THE MEASUREMENT AND SIMULATION OF CO_2 EFFLUX IN A FLORIDA SLASH PINE PLANTATION

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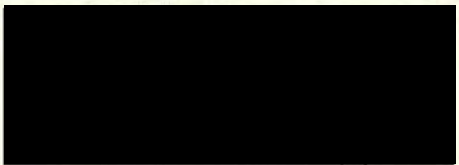
A thesis submitted for the degree of Doctor of Philosophy to the University of Edinburgh

Declaration

I declare that this thesis has been composed by myself from the results of my own work, except where stated otherwise, and has not been submitted in any previous application for a degree.



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ABSTRACT

Accurately measuring CO_2 efflux from the soil surface and adequately simulating the processes of CO_2 production and transport in the soil are crucial to enhance our understanding of carbon cycling in an ecosystem and at the global scale. However, significant uncertainty remains in both measurement and simulation of the efflux.

An open-top, dynamic chamber technique was developed for *in situ* CO_2 efflux measurement. The pressure difference between inside and outside the chamber was found to be a dominant factor controlling the measured CO_2 efflux from the soil surface with dynamic chamber methods as a change of a few tenths of a Pa in the pressure difference will cause a several fold variation in the measured CO_2 efflux. This influence is negligible in this new open-top chamber. A flow rate up to 8 $dm^3\ min^{-1}$ has no influence on the measured CO_2 efflux.

The mean carbon dioxide efflux, measured in a mature Florida slash pine (*Pinus elliottii* Engelm. var. *elliottii*) plantation in 1995-1996, was 0.217 mg $CO_2\ m^{-2}\ s^{-1}$ (varying from 0.179 to 0.253) in October 1995 and 0.087 mg $CO_2\ m^{-2}\ s^{-1}$ (varying from 0.031 to 0.146) in January 1996. Soil temperature, which accounts for about 90% of the variability in CO_2 efflux, is by far the most influential factor controlling the CO_2 efflux from the soil surface. The Q_{10} value for soil CO_2 efflux in relation to soil temperature measured at 5 cm is 2.5 and the activation energy of soil respiration has a value of 56.9 kJ mol^{-1}.

Soil respiration in the slash pine plantation is highly spatially variable, and generally increases with increase in fine root biomass, litter and humus amount on the forest floor but is inversely related to the amount of organic matter in the mineral soil. The spatial heterogeneity of CO_2 efflux in the plantation is mainly caused by the uneven distribution of palmetto plants and can be well explained by a simple model incorporating live and dead biomass and soil total porosity as predictor variables.

CO_2 concentration in the soil gas increases with depth, with ranges of 0.25 % to 1% by volume at a depth of 60 cm and 600-760 cm^3 m^{-3} at 2 cm depth during October and January in the slash pine ecosystem.

A process-based, one-dimensional model was developed to describe CO_2 production, transport and distribution in the soil and to predict the total CO_2 efflux from the soil surface.

Model sensitivity analysis shows that CO_2 evolution in the slash pine plantation is most sensitive to soil temperature and associated parameters. Moisture contents in the mineral soil hinder CO_2 transport in the summer and the autumn but slightly reduce soil respiratory activity in the winter. Simulated CO_2 efflux varies from 0.066 to 0.321 mg CO_2 m^{-2} s^{-1} during the year with an annual total of 5.1kg CO_2 m^{-2}. Soil respiration, including root and microbial respiration, is simulated to vary from 0.066 to 0.312 mg CO_2 m^{-2} s^{-1} through the year with an estimated annual production of about 5.1 kg CO_2 m^{-2} in 1995-1996. Of the total CO_2 released from the soil surface, about 53% comes from live root respiration and 47% from the decomposition of organic matter. Most CO_2 is produced in the litter and humus layer and the top 15 cm of the mineral soil, with contributions of about 43% and 32% of the total annual efflux, respectively.

