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Flower formation in different taxa of *Lonicera* L. (Caprifoliaceae) in a culture in southern Sakhalin (Russia)

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ABSTRACT

The floral meristem of many orthotropic honeysuckles starts to form nearly a year before flowering. Such an early formation may serve to support the Nedoluzhko's hypothesis that honeysuckle phenorhythm types evolved from summer/fall to early summer, passing through the stages of late autumn, winter and early spring. The relationship between flowering dates and the dates when floral meristems begin to form is distinct from that of the subgenus *Caprifolium* and orthotropic honeysuckles. This difference allows us to deduce that there is a special evolutionary pathway for phenorhythm types in the *Caprifolium* subgenus: a shift from a summer/fall flowering period to an earlier – not later – period. The relationship between flowering dates and dates of floral meristem formation in species of the *Tataricae* series, related to the *Lonicera* section, is almost identical to that of the *Rhodanthae* subsection. This supplements previously established arguments that suggest *Rhodanthae* is the closest subsection to the *Lonicera* section.

Key words: *Lonicera*, Caprifoliaceae, floral meristem, flowering periods

РЕЗЮМЕ

Шейко В.В. Продолжительность формирования цветков в разных систематических группах рода *Lonicera* L. (Caprifoliaceae) в условиях культуры на юге острова Сахалин (Россия). Флоральная меристема у многих ортотропных жимолостей формируется почти за год до цветения. Столь раннее формирование может служить аргументом в пользу гипотезы Недолужко, что феноритмотип жимолостей эволюционировал от летне-осеннего к раннелетнему через такие этапы, как позднеосенний, зимний и ранневесенний. Зависимость между датами зацветания и датами формирования флоральной меристемы разная в подроде *Caprifolium* и у ортотропных жимолостей. Данное различие позволяет предполагать в пределах подрода *Caprifolium* особый путь эволюции феноритмотипов: смещение от летне-осеннего цветения не к более позднему, а, наоборот, к более ранним срокам. Зависимость между датами зацветания и датами формирования флоральной меристемы у видов серии *Tataricae*, относящейся к секции *Lonicera*, почти совпадает с аналогичной зависимостью для подсекции *Rhodanthae* из секции *Isika*. Это дополняет ранее известные аргументы, позволяющие считать, что к секции *Lonicera* наиболее близка подсекция *Rhodanthae*.

Ключевые слова: *Lonicera*, Caprifoliaceae, флоральная меристема, сроки зацветания, микрофенология

Early-summer flowering is a characteristic feature of all species of the *Lonicera* section and many species of other sections (except for the *Nintooa* (Sweet) Maxim.) in the genus *Lonicera*. Nedoluzhko (1984) considered the early-summer flowering in the genus as evolutionary progressive trait that arose from summer-autumn flowering through the stages of winter and early spring flowering. One of the ways to test this hypothesis is a comparative study of the dynamics of the ontogenesis of flower primordia in different systematic groups. The calendar dates of laying the floral meristem and the duration of the development of flower primordia can serve as the simple criteria for determining the stages of ontogenesis. Differences in these indicators observed under identical conditions can be considered as a manifestation of specific characters inherent to the distant ancestors of these species. The comparison of the species of the *Lonicera*

section with species of other sections according to these criteria is of particular interest, since there are a number of paradoxical combinations of archaic and progressive traits among the traits of this section.

The contradictions in the analysis of the morphology of species of the genus *Lonicera* are reflected in the molecular systematics of the genus based on the analysis of nuclear and chloroplast DNA.

The objective of this study was to obtain data on the laying time of the floral meristem and the duration of the development of flower primordia in different systematic groups of the genus *Lonicera* in the collection of living plants of the Botanical Garden-Institute FEB RAS. Comparison of these data for species of different systematic groups in the genus *Lonicera* will open the possibility of testing the Nedoluzhko's hypothesis.

