Leaf Litter Decomposition Differences between Alien and Native Maple Species

DALIA JANUŠAUSKAITĖ[1*] AND LINA STRAIGYTĖ[2]

[1*]*Department of Plant Pathology and Protection, Institute of Agriculture, Lithuanian Research Centre for Agriculture and Forestry, Akademija, LT-58344, Kedainiai distr. Lithuania*
E-mail: daliaj@lzi.lt, phone +370 437 37263

Aleksandras Stulginskis University, Department of Silviculture, Studentu str. 11, Akademija, LT53361, Kaunas district, Lithuania, E-mail lina.straigyte@asu.lt

Abstract

This paper presents a comparative analysis of the leaf litter decomposition of two alien (*Acer negundo, A. pseudoplatanus*) and one native (*A. platanoides*) maple species. The leaf litter fall of *Acer pseudoplatanus* was collected in the Girionys Park, situated in the south-west of Kaunas, and leaves of *A. platanoides* and *A. negundo* were collected in the Santaka park, located in the eastern part of Kaunas in the autumn of 2008. A laboratory incubation experiment was conducted to evaluate the effect of alien and native maple species on ecosystem functioning, the response of microbial transformations and decomposition of maple litter. The study quantified the amount of CO_2 evolved from the decaying litters and the population of fungi, bacteria associated with the soil in forests under decomposing leaves. Decomposition of maple leaf litter was studied under laboratory conditions using the respiration technique. Chemical composition of the litters was determined before incubation by the dry combustion method. The decay rate of the maple litters varied significantly between species. *Acer negundo* litter decayed more rapidly (K_W = 0.003488) than *A. platanoides* (K_W = 0.002046) or *A. pseudoplatanus* (K_W = 0.00166). This variation in decomposition rate corresponded with indicators of litter quality (C/N ratio, N and C) with decomposition mostly being explained by C content. The CO_2 evolution differed significantly between the species; it was considerably higher in alien *A. negundo* litter. Bacteria and fungi quantities varied in soil associated with the three maple species. Microbial populations were similar in the soils associated with *A. platanoides* and *A. negundo*, while densities were lower on the site associated with *A. pseudoplatanus*. CO_2 evolution was positively correlated with the number of fungi and bacteria in the soil under maple litter. The leaves of *A. negundo* showed the fastest decomposition rate, and it is likely that faster nutrient cycling will occur in the soil where *A. negundo* grows and provides evidence how invasive species may alter the functioning of forest systems.

Key words: decomposition rates, litter respiration, maple species

Introduction

Bioinvasion is recognized as an important component of the global loss of species and habitats. Some have argued that bioinvasion is a greater threat than the greenhouse effect, industrial pollution or ozone depletion (Mack et al. 2001). Plant invasions can have serious ecological and economic impacts on native biodiversity and ecosystem processes (Sanchez-Flores 2007)**.** Alien plants either directly or indirectly have multiple impacts on plant communities including altering soil chemistry and ecosystem function (Riepšas and Straigytė 2008). For example, exotic plant species affect soil biota directly through root exudates during the growing season and through litter inputs during plant material decay (Wardle et al. 2004). Invasive trees that alter litter quantity and quality may have effects on processes that cascade from terrestrial environments into aquatic environments (Reinhart and Vande-Voort 2006). The long-term impact of litter and root exudates can modify soil nutrient pools, and there is evidence that alien plant species may alter nutrient cycles differently from native species (Weidenhamer and Callaway 2010).

The processing of leaf litter in forests is a key ecosystem function. Periodic litter inputs and its subsequent decomposition direct carbon into three main directions: back into the atmosphere, into the soil food web, and into pools of soil organic matter (Gartner and Cardon 2004). Tree species differ in their litter quantity and quality which affects decomposition processes. It is well documented that physical and-chemical properties of leaf litter caused important interspecific variability in decomposition rates (Mayer 2008).

Litter decomposition is controlled both by abiotic factors, such as climate (mainly temperature and humidity) and litter chemistry (in particular nitrogen, lignin and polyphenol concentrations and ratios), and by biotic factors, such as soil organism activity (the qualitative and quantitative compositions of decomposer communities including bacteria, fungi and invertebrates) (Sariyildiz and Anderson 2003, Aubert et al. 2010).

Initial litter quality influences the abundance, composition, and activity of the microorganisms, fungi and soil fauna that participate in litter decomposition (Bezemer et al. 2010), which, in turn, determines the decomposition rate and nutrient dynamics. Several factors such as N content, C/N ratio are often used as indicators of tissue quality because they correlate negatively with litter decomposition (Jacob et al. 2009). Invasive plants which can be dominant in ecosystems may also alter their functioning (Dukes and Mooney 2004). Understanding of how invasive trees alter nutrient cycling processes in the soil is important to comprehend how invaders impact on forest systems. Many alien trees have more rapidly decomposing leaf litter than the native species they replace (Ehrenfeld et al. 2001). Also alien plants may be responsible for important changes in soil microbiota affecting the structure and functions of microbial communities (Remigi et al. 2008). The available data suggest that invasive plant species frequently increase biomass and net primary production, increase N availability, alter N fixation rates, and produce litter with higher decomposition rates than co-occurring natives (Ehrenfeld 2003). Recently, it was found that on average, invaders were correlated with much higher litter decomposition rates and increases in soil nitrogen mineralization and nitrification (Ashton et al. 2005, Liao et al. 2008). Reinhart and Callaway (2006) reported that soil microbes in some ecosystems may promote 'exotic' invasion due to different plant–soil feedback processes between native and invaded ranges. However, the opposite patterns may also occur where litter may decompose faster in an area dominated by the native plant species, than in an area dominated by alien plant species (Gholz et al. 2000). Although much is known about litter dynamics in temperate forests, less is known about how alien trees alter decomposition and nutrient cycles compared to resident vegetation. Describing measures of litter quality and processes related to decomposition is an important approach helping evaluate how individual species affect ecosystem function.

According to the state forest cadastre data (2009), native maple *A.platanoides* stands grow on a 2,190 ha territory. The volume of this maple accounts for 0.43 % of the total growing stock (I and II storeys) volume (Kuliešis et al. 2009) in Lithuania's forests. The area covered by alien maple species *A.negundo* and *A.pseudoplatanus* is not known, but over the last decades we have recorded intensive spread of these maples in Lithuania. The spread of *A.negundo* seedlings is noticed near rivers, *A.pseudoplatanus* spreads rapidly in parks and older plantations.

The main goal of this study was to describe the litter quality and decomposition characteristics of one native maple species vs. two alien maple species. The main hypothesis was that alien maple species show different patterns of decomposition in relation to their chemical characteristics than native maple. Decomposition rates are lower in the litter with higher C/N content, and the higher microbial amount in the soil has a positive influence on the decomposition rate.

To address these issues, we designed a laboratory decomposition experiment using leaf litter of two alien and one native maple species. Such experiment has the advantage of being comparatively straightforward to perform and control environmental conditions, and is easier to understand than complex, real-world system. Results will give a better insight into how alien species' dominance may alter the processes relating to ecosystem function.

Material and methods

Site and experimental layout

We studied leaf litter quality and decomposition in maple plantations ca. 50 years of age. The leaf litter was collected in the autumn of 2008. The leaf litter fall of *Acer pseudoplatanus* was collected in the Girionys Park (*Planosol*) in the south-western part of Kaunas (54°51' N, 24°02' E), and leaves of *A. platanoides* and *A. negundo* were collected in the Santaka park (*Fluvisol*) in the eastern part of Kaunas (54°53'N, 23°53' E). The soil type was defined according to World Reference Base for Soil Resources (WRB 2006). Leaves were collected from the soil surface of one square meter size of randomly selected areas and about 2 meters from the tree trunk (n=3 for each maple species). The collected leaf litter was air dried and weighed.

Decomposition experiment

Fallen leaves were collected in the autumn of 2008. The litter samples were taken to the laboratory and kept at 20°C to let macrofauna escape.

The leaves were dried at 70°C for 48 h and half a gram of leaves was weighed in a beaker. The leaves of each maple species were inoculated with 8 ml of soil extracts, prepared from 15 g of soil taken from the plots under the tested trees. The soil was shaken with 250 ml water for 15 min, and the suspension served as the extract. Beakers with inoculated litter of the maple spe-

cies tested were put into 1l jars and tightly closed. Leaf weight loss was determined after every 21 days on three replicate samples for each treatment. After every 21 days of incubation, 3 replicate samples per treatment were removed from the incubator and analyzed. Decomposition rate was defined as the percentage of dry mass loss after incubation (Ayres et. al 2006).

Chemical analysis

Total C and N concentrations for leaf litter were determined using the ECS 4010 (dry combustion) analyzer at the Lithuanian Forest Research Institute. Total N concentration in litter was determined three times: after leaves fall, in March and in September. Total carbon concentration in litter was measured using the same method as for nitrogen. The chemical properties of maple litter are shown in Table 1.

performed to assess the cultivable bacterial and fungal colony forming units (cfu). For this purpose different media were used: for wide variety of cultivable bacteria enumeration Soy Tryptic agar (TSA/10 agar, Biochemika) was used; total fungal counts were determined on malt extract agar (Liofilchem Diagnostici). The plates were incubated at 25^0 C and bacterial and fungal counts were made after 4 and 7 days, respectively. Cfu were corrected for the moisture content of the soil before the final counts were expressed as the number of cultivable bacterial and fungal cells per 1 g of dry soil.

Statistical analysis

The data are reported as mean ±standard error, SE of the mean and were examined using Analysis of Variance (ANOVA) procedures. Before analysis, bacterial

Table 1. C and N composition, C/N rate in the fresh litter before decomposition experiments. Columns represent means and SE

Tree species	N, g kg^{-1}	C, g kg^{-1}	S, g kg^{-1}	C/N
A.negundo	17.45 ± 0.16	417.00 ± 5.11	1.56 ± 0.12	23.90 ± 0.09
A.platanoides	10.32 ± 0.07	465.02 ± 2.19	1.02 ± 0.04	45.05 ± 0.37
A.pseudoplatanus	12.35 ± 0.54	447.09 ± 1.89	1.49 ± 0.27	36.32 ± 1.41
LSD $_{0.5}$ to trial mean	0.64	4.49	0.39	1.97

Respiration rate

We measured respiration during litter decomposition by quantifying CO_2 production rate of litter samples placed in airtight Mason jars and incubated at 22^0 C (Alef 1995). CO_2 evolution was quantified by measuring the amount of remaining alkali. After precipitation of carbonate in $BaCl_2$, the remaining alkali concentration was determined by titration with HCl. Three replicates were used for each treatment, a total of 60 jars – 15 for each maple species and 15 for blank NaOH. Respiration was expressed as mg C-CO_2 µg^1 litter d^1 and measured in a closed environment after each 21 days. The daily decay rate (K) of litter calculated from litter mass loss in respiration experiment for the entire study was calculated through the negative exponential decay model:

$$W_t - W_0 = \exp(^{-kt}),$$

where, W_0 is initial weight and W_t is weight remaining after time t, representing the cumulative mineralization curves. The experimental period was completed after 105 days when respiration rates had ceased to decrease to any large degree between measurements.

Bacterial and fungi counts

Ten topsoil cores (8 cm diameter and 5 cm deep) were collected from each stand. Soil samples were homogenized after sieving, and used for the microbiological assays. We quantified population of bacteria and fungi. Conventional dilution spread-plating was

and fungal counts on plates were transformed from colony-forming units per gram using log10 transformation. Significant differences among treatment means were assessed by Fisher's least significant difference test (LSD, p <0.05) and using an F-test. Statistical computations were performed using the statistical software package STATGRAPHICS PLUS 6.0 software.