TABLE OF CONTENTS

TITLE PAGE AND DECLARATION i

ACKNOWLEDGMENTS ii

ABSTRACT iii

TABLE OF CONTENTS iv

LIST OF SYMBOLS ix

CHAPTER 1: INTRODUCTION AND AIMS 1

1.1 Background 1

1.2 Aims of this Study 6

1.3 CO_2 Efflux Measurement 8

1.3.1 Basic concepts 8

1.3.2 Laboratory techniques 10

1.3.3 Field techniques 12

1.3.3.1 Chamber methods 12

1.3.3.1.1 Enrichment chambers 12

1.3.3.1.2 Absorption chambers 15

1.3.3.1.3 Dynamic chambers 19

1.3.3.2 Soil CO_2 profile method 24

1.3.3.3 Micrometeorological methods 26

1.4 Estimation of the Root Respiration Fraction 28

1.4.1 Laboratory methods 28

1.4.2 Field methods 30

1.5 Modelling CO_2 Efflux 33

1.5.1 Empirical models 34

1.5.1.1 Single variable models 34

1.5.1.1.1 Temperature 34

1.5.1.1.2 Moisture 38

1.5.1.2 Multiple variable models 39

1.5.1.2.1 Linear models 39

1.5.1.2.2 Polynomial model 40
1.5.1.2.3 Other models 41
1.5.2 Non-empirical models 43
1.5.2.1 CO_2 transport in the soil 43
1.5.2.2 Models for CO_2 production 45
1.5.2.2.1 Bunnell's model 45
1.5.2.2.2 Šimunek's model 46
CHAPTER2: THE OPEN-TOP CHAMBER 48
2.1 Introduction 48
2.2 Materials and Methods 49
2.2.1 Chamber description 49
2.2.2 Measurements of CO_2 efflux 52
2.3 Results 54
2.3.1 Chamber setting and measured CO_2 efflux 54
2.3.2 Influence of pressure difference on measured CO_2 efflux 57
2.3.3 Influence of flow rate on measured CO_2 efflux 58
2.4 Discussion 60
2.5 Summary and Conclusions 63
CHAPTER 3: SOIL CO_2 EFFLUX FROM A SLASH PINE PLANTATION 64
3.1 Introduction 64
3.2 Materials and Methods 66
3.2.1 Site description 66
3.2.2 Measurement of CO_2 efflux 67
3.2.3 Soil gas collection and CO_2 concentration analysis 69
3.2.4 Measurements of environmental factors 72
3.2.5 Spatial variation of CO_2 efflux — theory 76
3.3 Results 79
3.3.1 CO_2 efflux and its temporal variation 79
3.3.2 Relation of CO_2 efflux to soil temperature 82

3.3.3 Spatial variation of soil respiration 83
3.3.4 CO_2 concentration in the soil 87
3.4 Discussion 89
3.4.1 Magnitude of CO_2 efflux 89
3.4.2 Temperature dependence of CO_2 efflux 90
3.4.3 Spatial variation of CO_2 efflux 92
3.4.4 CO_2 profile in the soil 96
3.5 Summary and Conclusions 97
CHAPTER 4: MODELLING SOIL RESPIRATION 99
4.1 Introduction 99
4.2 Model Description 100
4.2.1 CO_2 mass balance and transport in the soil 101
4.2.2 CO_2 production in the soil 106
4.2.3 Influences of environmental factors on soil respiration 109
4.2.4 Dynamics of soil litter and organic matter 113
4.3 Application in Slash Pine Plantation 114
4.3.1 Initial conditions in the slash pine site 114
4.3.2 Boundary conditions for model solution 116
4.3.3 Determination of parameters 117
4.4 Model Validation 119
4.4.1 CO_2 efflux 119
4.4.2 CO_2 concentration 120
4.5 Sensitivity Analysis 122
4.5.1 Sensitivity of annual CO_2 efflux to model parameters 122
4.5.2 Sensitivity of annual CO_2 efflux to initial conditions 126
4.5.3 Sensitivity of CO_2 efflux to model inputs 128
4.6 Results of Simulation 131
4.6.1 Seasonal pattern of total CO_2 efflux and soil respiration 131
4.6.2 Soil respiration at different depths 132
4.6.3 Contribution of roots and microbes to soil respiration 133

