

УДК 581.143.28

## HETEROBLASTY OF THE *LOLIUM PERENNE* L.

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The turfgrass heteroblasty has been investigated by the analysis of the gross intensity and the anatomy peculiarities of the first three leaves of *Lolium perenne* L. It was founded, that leaves differ from each other in physiology, morphology and anatomy parameters greatly. Primarily these are the leaf length and their growth rate, the square of cross sections, the square and the number of vascular bundles, the square of mesophyll and intercellular spaces, the number of chloroplasts. Different parts of leaves were concluded to contribute into the extent of heteroblasty display. Some parameters which are the most suitable for the heteroblasty estimation have been founded. The variety peculiarities in these parameters have been investigated too. The notion of heteroblasty coefficient was introduced. Some aspects of the interrelation between leaf anatomy structure and their physiology state was discussed.

*Key words:* chloroplasts, intercellular spaces, growth rate, leaf primordia, mesophyll, ryegrass, vascular bundles.

The phenomenon of heteroblasty is known and investigated long before [2, 7]. Such interest is caused by the possibility to use the morphology, anatomy and physiology changes in the leaves, which are observed during plant ontogenesis, to create a beautiful model of morphogenesis [6, 11]. It is common knowledge, that distinctions in gene expression in different parts of shoot apical meristem determine the further course of morphogenesis [11]. So it is possible to assume that the basis of heteroblasty is being founded during primordia formation which depends not only on apical meristem, but on early appeared primordia and leaves as well [4]. This problem is very interesting because the first leaves of crops are initiated already at the embryonic period. Therefore the greatest distinctions must be observed between these leaves and those, which are initiated at juvenile vegetative stage.

The heteroblasty investigation is not only of great theoretical significance. The physiological state of the whole plant is an amount of physiological states of each leaf, which are determined by their anatomical structure. It defines plant reaction on various agricultural treatments, such as sprinkling by herbicides, growth regulators and so on.

Heteroblasty is estimated mainly according to the leaf morphology [1, 2] or the results of the some simple histochemical tests [6]. Anatomical and cytological parameters usually are not regarded. It may be explained by the complexity and continuity of microscopical methods. But this approach is the most informative because it gives possibility to perform analysis at the deeper level of plant organization.

The majority of studies were performed at the dicots. Unfortunately less attention is paid to monocots. Among them maize, rice and wheat often become the objects of investigations [3, 7]. Although these plants are very important for the agriculture, they are not always convenient for such experiments. That is why ryegrass (*Lolium perenne* L.), the representative of turfgrass, which is widely spread in ecosystems attracts particular interest.

The purpose of study was investigation of morphology and anatomy features of the first three leaves of *L. perenne*, definition of their physiological states on that ground and elaboration of reliable criteria for the heteroblasty estimation.

For the experiments three varieties of ryegrass (RAPID, SAKINI, ESQUIRE) have been chosen. They were planted in greenhouse at the temperature of about 23°C. The illumination was natural with maximum intensity 1500 lux and day light length of July. The dynamics of leaf appearance was observed daily by accounting of their amounts during 10 days. The integral of obtained functions was calculated according to the programme of „Graphical analysis“. Besides, the leaf length was measured every day during indicated period. The moment growth velocity was defined as a tangent of angle ( $\text{tg } \alpha$ ) between abscissa and the tangent to the curve of functional dependence of leaf length of time in the point of measuring. Each variant included 100 plants.

For the anatomy and cytology study portion was taken from the middle part of leaves at the 10-th day of their appearance and was prepared as described early [9]. Their quantity estimation of cross sections was performed with the help of ImageJ program. As some parameters altered in various parts of the leaf in different manner for there estimation the whole square of cross sections was divided into some zones [9].

Statistical treatment involved determination of average quadratic deflection and coefficient of Student at 5% significance level.

