Ecological details of forming convergent corolla painting on example of flowering plants of Chişinău

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Abstract. The areal and temporal diversity of corolla painting in flowering plants was studied. One hundred and seventy five (175) species of the flora of Chisinau city were involved, and 317 species of herbaceous plants of Moldova were analyzed using literature sources. At flowering plants of *C* layer the seasonal convergence of corolla color was established. The conclusion deduced is that quantitative and qualitative parameters of solar spectrum are the limiting factor in the evolution of corolla color.
Key Words: corolla, solar spectrum, convergence, herbaceous plants, color, pigments.

Introduction. In the course of plant evolution the corolla (i.e. internal part of double perianth) evolved from transformed stamens lost anthers or from top leaves.

It is still not entirely clear what the biological significance corolla painting is, why different species have different paintings, does it make sense adaptive, and if so, what. The most consistent with corolla functional load is the theory of appearance of different pigments as a result of plant adaptation to solar radiation (Solovchenko & Merzlyak 2008; Hormaetxe et al 2005; Luu et al 2013). We hypothesized that seasonal changes in the spectrum of solar radiation should lead to a convergence in corolla painting of flowering plants. For this purpose we studied the territorial and temporal variability of corolla painting in flowering plants of Chisinau.

Material and Method. The main object of the study (2005-2009 year) was the plant cover of C layer in Chisinau. The species of plants were determined at the Department of Botany, Ecology and Forestry of the Chisinau State University. Flowering periods were established by four sources (Negru 2005, 2006, 2007; Ciocârlan 2000; Geideman 1986; Asseeva & Tikhomirov 1964). Vegetation relevés of stationary plots was carried out according to the classical method of Rabotnov (1987). Photometric characteristics of the solar spectrum are given by Rvachev (1966) on the first day of each month. Statistical analysis was carried out with the Excel Microsoft.

Results and Discussion. Evaluation of gamma diversity in C layer of urban flora showed the presence of 175 species of herbaceous plants from 42 families. The next 5 families are the most widely represented: Asteraceae (37 species), Poaceae (19 species), Fabaceae (14 species), Brassicaceae (11 species), Lamiaceae (8 species). Visual analysis of the corolla painting showed the presence of four color groups: blue (violet, indigo, blue, 13 species), white (white, cream, 34 species), yellow-orange (41 species), red (red, rose, purple, 34 species) (Table 1). Another group is not represented in the Table 1: with reduced corolla and/or with difficult color classification (53 species). For each color group the first month of flowering is given by four literary sources (Negru 2005, 2006, 2007; Ciocârlan 2000; Geideman 1986; Asseeva & Tikhomirov 1964).

Table 1

Distribution of flowering plants of C layer for flowering time and color of corolla

Species	*Source*				*Species*	*Source*			
	1	*2*	*3*	*4*		*1*	*2*	*3*	*4*
Blue, indigo, violet									
Cicorium intubus L.	5	7	5	6	*Myosotis arvensis L. (Hill.)*	5	4	5	-
Lactuca tatarica (L.) C.A.Mey	5	5	5	-	*Linum austriacum L.*	6	5	4	-
Veronica chamaedrrys L.	4	4	5	5	*Anagallis foemina Mill.*	4	5	5	-
Veronica spicata L.	6	-	5	-	*Vinca minor L.*	4	4	5	-
Ajuga genevensis L.	5	5	6	-	*Viola mirabilis L.*	4	6	4	-

