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SOIL BIOLOGY

Determination of Root and Microbial Contributions to the CO_2 Emission from Soil by the Substrate-Induced Respiration Method

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Abstract—The contributions of root and microbial respiration to the CO_2 emission from the surface of gray forest and soddy-podzolic soils under meadow and forest vegetation were determined in field and laboratory experiments. In the field, a new modification of the substrate-induced respiration (SIR) method was applied. According to this method, the contribution of root respiration was estimated at 41–50% for meadow cenoses and 33% for forest cenoses; similar values were obtained in the course of separate incubation of roots and soil in laboratory (42–57% and 29–32%, respectively) and with the use of the laboratory version of the SIR method (35–40% and 21–31%, respectively). The analysis of difference between the values of root respiration and microbial respiration obtained by the field and laboratory methods for the same experimental plots and the comparison of advantages and disadvantages of these methods made it possible to outline the ways for the further improvement of the field version of the SIR method.

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INTRODUCTION

The reduction of carbon dioxide emission to the atmosphere is one of most important challenges of the international community claimed in the Kyoto Protocol. The procedures for increasing the CO_2 fixation o in terrestrial ecosystems are an important component of measures on mitigating global climate changes, the because CO_2 emission from the soil surface is the second in magnitude flux of carbon in terrestrial ecosystems [19, 20, 23]. The mathematical simulation of the processes of carbon cycle serves as the theoretical basis for these measures. In turn, it is based on the experimental data on the components of carbon cycle. In particular, its simulation for terrestrial ecosystems is impossible without reliable data on the contribution of root respiration (RR) and microbial respiration (MR) to the total emission of CO_2 from the soil surface [13, 19]. These components of the CO_2 flux from soils have different sensitivities to temperature, moisture, and the composition of soil organic matter (SOM) [2, 9, 17, 22, 26]. Experimental data on RR and MR make it possible to predict changes in the CO_2 emission from the soil surface under the influence of biotic and abiotic factors and assess carbon fluxes at global and regional levels [22, 26].

Isotopic and nonisotopic methods are used to determine root and microbial respirations separately. Isotopic methods include artificial labeling of plants and soil in the air with carbon dioxide enriched in stable ^{13}C or radioactive ^{14}C isotopes, or the application of labeled organic substances into the soil. This group of methods makes it possible not only to assess the contributions of root and microbial respiration but also to estimate the fluxes of photoassimilated carbon in the rhizosphere (in the form of root exudates) and to determine the priming effect of root exudates relative to the SOM [1]. However, the use of isotopic methods in the field is restricted by the need in expensive sources of CO_2 and complex mass-spectrometric equipment (in the experiments with ^{13}C) and be the danger of radioactive pollution of the environment (in the experiments with ^{14}C) [11, 16]. Contrary to these methods, nonisotope methods for separation of root and microbial respirations do not require expensive equipment and cannot cause the environmental pollution. The impossibility to take into account the priming effect and the difficulties in separating the respiration of rhizosphere microorganisms (as a component of MR) and root respiration proper are the main disadvantages of nonisotopic methods [1]. Both isotopic and nonisotopic methods are connected with significant disturbances in the soil–microorganisms–plant system, i.e., with changes in the temperature and moisture regimes of soils, general soil disturbances, and mechanical injuries of roots [13, 16].

None of these methods has a universal character. Disadvantages of any particular method restrict its application and complicate the comparison of root and microbial respirations obtained with different methods in different ecosystems. The absence of a

reliable, cheap, and not time-consuming method for separating CO_2 fluxes from the soil under natural field conditions (with minimum disturbances of soils and roots) should be stressed.

Our choice of appropriate methodology for its testing in the field was based on the results of previous experiments [4, 28]. We compared the contributions of RR and MR to the CO_2 emission from the surface of gray forest soils in two ecosystems studied with the use of nonisotopic *laboratory methods* of incubation (the component integration method)and substrate-induced respiration. The component integration (CI) method consists of the separate determination of respiration from soil samples with and without roots, and both samples are prepared from the same freshly taken soil core sample. The contribution of root respiration is calculated as the difference between the respirations in the samples with and without roots [12]. The method of substrate-induced respiration suggested by Panikov with coauthors [5] is based on the application of glucose solution in concentration of no higher than 3 mg/g of soil into the soil sample with roots; this measure activates the microbial respiration and does not affect root respiration. In essence, this method represents a modification of the method of substrate-induced respiration developed for determining the microbial biomass in soil [7]. The coefficient of the increase in microbial respiration k_{mic} is determined in parallel after adding glucose into the soil sample without roots. The difference between respiration responses of the samples with and without roots after the addition is used to calculate RR [5]. It was demonstrated that the SIR method gives better estimates of RR and MR contributions in comparison with the CI method [4]. This advantage of the SIR method is probably related to the fact that it takes into account respiration of rhizosphere microorganisms (rhizomicrobial respiration) as a component of MR. In the CI method, the rhizomicrobial respiration is included in the root respiration, which leads to overestimation of the latter [4].

Despite the satisfactory results obtained with the SIR method in laboratory, the effect additional moistening of the soil with glucose solution under field conditions remains uncertain. The determination of contributions of RR and MR to the CO_2 emission from soils under field conditions is preferable because of the minimum soil disturbance and its natural water and temperature regimes [1, 14, 25]. We tested the SIR method under field conditions in soils with the high water holding capacity (WHC): mountainous meadow soils in the Austrian Alps near the city of Innsbruck) [28]. It was found that the method of substrate-induce respiration gives reliable results in the field; they are comparable with data obtained in laboratory experiments, in short-profile soils (with parent rock at the depth 30–40 cm). However, the applicability of this method for deep-profile heavy soils or for the soils with the low WHC was unknown.

Our study was aimed at determining of contributions of RR and MR to the total emission of CO_2 from the soil surface with the use of the direct field method of substrate-induced respiration. Soils with low the WHC were taken as the objects. We also compared the results of field determination of RR and MR with the results obtained in laboratory with the use of the SIR and CI methods.

OBJECTS AND METHODS

The study was performed on a loamy sandy soddy-podzolic soil (AY–EL–BEL–BT–C according to the new classification of Russian soils [6]) and on a medium loamy gray forest soil (AY-AEL([hh])-BEL([hh])-BT-C) in September 2007. The experimental plots on the soddy-podzolic soil were found in the Prioksko-Terrasnyi Biospheric Reserve under forest and meadow cenoses (C_{org} 1.5%, pH_{KCl} 5.4). The forest cenosis represented a mixed stand with the age of trees of about 80–100 years, and the meadow cenosis represented a sown meadow created in 1951. The plot on the gray forest soil (C_{org} 2.2–2.5%, pH_{KCl} 5.4) was found in a secondary mixed forest 4 km to the west of Pushchino; the age of the trees was about 50 years.

Three approaches to separate RR and MR were tested: the field modification of the SIR method and the laboratory determinations with the use of the SIR and CI methods.

The idea of the SIR method is that the respiration of microorganisms (V_{mic}) increases by k_{mic} times after the application of glucose (1 to 3 mg of glucose or other carbohydrate per one gram of soil or roots), whereas root respiration (V_{root}) remains at the same level [5]:

$$V1 = V_{root} + V_{mic}, \quad (1a)$$

$$V2 = V_{root} + k_{mic} V_{mic}, \quad (1b)$$

$$V_{mic} = (V2 - V1)/(k_{mic} - 1), \quad (1c)$$

where $V1$ is soil respiration before the application of carbohydrates, and $V2$ is soil respiration after the application of carbohydrates. Our previous experiments demonstrated that the coefficient of the increase in soil respiration under the impact of added glucose is equal to that in the case of added saccharose. Hence, these two carbohydrates can replace one another in the experiments on separation of root and microbial respirations with the SIR method.

The method of component integration (or the method of separate incubation [1]) is based on the manual separation of roots and soil. It is assumed that the disturbance of the natural soil morphology should change RR in the same way as MR, i.e., that the ratio between them should remain stable [13]. The emission of CO_2 from the soil with roots ($V1$) is calculated as the sum of RR (V_{root}) and MR (V_{mic}) according to Eq. (1a); respiration of the soil without roots is considered to be equal to V_{mic}.

We determined the CO_2 emission from the soil surface under field conditions in three variants: (1) control (without water and saccharose), (2) water control (with water added), and (3) variant with saccharose added. It was determined in four replicates with the use of the static chamber methods. Plastic vessels of 10.5 cm in diameter and 10–12 cm were used as the chambers. They were incised into the soil to a depth of 18–20 cm in 24–48 h before the experiment in order to eliminate the stress in respiration activity of soil microorganisms and roots caused by the installation of the chambers. The vessels were equipped with detachable covers with sealing gaskets and with sampler aperture closed by caps from penicillin flasks. Gas samples were taken into 15-ml hermetic evacuated penicillin flasks. In 2 h after adding water or water solution of saccharose the chambers were covered with detachable covers to allow the accumulation of CO_2 emitted from the soil. Gas samples were taken with 10–15 min intervals and the total time of the CO_2 accumulation was 30–40 min. After completing the determination of CO_2 emission in the field, soil cores of 10.5 cm in diameter and 18–20 cm in height were taken into the same vessels that were used in variant 1 of the field experiment. Soil cores were used in further laboratory experiments.

The volume of added saccharose solution or water was selected so that to ensure uniform soil moistening in the layer of 0–20 cm during 30 min. The regime of moistening of this particular layer is important, because the CO_2 emission from it is no less than 70% from the total CO_2 emission from the surface of gray forest and soddy-podzolic soils [3]. We added 750 ml of water or saccharose solution into the soddy-podzolic soil and 500 ml into the gray forest soil.

We determined the value of the coefficient of the enhancement of MR under the impact of added glucose (k_{mic}) in laboratory experiments with the soil free from roots. Weighed soil samples (50 g) were taken from each soil core and placed into 250-ml glass flasks hermetically sealed with rubber stopper and incubated at 20°C for 70–80 min. Then, gas samples were taken from the flasks to determine the CO_2 concentration. After this, the samples from the flasks were placed into Petri dishes and mixed carefully with the mixture of saccharose and calcined sand for an even distribution of saccharose in the samples (3–4 min). Then, the soil with added saccharose was placed back into the flasks and ventilated for 15 min. After this, the flasks were hermetically sealed and incubated for 60–70 min. At the end, gas samples for the analysis were taken with a syringe.

The k_{mic} values were calculated according to the following equation:

$$k_{mic} = V2_{mic}/V1_{mic}, \quad (2)$$

where $V1_{mic}$ and $V2_{mic}$ are the rates of CO_2 emission from the soil free from roots before and after saccharose adding, respectively. In fact, we determined the integral coefficient of the increase in respiration for the microbial community and for plant detritus, because the latter was not separated from the soil. This scheme somewhat differed from the previous scheme of the SIR method, in which the contribution of microorganisms decomposing SOM and plant detritus was separately estimated [4]. To calculate contributions of MR and RR to the CO_2 emission in the *field experiment*, the coefficient $k_{mic\text{-}field}$ was calculated according to the following equation:

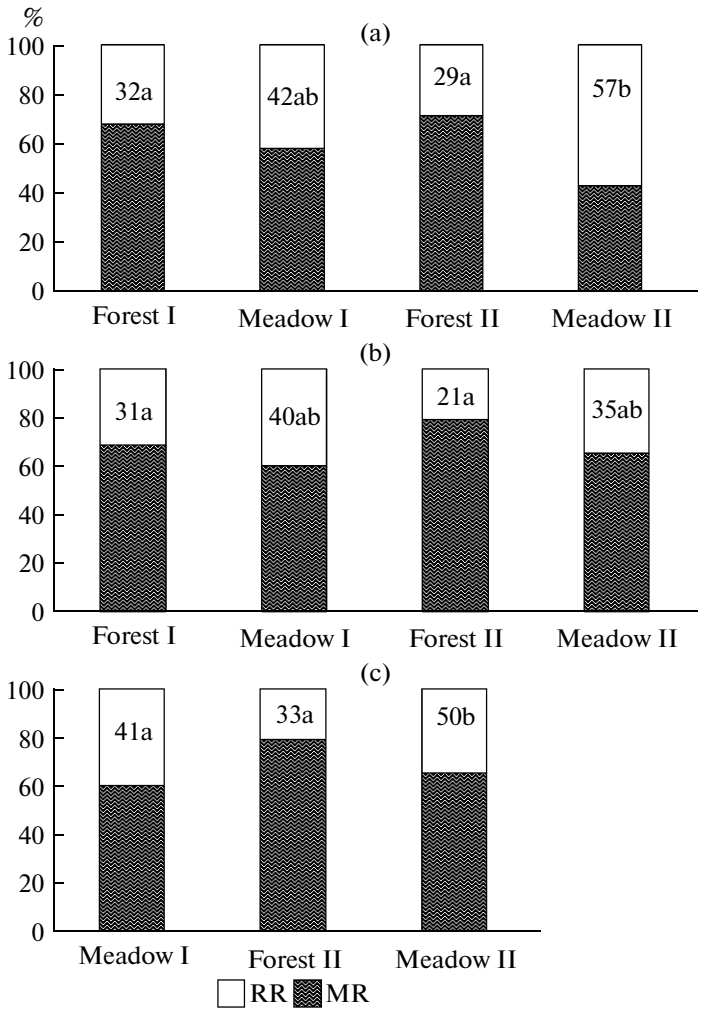
$$k_{mic\text{-}field} = k_{mic}/k_{comp}, \quad (3)$$

where k_{comp} is the compensation factor, which takes into account the effect of soil disturbance upon the soil loosening and mixing on respiration intensity. These procedures affect the microbiological activity due to the increase in the availability of easily decomposable organic substrates for microorganisms. At the same time, they affect the conditions of the CO_2 exchange between the soil and the atmosphere [2, 18]. In other words, not only the rate of the CO_2 production by microorganisms but also the rate of its emission from the soil are altered [3]. We determined the k_{comp} value in model experiments with the soil free from roots. For this purpose, we measured the coefficient of respiration increase in the soil compacted to the natural bulk density values and in the mixed soil. In the first variant, glucose solution was added without the soil mixing. In the second variant, the soil was carefully mixed to achieve the even distribution of the solution. The value of k_{comp} equal to 1.3 [28] was used in our calculations of contributions of RR and MR contributions in the field experiment.

All the experiments were performed in four replicates. The CO_2 concentration was determined on a gas chromatograph Kristall-4000M with thermal conductivity detector in the columns filled with Porapack *Q*. The results of calculations of contributions of root and microbial respirations to the CO_2 emission from the soil surface were grouped according to Duncan's test at $P < 0.05$.

RESULTS AND DISCUSSION

The k_{mic} values in soils of meadow cenoses (5.4 and 7.4 in the soddy-podzolic and gray forest soils, respectively) were higher than those obtained in our previous experiments (3.3–4.6 and 5.1–6.3 [4]). The coefficient of respiration increase was even higher in the soils of forest cenoses: 6.7 and 11.6 for the soddy-podzolic and gray forest soils, respectively. Such differences in the values of this coefficient in comparison with our data obtained in summer 2003 [4] can be explained by the changes in the hydrothermal regime of the soils, in the pool of microbial biomass and its activity, and in the availability of carbon substrate [18]. We do not know yet, which of these factors was of major importance. The revealing of relationships between k_{mic} values and the ecophysiological factors



Contributions of root (RR) and microbial (MR) respiration to the CO_2 emission from the soil surface determined with the (a) component integration method, (b) laboratory variant of the SIR method, and (c) field variant of the SIR method in ecosystems on (I) soddy slightly podzolic soil (AY-EL-BEL-BT) and (II) gray forest soil (AEL([hh])-BEL([hh])-BT-C). Numerals designate contribution of root respiration (% of the total CO_2 emission from the soil surface). The significance of differences (according to Duncan's test, $P < 0.05$, $n = 4$) is indicated by different letters.

will require further laboratory and field experiments with estimation of the biomass of soil microorganisms and the available carbon substrate under temperature and moisture conditions exactly corresponding to those in the field at the moment of sampling.

The contributions of root and microbial respiration to the total emission of CO_2 from the soil surface obtained with laboratory and field methods are shown in the figure. The contribution of RR to the total CO_2 emission in meadow ecosystems is higher than that in forest ecosystems on the same soils. The contribution of RR in meadow ecosystems measured by the CI, SIR, and field SIR methods comprises 42–57, 34–35, and 36–50%, respectively; in forest ecosystems, it reaches 29–32, 21–31, and 33%, respectively. We suppose that these differences are caused by the underestimation of RR in forest ecosystems, because the applied methods did not allow determining the contribution of roots at the depth of more than 20 cm, i.e., beyond the depth of installation of the chambers and samplers. The respiration of coarse (>10 mm) tree roots that may constitute up to 50% of RR [4] also was not taken into account. Thus, the reliable estimates of RR and MR in the total respiration from the soil surface in forest ecosystems can be obtained with due account for the percentage of the biomass of coarse roots and the roots found at the depths of more than 20 cm.

For all the variants, a tendency for higher values of RR determined with the CI method in comparison with the SIR method was observed, though this difference was statistically significant only in the variant of meadow on the gray forest soil. It is probable that

somewhat higher estimates of the contribution of RR to the total emission obtained by the CI method are related to the presence of dead roots in the determined root biomass. In this case, the respiration of microorganisms decomposing such roots is included in RR.

Application of the field variant of the SIR method on the gray forest soil gave higher estimates of the contribution of RR to the total CO_2 emission from the soil surface soil in comparison with estimates obtained by the SIR method in laboratory, though the difference between field and laboratory results was not great. However, we did not find systematic differences between field and laboratory determinations of RR with the SIR method in our experiments on the mountainous meadow soils in Austria [28]. At present, we cannot judge definitely about this tendency for forest and meadow cenoses on the gray forest and soddy-podzolic soils; the reasons for such differences have yet to be found. In fact, the differences in the estimates of RR and MR obtained by different methods were masked by the great spatial variability in the studied parameters. At least, we did not find a significant effect of additional moistening on the ratio RR and MR on the gray forest and soddy-podzolic soils. Native soil moisture comprised 29–30% of the WHC in the soddy-podzolic soils and 58–65% of the WHC in the gray forest soils. This allows us to suppose that the field modification of the SIR method can be applied not only to shallow-profile soils with the high WHC. At the same time, a significant increase in the portion of RR in the soils with additional moistening was demonstrated with the use of this method earlier [4, 28]. Thus, the question about the applicability of the SIR method in dependence on the ecophysiological conditions and the particular types of soils and ecosystems has yet to be investigated. In particular, the effect of temperature factor on the estimates of RR and MR should be studied. At present, the data on this problem are rather ambiguous. Some authors reject the effect of soil temperature on the ratio between RR and MR in the soil respiration [10]. Other researchers argue that RR is more sensitive to temperature changes in comparison with MR and, hence, temperature changes should lead to changes in the contributions of RR and MR to the total soil respiration [9]. The influence of temperature on the portions of RR and MR in the total respiration was not found in our experiments for the soil temperature range from 10–12°C (in the field) to 22°C (laboratory incubation experiments).

The estimates of the contribution of RR to the total soil respiration in meadow ecosystems obtained in this experiment agreed with the estimates of RR obtained by the same methods in meadow ecosystems formed on shallow-profile alpine soils (10–40% of the total CO_2 emission from the soil surface) and with laboratory CI and SIR methods in 2003 (about 1/3 of the total CO_2 emission from the soil surface). Moreover, our experimental estimates of RR and MR contributions corresponded to literature data. Despite the fact that other researchers used different methods or groups of methods, the predominance of microbial contribution over root contribution was determined as the major trend [4, 5, 8, 9, 24]. For example, the contribution of RR in prairie soils comprises 23–43% depending on the method of determination of root and microbial respiration [27]; for fertilized ameliorated, it reaches 40% [24], for grassed arable lands, 19–40% [10]. The only known exception for found for meadow ecosystems of New Zealand (74%, [15]). This is explained by the high root mass-to-aboveground phytomass ratio, extremely arid conditions, and essential infestation of meadows by a weed *Hieracium genera* [15]. So, our estimates of contributions of root and microbial respirations to the CO_2 emission from the soil surface seem to be realistic. As for separate determination of RR and MR in forest ecosystems, all the three methods gave similar values of RR and MR for the soddy-podzolic soil, and this allows us to argue that the modified SIR method can be applied in the field for forest ecosystems; necessary corrections for the contribution of large roots (see above) should be introduced into this method.

We consider that the use of both laboratory and field methods to distinguish between RR and MR is the most informative and efficient approach. To verify the results, isotopic methods should be used simultaneously, because they allow calculating the priming effect upon the decomposition of root exudates, plant detritus, and SOM. Further development of the field variant of the SIR method should be performed in the following directions: (1) the optimization of procedures for determining the coefficient of respiration increase, (2) the improvement of the method for measuring CO_2 fluxes in the field and laboratory, and (3) the testing of the method for a wide range of soils under different climatic and ecophysiological conditions. The improvement of the method for measuring CO_2 fluxes is seen in the performance of all necessary incubation laboratory experiments under thermostat conditions with incubation temperature equal to field temperature and the comparison of incubation regimes of different durations and with different frequencies of gas sampling. The k_{mic} values should be determined under field conditions. The testing of the field method for a wide range of soils will make it possible to determine the limits of its suitability, assess the influence of biotic and abiotic factors on the ratio between RR and MR [14], and evaluate the particular advantages and disadvantages of this method.

CONCLUSIONS

Our study represents the first attempt to determine contributions of root and microbial respirations to the total CO_2 emission using the substrate-induced respiration method for the soils of heavy texture (the gray forest soil) and of low water holding capacity (the soddy-podzolic soil). Earlier, the applicability of this

method was shown for the coarse-textured mountainous shallow-profile alpine meadow soils with the high water-holding capacity.

Though our data do not make it possible to indicate the preferable method for determining the contributions of root respiration and microbial respiration to the total CO_2 emission from the soil surface, we can state that the field modification of the SIR method gives the estimates comparable with those obtained by laboratory methods. An important advantage of the field method is that it allows one to separate root and microbial respirations under the conditions close to natural, i.e. under native temperature and natural soil texture with minimum disturbance in the ecosystem during measuring CO_2 fluxes, and this is always desirable upon determining CO_2 fluxes in ecosystems. Hence, we consider this methodological approach to be promising in the future after its refinement. The refinement of the field version of the SIR method should be performed in the following directions: (1) the determination of k_{mic} under natural conditions, (2) the optimization of measurements of CO_2 fluxes in the field and laboratory, and (3) the testing of the method for a wide range of soils under different climatic and ecophysiological conditions.

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