Poisson-Verteilung, in Blüten-Meristemen von *Trientalis europaea* auftreten. Meristeme mit geringer Organzahl (M_5 und M_6) sind anfällig für (+1) Abweichungen, während bei Meristemen mit höherer Organzahl (M_7 und M_8) (-1) Abweichungen gehäuft vorkommen. Wir meinen, dass stochastisches Ungleichgewicht in der Größe des Blütenmeristems von *T. europaea* die Schlüsselrolle für die phänotypische Plastizität spielt.

Keywords: phenotypic plasticity, flower development, *Trientalis europaea*, stochastic events

The origin of intraspecific variation has been subject of extensive studies for more than one century. As the result, three types of variation have been disclosed. The first one is genetic variation. It is generated by arising mutations and their further multiple combinations in the progenies (see AYALA & KIGER 1984; GRIFFITS et al. 1993; STERN 2000). The second one is ontogenetic variation. It occurs due to specific changes in gene expression while the organism consequently passes through different stages of the development (LAWRENCE 1992; KOROCHKIN 1999; LUTOVA et al. 2000). The third one is phenotypic plasticity within the norm of reaction (PHILIPCHENKO 1929). Its mechanisms appeared to be very wide and many of them are still poorly understood. Detailed investigation of these mechanisms is one of the central tasks for modern biology.

In many plant species, an amazing phenotypic plasticity is described. It usually affects all basic quantitative traits such as plant biomass, stem height, root length, leaf blade square, etc. (CLARKSON & HANSON 1980, KRAMER 1983, DOUGLAS 1994, FANKHAUSER & CHORY 1997). Some more specific traits may be also affected. For example, in the weedy angiosperm plant *Trientalis europaea* L., plasticity of the flower structure is demonstrated (CHARLIER 1913, HIIRSALMI 1969, TIKHODEYEV & TIKHODEYEVA 2001, 2002).

According to studies in natural populations, the flowers produced in this species may be divided into two groups (TIKHODEYEV & TIKHODEYEVA 2001, 2002):

1. Flowers possessing an equal number of sepals (S), petals (P) and stamens (St). Such flowers are designated as regular. In *T. europaea*, four types of regular flowers are described: 5-merous ($S_5P_5St_5$), 6-merous ($S_6P_6St_6$), 7-merous ($S_7P_7St_7$) and 8-merous ($S_8P_8St_8$);
2. Flowers possessing an unequal number of sepals, petals and stamens. These flowers are designated as irregular. When compared to regular flowers, the majority of irregular ones

have one extra or one missing sepal, petal or stamen (for example, $S_5P_6St_5$, $S_7P_6St_6$, $S_7P_6St_7$, $S_8P_8St_7$). Therefore, formation of an irregular flower is likely based on a local deviation which affects only one floral organ primordium and either blocks its further development (-1) or induces production of one extra organ (+1). Only few irregular flowers are of a more complex structure (for example, $S_8P_6St_6$, $S_6P_7St_8$, $S_8P_8St_6$). Each of these flowers seems to be the result of two local deviations that have occurred in the same floral meristem.

The most frequent type of *T. europaea* flowers is represented by $S_7P_7St_7$ (CHARLIER 1913, HIIRSALMI 1969, GRIVLOVA & VAHRAMEEVA 1990, TIKHODEYEV & TIKHODEYEVA 2001, 2002). Such flowers are considered as typical for this species. Notably, the joint frequency of all other types of regular flowers is usually higher compared to that of irregular ones (TIKHODEYEV & TIKHODEYEVA 2001, 2002). According to these data, formation of regular flowers $S_5P_5St_5$, $S_6P_6St_6$ or $S_8P_8St_8$ is not the result of multiple local deviations that have independently affected the same floral meristem. It is more likely that such flowers are the product of another mechanism: change of initial multiplicity of the organs primordia from usual 7 to unusual 5, 6 or 8.