MATERIAL AND METHODS

Forty species from the genus *Lonicera* from the collection of the Sakhalin Branch of the Botanical Garden-Institute FEB RAS were used in this study, in which we examined two characteristics: (1) the flowering start date, which was noted in the course of routine phenological observations recorded during the 2000–2018 period; (2) the dates of floral meristem formation in the generative buds, which were determined with a binocular microscope in microphenological studies during periods of 2004–2006 and 2017–2018. We examined buds from various sections from shoots of different types. The formation was set as earliest date in a particular season. In certain instances, it was impossible to establish the earliest appearance of floral meristem. We were only able to record a later development stage of the flower bud. In these cases, we studied the length of time between the appearance of floral meristem and that particular development stage in other (delayed) flower buds. These buds were selected either from plants of the same species or from closely related species with a similar phenorhythm. After determining the length of this period, we calculated an estimated date for the appearance of floral meristem in the species of interest. The years of 2004 and 2018 both saw abnormally cool summers. Since our microphenological observations lasted only five seasons, and occurrence rate for abnormally cool summers in the southern part of Sakhalin Island is less than 40%, the data for these years were not included in the calculation of means. The average delay in floral meristem formation during such years was about 10 days. Therefore, the dates for these years shifted by 10 days. Given that the flower development period were determined over several months in most cases, any errors resulting from this correction could not have significantly affected the findings.

RESULTS

Table 1 presents the collected data on flowering start dates, floral meristem formation dates and the duration of the flower development period in 40 species and one hybrid of the *Lonicera* genus. The species in the table are grouped according to their systematic position (after Rehder 1903). Supraspecific taxa, including *Lonicera xylosteum* L., were treated as generic taxa. Other supraspecific subdivisions examined:

Subgenera: *Caprifolium* (Adans.) Dipp. 1889 according to G. Krüssmann (1977).

Sections: *Isaxylosteum* Rehd. 1903, *Isika* Rehd. 1903, *Nintooa* (Sweet) Maxim. 1903, according to A. Rehder (1903).

Subsections: *Purpurascens* Rehd., *Pileatae* Rehd., *Caeruleae* Rehd. 1903, *Vesicariae* Kom. 1901, *Distegiae* Rehd., *Alpigenae* Rehd., *Rhodanthae* Rehd., *Pbenianthi* (Rafin.) Rehd., *Cypheolae* Raf. according to A. Rehder (1903); *Fragrantissimae* Rehd. emend. Nedoluzh., *Bracteatae* Hook. f. et Thoms. 1858 emend. Nedoluzh. 1986 according to V.A. Nedoluzhko (1986).

Series: *Praeflorentes* (Nakai) Nedoluzh. 1984, *Nigrae* Pojark. ex Nedoluzh. 1984, *Orientalis* Pojark. ex Nedoluzh. 1984, *Maximowiczianae* Pojark. ex Nedoluzh. 1984, according to V.A. Nedoluzhko, (1984 a); *Tataricae* (Rehd.) Nedoluzh. 1983, *Ruprechtianae* Pojark. ex Nedoluzh. 1983, *Maackinae* Pojark. ex Nedoluzh. 1983, according to V.A. Nedoluzhko, (1983) and the *Hispidae* Pojark. series. (1958. descr. ross.), *Asperifoliae* Pojark. (1958. descr. ross.), *Altmannianae* Pojark. (1958. descr. ross.), *Altmannianae* Pojark. (1958. descr. ross.), *Heterophyllae* Pojark. (1958. descr. ross.) according to Poyarkova (1958).

In most orthotropic honeysuckles, the floral meristems form 1–1.5 months after flowering begins. It may occur, although infrequently, two weeks earlier or later. For climbing honeysuckle, the situation is slightly different in that floral meristem starts forming at a minimum of more than two months after flowering begins. Most often, it occurs around four months after flowering, i.e. toward the end of autumn and sometimes even in spring of the following year. The latest recorded floral meristem formation was found in climbing *Lonicera henryi* from the *Nintooa* section. Therefore, different systematic groups of honeysuckle displayed different ranges in flowering periods (hereafter referred to as RFS) and in the lengths of the flowers' development periods (hereafter, RDFD). RFS in the *Caprifolium* subgenus is relatively small and significantly inferior its considerably more variable RDFD (Fig. 1). The *Lonicera* subgenus has a wider RFS and RDFD than *Caprifolium*. However, this difference in RDFD is due solely to the species from the *Nintooa* section. If we exclude this section from the *Lonicera* subgenus analysis, i.e. evaluate only orthotropic honeysuckles, then we find the opposite, where the RDFD is inferior to the RFS.

