Annals of Agri-Bio Research **28** (1): 23-31, 2023

Impact Score : 0.28
(Scopus)

Features of Physiological and Biochemical Processes of Grass Branching

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(Received: July 5, 2022; Accepted: September 8, 2022)

ABSTRACT

The aim of research was to study the features of grass sprouts. The research concentrates on morphological and physiological basis of this process. Tillering of grasses is based on the formation of the basal zone of shortened internodes and initiation of buds of a certain capacity, and it is completed by its transition to the growth, differing by peculiar morphological and biochemical features in its development.

Key words: Carbohydrate, protein, metabolism, physiological processes, ecological phases, grass tillering

INTRODUCTION

Many scientific publications are devoted to the study of grass tillering, but only some of them deal with its theoretical basis (da Silva *et al*, 2021; Sanches *et al*, 2021). Regulation of the process of scattered tillering is still a weak point (Yu *et al.*, 2020). As a result of analysis of the literature and our research on various aspects of grass tillering cytological and biochemical hypothesis of regulation of this process have been offered. This process is based on the features of mitotic cell activity of meristematic tissue depending on carbohydrate and protein metabolism, the ratio of different classes of growth substances and providing species with water and nutrients (Janska *et al.*, 2018; Chapman *et al.*, 2021). Belyuchenko (2014) summarized methods of sprout formation of grasses. In this paper, the features of sprout branching of grass species, the formation of the tillering zone and transition of lateral buds to growth are studied basing on this hypothesis. Comparative analysis of sprout formation of grasses in different environmental conditions will encourage more detailed study of their biology, ecology and morphology. The aim of our research was to study the features of grass sprouts. The research includes support of morphological and physiological basis of this process.

MATERIALS AND METHODS

Structure of the species and life forms were studied in terms of fodder grasses in conditions of field experiment in the former Soviet Union, Cuba, Sudan, and in South Africa. Observations were carried out permanently by means of the constant sampling and determination of biometric indexes. All materials (fresh and herbarium samples) were analyzed morphologically: Sprouts, their structure and branching were studied, branching diagrams were drawn, sprouts and buds were observed in the whole and segmented forms, by means of the unaided eye and the binocular increasing to ×120. The sprout structure of grasses was studied by means of monitoring the development of some species in natural herbage and of those species that were grown in field conditions and in vegetation vessels with subsequent laboratorium inspection. Observation was carried out every 5-6 days, determining the biometric indexes and describing the state of the plants. In some experiments, the whole plants were extracted every 15 days (up to 30-35 samples of each specie), described, and the

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information was written down for detailed study and anatomical and biochemical research.

The development of grasses was studied in the following way: the dates of sowing (or regrowth) and the beginning of some phenological phases were noted. During the first year of life every 2-3 days the seeds were examined and all changes were taken into account. In following years mono- and polydominant herbage was studied. In the process of studying of morphological changes in the vegetation period of plants the following phases were distinguished: in the vegetation cycle-germination (rooting) or aftergrowing, tillering, stem elongation; in the generative cycle-ear formation, flowering, bearing, the end of the vegetation period. Development of grasses was studied in terms of the most important fodder species in the economic relation. Seasonable monitoring of the plant development was carried out in the permanent study areas of seeded and natural pastures in Cuba, the former USSR, in Sudan, in Central Asia and the South Caucasus.

RESULTS AND DISCUSSION

The process of tillering in whole (from the formation of plumule in the caryopsis to the separation of the tillering zone and transition of its lateral buds to growth) was regulated by biochemical processes that are caused by the correlative relations of biochemical reactions (carbohydrate and protein metabolism and correlation of different hormone classes in certain periods of species development) and cytological activity (mitosis) of the organism that is largely dependent on environmental conditions (Yoon *et al.*, 2017; Jones *et al.*, 2017; Abid *et al.*, 2018; Rauf *et al.*, 2021). The proposed cytological and biochemical hypothesis of tillering process could explain the basic morphogenetic changes occurring in the plant, especially in the initial period of its development.