Thus the structure of *T. europaea* flower depends on two factors: (1) initial multiplicity of the organs primordia and (2) local deviations in the development of the floral meristem. As shown on two-flower *T. europaea* plants, each of these factors is not rigidly determined by the plant genotype or developmental stage, reflecting the significant role of phenotypic plasticity (TIKHODEYEV & TIKHODEYEVA 2002). Moreover, for local deviations in the development of the floral meristem, a stochastic manner of occurrence is demonstrated. The mechanism of such plasticity is still unknown.

In the present work, we have found that both (+1) and (-1) deviations occur in *T. europaea* floral meristems in good accordance with Poisson distribution. The meristems with low initial multiplicity of the organs primordia (i.e. M_5 and M_6) are predisposed to (+1) deviations. In contrary, in the meristems with higher initial multiplicity (i.e. M_7 and M_8), (-1) deviations are preferred.

Materials & Methods

Object of study

Trientalis europaea L. is the clonal weed plant common in the boreal zone of the Northern Hemisphere (HEGI 1908). In this species, seed set is low and seedling recruitment is quite rare (HIIRSALMI 1969, GRIVLOVA & VAHRAMEEVA 1990). During its vegetative pseudo-annual life cycle, the mother ramet produces several tubers and dies back (WARMING 1918, GRIVLOVA & VAHRAMEEVA 1990, PIQUERAS & KLIMES 1998). The daughter tubers retain in the soil until the new growing season which starts in May-June and completes in August-September. During this period, the mature plant produces one or several (sometimes up to 5) white actinomorphic flowers (CHARLIER 1913, MATTHEWS & ROGER 1941, HIIRSALMI 1969). In the North-West of Russia, flowering of *T. europaea* occurs in June.

Study area

This work has been carried out in natural populations of *T. europaea* in different plant communities of Konevitsa island (SW of Ladoga lake, Russia). Being formed by sandy and

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loamy deposits, this island is covered by multiple types of forests varying from pure *Pinus sylvestris* L. to pure *Picea abies* (L.) Karst. ones. Fragments of forests produced by *Betula pendula* Roth, *Alnus incana* (L.) Moench and *Populus tremula* L. are also present.

On Konevitsa island, *T. europaea* is quite common in all types of forests except pure *Pinus sylvestris* and most shaded *Picea abies* ones. From the forests, *T. europaea* successfully penetrates into the nearest open areas, like edges of forest swamps and floating bogs. In the present work, we have studied 24 samples of *T. europaea* flowers obtained from different plant communities of Konevitsa island (Table 1).

Analysis of *Trientalis europaea* flowers

In each plant community, we usually studied more than 100 randomly chosen, undamaged flowers of *T. europaea*. For every flower, we counted the number of sepals (S), petals (P) and stamens (St), getting the formula: $S_xP_ySt_z$.

The flowers with an equal number of sepals, petals and stamens will be further designated as regular (R). According to their structure, all regular flowers investigated were subdivided in four types: 5-merous ($S_5P_5St_5$ or R_5), 6-merous ($S_6P_6St_6$ or R_6), 7-merous ($S_7P_7St_7$ or R_7) and 8-merous ($S_8P_8St_8$ or R_8).

Table 1. Plant communities at Konevitsa island involved in the present study.