When comparing the same values in lower-ranking taxa, we see that the RFS within the *Caprifolium* subgenus is generally the same in the *Cypheolae* and *Caprifolium* subsections. Meanwhile, the RDFD is significantly higher in the *Caprifolium* subsection than in *Cypheolae* (Fig. 1). The RDFD exceeds the RFS in both subsections. The situation is different for orthotropic honeysuckle of the *Lonicera* subgenus. Within the *Isika* section, the genus's largest, both values are higher than in *Lonicera*. However, the RFS in the *Isika* section is larger than the RDFD, while this relationship is inverted in *Lonicera* (Fig. 1).

The relationship of these values for various subsections within the *Isika* section shows that the RDFD does not exceed the RFS. It also does not exceed the RFS for those series in the *Lonicera* section for which there is sufficient RDFD data (Fig. 1). A large RDFD for a section generally ensures variation among the series (for some of which there is insufficient RDFD data).

If we graphically represent the relationship between the length of the flower development period and the flowering dates for each of the 40 species (Fig. 2), then a large number of points for certain supraspecific taxa fall outside the main array. This is especially true for the subgenus *Caprifolium* and among the section *Nintooa* in the subgenus *Lonicera*.

Analyzing the relationship between flowering dates and the dates of floral meristem formation in those supraspecific taxa for which there is sufficient data yields the graph shown in Figure 3. Clearly, this relationship in the subgenus *Caprifolium* differs than that in the variety of subsections and series of this genus's orthotropic members.

An attempt to link flowering dates with the development stage observed in the plants at the beginning of winter did not reveal any connection with the species' systematic position.

DISCUSSION

Nedoluzhko (1984 b) considered the summer/autumn phenorhythm inherent in all species of the *Nintooa* section to be the primary flowering phenorhythm for the *Lonicera*

Table 1. Dates of flowering, formation of floral meristem and duration of the development of flowers

Section	Subsection	Series	Species	Date of flowering start	Date of floral meristem formation	Duration of flower development (days)
Subgenus <i>Lonicera</i>						
			<i>Lonicera mirtillos</i> Hook. f. et Thoms.	5.06	12.07*	327
	<i>Isaxylosteum</i>					