Among all the leaves the first one arouse most intensively (tab. 1). The 2-nd lagged behind but at last achieved the same level. The development of the 3-rd leaf distinctly differed from the mentioned above. Its appearance continued much longer and during the experiments not all plants initiated it. All three varieties had equal development dynamics of the first two leaves. In contrast to that, there were considerable difference between them and the 3-rd leaf. The highest leaf rate of appearance had ESQUIRE, the lowest – RAPID. The heteroblasty is shown best of all in the case with RAPID and it was the least in ESQUIRE. The appearance intensity of the 3-rd leaf besides the 1-st for RAPID decreased 2,04 times, but for ESQUIRE only 1,32 times. In-between position took up SAKINI (1,61 times). These results are possible to present in the next scheme:

Intensity of leaf appearance      ESQUIRE > SAKINI > RAPID  
Range of heteroblasty              RAPID > SAKINI > ESQUIRE

The absolute values of leaf length and the dynamics of their alterations are presented at the fig. 1. To the end of the experiment the 2-nd leaf was always longer than the 1-st and the 3-rd. The last was the shortest for RAPID plants and its growth was amazingly slow. In the case of SAKINI and ESQUIRE the situation was opposite. The 3-rd leaf became longer than the 1-st and its growth rate remained high up to the experiment end. The differences between leaves altered during their growth due to the distinctions in the growth rate. So it is better to analyze growth intensity but not absolute leaf length. The momentary velocity of growth is presented in tab. 2.

Table 1

The results of integration of functions of the arise intensity for the first three leaves of different *L. perenne* varieties

Variety	1-st leaf	2-nd leaf	3-rd leaf
RAPID	758	662	372
SAKINI	786	718	489
ESQUIRE	837	804	636

Evidently, the 1-st leaf of all varieties grew relatively uniformly. The tendency of steady and temperate decreasing of rate growth was remarkable. Slight increasing of the momentary growth rate took place at the 3-rd day for RAPID. For the 2-nd and 3-rd leaves the alterations of this parameter in the wave manner were typical. From the physical point of view they were damping oscillations. As for the wave-length of the 3-rd leaf it was more than for the 2-nd. But there were no trustworthy differences between them in the peak value. The analysis of average

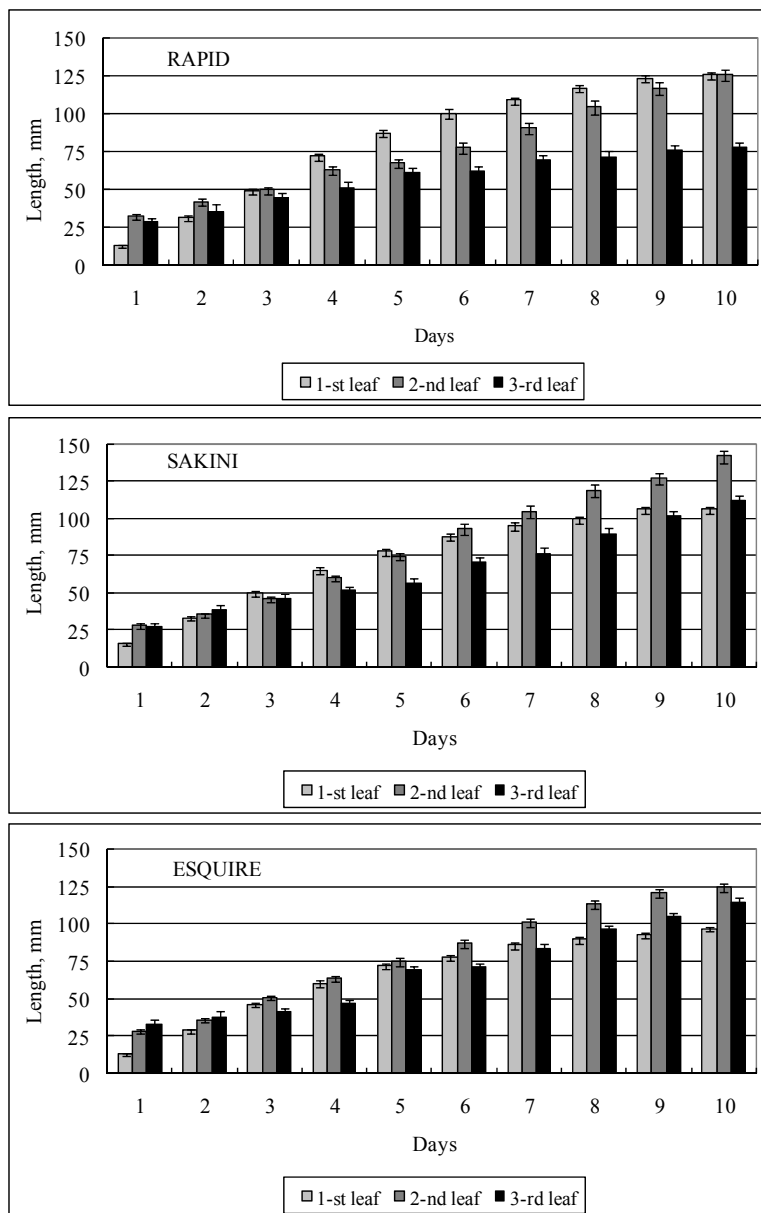


Fig. 1. The length of the first three leaves of *L. perenne* during 10 days after there appearance.

growth rate revealed substantial differences between leaves and plant varieties. The value of this parameter for RAPID was diminished with the increasing of leaf number. But if analyze the dynamics of momentary growth velocity, it was possible to assume that at the 12-13-th day the growth of the 1-st but not the 2-nd leaf stopped and then the simple average of growth rate for the 2-nd leaf became the largest as it took place for other varieties. So, the higher was oscillation frequency of a momentary growth velocity, the larger was the middle growth rate. These data let one assume that the continuity of leaf growth is a function of their number.

There are changes in the form, width and thickness of leaves (fig. 2). The tendency of decreasing the value of the angle between two parts of the leaf relative to central vascular bundle is distinctly traced. The bundle regions spread so that the interbundle sites decreased in their size and finally disappeared in the 3-rd leaf. The vascular system has changed greatly.

Table 2

The momentary growth rate (tg  $\alpha$ ) of the first three leaves of different *L. perenne* varieties and their simple average

Variety	Leaf	Days from leaf appearance										Simple average
		1	2	3	4	5	6	7	8	9	10	
RAPID	1-st	18,5	18,2	20,3	19,2	14,3	10,7	8,1	7,4	4,4	2,0	12,31
	2-nd	9,8	8,7	10,3	9,0	7,6	11,4	13,3	13,1	10,7	9,2	10,31
	3-rd	6,6	8,0	7,9	6,3	5,7	6,0	4,6	3,3	4,2	4,0	5,66
SAKINI	1-st	18,5	16,9	16,0	14,1	11,3	8,6	5,9	5,5	3,2	0,0	10,00
	2-nd	17,2	9,0	12,4	14,3	16,6	15,0	12,9	11,1	11,4	14,9	13,48
	3-rd	11,8	9,6	6,5	5,4	9,6	9,9	9,3	12,7	11,5	11,0	9,73
ESQUIRE	1-st	15,3	16,5	15,9	12,9	8,7	6,9	6,0	3,4	3,5	4,1	9,32
	2-nd	7,5	11,3	13,8	12,1	11,8	13,0	13,3	9,9	5,6	4,0	10,23
	3-rd	5,3	4,4	4,8	9,0	11,8	12,3	12,8	10,4	9,0	9,9	8,97

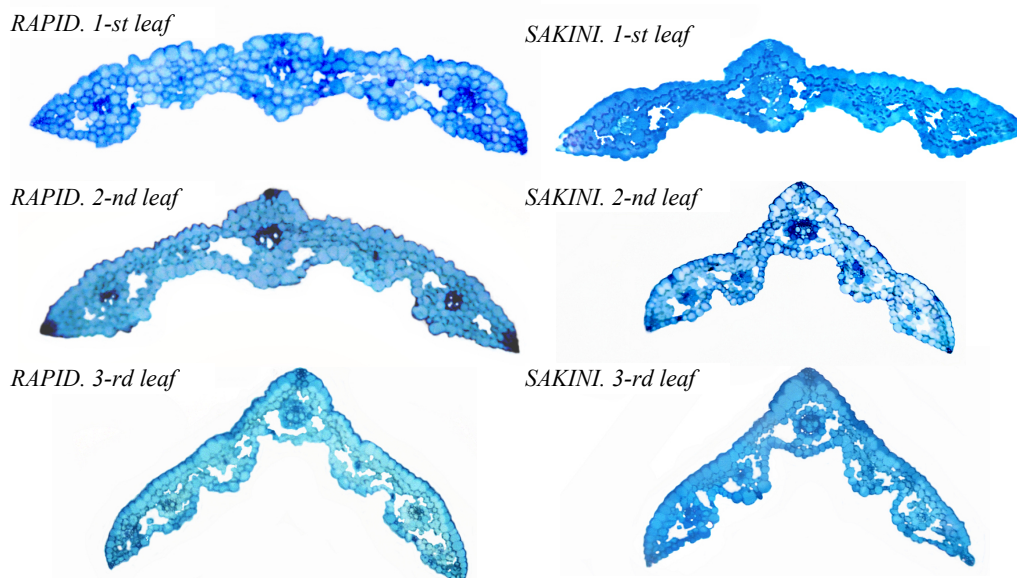


Fig. 2. The cross sections of the first three leaves of *L. perenne*. Ob. 8x, oc. 7x.

The quantity of bundles increased. Though mentioned tendencies are characteristic to both varieties the time of their appearance in each variant differs (tab. 3). Namely, the 1-st and the 2-nd leaves of RAPID differ from one another insignificantly. Absolutely opposite situation occurs with SAKINI. More similarity display the 2-nd and the 3-rd leaves. The morphometrical analysis points at the decreasing of cross sections square of the 2-nd and the 3-rd leaves and to a great extent, the 2-nd. The square and angle changes characterize variety peculiarities properly. In passing from the 1-st to the 2-nd leaf, the section square reduced at 1,38 and 1,43 times for the RAPID and SAKINI accordingly, but in passing to the 3-rd enlarged in comparison with the 2-nd at 1,06 and 1,24 times accordingly. So, SAKINI exhibits higher heteroblasty level. The angle between two parts of the leaf has changed abruptly in both varieties, but for SAKINI it becomes earlier than for RAPID. At that moment the amount of angle decreased at 1,54 and 1,41 times accordingly. Basing on these data one come to a conclusion that there is a moment in the course of ontogenesis when the structure of the leaves changes substantially. For the RAPID it is observed when passing from the 2-nd to the 3-rd leaf and for SAKINI when passing from the 1-st leaf to the 2-nd one.

The measuring of basic tissues square and the number of chloroplasts were performed only for the zones of the 1-st and the 3-rd bundles (tab. 4–5). The contribution of parenchyma into the structure of the zone around the 1-st bundle changes considerably than around the 3-rd bundle. If compare the 1-st and the 3-rd leaves, the square of parenchyma near the 1-st bundle decreases at 1,39 and 1,78 times for RAPID and SAKINI accordingly, but near the 3-rd bundle only at 1,03 and 1,16 times. Such alterations are accompanied by expansion of intracellular space and epidermis at these areas. These data point out that SAKINI has more remarkable variability except intracellular space, the volume of which increases for RAPID significantly. But in the area of the 3-rd bundle, the square of intracellular space (SAKINI) and epidermis (RAPID) increases only when passing from the 1-st to the 2-nd leaf and then reduces when passing to the 3-rd leaf. The amount of chloroplasts per unit square of parenchyma varies wider in the case of RAPID. But such changes do not always correlate with the alterations of parenchyma square for both varieties. Sometimes the maximum of chloroplast concentration is achieved in the 2-nd leaf (around the 1-st bundle of SAKINI and around the 3-rd bundle of RAPID). One can summarize that despite of decreasing of parenchyma square, the number of chloroplasts in it increases.

The changes in the square of vascular bundle tissues may have both positive (absolute square of whole bundle and its sheath, without the sheath of both bundles for RAPID), and negative (specific contribution of xylem and phloem in the square of the bundle) correlation with alterations of the entire section square. Against the background of decreasing of all varie-

Table 3

The quality estimation of the leaves of different *L. perenne* varieties

Variety	Leaf	Cross section Square, $\mu\text{m}^2$	Angle between two parts of leaf, degree	Number of vascular bunds, pieces
RAPID	1-st	177282±2156	133,6±5,2	5
	2-nd	128897±516	113,9±3,6	5
	3-rd	136990±764	80,9±5,1	6-7
SAKINI	1-st	140307±545	133,1±6,3	4
	2-nd	98429±661	86,5±2,4	5
	3-rd	121850±1129	78,8±3,6	5

Table 4

The quantity estimation of the 1-bundle zone of *L. perenne* leaves. The square of parenchyma, intercellular spaces and epidermis are pointed in percentage of general square of the zone. The square of phloem and xylem is pointed in percentage of general square of vascular bundle

Variety	Leaf	Parenchyma, %	Intercellular spaces, %	Epidermis, %	Vascular bundle, $\mu\text{m}^2$	Bundle sheath, $\mu\text{m}^2$	Phloem, %	Xylem conducting elements, %	Chloroplasts number per 1 $\text{mm}^2$ of parenchyma	Chloroplasts number per 1 $\text{mm}^2$ of bundle sheath
RAPID	1-st	34,0	7,3	33,1	3710 $\pm$ 33	5606 $\pm$ 53	5,8	24,0	8301 $\pm$ 234	8741 $\pm$ 49
	2-nd	31,2	14,0	33,2	2166 $\pm$ 5	3697 $\pm$ 18	15,2	30,5	15376 $\pm$ 402	11090 $\pm$ 189
	3-rd	24,4	18,1	37,0	2403 $\pm$ 22	2919 $\pm$ 35	14,6	28,6	17059 $\pm$ 474	13018 $\pm$ 480
SAKINI	1-st	34,9	11,2	30,5	3161 $\pm$ 34	5596 $\pm$ 44	12,9	27,7	10602 $\pm$ 177	9829 $\pm$ 536
	2-nd	24,7	16,8	38,4	1861 $\pm$ 22	2928 $\pm$ 25	15,1	29,7	18465 $\pm$ 712	16052 $\pm$ 376
	3-rd	19,6	19,3	43,7	2176 $\pm$ 24	3267 $\pm$ 48	14,9	29,0	17866 $\pm$ 459	11019 $\pm$ 337

Table 5

The quantity estimation of the 3-bundle zone of *L. perenne* leaves. The square of parenchyma, intercellular spaces and epidermis are pointed in percentage of general square of the zone. The square of phloem and xylem are pointed in percentage of general square of vascular bundle

Variety	Leaf	Parenchyma, %	Intercellular spaces, %	Epidermis, %	Vascular Bundle, $\mu\text{m}^2$	Bundle sheath, $\mu\text{m}^2$	Phloem, %	Xylem conducting elements, %	Chloroplasts number per 1 $\text{mm}^2$ of parenchyma	Chloroplasts number per 1 $\text{mm}^2$ of bundle sheath
RAPID	1-st	32,1	10,3	39,5	1617 $\pm$ 10	4340 $\pm$ 82	13,1	15,0	9959 $\pm$ 351	11060 $\pm$ 277
	2-nd	32,1	14,8	40,0	1018 $\pm$ 5	1820 $\pm$ 32	19,7	-	19384 $\pm$ 470	14286 $\pm$ 495
	3-rd	31,3	17,8	35,3	1261 $\pm$ 10	1489 $\pm$ 50	16,4	-	15146 $\pm$ 451	14775 $\pm$ 806
SAKINI	1-st	33,8	10,6	40,1	1500 $\pm$ 18	3295 $\pm$ 27	10,1	23,9	15721 $\pm$ 355	9105 $\pm$ 789
	2-nd	29,2	16,9	42,6	520 $\pm$ 6	1564 $\pm$ 24	26,9	-	18179 $\pm$ 464	16624 $\pm$ 831
	3-rd	29,1	15,9	44,0	762 $\pm$ 5	1711 $\pm$ 14	16,9	20,1	21247 $\pm$ 413	19871 $\pm$ 935

ties the 2-nd leaf bundles and their sheath square, contribution of phloem in their structure achieves maximum point. It is notable that at this moment it is impossible to identify conducting and parenchyma xylem elements apart in the 3-rd bundle at the cross section. As for the quantity of chloroplasts per unit of cell sheath square it increases according to the leaf index number. In such a way the correlation between sheath square and amount of chloroplasts in them is absent, excepting the zone of the 1-st bundle of RAPID where such correlation is negative. The increasing of chloroplast number per unit of parenchyma does not always occur simultaneously with the changes in chloroplast amount in the bundle sheath.

Quantitative estimation of heteroblasty may be done by comparing the leaves in all possible pairs by dividing the values of one certain parameter. After that heteroblasty factor (HF) will be defined as a product of all results. For example, one must calculate how many times the raise intensity of the 1-st leaf of RAPID is more than the 2-nd and the 3-rd ones: 1,15 and 2,04. Next step is comparison of the 2-nd and the 3-rd leaves: 1,78. The heteroblasty factor for the RAPID by the parameter of leaf raise intensity is 4,18. The calculations for other varieties and parameters are possible to perform similarly. These results are summarized in the tab. 6-7. Obviously HF will rise with the increasing of leaf number and its least value is equal to 1.

The heteroblasty estimation at the individual parameter may bring to the contrary results because there are differences in heteroblasty rate on the basis of definite features between various sorts. So the results show that heteroblasty of RAPID is more expressive than of SAKINI by the parameter of chloroplast number in the parenchyma and less if regard the chloroplast number in the sheath. In order to give general characteristic of the plants, it is necessary to calculate the simple average of all HF. But the calculation must be performed within the limits of one definite level of plant organization essentially, for example morphological. The reason is a ramification of regulatory systems and complexity of interconnections between various levels, where one component, for example, on the cytological level, may affect some anatomical or morphological features. If summarise physiological results, based on such parameters as intensity of their appearance and growth rate (tab. 6), general result will be the following: for RAPID – 4,45; for SAKINI – 2,27; for ESQUIRE – 1,52. If consider morphological features (tab. 6), the difference between the varieties is less: RAPID – 2,41; SAKINI – 2,23. And it is absent if to consider only anatomical features: RAPID – 2,23; SAKINI – 2,26.

Considerable contribution to the heteroblasty expression makes up heterogeneity of the leaf blade. The zone of the 1-st vascular bundle has greater value of HF practically at all parameters for the RAPID comparing with the zone of the 3-rd bundle. For SAKINI it is justly only for those tissues, which are not the components of the vascular bundle and do not contact with it directly. For this variety the largest value of HF is obtained for the 3-rd vascular bundle and its sheath.

It is possible to expect that the 1-st and the 2-nd leaf are characterized by similar properties. It is due to their formation at the embryo period. The 3-rd leaf may be characterized by the other anatomy and physiology features because at that time is represented as primordia. However, obtained results display substantial differences between the 1-st and the 2-nd leavers in the dynamics of their growth. The 2-nd leaf is more similar to the 3-rd one in this case. So that the environmental conditions do not influence the heteroblasty in growth rate and genetic

Table 6

The values of HF by some physiological and morphological features

Variety	Physiological features		Morphological features		
	Rate of leaf appearance	Growth rate	Length of leaf	Square of cross section	Angle between two halves of leaf
RAPID	4,18	4,72	2,62	1,89	2,72
SAKINI	2,60	1,93	1,79	2,04	2,86
ESQUIRE	1,73	1,30	1,66	-	-

Table 7

The values of HF by some anatomical and cytological features

Variety	Zone of the bund	Anatomical features					Cytological features	
		Specific square of parenchyma	Specific square of intercellular spaces	Specific square of epidermis	Absolute square of vascular bundle	Absolute square of sheath	Chloroplast number in the parenchyma	Chloroplast number in the sheath
RAPID	1-st	1,94	6,14	1,25	2,92	3,71	4,23	2,21
	3-rd	1,06	2,99	2,05	2,52	8,51	3,79	1,78
SAKINI	1-st	3,16	2,97	1,28	2,88	3,66	3,03	2,67
	3-rd	1,35	2,53	1,20	8,37	4,44	1,83	4,79

control must be taken as a key-factor [5]. One evidence more that heteroblasty is defined by genome is differences of its manifestation degree on the separate parts of the leaf.

Heteroblasty usually is estimated according to morphological indications [1, 2]. It is connected with easiness of observations. However Sylvester [6, 7] connected this phenomenon with the degree of leaf maturity which was estimated at epidermis metachromatic staining by toluidine blue-O. The results of own investigations testify that heteroblasty may be characterized by growth rate dynamics [8]. Heteroblasty is mostly expressed in growth processes, if it is considered on physiological level, which is integral since it is a result of all changes occurring on lower levels of plant organization during ontogenesis. Among morphological features it is difficult to find such ones which could be the best criteria for the heteroblasty estimation for *L. perenne* and probably for other monocots. Differences between the leaves disappear while joint examining of anatomical features. It means the higher is the level of plant organization the more is HF. But HF values may be rather great according to some parameters at any level. The cycle study of leaf growth is of a keen interest [8]. Essentially this is an oscillatory process of a damping character and its running is determined by two components: activity of intercalary meristem and cell expansion. To determine the contribution of each of them further cytological investigations are necessary. But the analysis of momentary growth rate describes this complicated process in general.

Analysis of obtained data demonstrates that such physiological parameters as leaf appearance intensity, their middle growth rate, cycle changes of growth rate are reliable criteria of heteroblasty estimation for turfgrass. They may add morphology and anatomy studies and may be used for the analysis of genetic experiment results as they first of all characterize the state of genome. These results may become the basis of similar investigations of other monocots.

The fact that the changes of morphometrical parameters in different parts of the leaf are different is very important [9]. That is why to estimate heteroblasty by simple generalization of the data of the whole leaf is impossible. It explains why Sylvester [6] does not consider anatomy criteria to be reliable and advises to use method of polychromic staining of epidermis. But such approach does not allow to estimate physiological state of each leaf. It can be done only using cytological methods with the further data analysis of the different parts of the leaf. Zone of central vascular bundle gives the most reliable results.

Exactly there one can observe considerable differences between the leaves and it may be connected with strong differentiation of that bundle. Heteroblasty is not properly expressed in the zone of less differentiated the 3-rd bundle. In general the problem of relation between heteroblasty rate and tissue differentiation requires further investigations. The principal parameters, which may become reliable criteria of heteroblasty estimation are square of cross section, intracellular space, parenchyma, epidermis and number of chloroplasts per square unit of parenchyma and bundle sheath. Some tissues in the vascular bundle can not be taken into consideration because sometimes it is very difficult to identify them or their parts at the cross sections. It may be connected with their various differentiation level and with separate tissue heterogeneity within the limits of one vascular bundle. It is not advisable to concentrate attention on one parameter from all viewed above because it may change within the wide limits for one variety and may be reliable constant for the other one.