Plant community	Position	Mature trees	Tree regrowth	Predominating species in plant soil cover	Illumination
<i>Pinus</i> forest	Dry sandy terrace, 12 m above the lake level	<i>Pinus sylvestris</i>	<i>Sorbus aucuparia</i> (rare)	<i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i> , <i>Calluna vulgaris</i> , <i>Pleurozium schreberi</i> , <i>Dicranum polysetum</i>	High
<i>Pinus</i> forest I	Dry sandy terrace, 6 m above the lake level	— " —	— " —	— " —	— " —
<i>Pinus</i> forest II	Dry sandy terrace, 10 m above the lake level	— " —	— " —	— " —	— " —
<i>Pinus</i> + <i>Picea</i> forest	Sandy terrace, 6 m above the lake level	— " —	<i>Picea abies</i> , <i>Sorbus aucuparia</i>	<i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i> , <i>Maianthemum bifolium</i> , <i>Lycopodium clavatum</i> , <i>Pleurozium schreberi</i> , <i>Pohlia nutans</i>	Comparably high
<i>Picea</i> + <i>Pinus</i> forest	Sandy terrace, 4 m above the lake level	<i>Picea abies</i> , <i>Pinus sylvestris</i> , <i>Sorbus aucuparia</i>	<i>Picea abies</i> , <i>Sorbus aucuparia</i>	<i>Vaccinium myrtillus</i> , <i>Calamagrostis arundinacea</i> , <i>Pleurozium schreberi</i> , <i>Rhizomnium punctatum</i>	Medium
<i>Betula</i> forest	Low-lying coast, 1 m above the lake level	<i>Betula pendula</i> , <i>Alnus cinerea</i> , <i>Populus tremula</i>	<i>Betula pendula</i> , <i>Alnus cinerea</i> , <i>Populus tremula</i> , <i>Picea abies</i>	<i>Calamagrostis epigeios</i> , <i>Vaccinium myrtillus</i> , <i>Rubus saxatilis</i> , <i>Oxalis acetosella</i> , <i>Anthyrium filix-femina</i> , <i>Dryopteris expansa</i>	Medium
<i>Picea</i> forest	Wet, loamy terrace, 10 m above the lake level	<i>Picea abies</i>	<i>Picea abies</i>	<i>Pleurozium schreberi</i> , <i>Dicranum scoparium</i> , <i>Hylocomium splendens</i> , <i>Vaccinium myrtillus</i> , <i>Oxalis acetosella</i>	Low

All other types of flowers (for example, $S_7P_6St_6$, $S_8P_8St_7$ or $S_6P_7St_8$) will be further designated as irregular (I). For each irregular flower, we reconstructed its most probable origin (TIKHODEYEV & TIKHODEYEVA 2002). A flower possessing 1 extra (+1) or 1 missing (-1) organ was suggested to be produced in result of a single local deviation that has occurred in an initially regular floral meristem. For example, the flower $S_6P_7St_7$ was considered to develop from initially 7-merous floral meristem due to damage or lack of 1 sepal primordium. Such flowers were designated as I_{7-1S} . By analogy, the flower $S_5P_6St_5$ reflected formation of 1 extra petal primordium in initially 5-merous floral meristem. Flowers of this type were designated as I_{5+1P} .

An irregular flower possessing more complex structure was suggested to be the result of two local deviations that have affected the same floral meristem. For example, the flower $S_6P_7St_8$ was considered to develop from initially 7-merous floral meristem due to damage or lack of 1 sepal primordium and simultaneous formation of 1 extra stamen primordium. Such flowers were designated as $I_{7-1S+1St}$. By analogy, the flower $S_8P_8St_6$ reflected damage of 2 stamen primordia in initially 8-merous floral meristem. Flowers of this type were designated as I_{8-2St} .

Analysis of distribution and frequency of (+1) and (-1) local deviations

Each sample of *T. europaea* flowers was subdivided in groups according to initial meristem structure: M_5 , M_6 , M_7 and M_8 . Then in every group of the flowers, the frequencies of (+1) and (-1) deviations for sepals, petals and stamens primordia were separately obtained. Basing on these data, we calculated expected ratio between the flowers with 0, 1 and 2 deviations of the certain type, in assumption that they correspond to Poisson distribution (GLOTOV et al. 1982):

$$p_k = \frac{\lambda^k}{k!} e^{-\lambda} ; \quad n_k = p_k \times N$$

wherein p_k = expected frequency of the flowers with k deviations;
 λ = obtained frequency of certain type of local deviations in the studied sample;
 n_k = expected number of the flowers with k deviations; and
 N = sample volume.

The expected ratio between the flowers with 0, 1 and 2 deviations of the certain type was compared to the real ratio using the criterion χ^2 (ROHLF & SOKAL 1995).

To compare the frequencies of local deviations in two different samples, we approximated Poisson distribution by the normal:

$$u = \frac{\lambda_1 - \lambda_2}{\sqrt{\lambda_1/N_1 + \lambda_2/N_2}}$$

and compared u value with table $u_{\alpha/2}$ (GLOTOV et al. 1982).

