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Root respiration and its importance for the carbon balance of beech saplings (*Fagus sylvatica* L.) in a montane beech forest

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Abstract

Root respiration of 10-year-old beech saplings (*Fagus sylvatica* L.) grown in the understorey (UND) and in a natural gap (GAP) of a mature beech forest in the Solling mountains, FRG, was investigated from April until December, 1990. Respiration rates of fine, medium and coarse roots were measured in situ by a PC-controlled cuvette system. Fine root respiration rates were in the range of 0.5 – 9.8 nmol CO_2 gDW^{-1} s^{-1} at both sites, but respiration rates of UND saplings were higher, compared to those of GAP saplings. The dependence of respiratory activity on soil temperature proved to be highly significant ($p < 0.001$) for both plots, following a quasi-Arrhenius type curve. Fine root respiration rates of UND saplings were highly significantly, negatively correlated with the water content of the attached organic material, whereas respiration rates of GAP saplings did not show such a correlation. Further, a significant correlation ($p < 0.01$) between mycorrhizal biomass and respiration rate was detected at the UND site, but not at the GAP site. Medium and coarse root respiration rates were very similar and no significant differences between the two sites were detected. Maximum respiration rates of 3.1 nmol CO_2 gDW^{-1} s^{-1} were reached in the middle of July. Due to low light intensities in the under storey, daily net CO_2 assimilation rates of UND saplings were much smaller than those of GAP saplings. At both sites, net CO_2 assimilation rates varied more than respiration rates and thus the carbon balance of beech saplings was more affected by the rate of carbon fixation than by the rate of respiratory carbon loss.

Introduction

Plant growth beneath the closed canopy of a mature deciduous forest is severely limited by light intensities which are only a fraction of full sunlight (Chazdon, 1986, 1988; Endler, 1993; Poulson and Platt, 1989). In a mature beech forest, less than 5% of the radiation above the canopy is available for assimilation by the herb layer (Eber, 1972; Ehrhardt, 1988; Schulte, 1993). Consequently, successful competition for light requires a highly efficient conversion of light into biomass, i. e. a high ratio of carbon gain to carbon loss for the plant as a whole. Studies on the aboveground growth patterns of shade-tolerant tree species showed large variations in height and lateral growth, leaf exposure, leaf area index (LAI) and other phenological parameters, when light intensity was altered by an opening in the canopy (Canham, 1988, 1989; Pearcy, 1983). Saplings of European beech (*Fagus sylvatica* L.) growing in the understorey (UND) show a clear suppression of lateral shoots and the main shoot grows plagiotrop, whereas saplings of the same age in a natural gap (GAP) distribute larger amounts of biomass into lateral shoots and growth is predominantly orthotrop (Roloff 1986; Schmaltz 1964; Stickan et al., 1992; Suner and Röhrig, 1980).

Photosynthetic gas exchange measurements of beech saplings revealed quantum yields of 0.04 (Stickan and Zhang, 1992) to 0.07 mol CO_2 mol $Photon^{-1}$ (Rees, personal communication), which is about twice as high as quantum yields of sun leaves of mature trees (Schulte, 1993; Schulze, 1970).

Further, light saturation of photosynthesis (I_s) of shaded beech saplings was measured in a range of 170 to 230 μmol Photons m^{-2} s^{-1} (Stickan and Zhang,

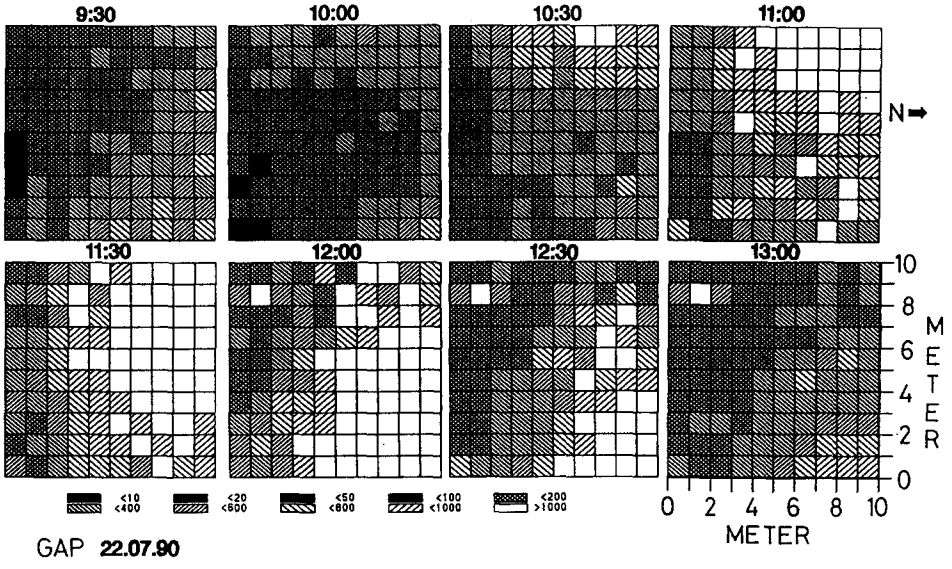

Fig. 1. Distribution of PPFD at the GAP site derived from the light measurement field on 22nd of July, 1990. Each square represents a half hour mean value of μmol Photons m^{-2} s^{-1} calculated from 1800 single measurements. At 11 a.m. a sunfleck occurs in the north-western part of the field, which extends and moves southward. At 1 p.m. the sunfleck has vanished.