Glechoma hederaceae L.	4	4	4	4	*Viola odorata L.*	5	3	4	-
Echium vulgare L.	6	5	5	6					
					White				
Achillea milefolium L.	6	-	-	6	*Bryonia alba L.*	6	6	5	-
Erigeron annuus (L.) Pers.	7	-	5	-	*Papaver dubium L*	5	5	4	5
Conyza canadensis L	6	6	6	6	*Galium aparine L*	5	-	5	-
Tripleurospermum inodorum (L.) Sch.Bip.	6	-	5	4	*Armoracia rusticana Gaerth.,Mey et Scherb*	5	5	6	-
Capsella bursa – pastoris (L.), Medik	4	-	4	4	*Silene moldavica (Klok.) Šourková*	5	-	6	-
Centaurea difussa Lam.	6	-	6	-	*Crambe tatarica Sebeok.*	4	5	4	-
Chamomilla recutita (L.) Rauschert	5	4	5	-	*Galinsoga parviflora Cav.*	6	-	7	-
Alliaria petiolata (Bieb) Cavara et Grande	4	5	5	-	*Arabidopsis thaliana (L.) Heynh.*	4	-	4	-
Datura stramonium L.	6	6	6	-	*Berteroa incana (L.)DC*	5	5	5	5
Connvalaria maialis L.	5	4	4	5	*Lepidium draba (L.) Desv.*	5	5	4	-
Daucus carota L.	6	5	5	-	*Melilotus albus Medik.*	6	-	6	6
Fallopia convolvulus (L.) A.Löve	6	-	5	-	*Trifolium montanum L.*	5	-	5	5
Heracleum sibiricum L.	6	6	6	6	*Stellaria media (L.)Vill.*	3	5	3	4
Anthriscus sylvestris (L) Hoffm.	5	5	6	5	*Saponaria officinalis L.*	6	-	6	6
Convolvulus arvense L.	5	5	5	6	*Solanum nigrum L.*	6	6	6	6
Calystegia sepium (L.) R. Br.	6	5	6	7	*Caucalis platycarpos L.*	5	-	6	-
Crepis pannonica (Jacg.) C.Koch	7	-	6	-	*Conium maculatum L.*	6	6	5	-
					Yellow				
Taraxacum officinalis Wigg.	4	4	4	4	*Galium verum Echtes Labkraut*	6	6	5	-
Sonchus arvensis L.	7	-	6	7	*Ranunculus acris L.*	5	-	5	-
Sonchus palustris L.	7	-	6	-	*Ranunculus oxispermus Willd.*	5	-	5	-
Inula germanica L.	7	6	5	-	*Sisymbrium altissimum L.*	5	-	6	-
Senecio vulgaris L.	6	-	4	5	*Sinapis arvensis L.*	5	5	6	6
Portulaca oleracea L.	6	6	5	-	*Potentilla erecta L.*	5	-	-	5
Hypericum perforatum L.	6	5	5	6	*Potentilla reptans L.*	6	5	5	-
Hypericum hirsutum L.	6	-	7	-	*Geum urbanum L.*	*5*	*5*	*5*	*6*
Rezeda lutea L.	5	-	5	-	*Potentilla anserina L.*	*5*	*5*	*5*	*5*
Chelidonium majus L.	5	5	5	5	*Agrimonia eupatoria L.*	*6*	*7*	*6*	*6*
Grindelia sqarrosa (Purch) Dun	7	7	7	-	*Rorippa austriaca (Crantz.)Bess*	*6*	*5*	*5*	-
Tanacetum vulgare L	7	6	6	6	*Euphorbia agraria Bieb.*	*7*	*5*	*4*	-
Crepis foetida L.,var.rhoeadifolia (Bieb.)Čelak	6	-	6	-	*Euphorbia peplus L.*	6	-	7	-
Crepis pannonica (Jacg.) C. Koch	7	-	6	-	*Euphorbia palustris L*	5	-	5	-
Tragopogon dubius Scop.	5	5	5	-	*Medicago romanica Prod.*	5	-	6	-
Scabiosa ucranica L.	6	-	6	-	*Medicago lupulina L.*	5	5	5	6
Asparagus officinalis L.	6	6	6	5	*Medicago minima (L.) Bartalini*	4	-	4	-
Verbascum nigrum L.	6	6	6	6	*Melilotus officinalis L. (Pall.)*	6	6	5	6
Linaria vulgaris Mill.	6	6	6	6	*Lotus corniculatus L.*	5	5	5	6
Sideritis comosa (Rochel ex.Benth) Stank	5	-	5	-	*Astragallus glycyphyllos L.*	5	5	5	6
Anchusa ochroleuca Schost.	5	-	-	-	*Potentilla argentea L.*	6	6	5	5
					Red, rose, purple				
Salvia nemorosa L.	6	6	6	-	*Urtica dioica L.*	6	6	6	6
Ballota nigra L.	6	5	5	-	*Fumaria officinalis L.*	5	4	5	6
Geranium robertianum L.	5	5	5	-	*Lythrum salicaria L.*	6	7	6	6
Vicia craca L.	6	-	5	6	*Lavatera thuringiaca L.*	6	7	6	6
Mentha piperita L.	6	-	7	-	*Hibiscus trionum L.*	6	-	6	-
Campanula persicifolia L.	6	6	6	6	*Althaea officinalis L.*	7	-	6	-
Solanum dulcamara L.	6	5	5	6	*Consolida regalis S.F. Gray*	4	6	5	-
Cardus acanthoides L.	6	-	6	-	*Trifolium pratense L.*	5	6	6	6
Cardus nutans L.	6	-	6	6	*Trifolium fragiferum L.*	6	5	5	-
Cardus hamulosus Ehrh.	6	5	5	-	*Vicia angustifolia Reichard*	5	-	5	-
Arctium lappa L.	7	-	6	-	*Lathirus tuberosus L.*	6	5	6	-
Cyrsium palustre (L.) Scop	7	-	6	-	*Coronilla varia L.*	6	-	6	6
Cyrsium arvense (L.) Scop	7	-	6	-	*Polygonum aviculare L.*	6	5	5	6
Leonurus cardiaca L.	6	-	7	7	*Polygonum hidropiper L.*	7	-	6	6
Xeranthemum annuum L.	7	6	6	-	*Polygonum persicaris L.*	7	7	7	-
Onopordum acanthium L.	7	-	6	-	*Rumex conglomerates Murray*	7	-	6	-
Allium rotundum L.	6	7	7	7	*Centaurea pseudomaculosa Dobrokz.*	6	-	6	-
Lamium purpureum L.	3	-	4	4					

1 – Negru (2005, 2006, 2007); 2 – Ciocărlan (2000); 3 -Geideman (1986); 4 - Asseeva & Tikhomirov (1964).

The value of mean month (Table 2) is the average (of the different literature sources mentioned in the table) number of month in which flowering begins. Table 2 shows that plants with blue flowers tend to begin flowering earlier than plants with white, yellow and red flowers. The average value of this parameter for purple flowers is higher than for the other color groups. We decided to check whether the pattern found in the flora of Chisinau is reproduced for the flora of the whole Moldova.

For this aim, the random sample of herbaceous plants from Negru (2005, 2006, 2007) was analyzed. Table 2 shows that both red and blue color groups significantly at level $p < 0.001$ different from the other color groups. As for the yellow and white color groups, between them there are no significant differences. Compared with the central (yellow-white) group the blue group shows a flowering shift 1.2 month, and the red group shows a shift +1.8 month. Thus, we can conclude that characteristic colors of early flower are blue and violet. For plants beginning to bloom on average in late June, the characteristic color of corolla are red, rose and purple. Therefore, with great certainty, we can argue a seasonal convergence of corolla color in herbaceous plants.

Table 2

Beginning flowering of herbaceous species in different color group

Number of month	*Blue group*		*White group*		*Yellow-orange group*		*Red group*	
	number of species	*%*	*number of species*	*%*	*number of species*	*%*	*number of species*	*%*
	Flora of Chisinau city							
3	1	33.3	1	33.3			1	33.3
4	6	31.6	8	42.1	4	21.1	1	5.2
5	5	9.4	13	24.5	25	47.2	10	18.9
6	1	2.3	10	22.7	12	27.3	21	47.7
7							1	100.0
Σ	13		32		41		34	
Mean month	4.46 ±0.22		5.00±0.15		5.20±0.09		5.59±0.13	
	Random sample from flora of Moldova							
2			2	100				
3	10	50	3	15	7	35		
4	17	43.6	14	35.9	8	20.5		
5	28	22.2	38	30.2	46	36.5	14	11.1
6			37	32.2	36	31.3	42	36.5
7					11	73.3	4	26.7
Σ	55		94		108		60	
Mean month	4.327±0.104		5.117± 0.095		5.370± 0.097		5.83± 0.068	

Integer value of “mean month” corresponds to middle of the month. For example, 5.0 = May 15. Thus, 5.5 = May 31 etc.

Considering the absorption of light by corolla in different color groups, if absorbent pigment is unknown we can approximately determine the absorption band from the table of complementary colors (Table 3). When the visible diapason is reflected totally, we observe white corolla. If one of colors is excluded from the total spectrum (in our case, absorbed by pigment-acceptor), the sum of remaining reflected colors will be perceived as a certain color called complementary to the excluded color (Gurevich 1950). Based on Table 3, for the blue color group should be expected light absorption in yellow and orange diapasons, for the yellow-orange group - in blue one, for the red group - in green one. This table gives an approximate solution, since it is assumes the ideal case when the absorption spectrum is stepped and lies within one of the traditional colors. Therefore, if we know the nature of the pigment, it is better to use the data on its real absorption spectrum.

Table 3

Complementary colors, λ (nm)

Excluded color	*Red* 780-630	*Orange* 630-600	*Yellow* 600-570	*Green* 570-490	*Blue* 490-460	*Indigo* 460-430	*Violet* 430-380
Complementary color	*Blue-green* 430-570	*Indigo* 460-430	*Violet* 430-380	*Purple* 380+780*	*Orange* 630-600	*Yellow* 600-570	*Yellow-green* 600-490

* This color is combined by extreme shades of spectrum.

Table 4 provides information about the known classes of pigments that are found in the corollas of flowers. Chlorophylls are not included because the green color group we had a small and therefore not included in the analysis.

Table 4

Pigments causing color of corolla

Pigment class	*Visible color*	*Peak or zone of absorption*	*Distribution and examples*
1. Carotenoids	Yellow	425-500 (blue, indigo)	Taraxacum, narcissus
2. Phenol compounds			
2.1. Quinones		UV, the batochrome shift to blue area is possible	
2.1.1. Chalcones	Yellow	360-425 (UV, violet)	Antirrhinum
2.1.2. Aurones	Orange, red	450-550 (blue, green)	Rarely (safflower)
2.2. Flavonoids			
2.2.1. Anthocyanines			Almost all red, blue and red-blue flowers, the most of orange ones
	Orange	480 (450-510), blue	
	Red	510 (blue-green)	
	Purple	460-540 (green)	
	Blue	500-640 (green, yellow, orange) – as result of intermolecular copigmentation or batochrome shift	
2.2.2. Flavones, flavonoles			
	White, cream	UV	
	Yellow	350-425 (UV, violet)	
3. Betalaines			Particular families
3.1. Betaxantines	Yellow	480 (blue)	
3.2. Betacyanines	Red-violet	534-554 (green)	

As the Table 4 shows, in the blue group the painting is caused by anthocyanins exclusively (with the possible intermolecular copigmentation with flavonols) at the absorption in broad band from green to orange inclusively. In the yellow-orange group the coloration may be caused by different pigments (carotenoids, quinones, anthocyanins, flavonoids, betaxantin), but in all cases the absorption takes place in the short-wave part of the spectrum (blue, indigo, violet) extending sometimes into the ultraviolet. In the red group the painting is caused mainly by anthocyanins and sometimes by aurone and betacyianin. The absorption zone in this case is green or blue-green. Pigments of the white group are flavonoids, which absorb in the ultraviolet. Thus, the true absorption spectrum roughly corresponds to that which can be derived by the additional colors. The most significant correction is that in blue color group the absorption band is not limited by yellow-orange area, but includes the green area too.

In the study of photochemical reactions caused by natural radiation in plants is of interest to the spectral distribution of the photons in the solar radiation. In the upper part of the Earth's atmosphere the most numerous photons are yellow with wavelength 560-590 nm. With the passage of sunlight through the upper atmosphere, the number of photons decreases gradually towards longer wavelengths and steeply toward short one: water vapor absorbs infrared radiation in several bands longer than 700 nm, oxygen has a number of narrow absorption lines near 687 and 761 nm, ozone strongly absorbs in the ultraviolet and visible regions of the spectrum, due to which the peak photon density is shifted from yellow to red (about 685 nm to). Plants are adapted to this spectrum, which is mainly determined by the oxygen supplied to the atmosphere by the plants themselves.

Irradiance produced by the solar radiation on the earth's surface, is determined by the height of the Sun above the horizon and, therefore, depends on the latitude, the time of year and time of day (Table 5). Moreover, this value is strongly dependent upon a number of meteorological factors, such as clouds, humidity and atmospheric transmittance. Seasonal reduction of solar radiation in the atmosphere is expressed by the Bouguer law:

$$E = E_0 \cdot R^{Tm},$$

where *E* is irradiance at the surface of the Earth produced by sunlight passing through a layer of *m* optical mass, E_0 is trans-atmospheric irradiance or solar constant, *R* is factor of atmospheric transparency, *T* is haze ratio.