Formation of the Tillering Zone

During the ripening of the grass caryopsides, the development of their grain kernels occurred, the formation level of which was due to environmental conditions (fertility, soil moisture, etc.; Carvalho *et al.*, 2021; de Oliveira and Viani, 2022). In wet years, the plumules of caryopsides of some species often germinated (at the grassroots). Fast germination (without a dormant period) of caryopsides was possible to observe during the seed cast of fountain grass, sugar cane and other grasses. Physiological after ripening of formed buds occurred during the dormant period of seeds (e. g. during the storage) and the activity of meristematic cells reduced by the means of specific physiological processes in the cytoplasm, not leading to the transformation of the nucleus. The transition of caryopsides to the dormant period was accompanied by accumulation in them (mostly in the covers) of large amounts of inhibitors (such as ABA – abscisic acid), that blocked mRNA and protein synthesis (Rehman *et al.*, 2021).

At a certain temperature and moisture the grass caryopsis absorbed much water that led to significant chemical changes stimulating mitotic activity in apical points; inhibitors were destroyed in the germ becoming glycosides or being leached by water; hormones that activated growth were synthesized (apparently mainly gibberellins); the synthesis of new proteins and mRNA will begin in the germs, if mRNA was not formed during the seed development and present in the germ; mRNA obviously encoded enzymes that were involved in the degradation of reserve constituents as only caryopsis began to absorb water (Abid *et al.*, 2018). The ratio of cytoplasm and nucleus by weight was disrupted in meristematic cells, which received the hydrolysis products, biochemical and biophysical activity of cytoplasmic structures increased and its nucleus pressure changed, the division of cells occurred and the seeds germinated.

Leaf formation in the tillering zone had certain specificity. The first leaf appeared in the plumule and had a very limited supply of mitotically active cells. The first leaf quickly appeared on the surface during the plumule germination. After the exposure of etiolated leaves to red light the part of its phytochrome (F_C) went to the form (F_{DC}), which regulated many biophysical, biochemical, histological and morphological processes in the plant. It changed the enzymes and hormones and their activity, chloroplasts developed from etioplasts, and chlorophyll synthesis was activated.

The time during which the first leaf grew was insignificant: it just took a few hours from plumule germination till appearing of the first leaf. The leaf received the light signal that caused the restructuring of the whole trophism of the forming specie involving the activity of photochromic system. The substrate specificity of organic substances took place. For example, movement of substances in the sugar cane had the following sequence: amino acids, then glucose and sugars. Light affected the outflow of assimilates from the chloroplasts by means of some poorly understood mechanisms that determined the reactions causing the evacuation of assimilates from the leaf. For example, in light the velocity of the assimilate outflow from the corn leaves significantly increased and reached up to 200 cm/h.

Light participated in the regulation of many processes, and this was important and genetically fixed property of plants. Light activated the chlorophyll work, stimulated oxidase of indoleacetic acid, and the latter inactivated auxin. Light intensified the formation of sugars and amino acids during the process of photosynthesis (Kurepa and Smalle, 2022). The ratio and nature of the usage of sugars and proteins that were formed in the process of photosynthesis depended on the plant requirement of them, on age and condition of the plants, as well as living conditions (Figs. 1 and 2). The main part of the products of photosynthesis went to stems: they went from the first leaves more than from those formed later (Zluhan-Martínez *et al.*, 2021).

The beginning of tillering in meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.] significantly increased amount of sugar content in their buds – up to 22% on dry basis. Increasing the amount of sugar was also observed in the aboveground leaf structures, but it was considerably less than in the buds of the tillering zone. The nitrogen content in the tillering zone of meadow fescue and aboveground leaves was high enough from 1.75 to 5.00%; the nitrogen concentration in growing buds of the tillering zone was the most stable; nitrogen content in the roots was relatively equated in comparison with other structures.

Protein areas in the form of lateral and apical buds affected turgor, osmotic pressure and the transport direction of metabolic products of plants. Transportation (low molecular weight) forms of sugars went primarily to the areas of accumulation of amino acids (meristematic areas), where they changed the concentration of the cytoplasm and the mass ratio of the cytoplasm and the nucleus. Auxin that is synthesized by the apical zone of the stem and first leaves by the means of enzymatic conversion of tryptophan, was obviously formed in low concentrations, and its impact on the growth of sprout structures was less effective than on the root structures. On the contrary, there was the growth inhibition of all structures of phytomer the leaf of which received the light signal (Roman *et al.*, 2016). Mitosis of meristematic cells in the first phytomers went fast, but its number was apparently very small. Firstly, this was due to