1992) which was about one third of I_s-values derived from the light-crown of mature trees (Larcher, 1969; Schulte, 1993; Schulze, 1970). Both low I_s-values and high quantum yields should be considered as adaptive reactions of the photosynthetic apparatus to insufficient light intensities (Boardman, 1977; Bolhar-Nordenkampf, 1985).

Hence morphological and physiological features of the aboveground organs of beech saplings ensure an efficient use of low light intensities for carbon fixation.

On the other hand, only limited information is available on the respiratory activity of understorey saplings and studies made so far concentrate exclusively on the investigation of leaf respiration (Masarovicova, 1980, 1988). Data on the respiratory carbon loss of the roots of tree saplings in a low-light climate is lacking, though this factor may contribute considerably to a plant's overall carbon loss.

Based on field experiments done in 1990, data on the respiratory activity of beech sapling roots and its dependence on climatic variables is presented here. Priority has been given to the investigation of fine root respiration rates, due to their high physiological activity in water and nutrient absorption.

Simultaneous measurements of rates of net photosynthesis and root respiration of saplings grown in a natural gap and in the understorey will give information about differences in the C-input : C-output ratio which indicates contrasting carbon economies of shaded and unshaded plant individuals.

Materials and methods

Study area

The study area is situated in the Solling mountains, Lower Saxony, Germany (51°46'N, 9°35'E) at 500 m above sea level. The annual mean temperature is 6.4°C and the annual sum of precipitation is about 1048 mm. The soil type is Typic Dystrochrept with a humus moder type and mean pH(H_2O)-values ranging from 3.8 to 4.2 (Ellenberg et al., 1986).

Two areas, each 600 m^2 were chosen in a 140 to 150-year-old natural beech forest. The density of trees is approximately 240 ha^{-1} with an average height of 30 m.

One plot (UND) was chosen beneath a closed canopy, the other plot was established within a natural gap (GAP) created by a storm in 1972. The average number of seedlings plus saplings at the UND site was only 1 m^{-2}, whereas the density at the GAP site was about 7 m^{-2}. As the subject of investigation, ten-year-old saplings were chosen which had reached an average height of 70 cm (GAP) and 35 cm (UND), respectively.

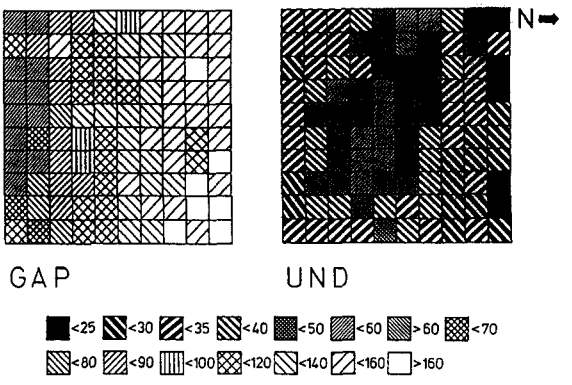

Fig. 2. Daily mean value of PPFD (μmol Photons m^{-2} s^{-1}) at the GAP and the UND site on 22nd of July, 1990. At the UND site PPFD did not exceed 70 μmol Photons m^{-2} s^{-1} but at the GAP site more than 160 μmol Photons m^{-2} s^{-1} were reached.

Methods

a) Light measurement system

To monitor the considerable spatial heterogeneity of the photosynthetic photon flux density (PPFD) a 'light measurement field' was installed at the centre of each plot. Each field consisted of 100 self constructed quantum sensors which were distributed regularly over an area of 10 by 10 m. The signal from each sensor was stored every second by a Pocket Computer (SHARP). Half hour mean values were calculated for each sensor and also stored. This procedure allowed the continuous registration of varying light conditions with special regard to sunflecks over a 3.5 day period (Stickan and Hentzelt, 1991).