	<i>Isika</i>	<i>Purpurascetes</i>	<i>L. utahensis</i> Wats.	15.05	16.06	331
			<i>L. canadensis</i> Marsh.	16.05	16.06**	332
			<i>L. gracilipes</i> Miq. var. <i>glandulosa</i> Maxim.	29.05	6.07*	324
			<i>L. tangutica</i> Maxim.	20.07	6.08	346
	<i>Caeruleae</i>		<i>L. caerulea</i> L.	18.05	16.06	334
	<i>Pileatae</i>		<i>L. pileata</i> Oliv.	27.06	21.08*	308
	<i>Vesicariae</i>		<i>L. vesicaria</i> Kom.	25.06	10.08	317
	<i>Fragrantissimae</i> s.l.	<i>Praeflorentes</i>	<i>L. praeflorens</i> Batal.	3.05	8.06**	327
		<i>Altmannianae</i>	<i>L. altmannii</i> Regel. et Schmalh.	20.05	16.06	336
	<i>Bracteatae</i> s. str.	<i>Hispidae</i>	<i>L. hispida</i> Pall. ex Roem. et Schult.	30.05	16.06	346
		<i>Asperifoliae</i>	<i>L. olgae</i> Regel. et Schmalh.	3.06	16.06*	350
	<i>Distegiae</i>		<i>L. tolmatchevii</i> Pojark.	15.05	15.06*	322
			<i>L. involucrata</i> Banks ex Spreng.	23.05	28.06	327
	<i>Alpigenae</i>	<i>Alpigenae</i>	<i>L. glehnii</i> Fr. Schmidt	25.05	25.06*	332
			<i>L. alpigena</i> L.	2.06	1.07	332
		<i>Heterophyllae</i>	<i>L. webbiana</i> Wall.	28.05	1.07*	328
	<i>Rhodanthae</i>	<i>Nigrae</i>	<i>L. chamissoi</i> Bunge	3.06	10.07**	326
			<i>L. nigra</i> L.	7.06	20.07*	320
		<i>Orientalis</i>	<i>L. caucasica</i> Pall.	23.06	15.08*	310
			<i>L. discolor</i> Lindl.	26.06	10.08	318
		<i>Maximowiczianae</i>	<i>L. sachalinensis</i> Fr. Schmidt	16.06	1.08	318
			<i>L. maximowiczii</i> Regel	16.06	1.08*	318
	<i>Lonicera</i>	<i>Lonicera</i>	<i>L. xylosteum</i> L. f. <i>mollis</i> Regel	5.06	5.07	332
			<i>L. chrysantha</i> Turcz. ex Ledeb.	14.06	12.07**	335
		<i>Ruprechtianae</i>	<i>L. morrowii</i> A. Gray	17.06	6.08	313
			<i>L. ruprechtiana</i> Regel	14.06	5.08**	311
		<i>Tataricae</i>	<i>L. karataviensis</i> Pavl.	7.06	16.07	324
			<i>L. tatarica</i> L.	18.06	7.08**	313
			<i>L. floribunda</i> Boiss. et Buhse	22.06	15.08*	309
		<i>Maackinae</i>	<i>L. prostrata</i> Rehd.	10.06	15.08*	297
			<i>L. maackii</i> Herd.	22.06	15.08	309
		hybrid	<i>L. quinquelocularis</i> Hardw. × <i>L. maackii</i>	25.06	7.09*	289
	<i>Nintooa</i>		<i>L. henryi</i> Hemsl.	28.07	10.05	79
Subgenus <i>Caprifolium</i>						
		<i>Phenianthi</i>	<i>L. sempervirens</i> L.	15.07	9.04	97
		<i>Cypbeolae</i>	<i>L. dioica</i> L.	17.06	31.08	288
			<i>L. dioica</i> × <i>hirsuta</i>	6.07	27.10*	250
			<i>L. prolifera</i> Rehd.	7.07	5.11*	242
			<i>L. hirsuta</i> Eaton	13.07	5.11*	248
		<i>Caprifolium</i>	<i>L. caprifolium</i> L.	25.06	28.08*	299
			<i>L. perichlymenum</i> L.	22.07	26.04	87

