
**SOIL
BIOLOGY**

Daily Dynamics of Cellulase Activity in Arable Soils Depending on Management Practices

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Abstract—The daily dynamics of cellulase activity was studied during 27 days by the cellophane membrane method on soils managed using the conventional high-input farming system (application of mineral fertilizers and pesticides) and the biological conservation farming system (application of organic fertilizers alone) in a microfield experiment. The regular oscillatory dynamics of the cellulase activity were revealed and confirmed by the harmonic (Fourier) analysis. The oscillatory dynamics of the cellulase activity had a self-oscillatory nature and was not directly caused by the disturbing impacts of both the uncontrolled (natural) changes in the temperature and moisture (rainfall) and the controlled ones (the application of different fertilizers). The disturbing impacts affected the oscillation amplitude of the cellulase activity but not the frequency (periods) of the oscillations. The periodic oscillations of the cellulase activity were more significant in the soil under the high-input management compared to the soil under the biological farming system.

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INTRODUCTION

Studies of the daily dynamics of the copiotrophic and oligotrophic bacteria in the rhizosphere and non-rhizosphere soil showed that both trophic groups displayed wave-like fluctuations in their development [16, 17, 22, 23, 25]. It should be noted that the fluctuating dynamics of prokaryotes (bacteria and actinomycetes) and of micromycetes in soils and other habitats was previously described [6, 7, 11, 12]. The most regular variations in the number of microorganisms and their activity (the CO₂ emission from soils) are revealed after disturbing natural or anthropogenic impacts: under an abrupt change in the soil moisture (drying–wetting), mechanical impacts, and the application of organic and inorganic substrates [1–5, 8, 20]. These variations are due to the cycles of growth and dying of the microorganisms caused by the temporary limiting of the microbial growth by the substrate [16, 17, 22, 23, 28]. It was supposed that the quantitative parameters of this oscillatory development of microorganisms (the periods (frequencies), amplitudes, and phases of waves) can be used for the comparative characterization of soil ecosystems [17, 24, 25].

The oscillatory temporal and spatial dynamics of microorganisms was heretofore revealed by the daily measurement of the number of organisms, the counting of colony-forming units (CFUs) on media, or the microscopic counting of stained cells in soil suspensions [6, 7, 11, 12, 22]. Sufficiently accurate and rapid methods have been developed by now for the instrumental registration of some functional processes of microorganisms in nature, which significantly exceed in efficiency the laborious counting of the number of microorganisms [19].

The cellophane membrane method is an efficient method for the determination of the soil cellulase activity under laboratory and field conditions [10]. The method can rapidly assess the cellulase activity in any ecotope and express the results in standard units of cellulase activity [13–15, 18, 21].

In nature, the decomposition of cellulose and many other processes are subjected to the effect of different factors: natural (temperature and precipitation) and agrotechnical ones, including different tillage practices, etc. In this context, it was important to thoroughly study the dynamics of the cellulase activity under the use of

conventional disturbing agrotechnical measures such as different tillage practices, the application of different fertilizers, and the growing of different agricultural crops.

The aim of this work was to study the daily cellulase activity in differently cultivated soils with different disturbing impacts and growing of different agricultural crops.

EXPERIMENTAL

Soil management. The cellulase activity was determined within the framework of a long-term experiment on measuring the resilience of microbial communities to disturbing factors and C and N sequestration in differently cultivated soils. The experimental plots were established on the territory of the Institute of Physicochemical and Biological Problems of Soil Science of the Russian Academy of Sciences (Pushchino, Moscow oblast) in 2005. The soil used in the experiment during the last 15 years was under a fallow meadow. Fifteen plots $2 \times 2 \text{ m}^2$ in size were prepared; 12 of them were managed, and 3 plots were used as the control. Six experimental plots were managed using the conventional high-input farming system (HIFS), including the application of mineral fertilizers and herbicide 2,4-D. The other six plots were managed using an environmentally safe, or biological farming system (BFS), with the application of organic fertilizers alone (cattle manure) from a biodynamic farm. In each farming system (the HIFS and BFS), three plots were sown with sugar beets (treatments 1, 2) and the other three plots were sown with mixed forage grasses (treatments 3, 4). The replicate plots were selected in accordance with the requirements for statistical randomization. The following treatments were used: (1) the high-input system—mineral fertilizers and 2,4-D for sugar beets; (2) the biological farming system—organic fertilizers for sugar beets; (3) the high-input system—mineral fertilizers and 2,4-D for forage grass; (4) the biological farming system—organic fertilizers for forage grass; and (5) natural meadow.