4.6.4 CO_2 concentration in soil gas 135
4.7 Discussion 137
4.7.1 The influence of soil moisture on CO_2 efflux 137
4.7.2 Response of soil respiration to O_2 concentration 139
4.7.3 Diffusion in liquid phase 140
4.7.4 Relation between respiration of different soil layers 141
4.7.5 Temporal variation in CO_2 efflux 141
4.7.6 Turnover rate of soil organic matter 143
4.7.7 Root respiration rate 144
4.7.8 Root : microbial contribution 146
4.7.9 CO_2 concentration in soil gas 146
4.7.10 Response of CO_2 efflux to climate change 148
4.7.11 Model limitation and applicability 150
4.8 Future Work 151
4.9 Summary and Conclusions 153
CHAPTER 5: SUMMARY AND FINAL CONCLUSION 156
REFERENCES 159
APPENDIX 185
A1 Pictures 185
A2 Publications 188

LIST OF SYMBOLS

A	soil surface area covered by a chamber, m^2.
B	live root biomass, g dry mass m^{-2}.
B_i	live root biomass of size class *i*, g dry mass m^{-2}.
B'	equivalent root biomass, g dry mass m^{-2}.
C_{dif}	CO_2 concentration difference between sample and reference gas.
C_g	CO_2 concentration in soil gas, mg CO_2 m^{-3}.
C_{gi}	concentration of component *i* in soil gas, mg m^{-3}.
C_T	total concentration of CO_2 in both gas and liquid phase in the soil, mg CO_2 m^{-3}.
C_w	CO_2 concentration in soil water, mg CO_2 m^{-3}.
C_{wi}	concentration of component *i* in soil water, mg m^{-3}.
d*c*/dz	vertical gradient of CO_2 concentration in soil gas, mg CO_2 m^{-3} m^{-1}.
D	Julian day in the year.
D_g	CO_2 gaseous diffusion coefficient in the air, m^2 s^{-1}.
D_{g_0}	CO_2 gaseous diffusion coefficient in the air at 273.16 K and 101.3 kPa, m^2 s^{-1}.
D_{gs}	CO_2 gaseous diffusion coefficient in the soil, m^2 s^{-1}.
D_w	CO_2 diffusion coefficient in soil water, m^2 s^{-1}.
$D_0^{CO_2} / D_0^{Rn}$	ratio of molecular diffusion coefficients for CO_2 and radon in the soil.
E	activation energy for soil respiration, kJ mol^{-1}.
f	gas flow rate through the chamber, dm^3 min^{-1}.
$f(O_2)$	scaling factor of O_2 concentration in soil gas on soil respiration.
$f(T)$	temperature dependence of soil respiration.
$f(W)$	influence of soil water content on soil respiration.
$f(W)_{max}$	maximum of $f(W)$.
F	CO_2 efflux, mg CO_2 m^{-2} s^{-1}.