Notes: * – adjustment in connection with the omission of the date of formation of the floral meristem; ** – adjustment due to cold summer

genus. While some species in this sections are common in the tropics, most are found in the subtropics. It is the opinion of this author that honeysuckle in the tropical climates of previous geological ages initially flowered during the late summer and in autumn. This autumnal flowering was replaced by a late autumnal one as a result of the differentiation by altitudinal belts in vegetation during orogenic processes, with a likely winter flowering period acting

as an intermediate stage. Further climatic cooling led to dormancy in winter and early springtime flowering. In modern honeysuckles, winter flowering is typically found in the Eastern Chinese *Lonicera fragrantissima* Lindl. et Paxt. (Yang et al. 2011). It is perhaps the most archaic member of its evolutionary branch, which includes an eponymous subsection and the *Bracteatae* subsection. The winter phenorhythm eventually transformed into a late spring period

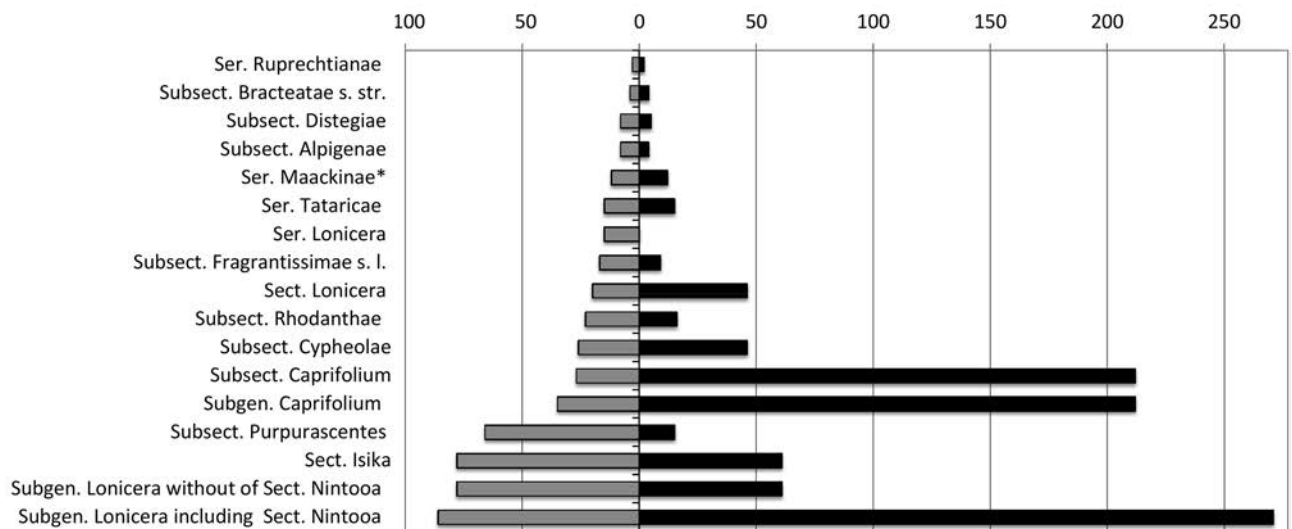


Figure 1 Ranges of flowering start dates (from earliest to latest for a systematic group) (left of zero axis) and of the duration of flower development (right of zero axis) in different systematic groups of the genus *Lonicera* L.

and, later still, early summer. Nedoluzhko did not distinguish between orthotropic shrubbery and climbing honeysuckle in his analyses on the phenorhythm shift in the *Lonicera* genus. The formation of the floral meristem almost a year before flowering can be considered as preserving the ontogeny of the traits inherent in the ancestors of these *Lonicera* species. A completely different relationship in *Caprifolium* between the flowering dates and floral meristem

formation dates suggests a different evolutionary pathway for the phenorhythms in this subgenus. Moreover, there are no species in this subgenus with winter or early springtime flowering. This subgenus likely experienced a shift from a summer/fall flowering period to an earlier—not later—period.

Figure 3 shows the relationships between flowering dates and dates of floral meristem formation in *Lonicera* species. The species from the *Tataricae* series (*L. floribunda*,

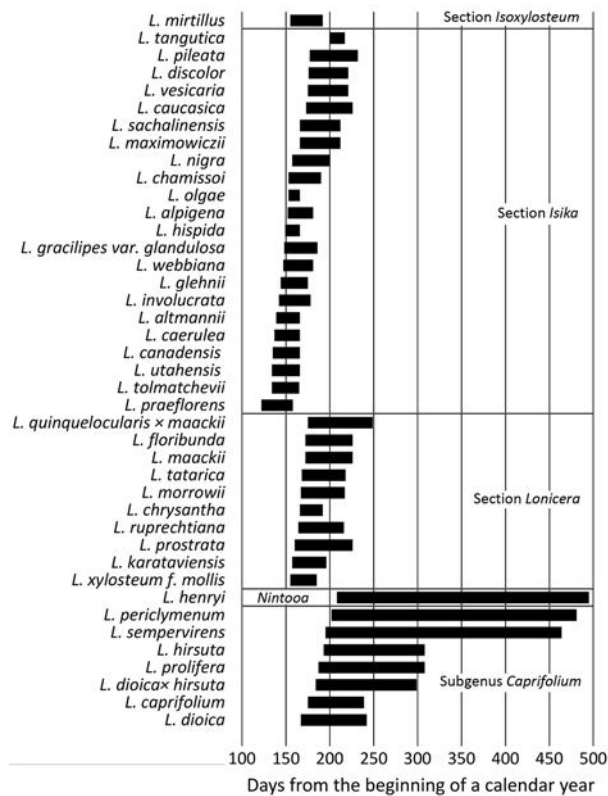


Figure 2 The time period of formation of floral meristem in different subgenera of the genus *Lonicera* L.