Basing on morphometric data analysis one can come to a conclusion regarding intensity of a number of physiological processes in separate leaves. In particular the increasing of specific volume of intracellular space can cause great changes in the gas and water regulations. The current of CO<sub>2</sub> to photosynthesised cells should be increased and it will demand



more chloroplasts for its fixation. Exactly such positive correlation between the number of chloroplasts per unit of parenchyma square and the volume of intracellular space is observed. It means that photosynthesis productivity of each following leaf should be increased but it is impossible without appropriate changes in vascular system structure and in sheath cells. Intensification of saccharose syntheses in the cytoplasm of photosynthetic cells and fructose-6-phosphate in the chloroplasts of the bundle sheath should be expected. Indirect evidence of such changes is the increasing of saturation of sheath cells by chloroplasts. Changes of intracellular space volume and a xylem part in the vascular bundles will cause changes of water potential in certain parts of the leaf and it may result in water supply of tissue. Phloem achieves its peak in the 2-nd leaf and it may cause more intensive outflow of saccharose to the leaf intercalary meristems, root apical meristems and zones of cell elongation in the roots. Probably it can explain that the 2-nd leaves have less width and cross sections square at simultaneous increasing of their length and is characterized by more intensive growth. It may be due to the intensification of cell proliferation but not cell expansion which probably decreased. So every leaf is characterized by its own gas and water regime, photosynthesis level and intensity of transport processes. It may cause different resistance of plants at different stages of ontogenesis to some unfavorable factors. These aspects should be accounted in practical work, for example in treatment of grasses by growth regulators, herbicides and other chemicals, in evaluating of competitive ability of plants in polycultural crops and in determining of terms of grass sowing according to local climatic conditions.

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**ГЕТЕРОБЛАСТІЯ *LOLIUM PERENNE* L.****І. Тіханков**

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Гетеробластію дерноутворюючих трав на прикладі *Lolium perenne* L. вивчали шляхом аналізу інтенсивності росту й анатомічних особливостей перших трьох листків. З'ясовано, що листки сильно різняться між собою за фізіологічними, морфологічними і анатомічними параметрами. У першу чергу це довжина листка, швидкість його росту та площа поперечного перерізу, а також площа та кількість провідних пучків, площа паренхіми, міжклітинників і кількість хлоропластів. Окремі частини листків різною мірою впливали на прояв гетеробластії. Були визначені параметри, які можна використати для кількісної оцінки гетеробластії у різних сортів. Запроваджується поняття коефіцієнта гетеробластії. Обговорюються деякі аспекти взаємозв'язку анатомічної структури листків із їхнім фізіологічним станом.

*Ключові слова:* хлоропласти, міжклітинники, швидкість росту, примордій, паренхіма, пажитниця, провідні пучки.

**ГЕТЕРОБЛАСТІЯ *LOLIUM PERENNE* L.****ІІ. Тіханков**

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Гетеробластия дернообразующих трав на примере *Lolium perenne* L. изучалась путем анализа интенсивности роста и анатомических особенностей первых трех листьев. Установлено, что листья сильно отличаются между собой по физиологическим, морфологическим и анатомическим параметрам. В первую очередь это длина листа, скорость его роста и площадь поперечного сечения, а также площадь и количество проводящих пучков, площадь паренхимы, межклетников и количество хлоропластов. Отдельные части листьев в разной степени влияли на проявление гетеробластии. Установлены параметры, которые можно использовать для количественной оценки гетеробластии у разных сортов этого вида. Вводится понятие коэффициента гетеробластии. Обсуждаются некоторые аспекты взаимосвязи анатомической структуры листьев с их физиологическим состоянием.

*Ключевые слова:* хлоропласты, межклетники, скорость роста, примордий, паренхима, плевел, проводящие пучки.

Стаття надійшла до редколегії 23.12.08

Прийнята до друку 19.02.09