The soil was sampled in all the plots with a soil auger from a depth of 0–20 cm every morning for 27 days. In the managed plots, soil samples were taken between the plant rows; in the meadow, the soil was sampled in a random manner after the local removal of the grass. The soil temperature and the precipitation were measured daily for the experimental plots. The cellulase activity was determined in a laboratory for soil samples taken only from two plots of each treatment. The soil was sieved through a 3-mm sieve, and the water content was determined by drying at 105°C for 8 h.

Disturbing impacts. The daily dynamics of the cellulase activity were determined in the spring (May–June) and fall (September) of 2006.

In the spring, the experimental HIFS plots (treatments 1 and 3) were subjected to a disturbing impact

(the application of mineral fertilizers: superphosphate, potassium sulfate, and ammonium nitrate at a rate of 200 kg/ha) 8 days after the beginning of the soil sampling. To eliminate weeds, 2,4-D was applied to these plots at a rate of 3 kg/ha. Organic fertilizers (manure at a rate of 50 t/ha) were applied to the BFS plots (treatments 2 and 4). As was noted above, treatment 5 was an undisturbed system (without any fertilizer or pesticide).

In the fall, the plants were removed from all the plots on the fourth day after the beginning of the soil sampling, and the crushed above-ground parts of the plants were incorporated into the soil of these plots. On the natural meadow plots, the grass was also cut, comminuted, and uniformly distributed over the soil surface. Thus, the experimental disturbing impact in the fall was the application of freshly cut plant residues.

Along with these controlled disturbing impacts, the plots were subjected to uncontrolled impacts (changes in the temperature and moisture due to rainfall).

The determination of the cellulase activity. The cellulase activity was determined by the cellophane membrane method, which involved the recording of the decrease in the cellophane membrane rupture strength after the incubation of the membrane on the soil [10, 21]. The membranes were fixed with a rubber ring on the neck of a vial without a bottom. The soil was put into a Petri dish; 12 vials with cellophane membranes were placed on the compacted soil surface and incubated for 49–96 h. The incubation time was selected in such a way that the decrease in the rupture pressure was statistically significant ($P = 0.10$). The membrane rupture pressure was then measured. The results obtained in the units of the rupture pressure (atm) were converted using a calibration curve into standard units of the cellulase activity (μg of reducing sugars in 1 ml of solution per 1 h of the reaction, $\mu\text{g}/(\text{ml h})$) [21]. The experiments were conducted in duplicate in a laboratory at constant humidity (85%) and 20°C .

Isolation and identification of the predominant micromycetes. The micromycetes from the cellophane membranes were isolated by transferring mycelium fragments with a sterile preparation needle onto the Czapek–Dox nutrient medium or by distributing membrane fragments overgrown by mycelium on the same medium. The dishes were incubated for 5 days. The grown colonies were identified by conventional methods using the corresponding guides.

Statistical analysis. Statistically significant oscillations of the cellulase activity were revealed by the harmonic (Fourier) analysis [9, 24, 25]. Data filtration and smoothing were performed before the harmonic analysis. Only the predominant statistically reliably harmonics exceeding the fluctuations due to noise are shown on the graphs. To reveal the possible effect of the variations of the temperature and soil moisture, a cross-correlation analysis of the corresponding data series was performed.

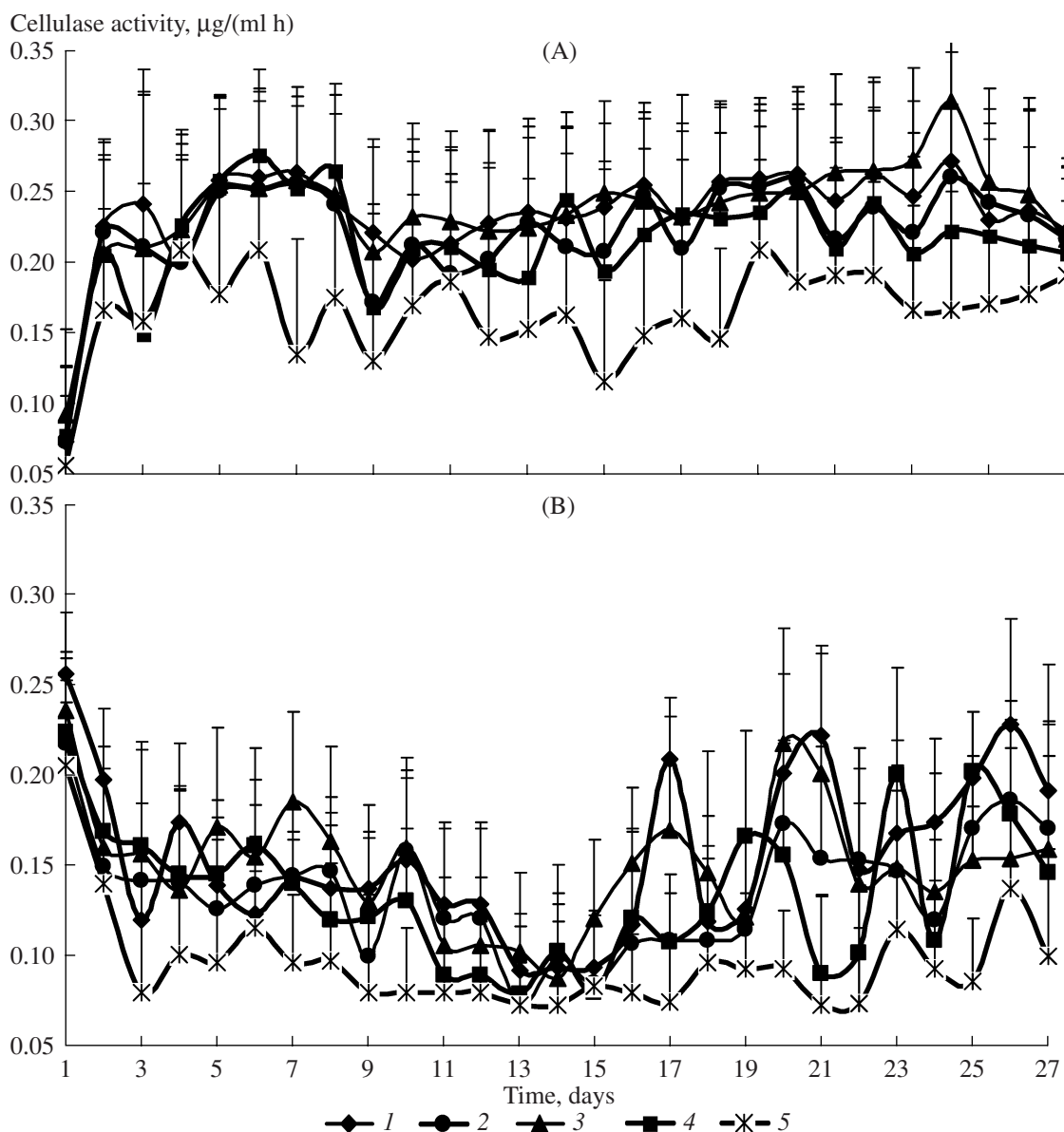


Fig. 1. Daily dynamics of the cellulase activity on soil plots managed using the high-input farming system (HIFS) and the biological farming system (BFS) in (A) May–June and (B) September of 2006. Treatments: (1) HIFS, beets; (2) BFS, beets; (3) HIFS, forage grass; (4) BFS, forage grass; (5) natural meadow.

RESULTS AND DISCUSSION

The dynamics of the cellulase activity during the spring and fall seasons. The daily dynamics of the cellulase activity was monitored in the spring (May–June) and fall (September) of 2006 (Figs. 1A, 1B). The dynamics of the cellulase activity in the soil were of a fluctuating character. In the spring, several maximums corresponding to 3, 6, 10, 16, 20, and 24 days of the experiment could be visually recognized in the dynamics of the cellulase activity. The comparison of the cellulase activities of the differently cultivated plots under the different crops showed that the lowest cellulase activity (apart from its value on the first day) was

observed in the natural ecosystem (meadow): 0.12–0.21 μg reducing sug./ (ml h) . The cellulase activity in the soils of the HIFS and BFS plots was slightly higher: 0.17 to 0.27–0.31 μg reducing sug./ (ml h) .

The application of organic and mineral fertilizers to the corresponding plots eight days after the beginning of the experiment decreased the cellulase activity, which is an interesting and hard to explain fact.

It can be supposed that the hydrothermal conditions of the environment affecting the dynamics of the microbiological processes in the soil could have also affected the dynamics of the cellulase activity, although the latter was determined in a laboratory at room temperature.

Table 1. Characteristics of significant harmonics ($P \leq 0.1$) revealed by the harmonic (Fourier) analysis of the daily dynamics of the biotic (cellulase activity, μg reducing sug./ml h) and abiotic (soil moisture and temperature) variables in the soil managed using the HIFS and BFS under different vegetation in May–June of 2006

Variable	G	R	ϕ , day	T , day	Frequency	ρ_k^2 , %	F	F_k
Soil T , °C	2	0.943	4.810	13	0.077	49.7	6.21	2.53
	3	0.668	-0.259	8.67	0.115	24.9	3.12	2.53
Treatment 1 (HIFS, beet)								
Cellulase activity, μg reducing sug./ml h	2	0.014	1.849	13	0.077	23.3	2.91	2.53
Soil moisture, %	2	1.104	1.301	13	0.077	37.8	4.72	2.53
	4	0.877	0.376	6.5	0.154	23.8	2.98	2.53
Treatment 2 (BFS, beet)								
Cellulase activity, μg reducing sug./ml h*	2	0.013	1.804	13	0.077	24.9	3.11	2.53
Soil moisture, %	2	0.720	2.391	13	0.077	23.7	2.97	2.53
	4	0.702	0.997	6.5	0.154	22.6	2.82	2.53
Treatment 3 (HIFS, forage grass)								
Cellulase activity, μg reducing sug./ml h*	3	0.014	2.803	8.67	0.115	33.6	4.19	2.53
Soil moisture, %	2	0.759	1.423	13	0.077	26.2	3.28	2.53
	3	0.748	3.990	8.67	0.115	25.5	3.18	2.53
Treatment 4 (BFS, forage grass)								
Cellulase activity, μg reducing sug./ml h*	2	0.015	2.231	13	0.077	41.8	5.22	2.53
Soil moisture, %	4	0.955	1.178	6.5	0.154	33.8	4.22	2.53
	6	0.750	1.827	4.33	0.231	20.9	2.61	2.53
Treatment 5 (natural meadow)								
Cellulase activity, μg reducing sug./ml h*	2	0.010	1.948	13	0.077	22.3	2.79	2.53
	3	0.014	0.851	8.67	0.115	41.0	5.13	2.53
Soil moisture, %	4	0.605	2.430	6.5	0.155	27.2	3.40	2.53
	5	0.625	0.897	5.2	0.192	29.0	3.62	2.53

Note: (G) harmonic number; (R) fluctuation amplitude, $\mu\text{g}/(\text{ml h})$; (T) period; (ϕ) phase determining the time of the first maximum harmonic value; (ρ_k^2) contribution to the variance, %; (F) Fisher F-ratio; (F_k) error set at a level of 10%.

It can also be supposed that the dynamics of the cellulase activity could have been affected by other disturbing factors: the application of the fertilizers and the incorporation of the fresh above-ground plant biomass.