Using the mean values as a data base for the creation of light plots by applying Statistical Analysis Software (SAS), the diurnal course of PPFD at each site could be mapped. Figure 1 gives an example of a drifting sunfleck at the GAP site on 22nd of July. Figure 2 demonstrates the daily mean PPFD at the GAP and the UND site on the same day. As an average of several days with diffuse radiation, about 8% of the above canopy light intensity was transmitted at the UND site and 20% was transmitted at the GAP site during the period of closed canopy.

b) Respiration cuvette system

The respiratory activity of different parts of the root system, i.e. fine ($\phi \leqslant 2$ mm), medium (2 mm $< \phi \leqslant 5$ mm) and coarse roots ($\phi > 5$ mm) was measured continuously by a PC-controlled cuvette system developed by Prof Kakubari at the University of Shizuoka, Japan. Twelve PVC cuvettes were connected in parallel with a PC-controlled value timing unit by PVC tubes (ϕ = 5 mm inside) up to 30 m long. The dimensions of a single PVC cuvette were 16.9×10×4.3 cm and it had a volume of 238 cm^3. At one narrow side two PVC tubes were inserted for the aeration of the interior. The opposite side was provided with a slit (ϕ = 6 mm) through which live fine roots, still attached to the sapling, could be inserted. The slit was sealed hermetically with an inert sealing compound. Additionally, each cuvette was equipped with an NTC-temperature sensor. After the insertion of a sample (fine roots, organic material or mineral soil) the cuvette was hermetically sealed with a thick PVC lid and buried at the depth at which the sample originated from.

The CO_2 evolution rate of an enclosed sample was measured by calculating the difference between the CO_2 content of fresh air - collected from just above the forest floor at a remote undisturbed place - pumped into the cuvette and the CO_2 content of the air leaving the cuvette. The duration of a single CO_2 accumulating period was 50 minutes. Previous experiments had shown that the rate of CO_2 evolution during this period was neither restricted by excessive CO_2 concentrations in the cuvette nor accelerated due to preceding aeration. Experiments were run for 3 days and thus, respiration data of 86 CO_2 accumulating periods were recorded. All data necessary for converting CO_2 concentration data into mass flow data (i.e. mass flow of air, time of accumulation, time of cuvette measurement) was logged automatically by an NEC Personal Computer.

c) Calculation of fine root respiration

Respiration rates of soil material were related to the dry mass of the samples, but respiration rates of fine roots were exclusively related to the dry weight of biomass of the samples i.e. without the fraction of necromass (see below). Fine root respiration was calculated as the difference between the respiration rate of a soil sample (O_f, A_h) taken from the immediate vicinity of the selected root and the respiration rate of the root plus attached soil material. For this purpose, the dry weight of the attached soil material had to be determined by treatment in the laboratory (see below).

Most of the investigated fine roots grew in the organic layer and were excavated carefully with a small fork. Care was taken not to tear off distal ramifications so as to avoid wound respiration.

d) Fine root sample treatment

Respiration experiments were conducted between April and December, 1990. As a rule, one sample per tree was investigated, but in some cases the respiration rates of three fine root samples of a single tree were measured simultaneously. At the end of an experiment, the enclosed fine root samples were detached with a pair of scissors and treated in the laboratory as follows:

1. The roots were washed under a binocular with a gentle jet of water and rinsed out soil material was collected quantitatively. Subsequently, soil matter was dried at 105°C for 24 hours.
2. Mycorrhiza species were determined following Agerer (1986, 1988) and Agerer et al. (1986) and collected quantitatively. Mycorrhizal necromass was also collected, but without regard to different species. Each fraction was dried in a freeze-drier (Alpha II–12, Christ) for 24 hours and its dry weight determined.
3. Non mycorrhized fine roots were separated into dead and living root fragments, considering the white colour of the central cylinder and its elasticity as live criteria. The texture of the root tissue, its colour and the condition of lateral root tips were used as supplementary criteria (Murach, 1984).

e) Medium and coarse root respiration

To measure medium and coarse root respiration, a small section was layed bare and washed carefully with a weak antiseptic solution (Orthocid 83: 5 g L^{-1}; Tetracycline: 100 mg L^{-1}; Tween 20: 2 mL L^{-1}). Subsequently the fraction was hermetically sealed in a cylindrical PVC cuvette (28.3 cm^3) and covered entirely with moist soil material. After the measurement period the sections were cut off and dry weight was determined. The percentage of dry weight of live tissue of such a section was calculated from the histochemical investigation of cross sections, applying staining methods for starch (Essiamah and Eschrich, 1985; Neemann and Stickan, 1991).

f) Photosynthetic measurements

During the vegetation period, assimilation and respiration rates of leaves of the GAP and UND saplings were investigated by a minicuvette gas exchange system using the IRGA technique (Walz, Effeltrich, FRG). Experiments were carried out with special regard to the influence of sunflecks on the net assimilation rate. For this purpose, sunflecks were simulated using halogen light of high radiant energy (200W) (Rees and Stickan, 1991).

Table 1. Biometric data of 10-year-old beech saplings grown in the understorey (UND) and in a natural gap (GAP). Mean values of six saplings are given which were harvested quantitatively at each site. Root systems were excavated with the aid of rinsing water minimizing loss of biomass

		Local-site	
		UND	GAP
Leaf area	dm^2	7.0	35.0
Leaf biomass	gDW	2.6	14.4
Mass of main shoot	"	3.0	22.0
Mass of lateral shoots	"	3.3	35.1
Mass of main root	"	3.8	19.9
Mass of lateral roots	"	0.5	11.4
Biomass of fine roots	"	1.0	6.5
Total mass	"	14.2	109.3
Root:Shoot ratio		1.7	1.9

DW = dry weight.

g) Statistics

Statistical Analysis Software (SAS) was applied for statistical calculations. The correlation of respiration rates with different independent variables was investigated by nonlinear regression analysis (Sachs, 1992, 489 ff). A student 't' test was used to determine significant ($p < 0.01$) differences between the respiration rates of UND saplings and those of GAP saplings.

Results

a) Biometric data

Table 1 gives the average biometric data of 10-year-old beech saplings grown at the GAP site and in the understorey (UND), respectively. At both sites, live fine roots make up about 20% of the entire root mass. Although total dry weight of GAP saplings is about 8 times higher than that of UND saplings, root : shoot ratios are very similar. The specific leaf area which will be defined here as leaf area per gram plant dry weight (cm^2 gDW^{-1}) is 50 for UND saplings and 32 for GAP saplings, respectively.

b) Carbon assimilation

Light saturation curves of net photosynthesis of leaves from UND saplings corresponded with those of shade leaves from mature trees and reached maximum PPFD values at the end of May (177 μmol Photons m^{-2} s^{-1}). Net photosynthesis of leaves from GAP saplings was light saturated by a PPFD of 258 μmol Photons m^{-2} s^{-1} (Rees and Stickan, 1991).

Net photosynthetic rates under light saturation (A_{max}) of GAP saplings exceeded those of UND saplings during the entire vegetation period and reached their maximum in July (6.7 μmol CO_2 m^{-2} s^{-1}). The maximum value for UND saplings was 4.4 μmol CO_2 m^{-2} s^{-1}, which was also reached in July (Rees, personal communication).

Experiments on the significance of sunflecks for carbon fixation were carried out at 10 minute intervals under light saturated conditions. It was detected that leaves of UND saplings reached half the maximum net photosynthetic rates after 3 minutes of illumination, whereas leaves of GAP saplings reached half the maximum values in half the time. About 29% of the net assimilation rate of GAP saplings under limited PPFD (20–50 μmol Photons m^{-2} s^{-1}) was due to the occurence of an artificial sunfleck i. e. when light saturation was generated for 10 minutes. For UND saplings, this fraction was only 10%. Thus, leaves of UND saplings showed no clear disposition to the efficient use of sunflecks. It seems more likely that a profound adaptation of the photosynthetic apparatus to continuously low light intensities is more important for UND saplings than short-term reactions to sunflecks (Rees and Stickan, 1991).

c) Fine root respiration

Figure 3 gives a typical graph of the respiration rate of a fine root sample at the GAP and UND site over three days at the end of May, 1990. The mean rate was 3.3 ± 1.7 nmol CO_2 gDW^{-1} s^{-1} for the former and 6. 2 ± 0. 9 nmol CO_2 gDW^{-1} s^{-1} for the latter, whereas mean values of temperature were very similar (GAP: 10.8 ± 1.3 °C, UND : 10.1 ± 1.3 °C). The respiration rates corresponded with the seasonal temperature curves which indicates a strong dependence of respiration on temperature.

This relationship could best be described by a quasi-Arrhenius type curve (Janecek et al., 1989): r(T) = exp (a· (T-b)) with r = respiration rate (mgC gDW $^{-1}$ d^{-1}) and T = temperature (°C). The parameters 'a' and 'b' were calculated by applying nonlinear regression anal-

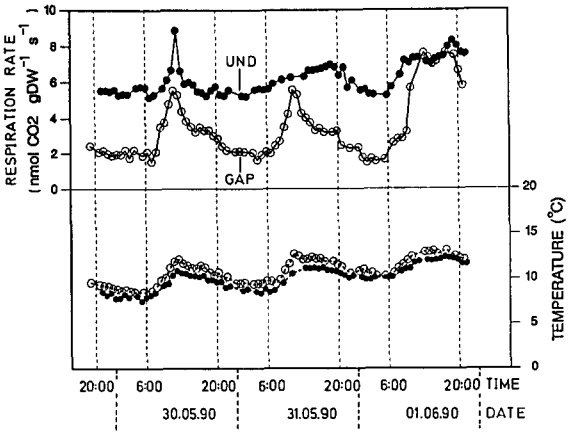

Fig. 3. Respiration rates of two fine roots at the UND and at the GAP site over a three-day period at the end of May. Both graphs coincided with the temperature graphs (UND: n=70, r=0.82; GAP: n=73, r=0.85).

ysis of the Statistical Analysis Software (SAS). Based on the respiration data throughout the year, correlation coefficients of 0.91 (n=24) for the UND site and 0.82 (n=20) for the GAP site were found ($p < 0.001$) (Fig. 4a,b). For the vegetation period from May until October correlation coefficients were 0.78 (n=19) for the former and 0.72 (n=16) for the latter ($p < 0.001$).