R and *T* are different for different wavelengths of the solar spectrum and increasing beginning winter towards summer. Reducing the solar height, the mass of air, penetrated by the beam with a single cross-section, increases in proportion to the length of the path traversed by the beam in the atmosphere (Rvachev 1966). So, the spectral composition, the peak position and short-wave limit of solar radiation on the Earth's surface are determined by the height of the Sun above the horizon. The lower the sun goes down, the richer spectrum of long-wavelength (red-orange) radiation and short-wavelength (violet-blue) boundary and the emission maximum shifts to longer wavelengths. Thus, from April to June, there is a rise of the sun over the horizon and the associated shift blue/red ratio (Table 5). In the same period, there is a shift in the color of the flowers: flowering species with blue, indigo and violet corolla (average start in April) is replaced by species with a red corolla (average start in June). We can assume some adaptive sense that corolla pigments absorb light in a certain range of the solar spectrum, and that this adaptation is often realized in the course of phylogeny, which is visually manifested in the observed seasonal changes of color distribution.

Table 5

Seasonal shift of parameters of solar spectrum at the latitude 47° (Chisinau)

	Parameters of solar spectrum								
1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*
March	41	1.55	560	400	11.5	12.2	18.7	12.8	0.953
April	53	1.30	660	480	13.0	12.9	18.9	12.1	1.066
May	62	1.15	770	560	14.5	13.2	19.0	12.0	1.100
June	66	1.06	805	640	16.0	13.4	19.0	11.9	1.126

1 – month; 2 **–** height of the sun above the horizon at midday; 3 - lens mass; 4 - average irradiance of a horizontal surface W/m^2; 5 - a daily dose of physiologically active radiation, W·sec; 6 – duration of day, hours; 7 - relative intensity of violet-blue band (380-490 nm), %; 8 - relative intensity of green-yellow band (490-600 nm), %; 9 - relative intensity of the orange-red band (600-780 nm), %; 10 – the ratio of the intensity violet-blue/orange-red.

The seasonal shift of the peak of solar radiation reaching the earth is consistent with our hypothesis.

Violet-blue tones of corolla are caused by the absorption of photons of yellow-green range. Preferential absorption of these photons is probably due to their relatively large part in the integer solar spectrum in the spring time. However, as in the case of photosynthetic the energy absorbed is utilized to create energetic equivalents (ATP and NADP*H) for assimilation of CO_2, in corolla CO_2 is not assimilated, energy equivalents is not formed, and the absorbed energy is channeled by the two circuits: the energy dissipation into the heat form and fluorescence. Hence, the temperature of corolla and reproductive organs (stamens and pistils) increases, which creates better conditions for the fertilization. Since most pollinators is partial or complete colorblind, their unmistakable recognition of flowers may be due to a slightly elevated temperature of the flower and the emanation of odors, which also increases with a higher temperature. The appearance of flowers of white, orange, yellow, yellow-green and white color coincides with an increase in the density of photons of blue-violet and ultraviolet range in the solar spectrum from April to June months (Table 5). The pigments responsible for this coloration absorb high-energy blue-violet and even ultraviolet photons. Absorbed energy is dissipated into heat and contributes to a more vigorous evaporation of water. Increased evaporation causes the decrease in temperature of flower in the hottest period and protects reproductive organs of plants from heat stress (Smolikova & Medvedev 2015). Leaves have the similar mechanism too. Leaf temperature is always lower than the air temperature in the hot. Finally, red and purple flowers appear which have the pigments absorbing green range (570-490 nm) of the visible spectrum. It may be associated with an increase in the intensity of green light reflected by tree layer A. This illustrates the adaptability of plants to use solar energy, obtained in the course of their evolution on the ground.

Conclusions. For the herbaceous flora of Moldova the seasonal differences between the types of corolla color are established. The species with a red corolla is characterized by a relatively late flowering, the species with a blue, indigo and purple corolla – relatively earlier.

Seasonal changes of corolla color correspond to seasonal changes of solar radiation reaching the earth's surface, providing probably the best conditions for the reproductive organs of flower.

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