===== **REVIEWS** =====

Growth Rhythms at Different Stages of Shoot Morphogenesis in Woody Plants

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Abstract—Research data on the rhythms of shoot growth in woody plants obtained in the second half of the 20th century are reviewed. Analysis of these data demonstrated different regulation of shoot growth processes at three stages of its development: (1) initiation of shoot primordia, (2) primordia development into phyllome primordia, and (3) visible shoot growth. The growth rhythm after the first stage was realized at the level of apical shoot meristem; at the second stage, at the individual shoot level; and at the third stage, at the whole plant level.

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The goal of this work was to review research data on the growth and morphogenesis of shoots in woody plants and to try systemic approach to the analysis of this process. Woody plants are the most convenient subject since their shoots do not die back each year as in herbs, which allows us to monitor their development for several years. The main research results of the shoot growth rhythms were obtained in 1950s–1970s. Later, the interest in this problem receded and researchers switched to physiological and genetic mechanisms underlying shoot growth control. However, systemic approach to all natural phenomena including shoot development requires revisiting the revealed mechanisms.

The shoots of woody plants have an annual rhythm manifested as a regular variation in the growth rate, which first increases to reach a peak and then decreases to zero. After a short pause, growth recommences. Woody plants can have several such waves or growth cycles in the vegetation season. The annual shoot growth in such plants can include several cycles. The shoot portion formed within such cycle was called the "elementary shoot" (Grudzinskaya, 1960; Gattsuk, 1974).

Since Sachs proposed the notion of the grand period of growth (Sachs, 1873; cited from Sabinin, 1973), botanists attack this periodicity; however, there are many obscure aspects in this phenomenon. Nevertheless, this process definitely depends on the internal plant processes rather than on seasonal variation in environmental conditions, i.e., the rhythm is endogenous (Serebryakov, 1952, 1962; Sabinin, 1963). This is confirmed by a rhythm in shoot growth in many plants growing under constant environmental conditions of humid tropics (Volkens, 1912; cited from Sabinin, 1963; Koriba, 1958; Alvim, 1964, 1978; Zimmermann and Brown, 1974; Kramer and Kozlovskii, 1983) as well as in growth chambers with constant light and temperature conditions (Lavarenne et al., 1971; Greathouse et al., 1971; Champagnat, 1978). However, natural selection has adjusted this endogenous rhythm to conform to the seasonal rhythm of environmental conditions (Serebryakov, 1966).

The rate and rhythm of shoot growth are reflected in the nascent shoot structure. Regions of successive growth can be usually recognized along the shoot axis. Each growth region starts from the bud ring—a zone of connivent nodes and scars of aborted bud scales. The bud ring is followed by the zone with extended nodes and progressively extending internodes, which reach the maximum length and then decrease so that the shortest of them are included in the bud ring zone of the next region of shoot growth (Figs. 1, 2). The structure of a grown perennial shoot makes it possible to precisely determine the number of its growth cycles and elementary shoots.

Two periods are commonly recognized in each shoot growth cycle—latent period within the bud and visible period starting from bud emergence and ending in arrested growth of internodes and leaves. The next period of latent growth that starts the next cycle is initiated in the shoot apex even before the visible growth of this shoot stops; however, the latent growth processes of the new cycle largely take place after the visible growth arrest (Artyushenko and Sokolov, 1955, 1958; Shilova, 1963; Borisovskaya, 1971).