In Figure 5, a comparison is made between the respiration rates of UND and GAP fine roots from April until December. Despite nearly identical temperature curves at both sites from April until July, the respiration rates at the UND site were higher than those at the GAP site.

During the vegetation period, a highly significant negative correlation of root respiration and water content of the attached organic material was detected at the UND site (Fig. 6a), whereas at the GAP site no such correlation was found (Fig. 6b).

Beside temperature and water content as climatic variables, the influence of ectomycorrhizal infection on the respiration rates was considered. As a rule, a single root sample was infected by the hyphae of several basidiomycetes e.g. *Xerocomus chrysenteron* ((Bull. ex St. Amans) Quel.), *Lactarius subdulcis* (Bull. ex Fr.) and *Russula ochroleuca* ((Pers.) Fr.). Hence, the mycorrhizal biomass, as a portion of the total respiring biomass of a sample was used as the reference quantity. At the UND site (Fig. 7a) a significant correlation ($p < 0.01$) of mycorrhizal biomass and respiration rate was detected (r=0.63, n=19) but this was not the case at the GAP site (r=0.5, n=14) (Fig. 7b).

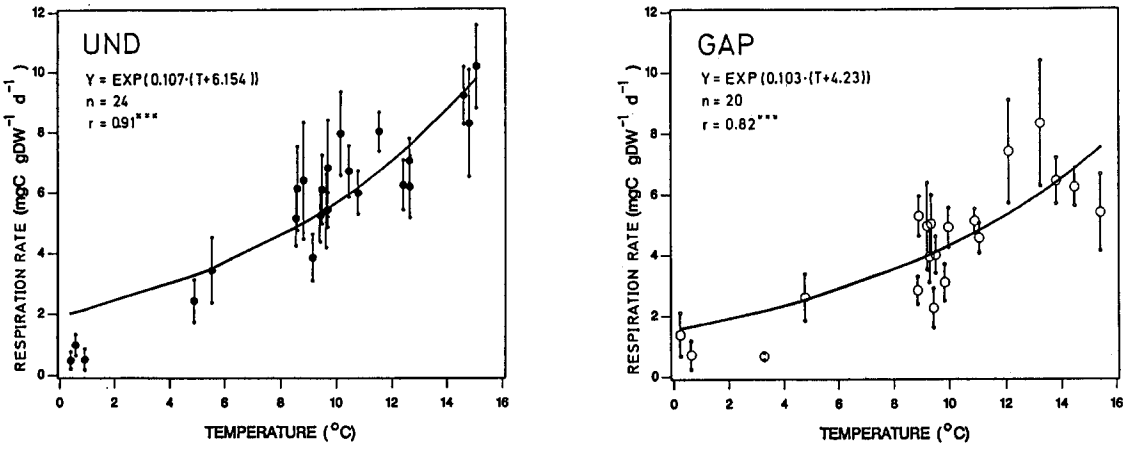

Fig. 4. Dependence of fine root respiration on temperature. Each dot (circle) represents a mean value of a three-day period which consists of 70 to 80 single measurements. Respiration rates were investigated from April until December, 1990.

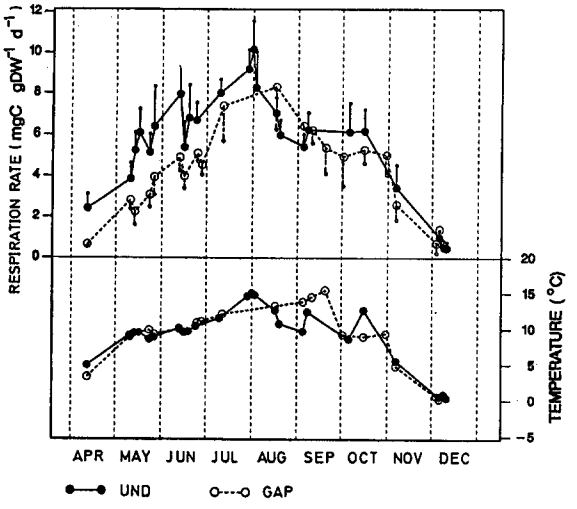

Fig. 5. Annual graph of fine root respiration of beech saplings grown in the understorey (UND) and in the natural gap (GAP). Root respiration at the UND site was higher than at the GAP site during the first half of the vegetation period, although temperatures were very similar.

d) Respiration of medium and coarse roots

Medium and coarse root respiration rates were found to be very similar. Furthermore, no significant differences between samples from the gap and the understorey could be determined. During spring, the mean respiration rates of 4 medium roots, which had been measured at each plot over 2 three-day periods, did not exceed 0.9 nmol CO_2 gDW^{-1} s^{-1} (T=3.9 ± 1.7 °C). Often at night no respiratory activity could be detected. During daytime, the respiration rates of five samples increased with increasing temperature, whereas the others did not follow such a temperature course. Here, respiration rates were more or less alternating with no clear pattern. In mid-summer, a mean rate of 1. 5 ± 0.2 nmol CO_2 gDW^{-1} (T=14.1 ± 1.5°C) was typical and daytime respiration did not differ significantly from night time respiration.

In Figure 8, an example of coarse root respiration at the end of July is presented. Although temperature shows a slight decrease at both sites during the experiment, the respiration rates (GAP and UND) were increasing. The mean values of 1.6 ± 0.4 (GAP) and 1.2 ± 0.2 nmol CO_2 gDW^{-1} s^{-1} (UND) were not significantly different from each other. The maximum respiration rate of this root class was measured in the middle of July and had a mean value of 3.1 ± 0.3 nmol CO_2 gDW^{-1} s^{-1} (T=13 ± 1°C). In comparison with fine root respiration rates, medium and coarse roots showed much lower respiratory carbon losses, but these were more constant during the diurnal course and even throughout the year.

e) Input: output ratios for carbon

In Table 2, mean values of daily net assimilation and fine root respiration per plant are given for each month during the vegetation period 1990. The calculation of net assimilation considers varying light saturation curves (Schulte, 1993; Schulze, 1970) of GAP and UND saplings as well as changes in light intensities at both plots during this period. Due to low light intensities at the UND site a net assimilation rate of only 0.3 mg C $plant^{-1}$ d^{-1} was calculated for September. During October, leaf respiration rates of UND saplings often exceeded assimilation rates and thus, a negative

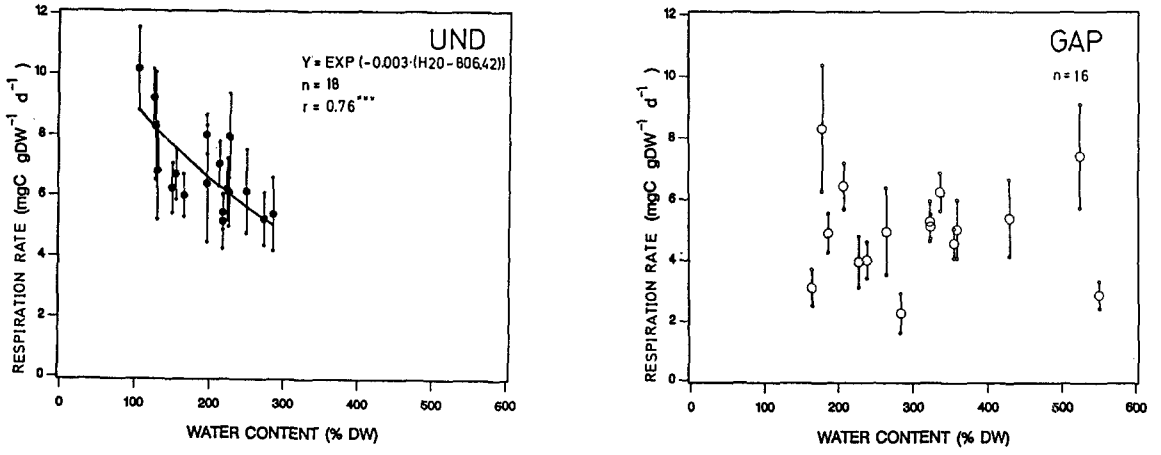

Fig. 6. Dependence of fine root respiration on the water content of the attached organic soil material ($O_f + O_h$) during the vegetation period in 1990. Water content is given in per cent of dry weight of the organic material.

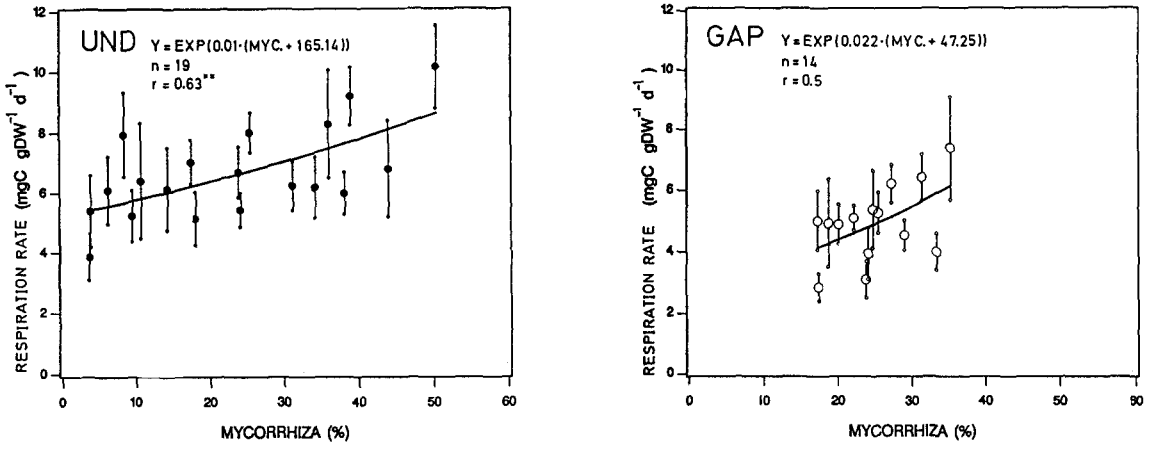

Fig. 7. Dependence of fine root respiration on the mycorrhizal infection rate during the vegetation period in 1990. The infection rate is given in per cent of dry weight of respiring biomass. Root samples were infected by the hyphae of several ectomycorrhiza forming basidiomycetes.

Table 2. Net assimilation rates (C_{in}) and fine root respiration rates (C_{out}) of a representative UND and GAP sapling calculated as a mean value for each month during the vegetation period in 1990

	Local site					
	UND			GAP		
	Net assimilation rate	Fine root respiration rate	$C_{in} : C_{out}$	Net assimilation rate	Fine root respiration rate	$C_{in} : C_{out}$
	(mgC plant^{-1} d^{-1})			(mgC plant^{-1} d^{-1})		
May	56 ± 15	5.4 ± 1	10	548 ± 95	19.7 ± 4.6	28
Jun	111 ± 19	6.7 ± 1	17	560 ± 113	30.1 ± 3.2	19
Jul	55 ± 21	8.9 ± 1	6	740 ± 141	48 ± 2.4	15
Aug	51 ± 22	6.5 ± 0.7	8	494 ± 113	54 ± 3.7	9
Sep	0.3 ± 17	5.8 ± 0.6	0	262 ± 100	39 ± 3.6	7
Oct	-2 ± 18	6.2 ± 0.1	0	241 ± 140	33 ± 1.5	7

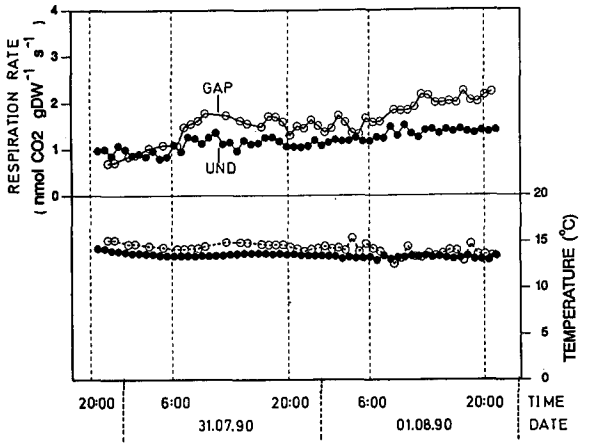

Fig. 8. Respiration rates of two coarse root segments at the GAP and at the UND site over a two-day period at the end of July, 1990. Although temperature graphs showed a slight decrease, respiration rates of both increased during this period.

mean value was calculated, whereas the net assimilation of GAP saplings reached a rate of 241 mgC plant^{-1} d^{-1}. Mean respiration rates of fine roots were derived from several three-day measurement periods each month. The comparison of C-input : C-output ratios of both sites revealed higher values for the GAP saplings each month, especially in May and July. These large differences are due to the high ratios of daily net assimilation (GAP : UND) compared to those of daily fine root respiration, which underlines the importance of light for UND saplings.

Discussion

The comparative study of photosynthesis and respiration as the two basic processes in carbon metabolism in saplings grown in the understorey and in a natural gap proved to be a useful tool for the interpretation of contrasting intraspecific growth patterns.

The optimized adaptation of leaves to low light intensities has been emphasized as a requirement for efficient growth (Canham, 1988, 1989; Chazdon, 1986, 1988; Gross, 1982), but it remains open, whether insufficient light alone is responsible for growth limitation. Therefore, emphasis was paid on the investigation of respiratory patterns of the root systems of GAP and UND saplings. Different respiration rates with varying dependencies on environmental variables may additionally strengthen divergent growth patterns.