Results

Respiration and decomposition

Litter of different maple species differed in respiration intensity (Figure 1). Respiration rates of samples initially increased and then began to gradually decrease. The respiration rate continued to increase until the 84th day. Some of the cumulative curves of CO_2 release are given in Figure 1 and show various patterns according to species.

The total release of CO_2 during 105 days ranged from 32.59 to 58.42 µg C g^{-1} of litter, i.e. approximately 0.0146-0.028 %. Respiration rate was significantly (p < 0.005) higher in *A. negundo*, intermediate in *A. platanoides* and slowest in *A. pseudoplatanus*, 58.42, 35.34 and 32.59, respectively. LSD test shows that the most significant split between the other maple species had *A.negundo*, except for 21 days, *A.platanoides* and *A. pseudoplatanus* differed significantly on the 42nd, 84th and 105th days.

Figure 1. Carbon release as CO_2 measurement during 105 d incubations of different maple leaf litters. Mean values ± SE are shown per each measurement. T-test significance between species at level 5 % is shown with different letters
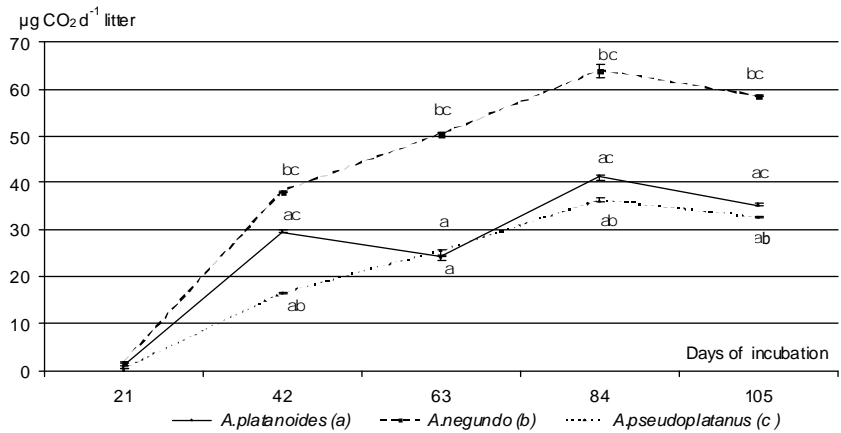
The decomposition rate constant (K_w), calculated from mass losses was 0.001661, 0.002046 and 0.003488 for *A. pseudoplatanus, A. platanoides* and *A. negundo*, respectively. The decomposition rate constant was significantly higher for *A.negundo* than the other tree species (p < 0.005). Respiration rate decreased in the order *A. negundo* > *A. platanoides* > *A. pseudoplatanus*. The leaf litter of *A.negundo*, which had the highest initial N concentration, showed the greatest decomposition rate constant. Measurements of litter quality (C, N, and C/N) explained much of the variation in respiration (r_C=0.92, r_N=-0.86, and $r_{C/N}$=-0.86, respectively). Decomposition rate (K_w) constants also varied predictably with measurements of litter quality (r_C=0.86, r_N=-0.79, and $r_{C/N}$=-0.78). Litter C/N ratio and N amount showed strong negative associations with decomposition rate, and C amount showed strong positive associations. The differences in N concentrations between *A. negundo* and the other two maple species were significant (p < 0.005) (Table 1). Also, the differences in C concentrations and C/N ratios between *A. negundo* and *A. platanoides* were statistically significant at one-way ANOVA. A strong

relationship was detected between leaf mass and respiration rate for all maples. When respiration increased, leaf weight decreased (Figure 2). Species varied in their rate of mass loss with *A. negundo* (30.68%) exhibiting the fastest decomposition rate, *A. platanoides* (19.4%) intermediate, and *A. pseudoplatanus* (16.0%) the slowest decomposition rate.

Fungal and bacterial contribution

The density of bacteria and fungi varied across the soils from the three different maple species. The amount of fungi in *A. negundo* soils differed significantly (F_{fact} -8.7**; p=0.034) compared with the other soils and reached 42.32 x10^4 cfu g^{-1} soil (Figure 3). The amount of fungi in the soil under *A. pseudoplatanus and A. platanoides* differed slightly. The amount of fungi reached 25.8 x10^4 and 28.9 x10^4 cfu g^{-1} soil, respectively. However, bacterial population did not vary significantly between the soils under *A. platanoides* and *A. negundo* litters. The lowest significant (F_{fact} -13.85**; p=0.0159) bacteria amount in the soil under *A. pseudoplatanus* was only 0.98 x10^4 cfu g^{-1} soil. In the soil under *A. negundo* and *A. platanoides* it was
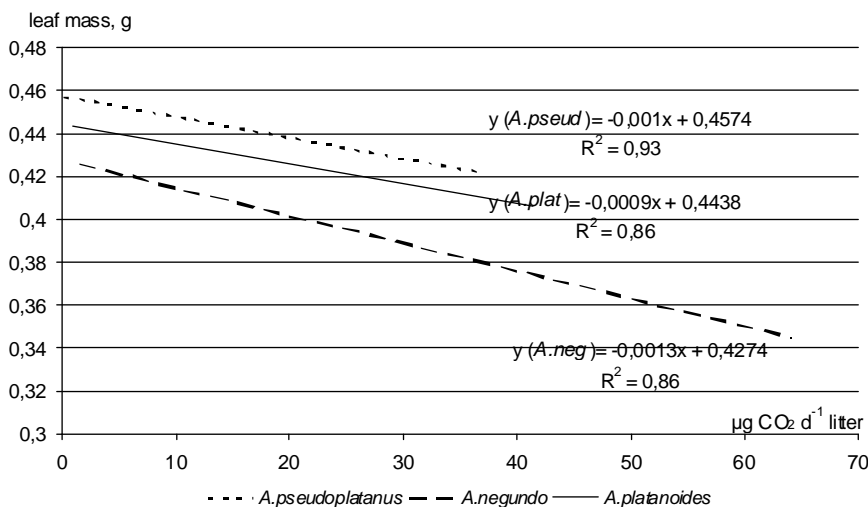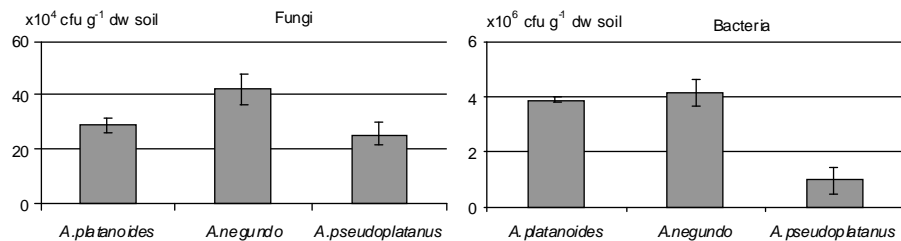

Figure 2. Relationship between leaf mass loss and respiration rate for maple

more than 3 times as high – 3.8 and 4.1 x10^4 cfu g^{-1} soil, respectively.

plants (Sanon et al. 2009). Sometimes litter decomposition rates were not significantly correlated with ob-

Figure 3. The distribution of microbial amount in the soils under the maple species. Columns represent means±SE

Discussion and conclusions

Alien plant species can alter the forest ecosystem and may also have significant ecological or economic consequences. For example, invasive trees can alter litter decomposition and nutrient cycling through variation in litter inputs (timing, quantity, and quality of litter). *Acer pseudoplatanus* affecting regeneration may relate to it altering decomposition rates and slowing nutrient cycling (Anon 2003). As a result, their potential to drastically alter ecosystem structure and function has been widely recognized in recent years (Levine et al. 2003). Here we compared the litter quality and decomposition rate of two alien maple species to a native maple species.

Studies on maple litter decomposition were done under laboratory conditions, but the findings may show how these processes occur in natural habitats. There was a considerable variation in litter quality among the studied maple species. Our results indicated that decomposition was related to leaf chemical composition. Decomposition rate was positively correlated with C and N concentration and negatively with C/N ratios of fresh litter. According to the general idea that C/N ratio is a good predictor of decomposition rates (Perez-Harguindeguy et al. 2000), the initial leaf litter C/N ratios of the *A. pseudoplatanus* and *A. platanoides* and K$_w$ values in our study were associated also. Thus it is evident that our and other studies indicate that tree species and litter quality can exert a strong control on nutrient cycling in forest ecosystems (Lovett et al. 2004, Perez-Harguindeguy et al. 2000, Wang et al. 2008), it seems likely that lower C/N ratio leads to increasing carbon and nitrogen mineralisation (Mansson and Falkengren-Grerup 2003). We may assume that higher decay rates for *A. negundo* might relate to the changes in ecosystem function due to accelerating nutrient cycling.

In the present study, litter quality as well as soil microbiota may be limiting factors for litter decomposition. Some plants may favour activity of soil biota by increasing their abundance and changing the com-

position of microorganisms in the soil (Hawkes et al. 2005). The decomposition of litter in the presence of biota extracted from the soil of each tree species shows that it is likely that litter decomposes in the same way as it occurs in natural conditions. The total abundance of bacteria associated with the soil under *A. platanoides* and *A. negundo* was large and was not related to litter decomposition rate of these two species. However, in the soil of *A. pseudoplatanus* site, bacteria population was significantly lower. This indicates that small amount of bacteria together with leaf properties may explain lower decomposition rate of *A. pseudoplatanus* litter. Bacteria and fungi differ in their contribution to breakdown, with fungi being apparently more important than bacteria in terrestrial ecosystem (Bailey et al. 2002). This is because they decompose the lignocellulose matrix in litter that other microorganisms are rarely able to decompose (Cooke and Rayner 1984). Also, bacteria were traditionally believed to be less abundant in soils than fungi, and therefore less important as decomposers. *A. negundo* litter exhibited the fastest decomposition rate, which might have resulted from greater densities of fungi and bacteria in the soil. Although we documented fewer fungi than bacteria in the soil, the variation in fungi abundance for maple species corresponded more closely with the variation in their litter quality and litter decomposition rates. In the litter with high C/N ratios microbial activity is significantly reduced, leading to N-immobilisation and reducing decomposition of litter. This suggests that the quality of litter inputs into the decomposer foodweb helps to regulate the abundance of these organisms. Some authors noted statistically significant correlation between the number of cellulose-degrading microorganisms and crop residue decomposition rate (Velička et al. 2009). Together, these data demonstrate an effect of plant community composition on decomposer abundance, confirming a link between above and belowground communities (Ball et al. 2009). Sanon et al. (2009) also found that microbial communities may have a role in the ecosystem-scale changes in soil biochemistry caused by invasive

served soil biological characteristics (Pavao-Zuckerman and Coleman 2005), and thus show not simple direct effects of soil microbes, but the occurrence of interaction of a few factors at the same time (Callaway et al. 2004). Such context-dependent relationships between litter decomposition, soil respiration rates and N mineralization rates defeating any attempt at easy summarization and interpretation of this relationship (Ehrenfeld 2010).

Alien maples *A. pseudoplatanus* and *A. negundo* had lower litter mass overall compared with native *A. platanoides* in previous study with litter bag method (Straigyte et. al. 2009). Due to low decomposition rates, the *A. platanoides* and especially *A. pseudoplatanus* site showed large litter accumulations (Straigyte et. al. 2009) in spite of a relatively low litter fall. The lower decomposition rates of the *A. pseudoplatanus* litter indicate quantitative changes in the decomposer communities (fewer fungi) of these systems that lead to a higher build-up of litter stocks on the forest floor. Thus, our study to clarify the reliability of the data from the field (Straigyte et. al. 2009) under controlled laboratory conditions, showed the same result. The strong correlations between decomposition rate and C/N ratio across the studied maple species seem also to be an important factor controlling the loss of litter mass. Consequently, decomposition rates determine the variation in below-ground ecosystem processes and change nutrient supply in forest ecosystem. For *A. negundo,* nutrient cycling is fast, while for *A. pseudoplatanus,* it is slow. The implications of these differing decomposition rates and soil biota amounts are that each studied alien species chooses an individual way to adapt or find a new niche or displace native species. Also, *A. platanoides*, which is not native to North America, decomposes faster than native maple species (Gomez-Aparichio and Canham 2008). Although our findings and other researches' results suggest that invaders tended to more quickly decompose, other authors indicate a slower nutrient cycling at ecosystem scale upon invasion (Godoy et al. 2010)

These results show that factors associated with decaying leaves, particularly decomposition rate, were significantly related to leaf properties and increasing amount of microbes. Our study has the limitation due to not representing the natural conditions; however, laboratory experiment enabled us to avoid other effects on litter decomposition. Measuring leaf breakdown rate by respiration method may be developed into a simple, powerful and low-cost tool for assessing an essential component of ecosystem functioning.

The main consequence of these changes is that the higher rate of litter decomposition of alien plants may be favourable for more rapid seed germination, quicker nutrient cycling and create better conditions for growing alien species. From our results we may predict which maple species will show a more rapid decomposition. The ecological significance of these results reveals considering the succession conditions that prevail in our region.

Our efforts to understand how alien tree species influence ecosystems and alter processes in the soils were focused on forest systems and their response to biological soil properties. This approach needs a more in-depth research to verify the validity of the results obtained. The research model can be successfully applied to other alien species in Lithuania, both in forest and other ecosystems. The results of the study also bear geographic relevance, and future investigations might be focused on microorganism community shift associated with host species. The present study may help to identify model species that might be used in similar studies.

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РАЗНИЦА МЕЖДУ РАЗЛОЖЕНИЕМ ЛИСТОВОГО ОПАДА ИНТРОДУЦИРОВАННЫХ И МЕСТНЫХ ВИДОВ КЛЕНА

Д. Янушаускайте, Л. Страйгите

Резюме

В статье анализируется разница между разложением опавших листьев клена местного вида (*Acer platanoides*) и интродуцированных видов (*A. negundo, A. pseudoplatanus)*. Листовой опад клена был собран осенью 2008 в парках Гирионис и Сантака (Каунас, Литва). Для оценки влияния интродуцированных и местных видов растений на реакцию микробного разложения и преобразование подстилки клена был проведен инкубационый эксперимент. Во время эксперимента измерялось количество CO_2, выделявшееся из листового опада, устанавливалось количество грибов и бактерий, обитающих в почве под кленами каждого вида. Разложение листьев клена изучались в лабораторных условиях с использованием техники дыхания.

Установлено, что суточная интенсивность разложения листьев различных видов клена k_w в расчете на потерю массы снизилась следующим образом: *A.negundo* ($K_w = 0.003488$) > *A. platanoides* ($K_w = 0.002046$) > *A.pseudoplatanus* ($k_w = 0.00166$). Исследовалась связь между качеством листьев (C / N, N и C) и интенсивностью респирации. Установлено, что скорость разложения (k_w) больше всего связана с содержанием углерода. Скорость разложения листьев клена различного вида значительно различается. Массу быстрее всех видов теряли листья *A.negundo*. Листья различных видов клена различались интенсивностью выделения CO_2, наиболее интенсивным выделением отличался вид *A.negundo*. Окружающая среда всех видов клена различаются по количеству бактерий и грибов в почве. Похожее количество установлено в почве под *A.platanoides* и *A.negundo*, значительно меньшее количество микроорганизмов было в почве под *A.pseudoplatanus*. Выделение CO_2 положительно коррелирует с количеством грибов и бактерий в почве под всеми видами клена. Результаты показывают, что самая большая скорость микробиологической деструкции листового опада было у *A.negundo*. Вероятно, качественные изменения и обмен питательных веществ в почве под этим видом клена будут происходить быстрее.

Ключевые слова: скорость разложения, листовой опад, виды клена