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Results

During 7 years (1995–2002), we studied the structural variation of *T. europaea* flowers in natural populations of Konevitsa island. The joint sample of 4,385 flowers comprised 3,783 regular and 602 irregular ones. All regular flowers obtained in this sample were represented by the following four types: R₅, R₆, R₇ and R₈, with predominance of R₇ flowers. Irregular flowers were shared in multiple types. For each of them, the most probable origin was reconstructed (Table 2).

Table 2. Structural variation of *Trientalis europaea* flowers on Konevitsa island (joined data from 1995 to 2002).

Initial floral meristem*	Regular flowers	Irregular flowers							Subtotal
		+1 S	-1 S	+1 P	-1 P	+ 1 St	-1 St	double	
M ₅	6 (0.1%)	4	0	0	0	2	0	0	12
M ₆	1242 (28.3%)	41	18	39	6	49	25	8	1428
M ₇	2442 (55.7%)	5	147	14	40	33	113	18	2812
M ₈	93 (2.1%)	0	15	1	3	0	15	6	133
Subtotal	3783 (86.3%)	50	180	54	49	84	153	32	Total
		230		103		237		32	4385

* M₅, M₆, M₇, and M₈: initially 5-, 6-, 7- and 8-merous floral meristems.

According to our reconstructions, the majority of *T. europaea* irregular flowers was the result of single local deviations of either (+1) or (-1) type. In addition, about 5% of studied irregular flowers appeared to be of more complex structure. Many of them possessed double deviations in the same whorl of organs (Table 3). Only in 9 irregular flowers obtained, two whorls of organs were simultaneously affected. In each of these flowers, the affected whorls were altered in opposite ways, i.e. the number of organs increased in one whorl and decreased in the other.

Table 3. Structure of *Trientalis europaea* flowers possessing several local deviations.

Flower type	Proposed flower origin	Number
S ₄ P ₆ St ₆	I ₆ -2S	1
S ₆ P ₆ St ₄	I ₆ -2St	1
S ₅ P ₆ St ₇	I ₆ -1S+1St	1
S ₇ P ₆ St ₅	I ₆ +1S-1St	1
S ₈ P ₆ St ₆	I ₆ +2S	2
S ₆ P ₆ St ₈	I ₆ +2St	2
S ₅ P ₇ St ₇	I ₇ -2S	5
S ₇ P ₇ St ₅	I ₇ -2St	6
S ₆ P ₈ St ₇	I ₇ -1S+1P	2
S ₇ P ₆ St ₈	I ₇ -1P+1St	1
S ₇ P ₈ St ₆	I ₇ +1P-1St	1
S ₈ P ₆ St ₇	I ₇ +1S-1P	1
S ₈ P ₇ St ₆	I ₇ +1S-1St	1
S ₉ P ₇ St ₇	I ₇ +2St	1
S ₆ P ₈ St ₈	I ₈ -2S	1
S ₈ P ₆ St ₈	I ₈ -2P	1
S ₈ P ₈ St ₆	I ₈ -2St	3
S ₆ P ₉ St ₈	I ₈ -2S+1P	1

It should be especially noted that we failed to obtain the flowers in which two different whorls were altered in the same way. Such flowers were undistinguishable from those produced in result of single local deviations (for example, the flower $I_{7-1S-1St}$ had the structure $S_6P_7St_6$ and thus resembled the flower I_{6+1P}). So for some *T. europaea* flowers, the reconstruction of their origin might be not correct. However, these flowers should be very rare and have no significant influence on general rules in development of *T. europaea* floral meristems.

Among all 9 flowers displaying simultaneous alterations in two whorls of the organs, in 6 flowers adjacent whorls have been affected. Such alterations may be explained by two different mechanisms. First, we could propose that single floral organ primordium has occasionally changed its developmental fate. For example, in the floral meristem M_7 , single organ primordium from the 2nd whorl might develop not in usual petal but in stamen. As the result, the flower with 1 missing petal and 1 extra stamen could be produced. Alternatively, formation of such flower might be due to double local deviations that have occurred in 2nd and 3rd whorls of the organs primordia.

