

Development and yield capacity of grass

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Abstract. Formation of grass sprouts is closely associated with generation of short internodes and bud set of specific capacity followed by growth and generation of yield. Process of grass sprout development consists of vegetative and generative phases. Process of sprout development at different stages is controlled by its heritable background within the frameworks of certain homeostatics, when the sprout reacts to changes in external environment, as well as by development of organism with the impact of internal (physiological, biochemical and energy) and external (environmental) factors.

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Introduction

Grass family *Poaceae* or *Gramineae* includes about 10000 species. This family is widespread in many climate zones, and it is of great economical significance because this grass is cultivated for food [1].

Furthermore, the grass is the basis for most of meadows in all natural areas of the country due to its high level of adaptability [2].

However, mechanisms of adaptation are barely studied. Most of the published works including the foreign ones [3-7] are dedicated to cultivated plants. There is a lack of information concerning wild plants, especially grass in forest-steppe areas. It means that research study of environmental and biological trends of grass development in the forest-steppe zone is still topical, and it will make a significant contribution to knowledge of grass adaptation to habitat [8-11].

The main structure of a grass specimen is a monocarpous sprout which goes through different phenological phases during its development. Grass specimen consists of various types of sprouts which differ in structure, lifespan, duration of development stages etc. [12]. The goal of our study is to receive more information on how grass sprouts of the forest-steppe zone in the Middle Volga area develop during the vegetation period. The target of our work is also to study development mechanisms for sprouts of different grass species during their vegetation.

Methodology

Reconnaissance and expeditions took a significant part of our work and were conducted throughout the whole forest-steppe zone of the

Middle Volga area during vegetation seasons in 2009-2013. We also provided fixed observations of various grass species, including sampling and determination of biometric parameters. Phenological research methods were implemented in the field (natural phytocenosis and agrocenosis). They included observations of development of different species in natural grass stands. Plant development was observed in different seasons and at different stations of seeded and natural pastures. We also cultivated plants in the field and in special vegetation pots with cameral treatment every 5-7 days and then determined their biometric parameters and described conditions of plants. During our experiments plants were extracted and described every 15 days (at the average of 30 exemplars of each species) with information saved for further detailed examination. During our work we based on methodology of I.G. Serebryakov [12], bud capacity is acc. to methodology of T.I. Serebryakova [5] and other scientists [13-15].

Main body

Grass sprout starts its vital activity with initiation of a bud of specific capacity inside a single seed or an axillary bud in the leaf base of a parent plant. Grass sprout ends its activity with die-off of all vegetative structures such as stem, leaves and roots. Sprout goes through various stages which have different morpho-physiological development. This development is determined by significant internal and external changes in life activity of the organism. Process of sprout development at different stages is controlled by its heritable background within the frameworks of certain homeostatics, when the sprout

reacts to changes in external environment, as well as by development of organism with the impact of internal (physiological, biochemical and energy) and external (environmental) factors [16, 17]. Taking it into account, we can say that grass sprouts develop as it is described in Table 1.