F_i	CO_2 efflux from the soil surface at location i, mg CO_2 m^{-2} s^{-1}.
F_{ag}	gaseous advective flux of CO_2 in the soil, mg CO_2 m^{-2} s^{-1}.
F_{agi}	gaseous advective flux of component i of soil gas, mg m^{-2} s^{-1}.
F_{aw}	advective flux of CO_2 in liquid phase in the soil, mg CO_2 m^{-2} s^{-1}.
F_{awi}	advective flux of component i in liquid phase, mg m^{-2} s^{-1}.
F_{dg}	gaseous diffusion/dispersion flux of CO_2 in the soil, mg CO_2 m^{-2} s^{-1}.
F_{dgi}	gaseous diffusion/dispersion flux of component i in the soil, mg m^{-2} s^{-1}.
F_{dw}	diffusion/dispersion flux of CO_2 in dissolved phase in the soil, mg CO_2 m^{-2} s^{-1}.
F_{dwi}	diffusion/dispersion flux of component i in dissolved phase in the soil, mg m^{-2} s^{-1}.
F_{Rn}	radon flux in the soil.
h, h_1, h_2, h_3	soil water pressure head (parameters related to soil water potential), m.
H	hour in the day.
k	decomposition constant of soil organic matter, g g^{-1} s^{-1}.
k_{lab}	decomposition rate of soil labile organic matter, g g^{-1} s^{-1}.
k_{ris}	decomposition rate of soil resistant organic matter, g g^{-1} s^{-1}.
K_1	Henry's law constant.
K_2, K_3	constants in ionizing reaction of hydrogen carbonates.
K_c	transfer coefficient of CO_2 in boundary layer.
K_M	Michaelis-Menten constant, mg m^{-3}.
L_0, L	litter amount at time *0* and *t*, g dry mass m^{-2}
$L(t)_l$	dynamics of litterfall for surface layer, g dry mass m^{-2} day^{-1}.
$L(t)_s$	input of root debris in the mineral soil, g dry mass m^{-2} day^{-1}.
M	amount of soil organic matter, g dry mass m^{-2}.
M'	equivalent amount of soil labile organic matter, g dry mass m^{-2}.
M_0	amount of soil organic matter initially, g dry mass m^{-2}.

M_{lt}	amount of litter and humus on the forest floor at time t, g dry mass m^{-2}.
M_{st}	organic matter in the mineral soil at time t, g dry mass m^{-2}.
M_t	amount of soil organic matter remaining at time t, g m^{-2}.
M_{tranl}	organic matter exchanged with other soil layers in surface layer, g m^{-2} per unit time.
M_{trans}	organic matter exchanged with other soil layers in the mineral soil, g m^{-2} per unit time.
N	number of bacterial colonies, 10^{-6} g air-dry $litter^{-1}$.
$[O_2]$	oxygen concentration in soil gas, mg O_2 m^{-3}.
P	air pressure, Pa.
P_{CO_2}	partial pressure of CO_2 in soil gas, Pa.
P_r	mean annual precipitation, mm.
Q_{10}	reaction rate increment with a temperature rise of 10 °C.
q_g	advective flux of soil gas, m s^{-1}.
q_w	advective flux of soil water, m s^{-1}.
R	universal gas constant, 8.314J $K^{-1}mol^{-1}$.
R_r	root respiration rate, mg CO_2 m^{-2} s^{-1}.
R_m	microbial respiration in the soil, mg CO_2 m^{-2} s^{-1}.
R_{ml}	microbial respiration rate in litter and humus layer, mg CO_2 m^{-2} s^{-1}.
R_{ms}	microbial respiration rate in the mineral soil, mg CO_2 m^{-2} s^{-1}.
S	source/sink of CO_2 in the soil, mg CO_2 m^{-2} s^{-1}.
S_i	source/sink of component i in the soil, mg m^{-2} s^{-1}.
S_T,	total CO_2 production rate, mg CO_2 m^{-2} s^{-1}.
t	time.
T	temperature.
T_m	temperature of maximal effect on microbial activity, °C.
V_{ch}	volume enclosed by a chamber, m^3.
V, V_{max}	reaction rate and its maximum.

V_g	volumetric fraction of air in the soil, $m^3\ m^{-3}$.
V_w	volumetric fraction of water in the soil, $m^3\ m^{-3}$.
W	soil moisture, g water g^{-1} dry mass.
W_d	depth of water table below the soil surface, m.
w'	fluctuations of vertical wind speed, m s^{-1}.
z	depth in the soil or height above a surface, m.
α	constant of organic matter transforming into CO_2, mg CO_2 g^{-1}.
ΔC	CO_2 concentration increment, mg CO_2 m^{-3}.
ΔC_{Rn}	concentration difference of radon.
ΔH	enthalpy change in ionizing reactions of hydrogen carbonates, kJ mol^{-1}.
Δt	time interval.
Δx	zero shift of IRGA, $cm^3\ m^{-3}$.
$\partial c/\partial z$	vertical gradient of CO_2 concentration, mg CO_2 m^{-3} m^{-1}.
$\varepsilon(\phi_g)$	tortuosity factor of gas diffusion in the soil.
$\varepsilon(\phi_w)$	tortuosity factor in water phase in the soil.
ϕ_g	air-filled soil porosity, $m^3\ m^{-3}$.
ϕ_{g1}	intra-aggregate air-filled pore space in the soil, $m^3\ m^{-3}$.
ϕ_{g2}	inter-aggregate air-filled pore space in the soil, $m^3\ m^{-3}$.
ϕ_T	total soil porosity, $m^3\ m^{-3}$.
ϕ_{T1}	intra-aggregate total pore space in the soil, $m^3\ m^{-3}$.
ϕ_{T2}	inter-aggregate total pore space in the soil, $m^3\ m^{-3}$.
γ_m	microbial respiration rate coefficient, mg CO_2 m^{-2} s^{-1}.
γ_{m0}	optimal microbial respiration rates at a given temperature T_0, mg CO_2 m^{-2} s^{-1}.
γ_r	respiration rate of the finest root, mg CO_2 m^{-2} s^{-1}.
γ_{r0}	optimal root respiration rate at a given temperature T_0, mg CO_2 m^{-2} s^{-1}.
γ_{r_i}	respiration rate constant of root size class i, mg CO_2 m^{-2} s^{-1}.
λ	ratio of soil labile organic matter to total organic matter.

λ_w	CO_2 dispersion coefficient in soil water, m.
ρ_c'	fluctuation of CO_2 concentration.

CHAPTER 1: INTRODUCTION AND AIMS

1.1 Background

Recently, a great deal of attention has been focused on the anthropogenic perturbations to the global carbon cycle and the possible consequences for the climate system (Foley, 1995). The concentration of atmospheric CO_2 has increased rapidly as a result of large scale deforestation and increasing industrial emissions. Soil organic matter and detritus represent a very large reservoir of carbon (more than 1500 Gt C), perhaps double that in the atmosphere (IPCC, 1995; Foley, 1995). The emission of CO_2 from the soil is estimated (50-75 Gt C yr^{-1}) to be equal to or greater than the estimated global terrestrial net primary productivity (50-60 Gt C yr^{-1}) and much greater than the CO_2 released into the atmosphere by burning fossil fuel (about 5-6 Gt C yr^{-1}, Raich and Schlesinger, 1992; IPCC, 1995). Any fluctuation in soil carbon storage, even if small, or in CO_2 efflux from the soil to the atmosphere, may result in a significant change in the atmospheric CO_2 concentration. The role of terrestrial ecosystems in determining, in part, the global carbon cycle has attracted growing attention not only because of the huge amount of CO_2 released from the soil but also because of the need to reduce the uncertainty in estimating the exchange of CO_2 between the atmosphere and biosphere (Taylor and Lloyd, 1992) and to establish the potential response of soil carbon to global climate changes (Trumbore *et al.*, 1996).

Measuring soil CO_2 efflux correctly and accurately is important at both ecosystem and global carbon cycle level. The CO_2 efflux density is regarded as a useful index of metabolic activity of ecosystems and can be used to examine the impact of disturbances, such as cutting and burning, on relative site productivity (Weber, 1990). An accurate estimation of soil CO_2 efflux provides useful information on heterotrophic activity, root respiration rates, soil-atmosphere interaction, soil energy and C budgets, and plant productivity (Raich *et al.*, 1990), as well as contributing substantially to a general understanding of the turnover rates that characterize and regulate ecosystems (Ewel *et al.*, 1987a). At the level of the global

carbon cycle, soil efflux measurements help to characterize the strength of CO_2 sources/sinks and their global distribution, to explain the interaction between soil CO_2 efflux and climate conditions, and to predict the variation of atmospheric CO_2 concentration and the potential response of terrestrial ecosystems to changing global climate.

Although many techniques have been used with varying degrees of success in estimating CO_2 efflux, all of them have some inherent problems which have either prevented them from giving an adequate estimation of CO_2 emission or restricted their use to limited conditions (Fang and Moncrieff, 1996). CO_2 efflux may vary to a great extent with the particular measurement techniques used (Raich *et al.*, 1990). The lack of a standardized system seriously reduces our ability to compare data collected by different researchers in different localities, and thereby hinders our understanding of this very important measure of ecosystem metabolism (Cropper *et al.*, 1985).

Emission of trace gases from the soil to the atmosphere is commonly measured by some kind of chamber-based technique. These can be categorized into three groups: *absorption*, *enrichment* and *dynamic* chamber methods. Absorption chambers use alkali to absorb CO_2 released from the soil covered by the chamber, and are simple and inexpensive enabling extensive replication in a variety of habitats. However, many factors affect the accuracy of such measurements. It has been found that static chambers generally produce underestimates of soil CO_2 emission (Livingston and Hutchinson, 1995; Jensen *et al.*, 1996), especially when effluxes are large (Kucera and Kirham 1971; Norman *et al.*, 1992). Enrichment methods estimate CO_2 flux by the increment of CO_2 concentration inside the chamber during a given period of time, and are complicated by the non-linear response of CO_2 concentration to the duration of enclosure (Nakayama, 1990). In dynamic chamber methods, air passes at a known flow rate through a chamber and the change of CO_2 density is monitored with time. Although the dynamic technique is considered to be a more precise method than the static method (Nakayama, 1990) and notwithstanding that different types of dynamic chamber methods have been developed, there are still some uncertainties and limitations associated with this particular technique (Fang and

Moncrieff, 1996). The most serious potential problem in the dynamic method is the influence of pressure differences between inside and outside the chamber on the measured CO_2 efflux. Large errors in CO_2 efflux may arise from extremely small pressure differences. However, little is known about the relationship between measured CO_2 efflux and pressure difference. Several issues remain unclear: how precisely does measured efflux relate to the pressure difference; does measured efflux respond similarly to a negative pressure difference as to a positive one; and is there an interaction between the pressure difference and some other environmental factors, such as soil properties?

In recent years, some micrometeorological techniques have been used to estimate CO_2 efflux from the soil surface, such as eddy covariance (Verma *et al.*, 1989; Baldocchi and Meyers 1991), Bowen ratio/energy balance (Dugas, 1993), and others (De Jong *et al.*, 1979; Denmead and Raupach, 1993). Micrometeorological techniques provide great potential for directly measuring CO_2 efflux at the floor of a forest and give an areally averaged estimation of CO_2 efflux with minimal impact on the local environment, but there are strict requirements which must be met for the technique to be applicable (Baldocchi and Meyers 1991).

No technique presently employed is perfect in its accuracy of measurement and also has a negligible impact on the microenvironment of the ecosystem studied. Continuously monitoring CO_2 efflux at various locations is necessary if we are to understand the temporal and spatial variation of soil respiration. Unfortunately, no method so far is satisfactory for that propose. Chambers permit replication in experiments with many surface treatments, but suffer both from their interference to the microclimate and the large spatial variability of soil fluxes (Denmead and Raupach, 1993). There is also a practical difficulty in continuously monitoring CO_2 efflux at various locations with existing dynamic chambers.

Soil respiration rates, as an index of the metabolic activity of heterotrophic microbes and plant roots, are different in different types of ecosystem and vary with environmental conditions (Singh and Gupta, 1977; Schlesinger, 1977; Raich and Schlesinger, 1992). Summarizing from the literature, CO_2 effluxes occur between 0 to 9540 mg CO_2 m^{-2} h^{-1}, but typically, are in the region of 50 to 1000 mg CO_2 m^{-2} h^{-1}

for most soils under various vegetation types (Singh and Gupta, 1977). Raich and Schlesinger (1992) compiled published data and gave a list of annual CO_2 efflux in different types of vegetation in the world. The lowest rate was in a tundra area (60 ± 6 g C m^{-2} yr^{-1}) and the highest in tropical moist forests (1260 ± 57 g C m^{-2} yr^{-1}). For other types of vegetation , except northern bogs and mires (94 ± 16 g C m^{-2} yr^{-1}), soil respiration rates varied between 224 (desert scrub) and 713 g C m^{-2} yr^{-1} (Mediterranean woodlands and heath).

The rate of soil respiration is apparently affected by many environmental factors, such as temperature, soil water content, litter and organic matter amount. Understanding the relationship of soil respiration to its influencing factors and the variable pattern of soil respiration in both time and space, is as important as quantifying the amount of CO_2 released from the soil, if we are to understand the global carbon cycle. The temperature-dependency of soil respiration has been well documented and the temporal variation of soil respiration was thought to be mainly controlled by temperature (Crill, 1991; Hanson *et al.*, 1993; Kicklighter *et al.*, 1994). High spatial variation of CO_2 efflux has been reported (Cropper *et al.*, 1985; Rochette *et al.*, 1991), but little is known about this spatial variation and its relation to environmental conditions.

Modelling soil respiration or CO_2 efflux has long attracted the attention of ecologists but is difficult because soil is a complex medium that consists of a broad range of types of organo-mineral particles and aggregates and contains numerous organisms with differing physiological processes. Soil properties vary temporally and spatially, both horizontally and vertically (Davidson and Trumbore, 1995). Many of the models for describing or predicting CO_2 spatial distribution in the soil or fluxes from the soil surface which have been published, mostly employ statistical correlation with specific parameters (Šimunek and Suarez, 1993). Empirical models help us understand the relationship of soil respiration to environmental conditions and to predict the CO_2 efflux in a specific ecosystem. For example, Oberbauer *et al.* (1992) fitted CO_2 efflux data from the field, to a regression model to describe the response of a riparian tundra soil to environmental factors. Hanson *et al.* (1993) developed an

empirical model to predict CO_2 efflux by relating it to soil temperature, soil water content and the percentage of soil coarse fraction. These models are likely to be case-specific and are, therefore, likely to be of little use in other ecosystems or under environmental conditions which are quite different from those for which the model was built. The lack of a biological framework in such empirical models, makes it very difficult to explain the role of the environment on soil respiration or carbon cycle in ecosystems. It is possible, for example, to draw unreasonable conclusions from an empirical model. Svensson (1980) developed a high order polynomial model for describing soil respiration in a subarctic mire in relation to soil temperature and soil moisture content. The soil respiration rate responded linearly to the increase of soil moisture at a temperature of 16 °C but was obviously inhibited by high moisture at 2.8 °C. It is commonly known that soil respiration is more responsive to soil moisture at an optimal temperature rather than at a low temperature (Howard and Howard, 1979).

Two major processes influence CO_2 emission from the soil: the production of CO_2 and its transport from the soil to the atmosphere. Published nonempirical or process-based models are inadequate in describing both of these processes. A mass balance model is commonly used to quantify CO_2 transport in the soil, and solutions (with different assumptions or simplifications) have been reported by Hendry *et al.* (1993), Šimunek and Suarez (1993), Suarez and Šimunek (1993), Wood *et al.* (1993), Freijer and Leffelaar (1996). For CO_2 production in the soil, few models give a satisfactory description of the respiration process and its response to environmental conditions and also have a sound biological basis. Šimunek and Suarez (1993) developed a submodel to define the relationship of soil respiration rate to soil water potential, temperature, CO_2/O_2 concentration, depth in the soil and time. Some of their assumptions can not be explained properly by our biological knowledge, such as the reduction functions relating to water potential or the CO_2 concentration in soil gas.

1.2 Aims of this Study

The first primary objective of this study was to develop a technique to enable the measurement of CO_2 efflux from the soil surface in the field correctly, accurately and continuously. In the open-top chamber system to be developed, field feasibility was of concern as well as reliability. Previous studies indicated that the pressure difference between inside and outside a dynamic chamber may be a dominant factor controlling measured CO_2 efflux. With this new open-top chamber, we were keen to learn the response of measured CO_2 efflux to pressure difference and other possible variables in the dynamic chamber technique.

The second objective of this thesis was to provide a reliable estimate of CO_2 effluxes from the forest floor as well as a comparison with other measurements made simultaneously in a forest, and to analyze the temporal pattern of CO_2 efflux and its possible relations to environmental conditions. For this purpose, field measurements were made in Florida, USA from May, 1995 to January, 1996 as a part of a project entitled " Exchanges of Energy and Radiatively Active Gases between Slash Pine and Cypress Ecosystems and the Atmosphere in the Southeastern United States".

High spatial variation in CO_2 emission from the soil has been recorded both in crop land and forest, and this causes a difficulty in measuring a representative CO_2 efflux with chamber techniques. The third objective of this study was to specify the spatial variation of CO_2 efflux on the slash pine site and to quantify the influence of major factors on such variation by analyzing the relationships between soil respiration, environmental conditions, root biomass and soil organic matter.

The fourth objective was to develop a process-based model suitable to describe CO_2 origin, transport and its distribution in the soil, and to predict CO_2 efflux from the soil surface as well as soil respiration. Soil was considered as an unsaturated porous system with one-dimensional gas and water flow. In addition to gas phase diffusion, which is thought to be the primary transport mechanism in unsaturated porous media, Šmunek and Suarez (1993) pointed out that the contribution of liquid phase diffusion is significant and may be higher than that from

gaseous diffusion when soils are close to saturation. CO_2 diffusion in the liquid phase is not considered here because the overall CO_2 production and efflux is small when soil is close to saturation. On the other hand, the CO_2 dispersive flux resulted from the advective flow of water in the soil is included as this flux may be significant when soil is warm but not very wet, as it was for most of the growing season of the slash pine plantation.

For the submodel of CO_2 production, both root respiration and microbial respiration were considered to be strongly dependent on temperature, soil water content and O_2 concentration. The amount as well as the quality of soil organic matter and root biomass in the soil were included in the model. There should be an influence of upper soil layers on respiration in the lower layers and such an influence is included in the model via their relation to O_2 concentration at different depths in the soil.

The thesis is arranged in the following order:

Chapter 1 is a literature review on the methodology of soil CO_2 efflux and root respiration measurements, and the simulation on CO_2 efflux and soil respiration. The aims of this thesis are also discussed here.

Chapter 2 describes an open-top dynamic chamber for measuring soil CO_2 efflux and discusses the influence of pressure differences between inside and outside the chamber on the measured efflux.

Chapter 3 presents the result of a field experiment in a slash pine forest in Florida. A simple model is developed for specifying the relationship between the spatial variation of CO_2 efflux and root biomass, soil organic matter and soil porosity.

Chapter 4 describes a process-based model for predicting CO_2 efflux, soil respiration and spatial distribution of CO_2 in the soil, and discusses application of the model in the slash pine forest.

Chapter 5 briefly summarizes the main finding of the thesis, as each preceding chapter is self-contained with its own discussion section.

Appendixes provide some additional information: A.1 photographs of the slash pine plantation and measuring equipment; A.2 list of publications.

1.3 CO_2 Efflux Measurement

1.3.1 Basic concepts

Soil respiration represents the sum of all soil metabolic functions in which CO_2 is produced (Lundegårdh, 1927). Although the CO_2 efflux from the soil surface is commonly referred as "soil respiration", they are different terms. CO_2 efflux represents all CO_2 produced from biological processes, i.e. soil respiration, and non-biological processes, e.g., chemical oxidation (Fung *et al.*, 1987), and the flux arising from changes in the CO_2 pool in the soil.

When the supply of oxygen in the soil is not limited, organic matter will be finally oxidized into CO_2, which will subsequently be released into the atmosphere via the process of diffusion and dispersion. This process is called oxic respiration. In the case of glucose, it can be expressed as (Glínski and Stepniewski, 1985):

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 2883 \text{ kJ energy} \qquad (1.1)$$

The molar ratio of carbon dioxide produced to oxygen consumed in respiration is called the respiratory quotient (RQ). The value of the RQ depends on both the character of substrates used and on the type of metabolism, and is typically 1.0 for aerobic respiration in soil (Rixon and Bridge, 1968; