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Flower development in *Trientalis europaea* L.: The possible role of environment and stochastic events

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Summary: We have studied structural variability of flowers in natural populations of *Trientalis europaea* L. The structure of flowers (i.e. number of sepals, petals and stamens) is shown to depend in this species on two main factors: (1) initial multiplicity of the organ-primordia and (2) regularity in the floral meristem development. According to our data, the last factor is controlled by local stochastic fluctuations of the environment.

Zusammenfassung: Wir präsentieren eine Studie der Blüten-Variabilität von *Trientalis europaea* L. in natürlichen Populationen. Es wird gezeigt, dass die Struktur der Blüten (Anzahl der Sepalen, Petalen und Stamina) bei dieser Art von zwei Haupt-Faktoren abhängt: (1) ursprüngliche Multiplizität der Organ-Primordien und (2) Regelmäßigkeit der Entwicklung des Blütenmeristems. Unseren Daten zufolge, wird der letzte Faktor von lokalen, stochastischen Fluktuationen des Milieus gesteuert.

Keywords: *Trientalis europaea*, Primulaceae, natural populations, flower variability

It is basically thought that all spectrum of intraspecific variability is due to some differences in (1) genotype, (2) developmental stage of the organism and (3) multiple influences of environment (for review see AYALA & KIGER 1984, GRIFFITHS et al. 1993, LUTOVA et al. 2000). To investigate the certain role of each factor, special laboratory studies are generally used. In such studies, two of the listed factors are made uniform, that allows to elucidate the role of the third factor alone (for example, studying organisms of the same genotype and developmental stage, it is possible to reveal the role of environment). This approach became fundamental in almost all phyla of modern genetics and developmental biology.

In natural populations, studies of intraspecific variability are far more complicated. The fact is that neither genotype nor certain environmental influences could be precisely controlled in such conditions. Thus, for the majority of species, the origin of natural variability is still poorly understood or completely unknown.

However, in some cases, when the organism (for example, flowering plant) produces multiple homologous structures (for example, flowers), the origin of intraspecific variability may be revealed even in natural populations. Actually, all homologous structures produced by the same organism or vegetative clone should possess the same genotype and thus resemble monozygotic twins. If these “twins” are closely similar to each other, their development is likely to be under strong genetic control. In contrary, if these “twins” possess multiple differences, the role of developmental stage or environment is also significant. Such approach appeared to be successful in studies, both on animals and plants (WOOLF 1995, KERSTETTER & POETHIG 1998).

Here we describe structural variability of flowers in natural populations of *Trientalis europaea* We have shown that structure of certain flower (i.e. number of its sepals, petals and stamens) depends in this species on two main factors: (1) initial multiplicity of the organs primordia and

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(2) regularity in the floral meristem development. According to our data, the last factor is controlled by local stochastic fluctuations of the environment.

Materials & Methods

Trientalis europaea (common names: Arctic Starflower and Chickweed Wintergreen) is one of the common weed angiosperms in boreal zone of the northern hemisphere (HEGI 1908). This clonal herb plant possesses pseudo-annual life cycle during which the mother ramet vegetatively produces several tubers and dies back (WARMING 1918, GRIVLOVA & VAHRAMEEVA 1990, PIQUERAS & KLIMES 1998). The daughter tubers retain in the soil untill new growing season that starts in May–June and completes in August–September. In the north-west of Russia, flowering of *T. europaea* usually occurs in June. During this period, the mature plant produces one or several (sometimes up to 5) actinomorph flowers predominantly possessing 7 sepals, 7 petals, 7 stamens and 1 pistil (CHARLIER 1913, MATTWES & ROGER 1941, HIIRSALMI 1969). However, the number of organs in *T. europaea* flowers is quite variable. This variability may be found even within the same vegetative clones, reflecting its uninheritable origin (CHARLIER 1913, HIIRSALMI 1969). In *T. europaea*, seed set is quite low and seedling recruitment is rare (HIIRSALMI 1969, GRIVLOVA & VAHRAMEEVA 1990).

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 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. For the present work, we have chosen 5 different plant communities situated along the south coast of the island, which continuously lowers from west to east. As a control, 2 additional plant communities situated in the internal part of the island have been used (Fig. 1):

1. *Pinus* forest I growing at the cleafy south-west coast, approximately 8 m above the lake level. In addition to mature *Pinus sylvestris* trees, rare *Sorbus aucuparia* L. young growth was detected. Weed cover was represented predominantly by *Vaccinium myrtillus* L, *V. vitis-idaea* L. and *Calluna vulgaris* L. Moss cover was formed by *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum polysetum* Sw.;

2. *Pinus* forest II situated in the internal part of the island (400 m away from the previous community, approximately 10 m above the lake level). Being quite similar to *Pinus* forest I, this plant community was chosen as its control;

3. *Pinus+Picea* forest growing at the cleafy south coast, approximately 6 m above the lake level. In addition to mature *Pinus sylvestris* trees, single mature and multiple young *Picea abies* and *Sorbus aucuparia* trees were present. Weed cover was formed predominantly by *V. myrtillus*, *V. vitis-idaea*, *Maianthemum bifolium* L., *Lycopodium clavatum* L. and *Rubus saxatilis* L. In moss cover, the most common species were *Pleurozium schreberi*, *Pohlia nutans* (Hedw.) Lindb. and *Dicranum polysetum*;

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4. *Picea+Pinus* forest situated at the south-east coast, approximately 4 m above the lake level. In addition to *Picea abies*, single mature *Pinus sylvestris* and *Sorbus aucuparia* trees were present. However, *Pinus sylvestris* regrowth was not found. Weed cover was represented predominantly by *V. myrtillus* and *Calamagrostis arundinacea* L. with presence of *Pteridium aquilinum* (L.) Kuhn. In moss cover, the most common species were *Pleurozium schreberi* and *Pohlia nutans*;

5. *Betula* forest growing at the low-lying and periodically flooded area of the south-east coast (approximately 1,5 m above the lake level). Tree cover was predominantly formed by *Betula pendula* Roth, *Alnus cinerea* L. and *Populus tremula* L. In weed cover, the most common species were *Calamagrostis epigejos*, *V. myrtillus*, *Rubus saxatilis*, *Oxalis acetosella* L., *Athyrium filix-femina* (L.) Roth and *Dryopteris expansa* (C. Presl.) Fraser-Jenkins et Jermy;

6. Edge of the floating bog at the low-lying area of the south-east coast. This plant community was situated immediately near the lake level and therefore suffered periodical floodings. Rare trees were represented by dwarf *Pinus sylvestris*. In moss and weed cover, the most common species was *Sphagnum sp*. with presence of *Comarum palustre* L., *Lythrum salicaria* L., *Carex lasiocarpa* Ehrh. and *C. caespitosa* L.;

7. Edge of the forest swamp situated in the internal part of the island, where *Picea* forest transited into sedge/sphagnum bog. Rare trees were represented by *Picea abies* plantlets. Moss cover was predominantly formed by *Sphagnum sp*. This plant community was chosen as a control for the edge of the coastal swamp.

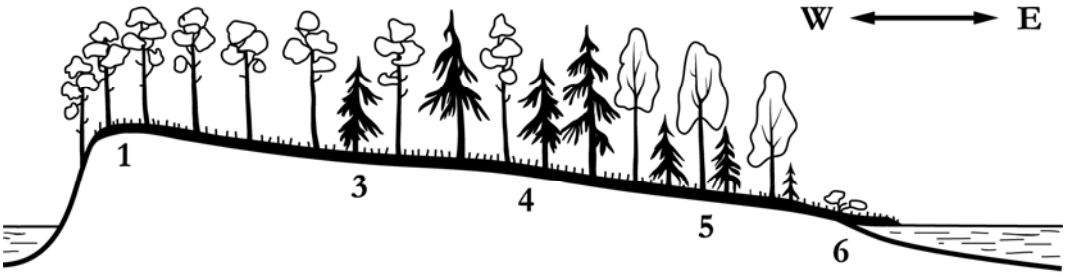

Figure 1. Schematic profile of the South coast of Konevitsa island. The studied plant communities are designated by the following numbers: 1 – *Pinus* forest I; 3 – *Pinus+Picea* forest; 4 – *Picea+Pinus* forest; 5 – *Betula* forest; 6 – the edge of the floating bog. Two other plant communities studied (2 – *Pinus* forest II; 7 – the edge of the forest swamp) were situated in the internal part of the island.

Analysis of *T. europaea* flowers

In each plant community, we investigated from 100 to 200 randomly chosen undamaged flowers of *T. europaea*. To prevent multiple testing of flowers produced by the same vegetative clone, the distance between any two studied flowers was taken no less than 1 m. For each flower, we counted the number of sepals (S), petals (P) and stamens (St), thus getting the formula: $S_xP_ySt_z$.

The flowers with equal number of sepals, petals and stamens (for example, $S_6P_6St_6$, $S_7P_7St_7$ or $S_8P_8St_8$) will be further designated as regular (R). All other types of the flowers (for example, $S_7P_6St_6$, $S_7P_8St_7$ or $S_6P_7St_8$) will be further designated as irregular (I). The frequency of irregular

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flowers was used as a quantitative character of flower variability in certain plant communities. For statistic analysis of this frequency, the Fisher's φ transformation has been used (ROHLF & SOKAL 1995).

Analysis of two-flowered plants

We investigated *T. europaea* plants simultaneously possessing two completely developed undamaged flowers. In each plant community studied, the sample of found two-flowered plants was divided in three following groups: the plants possessing 2 regular (RR), 2 irregular (II), and 1 regular + 1 irregular (RI) flowers. To estimate the role of stochastic factors in flower development, obtained ratio of the RR-, RI- and II-plants ($N_{RR} : N_{RI} : N_{II}$) was compared with corresponding expected ratio ($EN_{RR} : EN_{RI} : EN_{II}$) calculated in assumption that each flower developed in result of independent event. Expected ratio was calculated as follows:

$$EN_{RR} = r^2 (N_{RR} + N_{RI} + N_{II}); \quad EN_{RI} = 2ri (N_{RR} + N_{RI} + N_{II}); \quad EN_{II} = i^2 (N_{RR} + N_{RI} + N_{II});$$

wherein r and i correspondingly mean the frequencies of regular and irregular flowers within studied sample of two-flowered plants:

$$r = \frac{2N_{RR} + N_{RI}}{2N_{RR} + 2N_{RI} + 2N_{II}}; \qquad i = \frac{2N_{II} + N_{RI}}{2N_{RR} + 2N_{RI} + 2N_{II}}.$$

Comparison of observed and expected ratios was carried out by the χ^2 criterion (ROHLF & SOKAL 1995).

Results

Structural variability of *T. europaea* flowers

During 6 years (1996-2001), we studied structural variability of *T. europaea* flowers in natural populations of Konevitsa island. Within the sample of 3374 studied flowers (Table 1), the most frequent type was represented by regular 7-merous ones ($S_7P_7St_7$). This type of flowers seems to be basic for *T. europaea* and will be further designated as R_7. We also met three other types of regular flowers, namely 5-merous ($S_5P_5St_5$ or R_5), 6-merous ($S_6P_6St_6$ or R_6) and 8-merous ($S_8P_8St_8$ or R_8). The rest of the studied flowers appeared to be irregular, dividing in multiple types.

Table 1. Structural variability of *T. europaea* flowers on Konevitsa island (joined data from 1996 to 2001).

Initial floral meristem*	Regular flowers	Irregular flowers							Subtotal
		+1S	-1S	+1P	-1P	+1St	-1St	double	
M_5	6 (0.2%)	4	0	0	0	2	0	0	12
M_6	718 (21.3%)	39	18	28	5	35	24	6	873
M_7	2063 (61.1%)	3	117	14	39	31	105	18	2390
M_8	65 (1.9%)	0	12	1	3	0	13	5	99
Subtotal	2852 (84.5%)	46	147	43	47	68	142	29	
Total		193		90		210		29	3374

* M5, M6, M7 and M8 = initial floral meristem for R5, R6, R7 and R8.