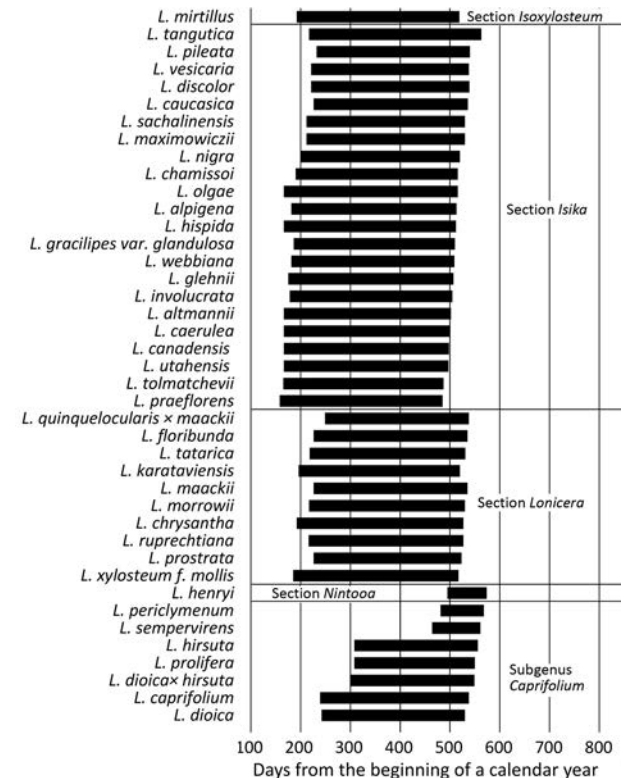


Figure 3 The time period from the beginning of flowering to the beginning of formation of floral meristem in different subgenera of the genus *Lonicera* L.

L. tatarica, *L. karataviensis*) have nearly the same dates of meristem formation as species of the *Rhodanthae* subsection. In this case, the correspondence can be viewed as additional confirmation of the *Lonicera* section's proximity to the *Rhodanthae* subsection (part of the *Isika* section), as evidenced by chloroplast DNA sequencing (Theis et al. 2008, Nakaji et al. 2015). Theis et al. (2008) reported a conflicting findings from the chloroplast DNA and nuclear DNA analyses, regarding the *Lonicera* section. Some inconsistencies in opinions on the phylogenetic relationships may arise when analyzing the morphological features of this section's species and the fact that there is no polyploidy (unlike in other sections). Primitive characteristics also appear in large shrubbery (the largest for orthotropic honeysuckle), immature buds, and evanescent pith (characteristic in relatives of the *Symphoricarpos* Duham. и *Leycesteria* Wall. genera). The origin of the this section could possibly be the result of introgression, but the morphological similarity, chloroplast DNA findings and the data from our microphenological studies suggests that the greatest contribution to this section's formation came from the *Rhodanthae* subsection. For further investigation into this matter, it will be necessary to conduct chloroplast DNA testing on a larger species sampling from both the *Lonicera* section and the *Rhodanthae* subsection. Most likely, analysis of relatively ancient species in the *Lonicera* section, such as *Lonicera quinquelocularis* Hardw., *L. arborea* Boiss., *L. floribunda*, and *L. brevisepala* Hsu et H.J. Wang (a widespread species to the west of the main habitats of the *Ruprechtianae* series), will be of particular interest. It would also be prudent to study the floral meristem formation periods in most of these species.

CONCLUSIONS

Research has found that the floral meristem of many orthotropic honeysuckles forms nearly a year before flowering, a feature that can be viewed as preserving the ontogeny of the character inherent in the distant ancestors of these *Lonicera* species. In turn, this may serve to support Nedoluzhko's hypothesis that honeysuckle phenorhythm types evolved from summer/fall to early summer, passing through the stages of late autumn, winter and early spring.

The relationship between flowering dates and the dates when floral meristems begin to form is distinct from that of the subgenus *Caprifolium* and orthotropic honeysuckles (species of the *Lonicera* subgenus, minus the *Nintooa* section). This difference allows us to deduce that there is a special evolutionary pathway for phenorhythm types in the *Caprifolium* subgenus. It is likely that this subgenus experienced a shift from a summer/fall flowering period to an earlier—not later—period.

The relationship between flowering dates and dates of floral meristem formation in species of the *Tataricae* series, from the *Lonicera* section, is almost identical to that of the *Rhodanthae* subsection. This supplements previously established arguments, based on morphological similarity and chloroplast DNA analysis that suggest *Rhodanthae* is the closest subsection to the *Lonicera* section.

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