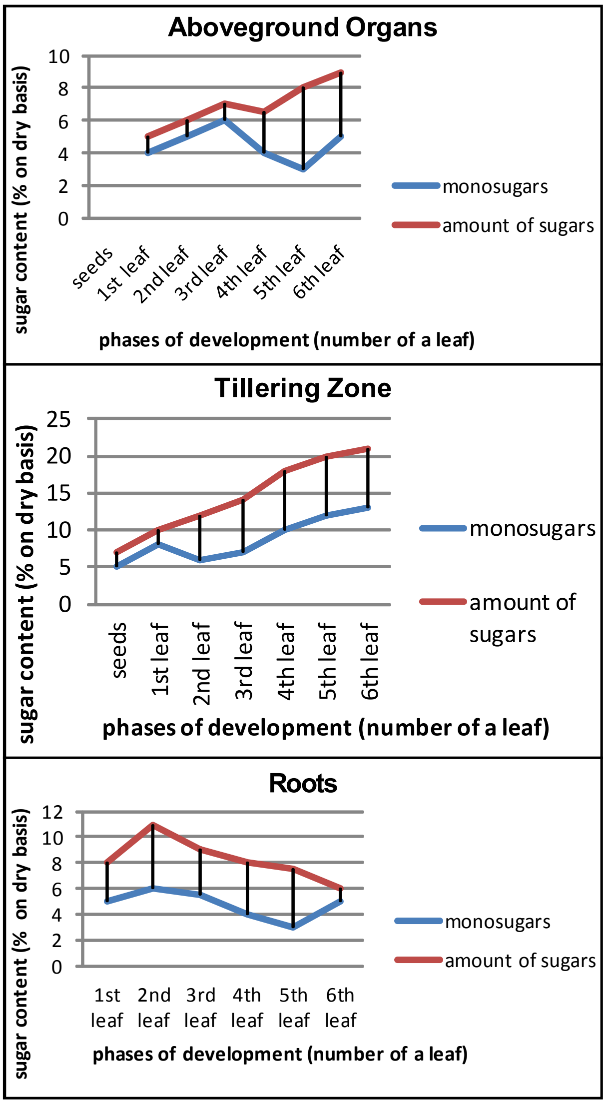

Fig. 1. Dynamics of sugars in sprout structures *Schedonorus pratensis* (Huds.) P. Beauv. in the process of forming of the tillering zone.

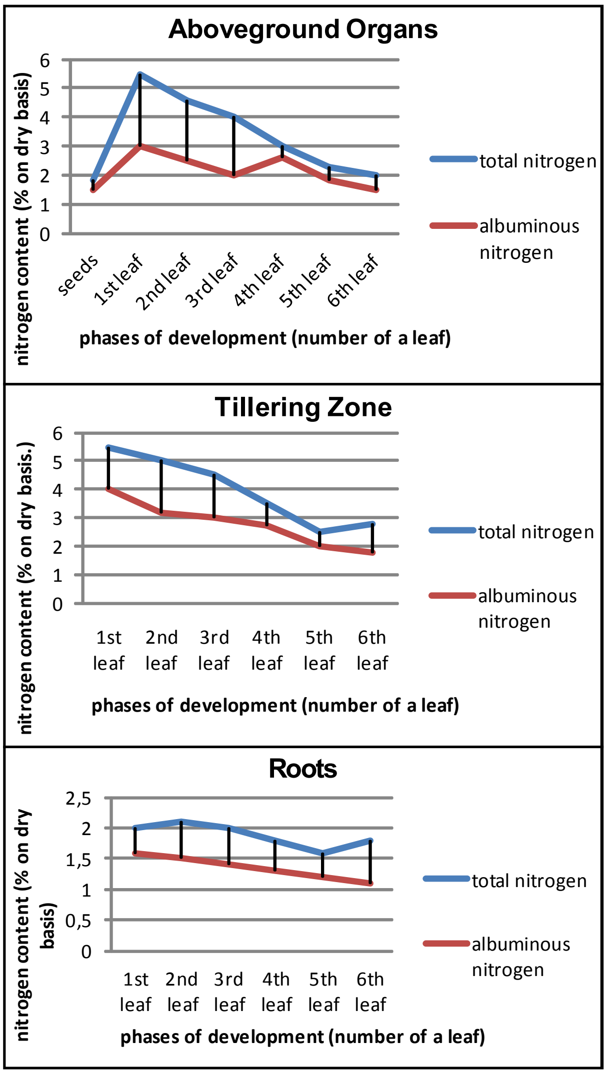

Fig. 2. Dynamics of nitrogen in the sprout structures *Schedonorus pratensis* (Huds.) P. Beauv. in the period of the transition to the tillering.

the age of the leaf; secondly, to the low stimulatory activity of growth substances; thirdly, to the increase of carbohydrates in meristematic cells, to the change of the ratio of the nucleus and the cytoplasm in this regard and a sharp deceleration and then the cessation of mitosis. Consequently, the blade and the axil of the first leaf were the shortest, and the duration of their active living was very low. The second leaf was younger than the first one and grew relatively longer in the dark (in the axil of the first leaf) till the receiving the light signal. Thus, activity of its meristems was prolonged and formed structures were notable for bigger sizes. The third leaf had more time of active growth in the dark till the receiving the light signal and the fourth had further time for it, etc. Moreover, the efficiency of growth substances increased (auxin and gibberellin) because of a reduction of their concentration.

Thus, the growth of the leaves depended on the duration of the dark period of vegetation, age, photosynthetic activity of the leaf, duration of spending assimilation products on the growth processes, vegetation conditions (high and low temperatures, drought decelerates mitosis and shortens structures of phytomers), the concentration of growth substances (ratio of stimulators and inhibitors), etc. In our opinion, separation of the truncated part of the tillering zone was due to; firstly, the conditions of caryopsis formation, its germination and early formation of the specie; secondly, to the physiological state of the meristematic cells of the plumule apex whose development was informatively (via DNA) designed to form some morphological structures; thirdly, to the differences in the number of the mitotically active cells in the intercalary meristem zone; fourthly, to the duration and the level of area isolation of the intercalary meristem; fifthly, to the duration of the (dark phase) of the appropriate leaf growth.

Internodes of the tillering zone being formed by the plumule metamers, were the shortest, and the following ones, initiation of which will take place in the apex during the formation of vegetative structures of the forming specie, became noticeably longer. In the tillering zone of not only different species, but of the same species the quantity of phytomers and their characteristics were not constant. Differences between species were due to their internal and external characteristics. Variation in the number of shortened internodes in the basal zone of species was due to the conditions of seed formation. For example, when sowing the hollow caryopsides the number of shortened internodes and forming sprouts was smaller than that of the sprouts, which appeared from the full caryopsides. Metamers with the leaf primordia became differentiated at the bottom of the plumule, and they were not significant in the upper structure. This was clearly seen in the diagrams of longitudinal sections with anatomical and histological analysis.

The formation of the tillering zone was also due to photoregulation and carbohydrate and protein metabolism. Internodes were elongated in case of shading of sprouts of their basal zone. This indicated that the light served as the main factor regulating the growth of internodes and other structures. Meristematic areas of internodes probably received a signal at coming of photosynthesis products of the leaves (sugars, proteins), which went to the final points of the phytomer, what were the nodes and internodes. Carbohydrates were moving quite fast (up to 2 m/h): it took about 1 min from the time of their formation in the first leaf till their appearance in the internode; formation and movement of growth substances, particularly auxin, occurred less rapidly (about 1 cm/h) and auxins got over the same way within 4-5 h. That's why its stimulating effect was not significant (Yoon *et al.*, 2017). Carbohydrates were accumulated in all cells very actively, their concentration increased sharply in cells of intercalary meristems, while mitosis of these cells was interrupted and they turned into the stocking one. However, the low concentrations of auxin stimulated mitotic activity in the pericycle, causing the primordium initiation of adventitious roots, and cytokinins caused the initiation of lateral buds. Indirectly, this was confirmed by our studies of the dynamics of sugars (mono- and amount) of meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.] in the process of development from the seed germination to its transition to the visible tillering phase.

The first internode, which had the least activity period of meristematic cells, was the shortest; the second and the following ones that had a larger amount of activity time of intercalary meristems, differed by the following elongation with the later differentiation of tissues. Early differentiation of sclerenchyma in the internodes of the tillering zone was explained by the lack of intercalary elongation in them (Fig. 3).

Growth of Lateral Buds

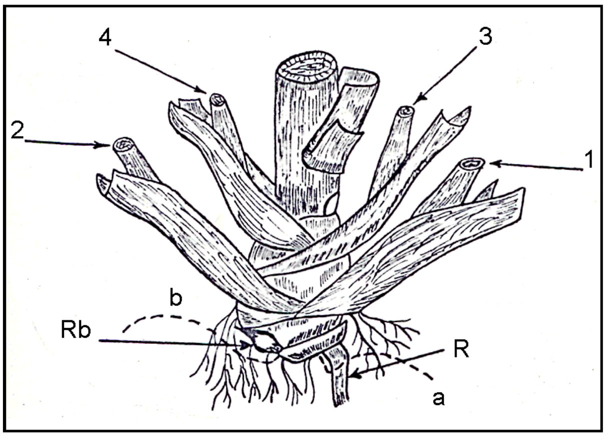

Fig. 3. Scheme of tillering of *Schedonorus pratensis* (Huds.) P. Beauv.; a, b – dead leaves, which are formed from the axils of the rhizome; Rb–resting bud and R rhizome; 1, 2, 3, 4 – sequence of appearing of lateral sprouts.

Some physiologists had an opinion that the development of lateral sprouts was subordinated to the hormonal regulation (Letham, 2019; Yu *et al.,* 2020). Indeed, in managed conditions the habitat differed from that in the natural ones and the injection of some hormones into the plant led to a significant change in its development. But "the plant need for hormones was usually extremely low, and in most cases, hormones were synthesized in sufficient quantities by the plant itself. The decisive criterion was the migration of hormone from the synthesis zone to the place of its influence, where it acted as a (chemical messenger). Besides hormones were metabolic products of plants, primarily of carbohydrate and protein metabolism.

Suggested earlier carbohydrate and nitrogen hypothesis of development of the organism proved to be unacceptable for reasoning vegetation features of the short-day plants. The suggested theory of hormonal development was used by many researchers to explain the process of grass tillering (Letham, 2019; Yu *et al.,* 2020). The grass transition to the tillering was obviously the result of the synthesis of organic compounds by plants and activity of total and primarily carbohydrate and protein metabolism. Due to various circumstances and first of all being provided with nutrients, ripening of lateral buds (a condition in which the bud is able to transit to the growth) usually fell behind the development of other structures of the appropriate phytomer (Robin *et al.,* 2021). Those buds, ripening of which coincides with the development completion of all structures of the appropriate phytomer, earlier transited to the growth: they had the largest supply of protein, which caused the going of the main traffic flows in them both from its leaf and leaves of other phytomers.

The lower (one or two) buds of the tillering zone were characterized by small capacity. They were formed during the initial period of the species formation when there was a lack of photosynthetic products and mitosis of their meristematic cells passed slowly. If the rhizomes were formed from these buds, their growth will be achieved by the coming photosynthesis products from the leaves. The upper part of the sprout was a young active structure with lateral buds that were able to transit to the growth. The deposition of photosynthesis products in stock and the conversion of cells into the stocking one were observed at the bottom of the rhizome. If lateral buds did not begin to grow at once, after a while they will lose this ability and become the stocking one. In the upper part of the buds, the carbohydrate concentration and the ratio of carbohydrates and proteins were longer supported in a favourable treatment for this process because of active mitotic division of the apex. This can be seen in a sugar cane, fountain grass and Guatemalan grass, the sprouts of which had been forming for a long time (more than 2-4 months). Apical parts of lateral buds and root primordia of the lower phytomers became the reservoirs of carbohydrates, mainly of compound polysaccharides (starch, hemicellulose, etc.), and lost their ability to germinate after planting. Therefore, the middle and upper segments of stems were used for planting, meristematic parts of which had not yet lost the ability to mitosis.

Sometimes about two or six buds were formed in the leaf axils of the aboveground phytomer of tropical grasses. Such cases occurred with *Eragrostis curvula*, *Panicum antidotale*, *Pennisetum purpureum*, etc. In such cases, the quantity of root primordia in the metamer zone usually reduced rather significantly (Silva *et al.*, 2019). When the bud became an elongated frondiferous sprout that had the capacity of (self-providing), the main traffic flow of the parent sprout switched to the following meristematic (points) (lateral buds). Stimulating or inhibiting of the lateral bud growth came from competitive action of two growth hormones: auxin, coming from the apex, and cytokinin, coming probably from the roots. Cytokinin was required for the beginning of mitosis. Constant protein synthesis was required for continuous cell division. Cytokinin did not accelerate protein synthesis, but it decelerated the protein proteolysis. The average molar ratio of auxin and cytokinin activated high cell division, caused the tissue initiation and low molar ratio of auxin and cytokinin caused the root initiation (Schaller *et al.*, 2015). If conditions were favourable, the species (strategy) will be the transition of all lateral buds to growth. Under adverse conditions, part of the buds did not grow: underdeveloped buds gradually lost turgor because of lack of water and nutrients and the ability to divide. Therefore, the underdeveloped buds did not affect the direction of traffic flow. They just turned into the stocking one.

Typically, the growth proceeded in two or three buds simultaneously. Favourable conditions of temperature, moisture, nutrient status, carbon dioxide and oxygen provided high tillering energy and shortening of its duration in each sprout. Under unfavourable conditions, the plant had a lack of nutrients. Because of the main development strategy of the specie, the nutrients were directed to the formation of individual axial sprout that led to reduction in the intensity of tillering. Under favourable conditions, plant (strategy) determined the direction of photosynthesis products to the formation of prospective structures (tillers) that were primarily capable to continue species living (Kapoor *et al.*, 2020).

Conditions permitting, the plant provided the transition of the lateral buds of elongated phytomers of usually lodging sprouts to the growth. Intensive branching of diageotropic sprouts in the zone of elongated phytomers emphasized the strategic direction of species living: taking of new space, intensifying of provision growing structures with nutrients, water, products of photosynthesis.

Lateral buds of diageotropic sprouts turned into the frondiferous sprout simultaneously with the transition of root primordia of the appropriate phytomers to the growth. If conditions did not provide a transition of root primordia to growth (e.g., dry soil), the sprout from the lateral bud will not be formed or it will be a rather weak and poorly branching one. This emphasized the relative autonomy of each phytomer of the diageotropic sprout and dependence of the development of its bud on the providing with water and nutrients.

Relations of various structures in the process of forming the tillering and branching zones and the section initiation of meristematic tissue (lateral buds and root primordia) were carried out as a response of the organism to the influence of the environment (light, temperature, moisture, etc.). This process was genetically determined because of cell excitability. After the perception of the light signal, physiological changes occurred in the leaf receptor that were transmitted to the internode, the bud, the zone of the root primordia and the node of the appropriate phytomer with incoming products of photosynthesis (carbohydrates, proteins, etc.). Nature of light effects was not clear, and one can only assume its biochemical, and probably biophysical basis. It was difficult to be doubtful about the occurrence of biochemical or biophysical (probably complex) changes associated with the distribution and dissemination of products of photosynthesis in structures (Fig. 4).

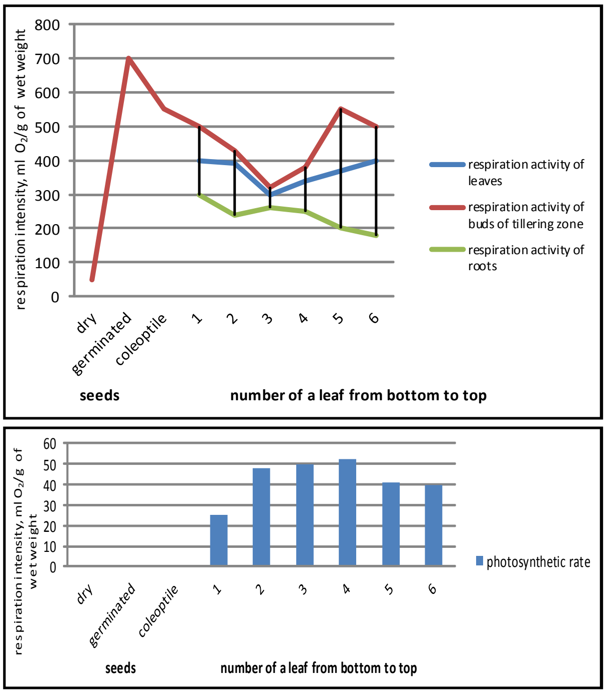

Fig. 4. The rate of photosynthesis and plant respiration activity of *Schedonorus pratensis* during the transition to the tillering.

Photosynthesis and respiration activity in seedlings of meadow fescue in the process of the transition to the tillering even in a short time interval differed quite significantly: buds of the tillering zone were notable for the highest intensity of respiration and relatively high photosynthesis fell on the middle part of the development of the sprout formation. Physiologists and biochemists' studies testified that as a result of changes in the receptor organs of grass species, products of these changes appeared - metabolites (mainly sugars), characterized by a very high mobility that is much greater than the translocation of growth substances (Canarini *et al.*, 2019). Metabolites from the leaves went to other structures, affected the metabolism, intensified or decelerated mitotic processes, thus determining the formation of some morphological structures. The growth polarity was strictly observed in structures of the first phytomers (two or three): the roots grew, and then the leaf grew. By the time it coincided with the dominance of hydrolysis in the exchange process. During this period, the lateral buds of these phytomers grew in size very little. When the synthesis (the phase of the third and fourth leaves) began to dominate in the metabolism, active growth of all grass buds occurred. The buds that were formed on the phytomers during this period grew faster and they began to grow simultaneously with adventitious roots of the appropriate structures. Intensification of synthesis led to the increasing of water discharge, which was actively absorbed by meristematic areas in the form of growing buds, leaves and roots the cells of which rapidly began to divide and use the energy generated by the functioning assimilation system (Kapoor *et al.,* 2020; de Bang *et al.*, 2021).

Lateral bud development of the tillering zone and elongated phytomers was due to the genetic characteristics of plants that determined the basic strategy of the whole organism development, and environmental conditions that affected carbohydrate and protein metabolism. The transition of the bud to the frondiferous sprout was regulated by correlative relationship of intensity of biochemical process (carbohydrate and protein metabolism and dynamics of physiologically active compounds) and the activity of cytological (mitotic) process (Letham, 2019).

The plant transition to the tillering was accompanied by a powerful accumulation of all the structures of dry matter, by the activation of nitrogen metabolism and primarily protein metabolism, by the sharp increase in the accumulation of phosphorus in the tissues, especially organic one, by the stabilization of respiration and photosynthesis indicators, etc. (Fig. 4). A similar trend was also observed in the vegetative reproduction. Vegetation conditions had a great impact on the tillering characteristics. Scattered branching, in the process of which the lateral sprouts were formed in the area of elongated phytomers, was typical for most tropical grasses and much less for the boreal ones. Apogeotropic sprouts began branching, usually after the apex differentiation or its removing and diageotropic ones began branching in each phytomer after the completion of its formation.

CONCLUSION

Tillering was due to the dynamic development of the various areas (apical and intercalary) of mitotically active meristematic cells and it had three phases : preparatory, hidden and visible tillering. Branching process was governed by the internal (genetic) characteristics and external conditions through the receptor system of leaf blades by means of obtaining the light signal and transmitting the products of photosynthesis to the various growth areas. Formation of sugars and proteins in the photosynthesis process, their coming to some sections of the apical and intercalary meristems and the accumulation of various growth substances helped to stimulate or cease mitosis, initiation and isolation of some metamer structures. Species characteristics and environmental factors regulated the development of all parts of a multi-phase process of perennial grass branching of tropical and boreal origin through the nutrition system (primarily carbohydrate and protein metabolism).

Seasonal development of grasses had great theoretical and practical importance. But this phenomenon was clearly observed in the arid and monsoon regions of tropics and subtropics, was not studied properly. Seasonality in the plant development occurred in the nature of sprout formation and it was due to the different environmental factors. Development of grass sprout was mainly controlled by physiological and biochemical processes and determined by correlation between various biochemical reactions (trophism of organism) and cytological activity of organism. These reactions were substantially dependant on environmental conditions. Tropical and boreal grasses developed certain types of sprouts in different ways and had unequal duration of this development process in various seasons and years of vegetation.

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