Three stages can be recognized in the elementary shoot growth and morphogenesis (Fig. 2). At the first
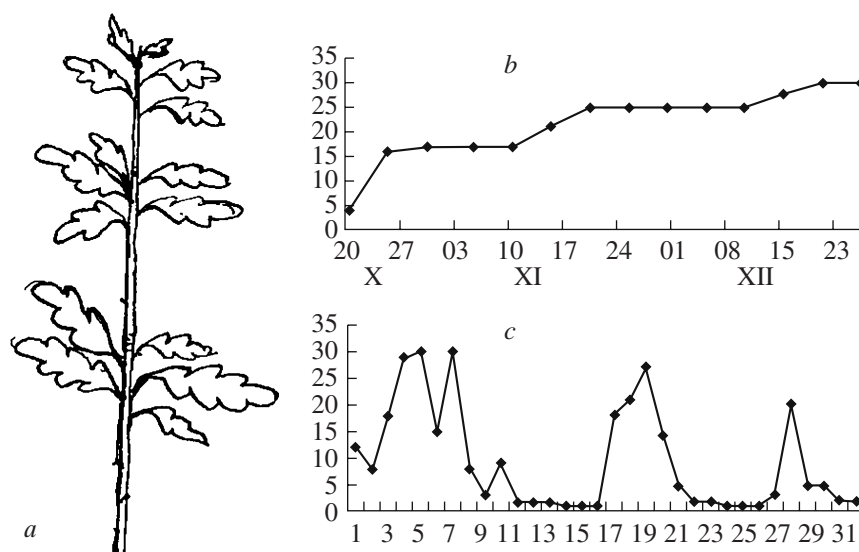
Fig. 1. A shoot of *Quercus robur* seedling growing in chamber under continuous light and constant temperature that formed through the elementary shoots; *a*, general view; *b*, growth curve (ordinate: cm); *c*, shoot structure expressed as internodal length variation (ordinate, mm) along the axis in consecutive shoot metameres (abscissa).

stage, the peripheral zone of the shoot growing point gives rise to primordial outgrowths, which provide the development of future shoot metameres. At the second stage, these primordial outgrowths are developed into leaf primordia, which start to grow at the third stage. The first two stages take place in the period of latent growth; and the third stage, in the period of visible growth (Mikhalevskaya, 2002a).

The processes at each stage go relatively autonomously, do not depend on processes going at other stages, and are controlled by different physiological mechanisms. This can be demonstrated by their detailed consideration.


Fig. 2. Metameres: *a*, inside the bud at the first and second stages of shoot development; *b*, after visible growth termination at late third stage of shoot development; *1*, primordial outgrowth, *2* leaf primordia; *3*, bud ring metameres; *4*, elementary shoot.

FIRST STAGE OF SHOOT GROWTH AND MORPHOGENESIS

The first stage demonstrates certain periodicity in the formation of the primordial outgrowths. The plastochron—time interval between the appearance of two neighboring primordial outgrowths—periodically changes. This has been demonstrated by Shilova (1962, 1963, 1967, 1969, 1988, 1991) in the studies of bud development in some species of the Ericaceae, Rosaceae, and Saxifragaceae families as well as in *Crataegus, Rododendron, Juglans*, and other species. The revealed periodic changes in plastochron did not always coincide with the changes in the rate of visible shoot growth. The buds of many species had two periods of primordial initiation in the vegetation season, and the rate of primordia emergence first increased and then decreased in each of the periods. However, only a single period of visible shoot growth was observed in the same vegetation season. This points to different mechanisms of rhythm regulation after the first and third stages of shoot morphogenesis.