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When compared to regular flowers, the majority of irregular ones possessed either 1 lacking (-1) or 1 extra (+1) sepal, petal or stamen. According to these data, the mechanism of irregular flower formation is based on some local deviations that occur in the development of floral meristems. Each deviation usually affects only one single floral organ primordium and either blocks its further development or induces production of 1 extra organ.

We have found that total quantity of irregular flowers (522) was significantly lower that of R_6 ones (718). Thus formation of the flower R_6 could be hardly explained by multiple local deviations which independently occurred in the same floral meristem. It is more likely that in such floral meristem, initial multiplicity of the organ primordia has been modified from usual 7 to unusual 6. This type of the meristems will be further designated as M_6. We propose that production of the flowers R_5 and R_8 was due to formation of unusual meristems M_5 and M_8, correspondingly.

These results allowed us to reconstruct the origin of irregular *T. europaea* flowers. For example, the flower $S_6P_7St_7$ was considered as the result of a single local deviation (namely, damage or lack of 1 sepal primordium) which occurred in the meristem M_7. Similarly, the flower $S_6P_7St_6$ manifested formation of 1 extra petal primordium in the meristem M_6. Therefore irregular flowers like $S_6P_7St_7$ and $S_6P_7St_6$ will be further designated as $I_{7\text{-}1S}$, I_{6+1P} and so on.

Only 29 irregular flowers appeared to be of more complicated origin. Each of these flowers seemed to suffer 2 local deviations that have independently occurred in the same floral meristem (Table 2).

Table 2: Structure of *T. europaea* flowers with double developmental deviations.

Flower type	Proposed flower origin	Number
$S_4P_6St_6$	$I_{6\text{-}2S}$	1
$S_6P_6St_4$	$I_{6\text{-}2St}$	1
$S_5P_6St_7$	$I_{6\text{-}1S+1St}$	1
$S_8P_6St_6$	I_{6+2S}	2
$S_6P_6St_8$	I_{6+2St}	1
$S_5P_7St_7$	$I_{7\text{-}2S}$	5
$S_7P_7St_5$	$I_{7\text{-}2St}$	7
$S_6P_8St_7$	$I_{7\text{-}1S+1P}$	1
$S_7P_6St_8$	$I_{7\text{-}1P+1St}$	1
$S_7P_8St_6$	$I_{7+1P\text{-}1S}$	1
$S_8P_6St_7$	$I_{7+1S\text{-}1P}$	1
$S_8P_7St_6$	$I_{7+1S\text{-}1St}$	1
$S_9P_7St_7$	I_{7+2St}	1
$S_6P_8St_8$	$I_{8\text{-}2S}$	1
$S_8P_6St_8$	$I_{8\text{-}2P}$	1
$S_8P_8St_6$	$I_{8\text{-}2St}$	3

So, the studied sample of 3374 *T. europaea* flowers has been divided in 3 following groups: (1) regular flowers R_5, R_6, R_7 and R_8, (2) irregular flowers produced due to single developmental deviations and (3) irregular flowers produced in result of double developmental deviations. In the flowers derived from the meristems M_7 or M_8, the majority of deviations led to decrease of the organ number (Table 1). The opposite situation has been found in the flowers developed from the meristems M_5 or M_6. In both cases, the most variable organs were sepals and stamens.

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Environmental influence on frequency of irregular flower formation

In June 1996, we investigated the frequency of irregular *T. europaea* flowers in 7 natural plant communities of Konevitsa island (Table 3). In similar plant communities, this frequency appeared to be very close. For example, in dry *Pinus* forests I and II, 95% CIs for this frequency were almost the same. An analogous situation has been obtained at the edges of the forest swamp and the floating bog. However, in several plant communities, the frequency of irregular flowers was significantly different. This difference appeared to be most dramatic between wet *Picea+Pinus* forest on one hand (CI: 0.02–0.09) and dry *Pinus* forests I and II on the other (CI for the joint two samples: 0.15–0.23), $P < 0.001$. According to our data, soil humidity seems to be one of the major environmental factors that determines structural variability of *T. europaea* flowers.

Table 3. Structural variability of *T. europaea* flowers in different plant communities of Konevitsa island.

Plant community	N	Regular flowers	Irregular flowers		
			single	double	total
Picea+Pinus forest	164	156	8	0	8 (0.02–0.09)*
Edge of the floating bog	170	157	13	0	13 (0.04–0.12)
Edge of the forest swamp	116	105	11	0	11 (0.05–0.16)
Betula forest	200	179	19	2	21 (0.07–0.15)
Pinus+Picea forest	161	135	24	2	26 (0.11–0.22)
Pinus forest I	150	123	26	1	27 (0.12–0.25)
Pinus forest II	199	161	36	2	38 (0.14–0.25)

* In parenthesis, 95% CI for the frequency of I flowers is shown.

Initial multiplicity of the floral organ primordia in different plant communities

Each *T. europaea* flower studied in 1996, was also described for initial multiplicity of the organ primordia. We have found that even in similar plant communities, the ratio $M_6 : M_7 : M_8$ was significantly different (Table 4). Namely, for dry *Pinus* forests I and II, the χ^2 value was about 39; $\nu = 2$; $P < 0.001$. For the edges of the forest swamp and the floating bog, the difference was especially sharp ($\chi^2 = 325$; $\nu = 2$). This means that initial multiplicity of the organ primordia is determined in *T. europaea* by different mechanisms than regularity of the floral meristem development.

Table 4. Initial multiplicity of the organs primordia in *T. europaea* flowers from different plant communities.

Plant community	N	$M_6 : M_7 : M_8$
Picea+Pinus forest	164	34 : 125 : 5
Edge of the floating bog	170	115 : 54 : 1
Edge of the forest swamp	116	15 : 91 : 10
Betula forest	200	10 : 188 : 2
Pinus+Picea forest	161	33 : 126 : 2
Pinus forest I	150	26 : 123 : 1
Pinus forest II	199	65 : 124 : 9

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Special attention should be paid to the data obtained at the edge of the floating bog. In this plant community, initial multiplicity of the organ primordia was strongly shifted from usual 7 to unusual 6. These data may be explained in two different ways. First, one could propose that the plants at the edge of the floating bog were genetically different from those at the other communities studied. Second, initial multiplicity of the organ primordia could be modified by some environmental factor(s) that were mostly characteristic to the edge of the floating bog.

To elucidate the possible roles of the genotype and environment, we have studied two-flowered plants of *T. europaea*.

Structural variability of *T. europaea* flowers in two-flowered plants

In June 2000, we investigated 189 two-flowered *T. europaea* plants from *Pinus* I and *Pinus+Picea* forests (in previous years, it appeared to be impossible due to very low quantity of two-flowered plants). During the analysis of each plant, we distinguished the lower and the higher flowers (Fig. 2). This allowed us to compare the structure of flowers in respect to their position on the shoot, i.e. to the order of their opening. For both plant communities investigated, we have found no significant difference between the samples of the lower and the higher flowers (Table 5). Thus structural variability of *T. europaea* flowers does not reflect their position on the shoot.

Figure 2. Two-flowered plant of *T. europaea*. The flowers have different positions on the shoot: the left one is lower. This corresponds with the order of their opening. The lower flower usually opens earlier.

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Table 5. Structural variability of *T. europaea* flowers in respect to their position on the shoot.

Plant community	Type of ratio	Lower flowers	Higher flowers
Pinus I forest	R : I	73 : 6	76 : 3
		χ^2 = 1.623; ν = 1; P = 0.20	
	$M_6 : M_7 : M_8$	17 : 59 : 3	21 : 57 : 1
		χ^2 = 2.344; ν = 2; P = 0,31	
Pinus+Picea forest	R : I	98 : 11	98 : 11
		χ^2 = 0.000; ν = 1; P = 1.00	
	$M_6 : M_7 : M_8$	24 : 81 : 4	26 : 80 : 3
		χ^2 = 0.429; ν = 1; P = 0,51	

A significant portion of the studied plants appeared to produce structurally different flowers (Table 6). According to these data, development of *T. europaea* flowers was not strongly controlled by the plant genotype. This suggestion seems especially true in respect to regularity of the flower meristem development. Actually, the ratio of RR-, RI- and II-plants corresponded to the assumption that the flowers produced by the same plant have developed independently from each other. The simplest explanation of this fact is that the choice between regular and irregular development of floral meristems in *T. europaea* is stochastic.

Table 6. Ratios of two-flowered plants of *T. europaea* in different plant communities.

Plant community	Observed ratio	Expected ratio	Observed ratio	Expected ratio
	$N_{RR} : N_{RI} : N_{II}$	$EN_{RR} : EN_{RI} : EN_{II}$	$N_{7-7} : N_{7-6} : N_{6-6}$	$EN_{7-7} : EN_{7-6} : EN_{6-6}$
Pinus I forest	72 : 5 : 0	68.53 : 8 .47 : 0.00	45 : 22 : 8*	42.00 : 28.50 : 4.50
	χ^2 = 1.598; ν = 1; P = 0.21		χ^2 = 4.418; ν = 1; P = 0.03	
Pinus+Picea forest	88 : 19 : 2	86.11 : 21.80 : 1.09	64 : 29 : 10*	59.74 : 37.08 : 6.18
	χ^2 = 1.161; ν = 1; P = 0.28		χ^2 = 4.426; ν = 1; P = 0.03	

* Several plants possessed initial floral meristem M_8. These plants were excluded from the analysis.

Being able to reconstruct the origin of irregular flowers, we divided each sample of two-flowered plants in 3 following groups: plants with 2 M_7 (7-7), 2 M_6 (6-6) and 1 M_7 + 1 M_6 (7-6) floral meristems. Observed ratios of 7-7-, 7-6- and 6-6-plants ($N_{7-7} : N_{7-6} : N_{6-6}$) were compared to the corresponding expected ratios ($EN_{7-7} : EN_{7-6} : EN_{6-6}$) calculated in assumption that each flower has developed in result of an independent event. The principle of such calculation was similar to that of expected ratio $EN_{RR} : EN_{RI} : EN_{II}$ (see Materials and Methods). In each plant community, the difference between observed and expected ratios was significant (Table 6). So initial multiplicity of the organ primordia was not determined in *T. europaea* by stochastic events, disclosing some influence of the plant genotype. This influence seems to be also not crucial but quite important for young floral meristem.

Structural variability of *T. europaea* flowers in 2 closely neighbouring clumps

In June 2001, we studied structural variability of *T. europaea* flowers within the same population on Konevitsa island. For this purpose, we selected 2 closely neighbouring clumps of *T. europaea* situated in *Pinus+Picea* forest at the distance of only 3 m from each other. The environmental influences in both clumps seemed to be completely identical.

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For each clump, we have analyzed all the flowers, without consideration of the distance between them. Comparing the data obtained, we have found that in these neighbouring clumps the frequency of irregular flowers was very similar (Table 7). In contrary, the ratio M_6 : M_7 : M_8 appeared to be significantly different. Since the environmental influence was completely identical, we believe that the data obtained were due to some genetic differences between the clumps.

Table 7. Structural variability of *T. europaea* flowers in two closely neighbouring clumps.

Plant community	Type of ratio	Clump no. 1	Clump no. 2
Pinus+*Picea* forest	R : I	102 : 4	82 : 3
		$\chi^2 = 0.018$; $\nu = 1$; $P = 0.89$	
	$M_6 : M_7 : M_8$	5 : 89 : 12	20 : 63 : 2
		$\chi^2 = 90.901$; $\nu = 2$; $P < 0{,}001$	

Discussion

The structure of flowers in *T. europaea* is quite variable (CHARLIER 1913, MATTWES & ROGER 1941, HIIRSALMI 1969). Although this variability is well documented, its certain mechanisms remain completely unknown. One of the causes of such situation is the following. In previous studies, structural variability of the flowers was described for sepals, petals and stamens separately. In the present work, all the organs have been analyzed in complex. This approach allowed us to reconstruct the origin of each investigated flower.