The harmonic analysis of the cellulase activity data (May–June, 2006) revealed only one significant harmonic for each treatment, except for the natural meadow ecosystem, where two harmonics were found (Fig. 2A (1–5), Table 1). These were usually second-order harmonics, except for the treatment with HIFS, where a third-order harmonic was revealed under the forage grass and second- and third-order harmonics were revealed under the natural meadow. The equal harmonics of the corresponding orders had similar amplitudes, periods, etc. It may be stated with some assumptions that each statistically significant harmonic reflects the existence and functioning of a microbial group significant for the process studied in the soil analyzed. Hence, the dominating microbial populations responsible for the cellulase activity in the differently cultivated soils were similar in their functional kinetic properties. At the same time, the harmonic analysis also

revealed other, less significant harmonics reflecting the activity of other, less significant cellulolytic groups that also contributed to the cellulase activity, although their contributions were low and the revealed harmonics were statistically insignificant. Therefore, they are not listed in the table of the harmonic analysis parameters. Our results show that, even after the soil was managed using the different technologies with the growing of the different crops for two years, it still significantly retained microbial populations similar in their functional kinetic properties (primarily in the growth and dying rates and apparently in the properties of the cellulolytic enzymes). At the same time, a strong succession process was already induced in the managed soils. This was evidenced by the number of harmonics and their parameters in the natural meadow ecosystem, where two (rather than one) dominant populations responsible for the cellulase activity in these plots were revealed.

Up to six peaks were visually identified in the dynamics of the cellulase activity, but the harmonic analysis revealed only two or three peaks. This differ-