Our studies on several species of oak growing under different conditions (Moscow Region, Caucasian Black Sea coast, and Pamir Mountains) have also demonstrated a periodicity in leaf primordium initiation, which was manifested as polymodal distribution of the studied elementary shoots by the number of their metameres. Each sample including two or three hundreds of shoots had several modal classes differing by five metameres (Mikhalevskaya, 1987; Mikhalevskaya and Abdrakhmanova, 1991). Such polymodality indicated rhythmic primordial initiation, which likely depends on phyllotaxis (2/5 in oak). The polymodality resulted from the alternation of periods of apical mer-
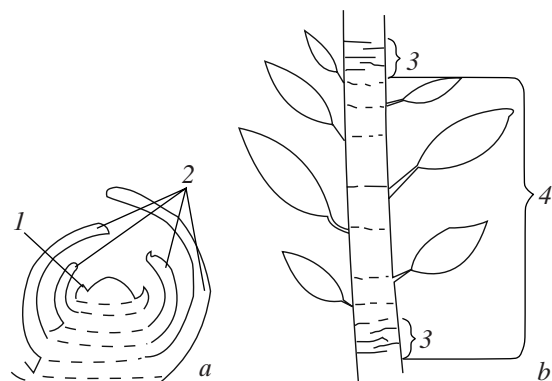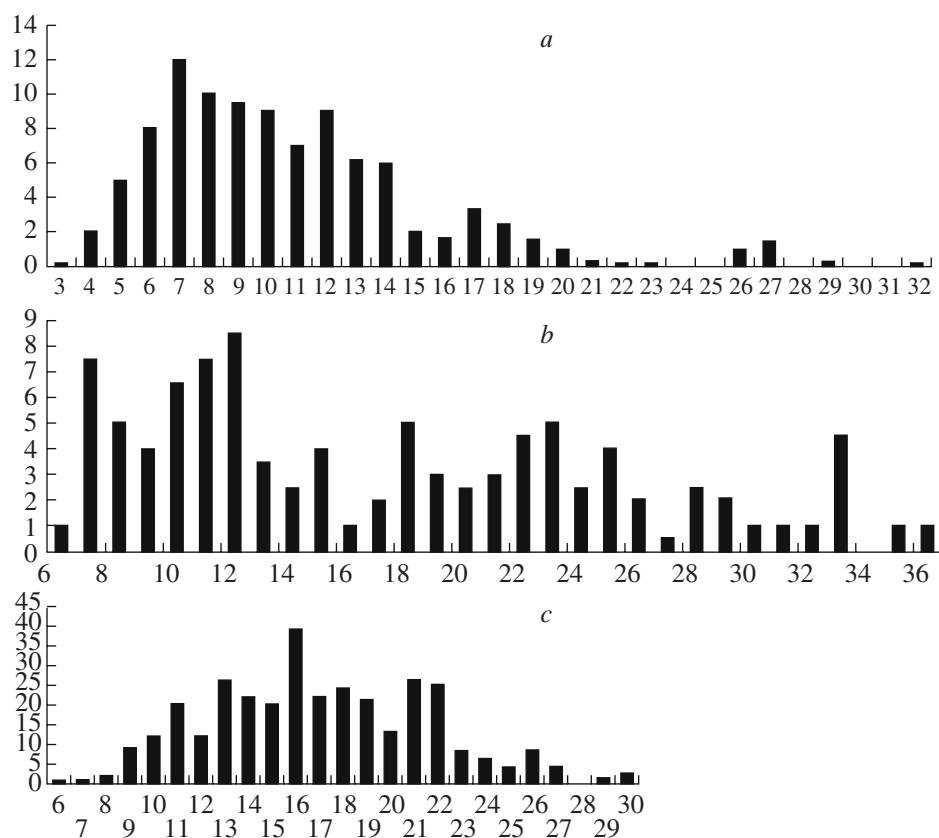
Fig. 3. Distribution of oak elementary shoots (ordinate) by the number of their metameres (abscissa); modal classes in: *a, Quercus robur* with metamere numbers of 7, 12, and 17 (245 shoots studied); *b, Q. rubra*, 8, 13, 19, 24, 29, and 34 (153 shoots studied); and *c, Q. acuta*, 11, 16, 21, and 26 (298 shoots studied) (Mikhalevskaya, 1987).
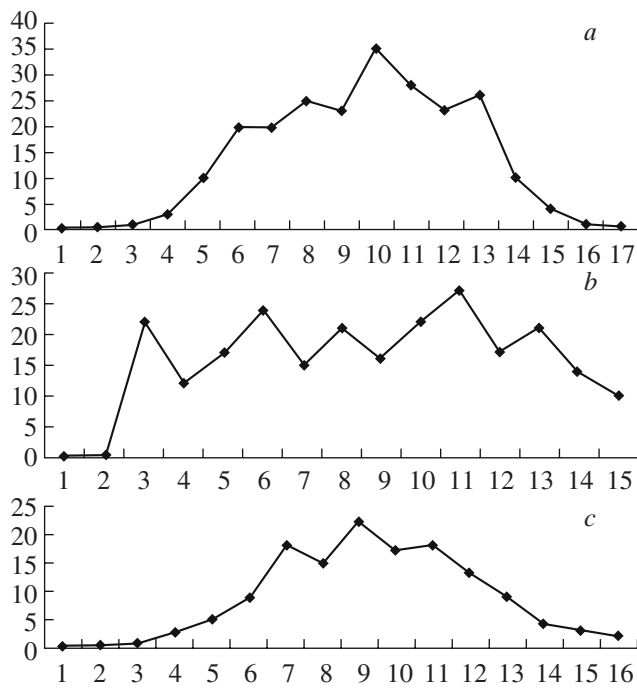
istem activity (when primordial outgrowths emerged to give rise to shoot metameres later) and inactivity (when the number of primordia did not increase). Accordingly, the number of shoots with a constant number of metamere primordia was greater than that of shoots with the increasing number of primordia. This was reflected by the histograms of shoot distribution by the number of their metameres (Fig. 3). The classes consisting of numerous shoots (i.e., modal classes) included the shoots with inhibited metamere initiation, where the number of primordia remained constant for some time. Conversely, the classes consisting of less shoots included those, where the number of primordia changed as a result of their initiation. This approach allowed Shmidt (1961, 1968) to reveal rhythmic processes that determined the number of perianth parts in the flowers of some Ranunculaceae and the number of umbels in some Umbelliferae.

The polymodal distribution of individuals by some parameters indicates quantized growth in plants (Shmidt, 1984; Magomedmirzaev, 1990). Such quantized growth was manifested as rhythmic initiation of primordia at the first stage of shoot morphogenesis; however, no such rhythm was observed at the subsequent stages. This is confirmed by the dynamics of

changes in the metamere size along the shoot axis. The pattern of changes in the internodal length along the shoot axis, which reflects the shoot structure, is described by a unimodal curve typical of many plants. Figure 4 presents such curve for the most common structure of individual shoots in three oak species. One can see minor variations in the length of neighboring internodes; however, the internodal length first increases and then decreases throughout the shoot and this unimodal curve has no peaks for each five metameres. This demonstrates that the rhythm reflected in the polymodal distribution of the shoots by the number of their metameres is limited to the first stage, when leaf primordia are initiated, and is not observed at the subsequent stages. The regulation of the processes driving the rhythm of the first stage is realized in the shoot apical meristem cells. The same processes likely underlie the phyllotaxis in oak shoots.

SECOND STAGE OF SHOOT GROWTH AND MORPHOGENESIS

At the second stage, the primordia of leaves and other similar organs (cataphylls, bud scales, or perianth parts) are formed from the primordial outgrowths. Its

Fig. 4. Variation in the internodal length along the elementary shoot axis in different oak species: *a, Quercus robur*; *b, Q. rubra*; and *c, Q. acuta*; abscissa, number of consecutive metameres above the bud ring; ordinate, internodal length, mm (Mikhalevskaya, 1987).

leaf blades leads to the formation of primordia of normal leaves with blades. This abolishes the rhythm at the second stage of shoot development, which is manifested by alternation of the regions with scales and leaves along the shoot axis (Mikhalevskaya et al., 2004). The experiments on the removal of growing leaves on the shoot apex demonstrate that the development into phyllome primordia is regulated not in the apical meristem but rather in the underlying zone of the growing shoot.

Essentially, the emergence of bud scales in plants results from the rhythm at the second stage of shoot morphogenesis rather than from the plant evolutionary adaptation of protecting the apical meristem from unfavorable environmental conditions, although the bud scales clearly have such protective function. Leaf primordia realize this protective function in many plants with open buds, i.e., without bud scales. Such species demonstrate no alternation of metameres with scales and leaves along the shoot axis since the leaves with blades develop in all metameres. The shoot structure in these species is likely due to be absence of rhythm at the second stage of shoot development.

Different regulation of primordial outgrowth initiation and their development into leaf primordia were also demonstrated by genetic studies. Analysis of these processes in *Arabidopsis* and maize mutants demonstrated independent genetic control of leaf initiation and formation (Lutova et al., 2000).

THIRD STAGE OF SHOOT GROWTH AND MORPHOGENESIS

This stage of shoot growth begins with budbreak and onset of visible growth. As a result, the metamere size increases, internodes elongate, and leaf blades sprout. The growth rate during this stage commonly varies along a unimodal curve: it first increases, reaches to the peak, and then decreases. The lower and upper metameres stop growing first and last, respectively. The pattern of changes in the internodal length and leaf blade area in the series of shoot metameres reflects the changes in their growth rate (Fig. 1) and these changes do not reflect the rhythm of the first stage of shoot growth when primordial outgrowths are initiated.

At the third stage of shoot development, the first stage of the next shoot (new elementary shoot) growth is initiated in the apical meristem. The primordial outgrowths of this daughter shoot, initiated during visible growth of the parental shoot, commonly give rise to scale primordia and, after parental shoot growth completes, to leaf primordia. This was shown in many woody species (Artyushenko and Sokolov, 1955, 1958; Shilova, 1963, 1988; Borisovskaya, 1971).

The duration of the third stage of shoot growth as well as the timing and rate of its visible growth are set not at the individual shoot level but rather at the level of the crown shoot system or even at the level of the whole

regulation is different from that of outgrowth formation, as indicated by experiments with the removal of leaf blades or bud scales from the growing shoot. In the experiments on horse chestnut shoots, the removal of outer bud scales in emerging apical buds induced the emergence of new bud scales from the leaf primordia in the bud. In the intact buds, nascent primordia gave rise to primordial leaves with blades (Dostal', 1956). In *Theobroma cacao* and *Gleditsia triacantos* with a pronounced rhythm of shoot growth, the removal of growing leaves induced the development of primordia following these leaves into green leaf primordia rather than into bud scales, what is normally observed. Such removal also abolished the rhythmic structure of the shoot manifested as the alternation of regions with scales and leaves along the shoot axis (Nozeran, 1978). The removal of growing leaves in rubber tree (*Hevea brasiliensis*) also abolished the rhythm of shoot growth typical of this species (Halle and Martin, 1968).

Our experiments on the shoots of oak (*Quercus robur*) seedlings have demonstrated the same effect of growing leaf blade removal. An apical bud externally covered by bud scales that developed from leaf primordia is commonly formed on the tip of oak shoot before its growth stops. The scale formation is mediated by inhibiting the development of leaf blade primordium. In this case, the stipules continue development into bud scales. The additional removal of the youngest growing

plant including its root system. Grudzinskaya (1959, 1960) studied the development of *Quercus robur* shoots and demonstrated that the rhythm of their growth and the capacity to form lammas shoots depends on the proportion between the shoot and root systems, since improved root growth conditions favored lammas shoot formation. Borchert (1973, 1975, 1978) has reached the same conclusion after removing a part of the root or shoot system in *Quercus palustris* seedings, which affected the shoot–root balance and altered the rhythm of visible shoot growth.

Analysis of the length and metamere number in shoots that ceased growth also demonstrates independent regulation of the growth rhythms at the first and third stages of shoot development. Such analysis performed for a number of woody plants (Mikhalevskaya, 2002b) demonstrated that the shoot length does not depend on the number of metameres in it. The shoots with the same number of metameres can considerably differ in length (Table 1) and the coefficients of variation of the number of metameres are several times smaller than those of the shoot length (Table 2), which also indicates independent regulation of these two parameters.

In early ontogeny of some woody plant species, neither the rhythm of visible shoot growth nor alternation of regions with scales and leaves are observed in seedlings. Such rhythm appears in the shoot structure later and is maintained at the subsequent ontogenetic stages. This also indicates the regulation of this rhythm at the whole plant level rather than at individual shoot level. Such developmental pattern has been revealed in seedlings of *Hevea brasiliensis, Mangifera indica* (Alvim, 1964), *Picea* and *Abies* species (Kozlowski, 1992), and many tropical trees (Borchert, 1978).

The regulation of visible shoot growth at the whole plant level does not exclude its regulation at the individual shoot level. Experiments on *Arabidopsis* shoots (Lake et al., 2001) demonstrated that mature leaves that ceased growth influence histogenesis in young growing leaves. The exposure of mature leaves in individual

Table 1. Length variations in elementary shoots with the same number of internodes in different woody plant species

Species	Number of internodes in shoot	Number of studied shoots	Shoot length, mm
Populus tremula	6	12	12–115
	7	14	29–155
P. "canadensis"	6	11	3–38
	8	11	15–160
Acer platanoides	2	16	3–94
	3	18	15–209
A. negundo, ♀	3	11	38–143
	4	9	60–215
Fraxinus pennsylvanica	3	19	8–80
	4	26	25–160
Sorbus aucuparia	4	14	7–232
	6	11	35–284
Cinnamomum japonicum	10	10	51–206
C. glanduliferum	18	13	141–725
C. camphora	15	7	66–252

chambers with high CO_2 concentration decreased the number of stomata in the growing leaves exposed to low CO_2 concentration, while increased illumination of the mature leaves increased the number of stomata in the growing leaves. The physiological mechanism of this interaction between the leaves of the same shoot remains unclear. However, such morphogenetic changes in young developing leaves are clearly beneficial, since increased number of stomata at high light intensity increases the photosynthetic rate through accelerated CO_2 influx. At the same time, the gas exchange rate required for photosynthesis at high CO_2 concentration is provided by a low number of stomata, and their low number decreases water loss through transpiration.

**Table 2.** Length of elementary shoots and number of their metameres

Species	Number of studied shoots	Shoot length, mm			Number of metameres in shoot		
		Mean ± SEM	CV, %	Lim	Mean ± SEM	CV, %	Lim
Populus tremula	55	209 ± 25	89	20–670	15.2 ± 0.7	35	8–29
P. "canadensis"	40	75.6 ± 7.5	63	20–167	11.6 ± 0.5	27	7–17
Acer platanoides	44	76.8 ± 13	115	3–357	7.5 ± 0.18	16	5–11
A. negundo ♂	62	163 ± 19	92	9–599	7.8 ± 0.3	26	5–12
A. negundo ♀	44	162 ± 20	84	10–525	7.4 ± 0.3	25	4–12
Sorbus aucuparia	70	166 ± 16	80	4–475	10.5 ± 0.34	27	4–16
Fraxinus pennsylvanica	57	114 ± 18	117	6–694	6.3 ± 0.2	24	4–11

Notes: SEM, standard error of the mean; CV, coefficient of variation; Lim, variation limits.
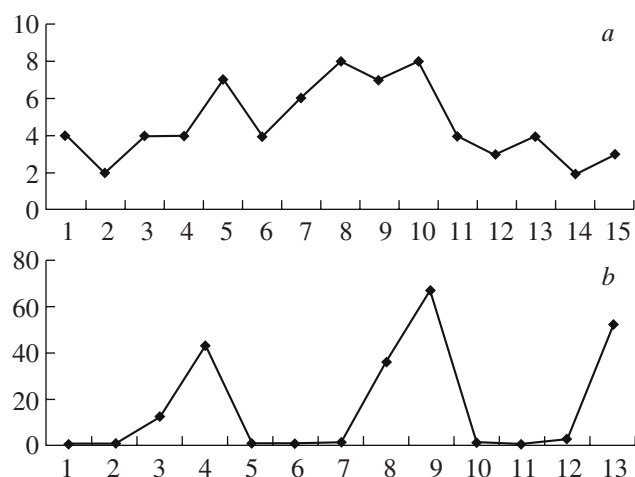
Fig. 5. Structure of a typical shoot in *Viburnum* spp.: *a, V. lantana*, 125 shoots studied; *b, V. dentatum*, 26 shoots studied; in contrast to *V. lantana*, the rhythm is apparent in the structure of *V. dentatum* shoot (Mikhalevskaya, 1999).

Tropical trees include species with no rhythmic structure in the grown shoots (Koriba, 1958). They demonstrated no periodic changes in the internodal length or leaf size, no bud scales were formed, and their buds were open. Visible growth of their shoots was not limited to particular months and growing shoots could be found in the crown throughout the year. Koriba called such species evergrowing as distinct from intermittent ones with a pronounced rhythm in the shoot
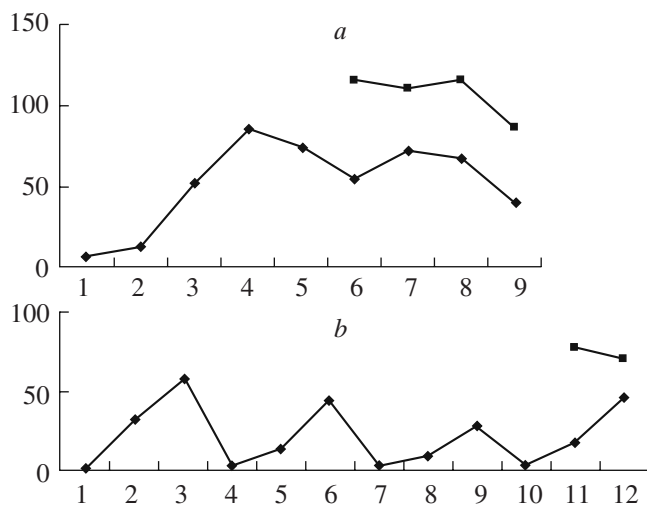
Fig. 6. A typical shoot structure in *Cornus* spp.: *a, C. alba* (144 shoots studied); *b, C. mas* (145 shoots studied); the shoot leaves remained only on the last annual increment; a clear rhythm can be seen in a *C. mas* perennial shoot, while it is not pronounced in the two-year-old lateral shoot in *C. alba* (Mikhalevskaya and Sycheva, 2003). Abscissa: metamere number; ordinate: internodal and leaf blade length, mm; ◆, internode; ■, leaf.

structure. He has found that about 20% of species in the Singapore Botanical Gardens were evergrowing; however, they were not limited to some taxonomic group and occurred in different families and genera.

We have found similar tree species with no periodic changes in the structure of grown shoots among subtropical trees in the Batumi Botanical Gardens and in the greenhouse of the Main Botanical Gardens of the Russian Academy of Sciences (Mikhalevskaya, 2004) as well as among species of the temperate zone (Mikhalevskaya, 1999; Mikhalevskaya and Sycheva, 2003). The latter included *Cornus alba, Viburnum lantana, Cotoneaster licidus, C. ignavus*, and *H. virginiana*. There are no bud rings or periodic changes in the internodal length along the axis of their perennial shoots, that is why the boundary between annual shoot increments is not always apparent. Similar species of the same genera living nearby in the Arboretum of the Main Botanical Gardens demonstrate clear rhythm in the structure of grown shoots (Figs. 5, 6). The absence of such rhythm in the shoot structure of the above-mentioned species is clearly due to the absence of rhythm in the formation of phyllome primordia from the primordial outgrowths at the second stage of shoot development going in the bud.

Alterations in the second stage of shoot development can be observed in individual shoots in the crown. Such alterations have been revealed in *Acer, Populus, Salix*, etc. species. They have "neoformed" leaves developed from the primordia not initiated in the buds before budbreak, rather they are initiated at the third stage of shoot development and immediately start visible growth. The blades of such neoformed leaves slightly differ in shape from those developed from primordia preformed in the bud before budbreak (Critchfield, 1960, 1971). In the metameres with neoformed leaves, the second stage of development goes much faster compared to metameres with preformed leaves. Neoformation is commonly observed in the shoots demonstrating active visible growth in the crown. This indicates that its regulation is realized at the whole plant level.

The distribution of plastic materials (assimilates) used to build different shoot parts plays a significant role in the regulation of morphogenetic processes at the second stage of shoot development. Thorough analysis of bud development in horse chestnut and lilac allowed Borisovskaya (1971) to propose that the development of scales in buds going during active growth of upper leaves of the parental shoot results from the deficiency of nutrients actively assimilated by growing leaves. Nozeran (1978) proposed a similar explanation of physiological mechanisms controlling the rhythm of shoot growth in rubber tree: actively growing leaves consume a lot of assimilates arriving to the growing shoot apex, thus, cutting down feeding of nascent leaf primordia. A negative feedback is established between the growing leaves of the parental shoot and leaf pri-

mordia in its apical meristem, which inhibits growth of the primordia and they give rise to scales. The experiments with the removal of growing leaves, which abolishes the rhythm of shoot growth, confirm this hypothesis.

The physiological processes underlying the regulation of growth rhythms as well as morphogenesis in general remain largely unclear despite numerous studies, although the role of the phytohormonal system in the regulation of the rate of growth processes and donor–acceptor relationships directing assimilate fluxes to the growing plant parts has been studied in detail. The role of cytokines in the regulation of assimilate transport to the growing points has been shown; although the mechanism of their effect remain obscure (Ron'zhina and Mokronosov, 1994; Ron'zhina, 2002). The role of auxin in the vascular network patterning is known (Berleth et al., 2000), and the genetic control of morphogenesis is actively studied. A gene involved in the regulation of leaf blade primordia development was identified in poplar (Rohde et al., 2002). A study of rhythm variation in shoot growth should also contribute to understanding morphogenesis control in plants.

Analysis of the shoot structure and development in woody plants demonstrated that the rhythm of shoot growth arises from many different rhythms simultaneously observed in different morphological parts of the growing shoot. The primordial outgrowths, which determine the future metameres, are initiated in the shoot apical meristem. Their initiation is regulated by the physiological processes going in the apical meristem cells.

As phyllome primordia develop in the bud, a different rhythm is observed, which provides for the alternation of bud scales and assimilating leaves along the shoot axis. This rhythm depends on the physiological processes going in the growing leaves of the preceding elementary shoot.

The third rhythm is observed during visible shoot growth starting from budbreak. This rhythm is governed by the physiological processes regulating the distribution of assimilates between different plant organs and is realized at the whole plant level.

All three rhythm types form a hierarchical system regulating plant growth and development, where the upper level that defines the processes in individual shoots and apical meristem in each shoot is the whole plant level.

ACKNOWLEDGMENTS

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