To distinguish these mechanisms, we compared the numbers of irregular flowers displaying different pairs of affected whorls: sepals-petals (S-P), petals-stamens (P-St) and sepals-stamens (S-St). We have found that the numbers of flowers in which two adjacent or two opposite whorls were simultaneously altered appeared to be very similar (4 flowers of the S-P type, 2 flowers of the P-St type and 3 flowers of the S-St type). According to these data, all *T. europaea* flowers displaying simultaneous alterations in different whorls are the result of the same mechanism, i.e. several local deviations occurred in the same floral meristem.

Only for one single *T. europaea* flower, it's origin could not be reconstructed even proposing double local deviations. This flower ($S_6P_9St_8$) seemed to be the result of triple local deviations that have occurred in the meristem M_8 : two (-1) deviations in the whorl of sepals and (+1) deviation in the whorl of petals. So we have shown that the same *T. europaea* floral meristem can suffer multiple, more than double local deviations.

Distribution of (+1) and (-1) local deviations in *Trientalis europaea* floral meristems

To carry out detailed statistic analysis of (+1) and (-1) local deviations, one should know the character of their distribution. These deviations turned out to be quite rare events which could occur in the same floral meristem for several times. Therefore we proposed that both (+1) and (-1) deviations arise in the meristems in accordance with Poisson distribution. We have verified this proposition in 10 samples of *T. europaea* flowers displaying comparably high frequency of local deviations. For this purpose, each sample was subdivided in flowers derived from the meristems M_5 , M_6 , M_7 and M_8 . After that in every group of the flowers, we have obtained the media numbers of (+1) and (-1) deviations for sepals, petals and stamens primordia separately. For the flowers derived from the meristems M_5 and M_8 , such deviations were very rare in each studied sample. Therefore we have used only the flowers developed from the meristems M_6 and M_7 .

Basing on the obtained media numbers, we have calculated the expected ratio between flowers with 0, 1 and 2 deviations of the certain type (see Materials & Methods). We have shown that in the majority of samples, the expected ratio was closely similar to the real one (Table 4). Notably, such similarity was characteristic to different types of local deviations (+1 and -1), floral organs (sepals, petals and stamens), floral meristems (M_6 and M_7) and plant communities (*Pinus*,

Deviations in floral meristem development of *Trientalis europaea* L.Table 4. Expected and real ratio between *Trientalis europaea* flowers with 0, 1 and 2 local deviations.

Year of study	Plant community	Floral meristem	Type of local deviation	Number of flowers	Expected ratio* 0 : 1 : 2	Real ratio 0 : 1 : 2
1995	Pinus forest	M ₆	+ 1S	92	78.2 : 12.8 : 1.0	77 : 15 : 0
			+ 1St	92	80.8 : 10.5 : 0.7	80 : 12 : 0
		M ₇	- 1S**	108	84.1 : 21.1 : 2.6	81 : 27 : 0
			- 1St	108	97.4 : 9.9 : 0.5	96 : 11 : 1
	Pinus+Picea forest	M ₆	+ 1S	84	79.8 : 3.8 : 0.1	80 : 4 : 0
			+ 1P	84	73.6 : 9.7 : 0.6	73 : 11 : 0
			- 1St	84	79.1 : 4.7 : 0.2	79 : 5 : 0
		M ₇	- 1S	159	142.9 : 15.3 : 0.8	143 : 15 : 1
			- 1P	159	147.6 : 11.1 : 0.4	147 : 12 : 0
			+ 1St	159	150.9 : 8.8 : 0.1	150 : 9 : 0
			- 1St	159	141.9 : 16.1 : 0.9	142 : 16 : 1
			Picea+Pinus forest	M ₇	- 1S	102
	- 1St	102			95.2 : 6.5 : 0.2	97 : 3 : 2
	Picea forest	M ₆	+ 1S	87	81.2 : 5.6 : 0.2	82 : 4 : 1
		M ₇	- 1S	112	97.9 : 13.1 : 0.9	98 : 13 : 1
			- 1P	112	104.2 : 7.5 : 0.3	104 : 8 : 0
1996	Pinus forest I	M ₇	- 1S	182	174.1 : 7.6 : 0.2	175 : 6 : 1
			- 1St	182	167.6 : 13.8 : 0.6	168 : 13 : 1
	Pinus forest II	M ₇	- 1S	123	112.3 : 10.0 : 0.5	113 : 9 : 1
	Pinus+Picea forest	M ₇	- 1S	124	118.1 : 5.7 : 0.1	118 : 6 : 0
	Picea+Pinus forest	M ₇	- 1St	126	112.7 : 12.5 : 0.7	112 : 14 : 0
	Betula forest	M ₇	- 1S	189	184.0 : 4.9 : 0.0	184 : 5 : 0
			- 1St	189	178.3 : 10.4 : 0.3	180 : 7 : 2
2002	Pinus forest	M ₆	+ 1St	231	219.4 : 10.5 : 0.3	220 : 10 : 1
		M ₇	- 1S	74	62.9 : 10.2 : 0.8	62 : 12 : 0
Joint sample (1995–2002)	M ₆	+ 1S	1428	1382.6 : 44.5 : 0.7	1384 : 42 : 2	
			- 1S	1428	1405.7 : 20.7 : 0.2	1408 : 19 : 1
			+ 1P	1428	1389.6 : 38.0 : 0.5	1389 : 39 : 0
			- 1P	1428	1421.9 : 5.9 : 0.0	1422 : 6 : 1
			+ 1St	1428	1375.1 : 52.0 : 1.0	1376 : 50 : 1
			- 1St	1428	1400.3 : 27.4 : 0.3	1401 : 26 : 1
		M ₇	+ 1S	2812	2805.4 : 6.9 : 0.0	2805 : 7 : 0
			- 1S	2812	2657.3 : 150.2 : 4.2	2658 : 149 : 5
			+ 1P	2812	2795.1 : 16.8 : 0.1	2795 : 17 : 0
			- 1P	2812	2770.1 : 41.3 : 0.3	2770 : 42 : 0
			+ 1St	2812	2776.3 : 35.6 : 0.2	2776 : 36 : 0
			- 1St	2812	2687.7 : 121.3 : 2.9	2692 : 115 : 6
		M ₈	- 1S	133	115.2 : 16.5 : 1.2	114 : 15 : 2
			- 1P	133	12.2 : 4.8 : 0.1	129 : 3 : 1
			- 1St	133	117.2 : 14.9 : 0.9	117 : 15 : 1

*The expected ratio was calculated in assumption that local deviations occurred in *T. europaea* floral meristems according to Poisson distribution. Numbers 0, 1 and 2 mean the flowers displaying 0, 1 and 2 local deviations of appropriate type.

**The samples possessing significant differences (at 95% significance level) between the expected and real ratio are shown in bold letters. Such differences are rare and not specific to certain plant community, type of the meristems or local deviations. So these differences are likely due to not enough volumes of the studied samples.

Pinus+Picea, *Picea+Pinus*, *Picea* and *Betula* forests). So both (+1) and (-1) local deviations actually occur in *T. europaea* floral meristems in accordance with Poisson distribution.

The frequency of (+1) and (-1) deviations in *Trientalis europaea* floral meristems with different initial multiplicity of the organs primordia

We have found that in joint sample of *T. europaea* flowers (1995-2002), distribution of both (+1) and (-1) local deviations also corresponded well to Poisson distribution (Table 4). This allowed us to compare the frequency of (+1) and (-1) deviations in the same type of floral meristems using joint data from all 24 samples studied (Table 5). The meristems M_8 and M_7 appeared to be predisposed to local deviations of (-1) type. Meanwhile the meristems M_6 preferably suffered (+1) deviations. Unfortunately, we could not make a statistically supported suggestion for the meristems M_5 because of their rarity in *T. europaea*. However, all 6 local deviations obtained in these meristems were of (+1) type only. So we believe that the meristems M_5 were also predisposed to (+1) deviations.

Thus the meristems with high initial multiplicity of the organs primordia (i.e. M_8 and M_7) preferably suffer (-1) deviations. In contrary, in the meristems with lower initial multiplicity (i.e. M_6 and M_5), local (+1) deviations are preferable.

Using joint sample of *T. europaea* flowers, we have also compared the frequency of (+1) and (-1) deviations in the meristems with different initial multiplicity of the organs primordia (Table 6). For both, sepal and stamen primordia, the frequency of (+1) deviations decreased gradually from the meristems M_6 to the meristems M_8 . In contrary, the frequency of corresponding (-1) deviations was shown to increase in the same range. So the frequencies of these types of local deviations depend on initial multiplicity of floral meristems.

Table 5. The frequency of local (+1) and (-1) deviations in the same type of *Trientalis europaea* floral meristems.

Initial floral meristem	Type of local deviation	Number of flowers	Number of local deviations	Frequency of local deviations	$P_{H_0}^*$
M_6	+ 1S	1428	46	0.032	
	- 1S	1428	21	0.015	< 0.001
	+ 1P	1428	39	0.027	
	- 1P	1428	8	0.006	< 0.001
	+ 1St	1428	52	0.036	
	- 1St	1428	28	0.019	0.009
M_7	+ 1S	2812	7	0.002	
	- 1S	2812	159	0.057	< 0.001
	+ 1P	2812	17	0.006	
	- 1P	2812	42	0.015	0.02
	+ 1St	2812	36	0.013	
	- 1St	2812	127	0.045	< 0.001
M_8	+ 1S	133	0	0.000	
	- 1S	133	19	0.143	< 0.001
	+ 1P	133	1	0.008	
	- 1P	133	5	0.038	0.11
	+ 1St	133	0	0.000	
	- 1St	133	17	0.128	< 0.001

* H_0 : the frequencies of (+1) and (-1) deviations in the same type of floral meristem are equal. In all cases except one (+1P and -1P deviations in the meristems M_8), the difference appeared to be significant. This single exception is likely due to not enough number of studied meristems M_8 because of their rarity in *T. europaea*.

Deviations in floral meristem development of *Trientalis europaea* L.Table 6. The frequency of local (+1) and (-1) deviations in different types of *Trientalis europaea* floral meristems.

Type of local deviation	Floral meristem	Frequency of local deviations	Statistical result of comparison*
+ 1S	M ₆	0.032	$\lambda(+1S)_6 > \lambda(+1S)_7 > \lambda(+1S)_8$
	M ₇	0.002	
	M ₈	0.000	
+ 1P	M ₆	0.027	$\lambda(+1P)_6 > \lambda(+1P)_7$
	M ₇	0.006	
	M ₈	0.008	
+ 1St	M ₆	0.036	$\lambda(+1St)_6 > \lambda(+1St)_7 > \lambda(+1St)_8$
	M ₇	0.013	
	M ₈	0.000	
- 1S	M ₆	0.015	$\lambda(-1S)_6 < \lambda(-1S)_7 < \lambda(-1S)_8$
	M ₇	0.057	
	M ₈	0.143	
- 1P	M ₆	0.006	$\lambda(-1P)_6 < \lambda(-1P)_7$
	M ₇	0.015	
	M ₈	0.038	
- 1St	M ₆	0.019	$\lambda(-1St)_6 < \lambda(-1St)_7 < \lambda(-1St)_8$
	M ₇	0.045	
	M ₈	0.128	

* Symbols $\lambda(+1S)_n$, $\lambda(+1P)_n$, $\lambda(+1St)_n$, $\lambda(-1S)_n$, $\lambda(-1P)_n$ and $\lambda(-1St)_n$ mean the frequency of respective type of local deviations in n-merous floral meristems. All the differences shown are of at least 98% significance level.

Similar tendencies were also characteristic to (+1) and (-1) deviations affecting petals primordia. But in this case, significant differences were found only between the meristems M₆ and M₇. We propose that such a result is due to rather small number of the meristems M₈ investigated because of their rarity in *T. europaea*.

Discussion

Trientalis europaea is the well known plant species showing phenotypic plasticity of flower structure (CHARLIER 1913, MATTHEWS & ROGER 1941, HIIRSALMI 1969, TIKHODEYEV & TIKHODEYEVA 2001, 2002). However, the mechanisms of this plasticity are still unknown. In the present work, we have shown that formation of irregular flowers in *T. europaea* is due to (+1) or (-1) local deviations which occur in the floral meristems in good accordance with Poisson distribution. This means that both (+1) and (-1) deviations are the results of some stochastic developmental events. Moreover, such events are independent even when occurred in the same floral meristem. These data are in good agreement with our previous finding that the flowers produced by the same *T. europaea* plant are independent in respect to regularity of their meristems development (TIKHODEYEV & TIKHODEYEVA 2002).

We have demonstrated that *T. europaea* floral meristems with low initial multiplicity of the organs primordia (i.e. M₅ and M₆) are predisposed to (+1) local deviations. In contrary, in floral meristems with higher initial multiplicity (i.e. M₇ and M₈), (-1) deviations were preferable. So phenotypic plasticity of *T. europaea* flowers predominantly results in formation of not marginal but intermediate numbers of floral organs: 6 or 7.

It should be stressed out that 7-merous flowers are considered as typical for this species (CHARLIER 1913; MATTHEWS & ROGER 1941; HIIRSALMI 1969; GRIVLOVA & VAHRAMEEVA 1990). However, in some studied samples, 6-merous flowers were shown to be most abundant (TIKHODEYEV & TIKHODEYEVA 2002, and unpublished). Perhaps this is due to genetic differences between the samples. Such explanation is in good accordance with our finding that initial multiplicity of the organs primordia in *T. europaea* floral meristems is determined by both stochastic events and the genotype (TIKHODEYEV & TIKHODEYEVA 2002).

As we have already noted, phenotypic plasticity of 7-merous flowers predominantly resulted in decrease of the organs number. Meanwhile, in 6-merous flowers, its effect was quite opposite. So *T. europaea* flowers are likely predisposed to produce intermediate number of the organs, between 6 and 7. But what are the possible mechanisms of such developmental feature?

In model plant species *Arabidopsis thaliana* L., it is shown that the number of floral organs depends on the size of the floral meristem which in turn is controlled by the plant genotype (CLARK et al. 1993, RUNNING et al. 1998). We believe that similar mechanism is also characteristic to *T. europaea*. The floral meristems in this species seem to be usually of intermediate size: not large enough to produce 7-merous flowers but not so small to form only 6-merous ones. Moreover, the size of *T. europaea* floral meristems is not rigidly controlled by the genotype and therefore shows phenotypic plasticity under several environmental influences and stochastic events. As the result, not inheritable variation of flower structure happens quite often in this species.

We also propose that different regions of *T. europaea* floral meristem are poorly coordinated in their size. So the same meristem may produce different number of sepals, petals and stamens primordia. Usually only one whorl of the organs primordia is affected and such an affect is comparably slight. As the result, the flower with single (+1) or (-1) deviation is formed. Sometimes misbalances in meristem development are so strong that the flower displays several deviations at the same or even different whorls.

In the previous work (TIKHODEYEV & TIKHODEYEVA 2002), we have shown that one of the possible factors controlling the frequency of (+1) and (-1) deviations is local temperature fluctuation. This fluctuation is hardly predictable and so resembles some stochastic events. As the result, both (+1) and (-1) deviations occur in *T. europaea* floral meristem in stochastic manner. The role of temperature fluctuations in triggering phenotypic plasticity is recently demonstrated in *Arabidopsis thaliana* (QUEITSCH et al. 2002). The similar mechanism may also work out in *T. europaea*, as it seems.

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O. N. TIKHODEYEV ET AL.

Addresses of the authors:

Associate Prof. Dr. Oleg N. Tikhodeyev
Department of Genetics
Faculty of Biology and Soil Science
St. Petersburg State University
University emb. 7/9
Russia
E-mail: tikhodeyev@mail.ru

Senior Student Maria A. Neustroeva
Department of Genetics
Faculty of Biology and Soil Science
St. Petersburg State University
University emb. 7/9
Russia

Senior Sci. Res. Dr. Marina Y. Tikhodeyeva
Department of Plant Ecology
Faculty of Biology and Soil Science
St. Petersburg State University
University emb. 7/9
Russia

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Autor(en)/Author(s): Tikhodeyev Oleg N., Tikhodeyeva Marina Y., Neustroeva Maria A.

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