The most frequent type of *T. europaea* flowers is R_7 (CHARLIER 1913, MATTWES & ROGER 1941, HIIRSALMI 1969, GRIVLOVA & VAHRAMEEVA 1990). However, the number of sepals, petals or stamens may vary between certain flowers from 5 to 8. We have shown that all this structural variability could be simply explained by 2 types of events. First, in the developing floral meristem, initial multiplicity of the organ primordia may be shifted from usual 7 to 8, 6 or 5. The flower produced by this meristem would be regular: R_8 , R_6 or R_5. Second, developing floral meristem may suffer some local deviation which affects only one of the organ primordia. The flower produced by this meristem would be irregular.

What are the possible causes of such events? We have shown that significant portion of the plants may produce 2 structurally different flowers. So in this species, development of flowers is controlled not only by the genotype.

One could propose that the structure of *T. europaea* flowers depends on their position on the shoot. However, in our study of two-flowered plants, this proposition could not be supported. Thus, there are some environmental influences which are also important for the structure of *T. europaea* flowers.

Unfortunately, we failed to disclose certain environmental factor(s) that affect initial multiplicity of the organ primordia. We have shown that in very similar conditions (for example, in dry *Pinus* forests I and II), the ratio M_6 : M_7 : M_8 was significantly different. Moreover, analogous result has been obtained in 2 very closely neighbouring clumps situated in the same plant community, at the distance of only 3 m from each other. The simplest explanation of these

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data is spacial heterogeneity of natural populations of *T. europaea*. It is known that reproduction strategy of this species is predominantly based on vegetative propagation (HIIRSALMI 1969, GRIVLOVA & VAHRAMEEVA 1990, PIQUERAS & KLIMES 1998). Therefore, even closely neighbouring habitats may be occasionally occupied by the members of different clones. It seems very likely, that the clump no.1 was enriched with the members of some vegetative clone which were able to produce unusual meristems M_8 (Table 7). In contrary, the clump no.2 was enriched with the members of another vegetative clone which were able to produce unusual meristems M_6.

The difference between these putative clones could be simply explained by the difference between their genotypes. So we believe that initial multiplicity of the organ primordia is controlled in *T. europaea* by (1) the genotype and (2) yet unknown environmental factor(s).

In respect to regularity of floral meristem development, the important environmental factors are more obvious. We have found that in wet and shaded *Picea+Pinus* forest, the frequency of irregular flower formation was significantly lower than in dry and well illuminated *Pinus* forests. Moreover, in similar conditions (for example, in *Pinus* forests I and II, or in neighbouring clumps from *Pinus+Picea* forest), this frequency appeared to be very close. According to these data, the local deviations in *T. europaea* floral meristems are induced by simultaneous action at least of two factors: (1) low soil humidity and (2) high illumination.

Especially interesting results have been obtained in the study of two-flowered plants. We have found that the ratio RR : RI : II well corresponded to assumption that the flowers produced by the same plant have developed independently from each other. The simplest explanation of this fact is that the choice between regular and irregular development of floral meristem in *T. europaea* is stochastic.

We propose that the floral meristems in this species are very flexible under environmental influences. On their turn, such influences are not stable but spacially and temporally fluctuating. For example, temperature fluctuations could be a possible candidate for that role. This proposition seems to be quite true since in the hottest year of our studies, the frequencies of irregular flowers formation appeared to be much higher than usually (Tikhodeyev & Tikhodeyeva, unpublished). We also propose that the floral meristem in *T. europaea* has a crucial developmental stage, which is especially responsible for temperature rising. So the structure of certain flower is determined by a local temperature value at this crucial stage of the meristem development. The flowers produced by the same *T. europaea* plant are known to develop and open not simultaneously. Therefore, at the crucial stages for the first and the second floral meristem, the local temperature values could be different, resulting in production of two different flowers.

The local temperature value may be modified by many other environmental factors, for example, by soil humidity and level of illumination. Therefore, the listed environmental factors are also important for the structure of flowers in *T. europaea*. That is why in different plant communities, irregular flowers are produced in different frequency.

In the present study we have shown that regularity of the floral meristem development is likely determined in *T. europaea* by fluctuation of some environmental factor(s). Such fluctuations could be hardly predicted and thus resemble some stochastic events. As the result, regularity of the meristem development manifests in *T. europaea* in stochastic manner.

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