Basically, in situ measurements of root respiration can only yield approximate data, because any disturbance of the root and its environment e.g. alterations in soil moisture, nutrient supply, O_2 : CO_2 ratio, microbial density etc. may cause deviations from the natural respiratory state. Chapman (1979) suggested, that washed root material had up to five times higher respiration rates than estimated from his regression models. Our measurements on washed fine roots which had been embedded in sterilized and moistened silica sand however, revealed a distinct decrease in respiration and almost no reaction to temperature variations.

On the other hand, indirect measurement of fine root respiration rates as described here, must consider the respiratory activity of microbes, living on the root surface and in the adhering soil material, i.e. the rhizosphere (Campbell and Greaves, 1990; Newman, 1985). The investigation of harvested beech fine roots showed that the ratio of microbial density of the rhizosphere to root-free organic soil material ranged from 9 to 22 (Carlberg, 1992), but this was not in accordance with similar ratios of the respective respiration rates measured in our laboratory (Gansert, unpubl. data). Thus, it is likely that the respiration rate as calculated here, was not overestimated due to an underestimation of rhizosphere respiration.

At both sites, root respiration showed a close dependence on soil temperature throughout the year. This was also valid during the vegetation period, when the temperature varied only 7°C. Although the relationship between temperature and respiration rate has been well documented (Larcher, 1980; Long and Woodward, 1988 ; Lyr et al., 1992; Precht et al., 1973), it should be kept in mind, that root respiration in the field is affected by several other interacting variables such as water and nutrient supply (Lambers, 1985; Lambers et al., 1991; Palta and Nobel, 1989), root growth activity (Veen, 1981; Waisel and Eshel, 1991) and internal carbohydrate levels (Amthor, 1989; Farrar and Williams, 1991). Hence, a clear correlation of temperature with root respiration will only be possible, when such variables have no important influence.

The correlation of fine root respiration and water content at the UND site and the absence of such a relationship at the GAP site points to an influence of water content on root respiration. During the vegetation period, the water content of the organic layers (O_f plus O_h) at the UND site was 30% lower than at the GAP site and water shortage occured for several days during July and August. This phenomenon was probably caused by the water uptake of mature trees, which accumulate a large part of their fine roots in these layers (Ellenberg et al., 1986; Rapp, 1991).

Ladefoged (1939) observed that beech fine roots originating from thick taproots showed an increase in growth rate during periods of drought, whereas those originating from thin horizontal roots of the same tree were often supressed. He assumed, that the former could be sufficiently supplied with water from deeper soil layers and, thus, an increased growth rate could be due to higher temperatures. This assumption may be of importance for the interpretation of increased fine root respiration rates of UND saplings during dry periods, because these roots often originated from the main root. Other authors, however, observed a decrease of fine root biomass during the dry summer months and related this finding to the prevailing low soil moisture (Deans, 1979; Göttsche, 1972; Hoffmann, 1972). On the other hand, Comeau and Kimmins (1989), Nisbet and Mullins (1986) and Santantonio and Hermann (1985) determined an increased production of fine roots on dry sites which is in accordance with Gales (1977, 1979) who reported that the root : shoot ratio increased in response to drought. From these reports can be concluded that further information on the interaction of root respiration and water availability is of great importance for the understanding of carbon economy under various climatic conditions.

A significant relationship between rates of fine root respiration and rates of mycorrhizal infection could only be detected for UND saplings but not for GAP saplings. This may be due to the small range of mycorrhizal infection of fine roots from this site. Additionally, results from laboratory experiments (Gansert, unpubl. data) showed that respiration rates of non mycorrhized fine roots of 3-year-old beech saplings were of the same magnitude as rates of mycorrhized roots in the field. Harley (1969, pp 98) emphasized that 'on a dry weight basis, uninfected and mycorrhizal roots of *Fagus sylvatica* respired at much the same sort of rate and no explanation of function or difference of behaviour could really be linked with their rates of respiration'. Similarly, Kramer and Hodgson (1954) pointed out that the oxygen consumption of mycorrhizal roots of *Pinus taeda* was about 1.4 times as great as that of non mycorrhizal roots on a fresh-weight basis, but was considerably smaller on a dry-weight or surface-area basis. Thus, it is of importance to look much closer at the relationship between fine root respiration and mycorrhizal infection under field conditions.

With respect to the ratios of net assimilation and those of fine root respiration of the GAP and UND saplings during the vegetation period it should be concluded that limited net assimilation rates due to insufficient light intensities are largely responsible for limited growth of UND saplings. Additionally, the relationships of respiration rates and water content as well as mycorrhizal infection rate for the UND saplings indicate an increased sensitivity of fine root respiration to other abiotic and biotic variables. Thus, it is likely that under detrimental environmental conditions like water shortage in dry summer periods the growth rate of understorey beech saplings will be retarded, whereas that of GAP saplings remains unaffected.

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