Table 1. Sprout development during vegetation

Development phase	Development stage	Conditionality of factors	
		internal factors	external factors
1	2	3	4
Vegetative period			
Preparatory tillering phase	Plumule formation (lateral bud of the sprout)	Free water loss, high concentration of C and N, accumulation of inhibitors such as ABA	Temperature, light, moisture and fertility of soil, CO ₂
Hidden tillering	Plumule sprouting (lateral bud of the sprout)	Water absorption, activation of carbohydrate-protein metabolism, inhibitors destruction, formation of gibberellins	Temperature, moisture, O ₂
	Formation of leaves of undifferentiated internodes	Photoccontrol, carbohydrate-protein metabolism and water metabolism, proportion of different types of growth substances	Quality of light, soil fertility, moisture, temperature, O ₂
	Formation of axillary buds	Carbohydrate-protein metabolism, cytokinin / auxin proportion shifts towards cytokinin	Soil fertility, moisture, temperature, CO ₂ , O ₂
	Formation of secondary root bases	Carbohydrate-protein metabolism, cytokinin / auxin proportion shifts towards auxin	Moisture, temperature, soil fertility, CO ₂ , O ₂
Viable tillering	Start of visible growth of axillary buds	Carbohydrate-protein metabolism, cytokinin accumulation, sharp reduction of auxin generation	Fertility and moisture of soil, temperature, CO ₂ , O ₂
Sprout elongation	Formation of extended aerial phytomers, apical and intercalary growth of all new structures	Intensive mitosis in areas of apical and intercalary meristems, protein-carbohydrate metabolism, increased activity of gibberellins	Temperature, light, moisture, soil fertility, CO ₂ , O ₂
	Intensive tillering of sprouts (formation of shortened, extended, stolon and stolon-shaped sprouts and rhizomes), growth of root mass	Protein-carbohydrate metabolism, stabilization of growth substances with high amount of gibberellins and cytokinins	Soil fertility, temperature, moisture, light, O ₂ , CO ₂
	Cessation of phytomer formation and sprout elongation	Photoccontrol, protein-carbohydrate metabolism, reduced activity of gibberellins and cytokinins within the complex of growth substances, increased amount of starch in storage organs	Light, moisture, fertility and temperature of soil, CO ₂
Generative period			
Formation of inflorescence	Differentiation of apical bud, inflorescence initiation	Photoccontrol, carbohydrate-protein-lipid metabolism, increased amount of cytokinins within the complex of growth substances	Light, temperature, soil fertility, moisture, trace elements, CO ₂ , O ₂
	Formation and growth of inflorescence	Photoccontrol, carbohydrate-protein-lipid metabolism, reduction of auxin amount	Light, moisture, soil fertility, trace elements, temperature, O ₂
Blooming	Development and ripening of floral structures	Carbohydrate-protein-lipid metabolism, water metabolism, dominance of gibberellic acid amidst growth substances	Light, temperature, moisture, soil fertility, trace elements, O ₂
	Blossom opening	Carbohydrate-protein-lipid metabolism, water metabolism, dominance of auxins amidst growth substances	Light, temperature, moisture, soil fertility
Seed formation	Ovary fertilization, formation of seeds	Carbohydrate-protein-lipid metabolism, water metabolism, evolution of growth substances towards the proportion "indoleacetic acid - cytokinins - gibberellins"	Light, temperature, moisture, soil fertility, trace elements
	Ripening of seeds	Carbohydrate-protein-lipid metabolism, water metabolism, increased amount of ABA within the complex of growth substances, seeds dehydration	Light, temperature, moisture, O ₂ , CO ₂
Sprout die-off	Transition of axillary buds to quiescence or to storage structures	Reduction of turgor and reduced water content in cells, carbohydrates prevail amidst organic substances, accumulation of lipids and phenols in quiescent organs	Temperature, moisture, light, CO ₂
	Die-off of aerenchyma sprout structures	Reduction of osmosis, hydrolysis of protein, carbohydrate and lipid, nutrients outflow to basal zone and to roots, partial plasmolysis of cells	Moisture, temperature, light, CO ₂
	Die-off of tillering area and secondary roots	Osmosis drop, cells dehydration, hydrolysis of organic substances, plasmolysis of cells, high level of inhibitors in quiescent organs	Moisture, temperature, CO ₂

Vegetative phases lay the foundation of the organism and prepare it for reproductive development. These phases depend on genetic properties of species, intensity of carbohydrate-

protein and water metabolisms and dynamism of growth substances on the one hand, and environmental conditions, such as light, temperature, soil fertility and moisture on the other.

Generative phases determine seed productivity of the organism and include differentiation of apical bud and inflorescence initiation. These phases are characterized by significant changes of carbohydrate-protein-lipid metabolism and growth substances, as well as by external conditions, such as light, temperature, soil fertility and moisture.

Analysis of different aspects of grass sprout life activity allowed us to draw a conclusion that its development at some stages is determined by mitotic activity of meristematic tissue cells (apical and intercalary meristems) and nutrients supply (trophism of organism) on the background of optimal temperature, light and moisture conditions. Changes in development conditions of grass specimens lead to boosts or delays in development of their sprouts, variation of biomass parameters or even elimination of certain phases etc.

Various types of sprouts develop unequally in different seasons and years of vegetation, creating a significant difference between grass species.

Vegetative period of all species finishes later in the seedling year than in the second and the following years. In relation to the latter it is obviously connected to the fact that vegetative structures grow earlier in comparison to sprouting of seeds in spring. Grass develops unequally in different years of vegetation and has specific rhythmicity of development throughout the year. All tropical grasses start to form extended and generative sprouts much earlier in the second year of vegetation. Grasses also differ in how they form short sprouts and in duration and intensity of this formation in different seasons.

The studied grasses can be divided into the following groups according to how they produce short sprouts: 1) plants forming short sprouts throughout the whole vegetative period (*Bromopsis inermis* (Leyss.) Holub, *Festuca orientalis* (Hack.) V. Krecz. et Bobrov, *Eragrostis suaveolens* A. Beck. ex Claus); 2) plants forming short sprouts in spring and autumn (*Dactylis glomerata* L., *Calamagrostis arundinacea* (L.) Roth.). Tropical grass forms the highest amount of short sprouts in spring, whereas boreal grass generates these sprouts mostly in spring and autumn. Period of generation of short sprouts by boreal grass is 3-4 months longer in comparison to the tropical grass. All tropical grasses start to form their sprouts 1-2 months later in the seedling year than in the following years. Percentage of extended sprouts of all grasses varies in different seasons and vegetation years. It is caused by biological specifics

of certain species. Seasons have different duration of the period when sprouts are extended. This period is longer in spring and shorter in summer and autumn. It impacts the contribution of different seasons to the amount of extended sprouts. Tallgrowing species have the highest percentage of extended sprouts, whereas shortgrowing species possess the lowest percentage.

All grasses form generative sprouts faster in the second year of vegetation. This feature is clearly visible for all tropical grasses and for a boreal grass *Bromopsis inermis*. Different species have unequal duration of generative sprout formation. Tropical grasses like *Eragrostis curvula* (Schrad.) Nees, *E. robusta* Stent, *Panicum antidotale* Retz., *Paspalum dilatatum* Poir start to form their generative sprouts quite early (end of May – beginning of June) in the second and in the following years of vegetation. Boreal grass has similar phase at the end of April, but the highest amount of generative sprouts is formed in May. *Eragrostis* Wolf has the longest formation period of generative sprouts among all tropical species, which lasts from the end of May till the beginning of November. *Panicum antidotale* and *Paspalum dilatatum* have the shorter period (end of May – beginning of October), *Sorghum alnum* Parodi obtains the shortest period from June to October [17].

All tropical grasses generate lateral aerial sprouts which mostly pass into extended sprouts and then into generative sprouts. Tallgrowing grasses *Panicum antidotale* and *Sorghum alnum* ramify more intensively in comparison to the faster vegetating species, such as *Paspalum dilatatum*. Low-growing forms *Paspalum dilatatum* and *Pennisetum orientale* Rich. have small amount of lateral aerial sprouts in their yield of fodder mass. Boreal grass does not form lateral aerial sprouts.

Seasonal development of grass and its yield capacity

Many researchers mention the strong correlation between productivity and rhythmicity of seasonal development of tropical and boreal grass [18]. Difference in productivity of grass in various seasons is caused by specifics of structures that different species have in different periods of vegetation. In spring such plants as *Eragrostis curvula* are able to form most of the short sprouts which are the main part of their yield. In summertime the plants form significant amount of generative sprouts and reduce the amount of short vegetative sprouts in comparison to springtime. The short sprouts start to prevail again in autumn. Boreal grass obtains quite a different aspect of grass stand in various seasons. Generative sprouts form the main

part of their yield in spring, with short sprouts dominating in summer. Our study confirms that differences between certain species make a significant impact on tops yield in different seasons.

Grasses are characterized by significant differences in terms of yield in different seasons. In the seedling year tropical grass forms most of its annual yield in summertime. This number varies from 67% by *Sorghum alnum* to 72% by *Eragrostis curvula* and *Panicum antidotale*. In the first year of vegetation boreal grass delivers the maximal yield in spring and autumn, and it brings the minimal yield in summer. If tropical grasses had been planted a few years ago, they accumulate the highest yield above 50% also in hot periods of year. Grasses of this group have the equal yield capacity in spring which is below 40% of their total annual yield. Regarding the second and the third years of vegetation, productivity of tropical grass is almost equal in all seasons. Difference in yield for this group in spring and autumn is obviously correlated to temperature variations in different seasons. For instance, all tropical species delivered rich harvest in spring 2010 due to high temperature in this period of time. In 2011 temperature was more moderate which caused significant reduction of yield. On the contrary, boreal grass developed poorly in early spring 2010 in conditions of high temperature, having the better yield in 2011 with more moderate temperatures. High temperature in summer 2010 resulted in rich yield of tropical grass, but caused depression for boreal grass. Analysis of development and dynamics of harvest for certain species shows that productivity depends significantly on rhythmicity of seasonal vegetation [19].

Development rhythmicity determines distribution of yield throughout vegetation phases and seasons, which is confirmed by our data received in Mordovia in 2011-2012 (fig. 1). *Alopecurus pratensis* L. and *Bromopsis inermis* are the widespread meadow grass species. In summer they generate 100% of their yield during stem elongation phase, whereas in autumn the maximal yield is developed during blooming and seed formation.

Difference in productivity dynamics of grass species is profound and determined by biological specifics of their development (fig. 2). For example, the stolon-forming grass *Agrostis stolonifera* L. forms all sprouts only in summer and has the highest photosynthetic activity of leaf apparatus during this season. It makes it possible for this species to increase the photosynthesis rate intensively and to achieve the highest level of photosynthesis by the age of 30 days. *Festuca rubra* and especially *Bromopsis inermis* have the delayed transition from one development phase to the other, but they are able to

increase their productivity gradually. *Agrostis stolonifera* rapidly gains in yield during the first period of development which lasts up to 30 days, but later the effectiveness of leaf apparatus goes down. Other species have a different situation. Smooth increase in productivity of the leaf apparatus at the beginning changes into gradual reduction of productivity at the end.

It is to be noticed that maximal productivity is synchronous with optimal development of the main sprout types. For instance, *Agrostis stolonifera* has the highest daily productivity at the age of 30 days and generates all types of sprouts, including short and extended vegetative sprouts, stolons and stolon-shaped sprouts, lateral aerial sprouts and generative sprouts. *Bromopsis inermis* has similar period, when vegetative sprouts achieve about 85% of normal height before bottom leaves start to dry up.

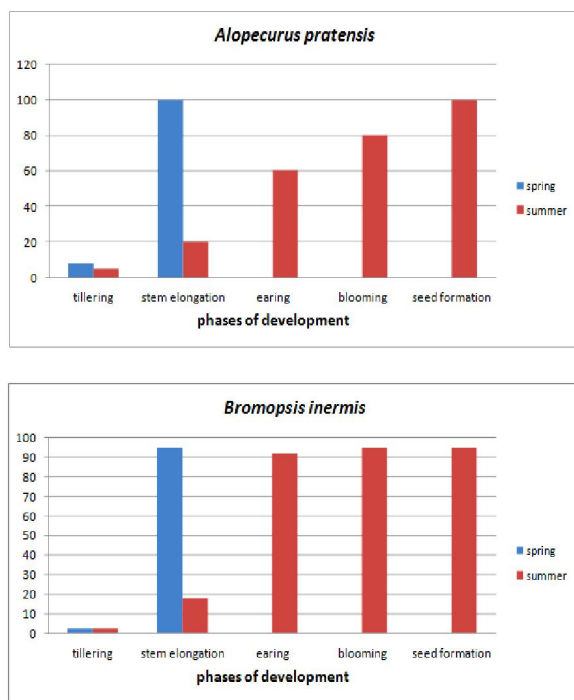


Figure 1. Development of tops yield by certain grass species (Republic of Mordovia, 2011-2012), in percents to the maximal yield

Rhythmicity of grass development determines how yield is allocated through all seasons of the year, and it is confirmed by our experiments at fertilized irrigation sites (table 2).

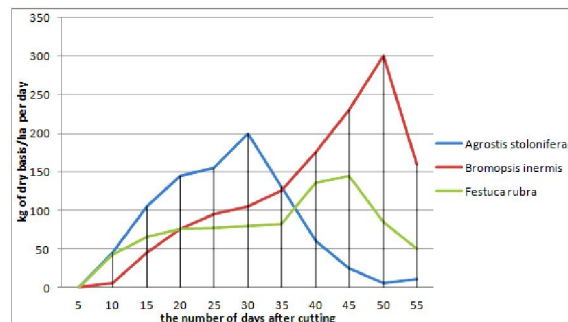


Figure 2. Dynamics of tops after cutting in summertime (Republic of Mordovia, 2009)

Table 2. Yield capacity of grass in different seasons (Republic of Mordovia, 2011-2012)

Species	Annual yield, g/ha of dry basis, $(\bar{X} \pm \delta)$	Yield in seasons, %	
		summer	autumn
<i>Dactylis glomerata</i>	19.6 ± 0.82	66	34
<i>Alopecurus pratensis</i>	11.6 ± 0.45	56	44
<i>Agrostis stolonifera</i>	16.1 ± 0.68	74	26
<i>Schedonorus pratensis</i>	12.9 ± 0.61	57	43
<i>Festuca rubra</i>	17.8 ± 0.74	67	33
<i>Bromopsis inermis</i>	25.3 ± 1.09	63	37

Average long-term productivity of some grass species is lower in summer than in spring. This is typical for *Agrostis stolonifera* which forms almost nothing but short sprouts in dry season, or *Bromopsis inermis* which rapidly goes through vegetative period and then reduces sprout formation and yield capacity. *Schedonorus pratensis* and *Alopecurus pratensis* are more labile to conditions of certain seasons.

Grass species from the Middle Volga area have certain level of rhythmicity in process of tops formation. It is caused by temperature conditions. The main part of their harvest is formed in summer with hot temperatures and high moisture (fig. 3). Thermophilic grass with C₄ photosynthesis has the greater biomass in summertime, whereas the temperate species such as *Bromopsis*, *Dactylis glomerata*, *Lolium* etc. receive more biomass in late

autumn and in winter. Grasses with C₄ photosynthesis accumulate their maximal harvest in July and August or in the second half of June – the first half of August if spring comes early. Grasses generate their yield in early spring and at the beginning of summer, with their productivity going down rapidly after this period. It happens due to their photosynthetic apparatus with C₄ fixation of CO₂, unadapted to intensive activity in hot temperature and intense insolation conditions. In such conditions species of this group have to spend a lot of energy for photorespiration, and they stop tillering and start to form more extended sprouts.

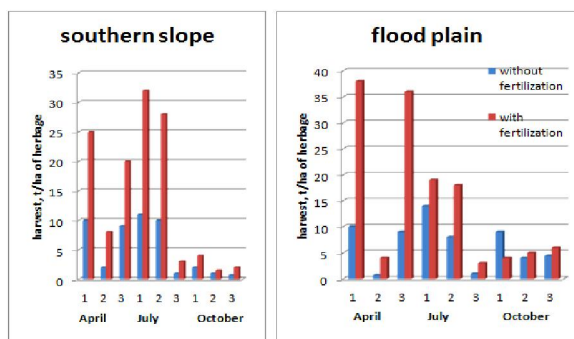


Figure 3. Grass productivity in coastal zone of the river Issa (Insarskiy district, Republic of Mordovia, 2011-2012)

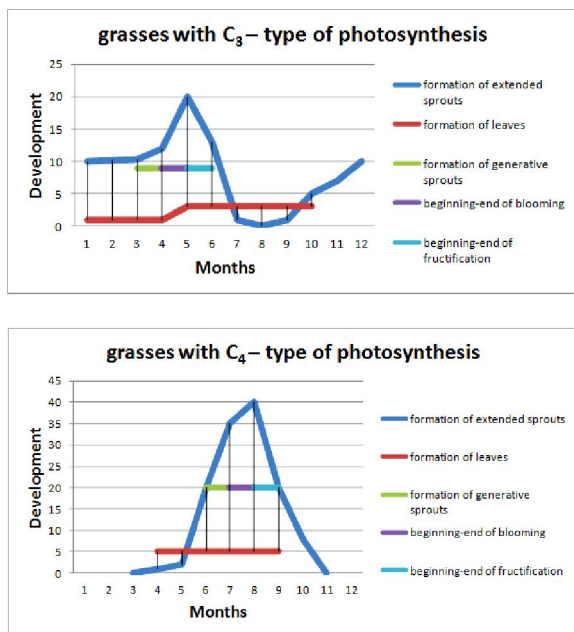


Figure 4. Grass development in coastal zone of the river Issa (Mordovia, 2011)

Fertilization gives a rapid boost to development and raises productivity of grass, especially of grass species with C₄ type of

photosynthesis. It increases their amount in grass stands by several times in comparison to grasses with C₃ type of photosynthesis (fig. 4, fig. 5).

Conclusions

Development of grass sprout is 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 are substantially dependant on environmental conditions.

Tropical and boreal grasses develop certain types of sprouts in different ways and have unequal duration of this development process in various seasons and years of vegetation.

Species have different rhythmicity of development. This rhythmicity determines productivity of grasses in different seasons and reflects their evolution path in certain climate conditions. Most of the species have active summer vegetation. If conditions are changed (irrigation, fertilization), it impacts vegetation phases and duration of certain periods of development, but it does not change the overall picture of phenological spectra.

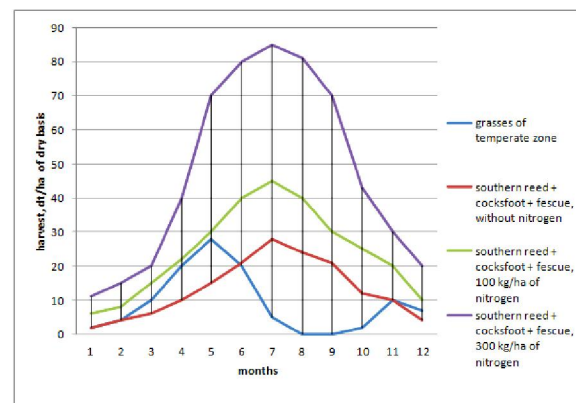


Figure 5. Pasture harvest in coastal zone of the river Issa (Mordovia, 2011)

Credits

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