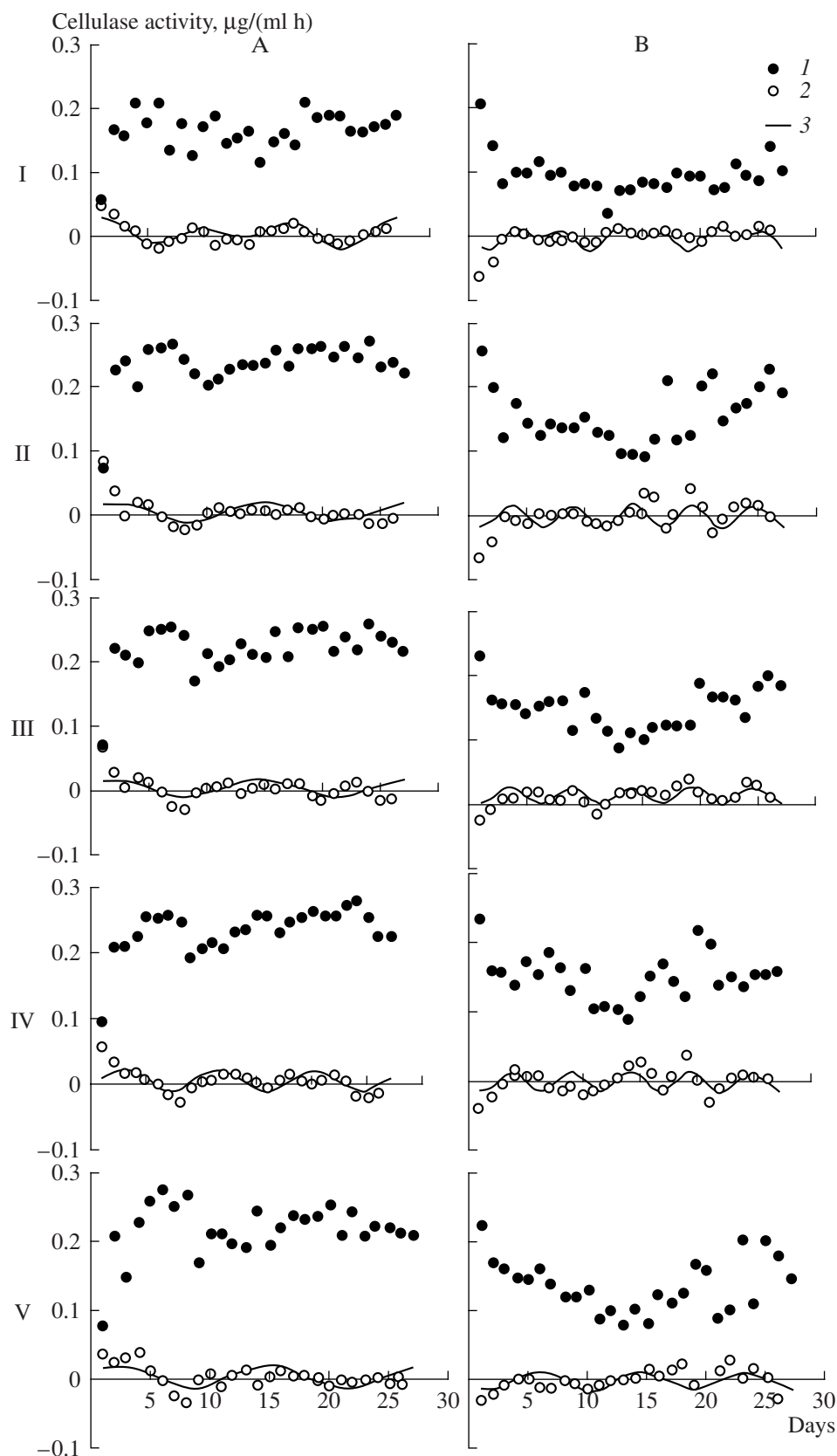


Fig. 2. Harmonic analysis of the daily dynamics of the cellulase activity on differently cultivated soils in (A) May–June and (B) September of 2006. Treatments: (I) HIFS, beets; (II) BFS, beets; (III) HIFS, forage grass; (IV) BFS, forage grass and (V) natural meadow; (1) experimental data; (2) filtered and smoothed experimental data; (3) harmonics.

Table 2. Characteristics of significant harmonics ($P \leq 0.1$) revealed by the harmonic (Fourier) analysis of the daily dynamics of the biotic (cellulase activity, μg reducing sug./ (ml h)) and abiotic (soil moisture and temperature) variables in the soil managed using the HIFS and BFS under different vegetation in September of 2006

Variable	G	R	ϕ , day	T , day	Frequency	ρ_k^2 , %	F	F_k
Soil T , °C	3	0.7	-0.29	8.67	0.115	26.8	3.35	2.53
	5	0.8	-0.53	5.2	0.192	31.3	3.91	2.53
Precipitation, mm	2	0.50	0.10	13	0.077	20.5	2.56	2.53
Treatment 1 (HIFS, beet)								
Cellulase activity	5	0.016	3.77	5.2	0.192	25.6	3.20	2.53
Soil moisture %	1	0.66	-1.81	26	0.039	24.4	3.05	2.53
Treatment 2 (BFS, beet)								
Cellulase activity	5	0.012	3.69	5.2	0.192	32.0	4.00	2.53
Soil moisture %	1	0.66	-1.61	26	0.039	38.9	4.86	2.53
	7	0.51	-0.42	3.71	0.269	23.5	2.94	2.53
Treatment 3 (HIFS, forage grass)								
Cellulase activity	5	0.013	3.80	5.2	0.192	28.8	3.60	2.53
Soil moisture %	1	0.72	-1.44	26	0.039	22.6	2.82	2.53
	7	0.73	-0.47	3.71	0.269	23.4	2.93	2.53
Treatment 4 (BFS, forage grass)								
Cellulase activity	3	0.011	5.90	8.67	0.115	23.6	2.95	2.53
Soil moisture %	6	0.80	-0.74	4.33	0.231	24.2	3.03	2.53
Treatment 5 (natural meadow)								
Cellulase activity	3	0.011	5.66	8.67	0.115	22.6	2.83	2.53
	6	0.011	-0.44	4.33	0.231	23.0	2.88	2.53
Soil moisture %	3	0.513	-0.17	8.67	0.115	32.4	4.06	2.53
	7	0.454	-0.24	3.71	0.269	25.5	3.19	2.53

ence was indicative of the presence of numerous and usually unregistered (unnoticed) disturbing impacts. In this context, it was interesting and important to analyze the parameters of the harmonics revealed in the analysis of the soil moisture and temperature, which are the most obvious disturbing factors.

The harmonic analysis of the soil moisture and temperature dynamics always revealed at least two harmonics, usually of higher orders up to the sixth order. The differences in the number and orders of the significant harmonics identified for the cellulase activity and for the dynamics of the moisture and temperature indicated the different nature of the oscillations of the latter parameters compared to the oscillations of the cellulase activity, as well as their mutual independence.

Thus, the harmonic analysis permitted us to discriminate the nature of the oscillatory dynamics of the biotic component from that of the abiotic factors. The latter factors obviously affect the biotic component, and researchers frequently recognize them as the major causal factors of the oscillatory dynamics of biotic components, which contradicts the results of our experiments. The contribution of the abiotic factors to the variance of the significant harmonics was 21 to 38% for the moisture and 25–50% for the temperature. The con-

tribution of the significant harmonics to the variance of the cellulase activity was lower and varied from 23% for the HIFS (beets) to 42% for the BFS (grass). In the meadow soil, the succession processes proceeded more slowly, and it could be supposed that at least two relatively strong cellulolytic populations were therefore developed with the total contribution of the two significant harmonics being 63.3%.

The daily dynamics of the cellulase activity in the soil samples taken in the fall of 2006 revealed more significant differences between the experimental treatments, although the total oscillation amplitude of the cellulase activity was smaller than in the spring (Figs. 1B, 2B; Table 2).

In the fall, peaks of increasing cellulase activity were noted on the 4th, 7th, 10th, 17th, 20th, and 26th days, which largely coincided with the dynamics of the cellulase activity in the spring. At the same time, a decrease in the cellulase activity was observed after the application of the plant residues, which was followed by its increase 13 days after the beginning of the determination of the cellulase activity. The value of the cellulase activity varied from 0.09 to 0.23 $\mu\text{g}/(\text{ml h})$ in the soil of the managed plots and from -0.03 to 0.14 $\mu\text{g}/(\text{ml h})$ in the soil under the meadow. The decrease in the cellulase

activity observed between the 5th and 14th days in the fall could be related not only to the application of the fresh plant residues but also to the significant decrease in the temperature during this period (to +4°C on some nights).

The harmonic analysis of the daily dynamics of the cellulase activity in the fall also revealed significant harmonics, but they were of higher orders compared to the spring. Only one significant harmonic was found in the HIFS (beets, forage grass) treatments and one in the BFS (beets) treatment, and they were of the fifth order. In the BFS (forage grass) treatment, one harmonic of the third order was found; two harmonics were found for the natural meadow, as in the spring period, but they were of the third and sixth orders. The revealed tendencies were unexpected and hardly interpretable. In the fall, after the incorporation of the plant residues into the soil and at low temperatures, one significant population of cellulolytics was mainly predominant, as in the spring. However, this population was characterized by shorter periods of growth and dying (4–5 days) but similar amplitudes (0.011–0.016 µg/(ml h)) as compared to those revealed in the spring; the contributions to the variance were also similar (23–32%).

In the fall, significant harmonics were also revealed in the oscillations of the abiotic factors (the temperature and soil moisture). These harmonics differed in their order from those revealed in the spring. For the soil moisture, harmonics of the first order were revealed in three treatments and were significant but of little information value for the analysis. In both cases (with and without consideration of the contribution of the first-order harmonics), the variances of the moisture and temperature were higher or lower than the variance of the cellulase activity in this season. Hence, the differences in the oscillatory dynamics of the biotic component and the abiotic factors were of nonrandom nature.

The possible correlation of the temperature and moisture variations with the oscillatory dynamics of the cellulase activity was tested using the cross-correlation analysis by calculating the correlation coefficients R of the following variables: the cellulase activity, the temperature, and the soil moisture (Table 3). It was shown that significant positive correlations mainly existed between the cellulase activity and the soil moisture in the spring. However, the correlation was reliably negative (–0.528) for the HIFS (forage grass) and insignificant for the natural meadow ecosystem. In all the cases, a significant negative correlation was found between the cellulase activity and the precipitation.

A correlation between the cellulase activity and the soil temperature was always observed with a significant time lag always equal to 6 days, although rainfall events were rare and irregular.

A significant positive correlation was also observed between the cellulase activity, the soil moisture, the temperature, and the precipitation in the fall (Table 3). A significant negative correlation was found between

Table 3. Significant cross-correlation functions (CCFs) ($P < 0.05$) for the comparable data on the cellulase activity and the soil moisture and temperature for the plots managed using the HIFS and BFS in May–June and September of 2006

Parameter	June		September	
	CCF	lag	CCF	lag
HIFS, beet				
Soil sample moisture	0.447	1	0.510	6
Soil T	0.434	3	0.416	2
Precipitation	–0.463	6	0.496	3
BFS, beet				
Soil sample moisture	0.559	1	0.510	6
Soil T	0.484	3	0.416	2
Precipitation	–0.544	6	0.496	3
HIFS, forage grass				
Soil sample moisture	–0.528	6	0.491	7
Soil T	*		0.536	2
Precipitation	–0.481	6	*	
BFS, forage grass				
Soil sample moisture	0.411	1	0.525	4
Soil T	–0.500	9	–0.600	–10
Precipitation	–0.471	6	0.411	2
Natural meadow				
Soil sample moisture	*		*	
Soil T	*		0.555	4
Precipitation	–0.497	6	0.664	3

Notes: * (CCF) cross-correlation function; (lag) time period, days. No statistically significant coefficient was revealed.

the cellulase activity and the soil temperature in BFS treatment 4 (forage grass). In distinction from the spring, a positive correlation between the cellulase activity and the precipitation was always found in the fall. Another distinction of the spring period was that a significant positive correlation between the cellulase activity and the other variables was found only with regard for lag periods (shifts), frequently of 7 days.

The correlation analysis used for revealing the possible effect of the hydrothermal parameters of the soil on the oscillatory dynamic of the cellulase activity showed that these relationships were uncertain and even illogical in some cases. In other words, the observed spontaneous changes in the soil moisture and temperature could not be considered as decisive reasons for the oscillatory dynamics of the cellulase activity in the soil, and their effect stayed within the conven-

tional temperature and moisture dependences of the biological objects.

The response of the cellulase activity to the different disturbing impacts. The microbial community responds to the application of a substrate to the soil or another active disturbing impact by conspicuous variations in the abundance and activity of the community components [2, 3, 4, 17, 18, 27, 28]. The application of mineral and organic fertilizers resulted in a temporary decrease of the cellulase activity. At the end of the monthly period, the cellulase activity was restored to the initial level or even exceeded it. Our studies showed that the application of the fertilizers or plant residues had a suppressing but transient effect on the cellulase activity. The harmonic analysis revealed no significant differences in the cellulase activity among the experimental treatments.

The dynamics of the cellulase activity in the soil were similar under the beets and grass, and the differences were observed only in terms of the amplitudes. In the spring, the dynamics of the cellulase activity in the HIFS plots were more smoothed, which could be related to the stable supply of the cellulolytic community with mineral components. A more pronounced oscillatory character of the changes in the cellulase activity was observed in the soil of the BFS (beets) treatment, which could be due to the growth and dying of the cellulolytic community because of the periodic lack of mineral components in the soil.

On the whole, the dynamics of the cellulase activity in the managed soils were higher compared to the natural meadow. The revealed tendency is quite logical, because the decomposition of organic matter is more intensive in managed soils [26].

The analysis of the dominant micromycetes on the cellophane membranes. In the early period (the first 3–5 days of the observations), *Fusarium oxysporum*, *Trichoderma koningii*, and *T. avatavirida* were the predominant micromycetes. Towards the end of the observation period, *Penicillium* sp. group 1 and *Mucor* sp. were mainly found; i.e., a pronounced change of the dominating micromycetes occurred.

CONCLUSIONS

The daily determination of the cellulase activity in the differently cultivated soils revealed the regular oscillatory dynamics of this activity. The significance of the regular oscillatory dynamics of the cellulase activity in the differently cultivated soils was confirmed by the harmonic (Fourier) analysis. The values of the cellulase activity, as well as the parameters of the harmonics, in the differently cultivated soils in the spring differed from those in the fall.

The disturbing effects, both the uncontrolled (the changes in the temperature and moisture (precipitation)) and the controlled (the application of the fertilizers), are important for the oscillatory dynamics but are

not decisive factors. Although the conventional correlation analysis shows significant correlations between the cellulase activity and the soil moisture and temperature dynamics, the logic of such correlations is, obviously, only formal.

The oscillatory changes in the cellulase activity were accompanied by succession changes in the dominant micromycetal species. It can be suggested that more significant differences will be accumulated between the microbial communities and the physicochemical properties of the soils under the more lasting application of different land use systems (HIFS and BFS). It can be supposed that the long-term use of the organic farming system will result in a decrease in the cellulase activity and, hence, the accumulation of organic matter in the soil.

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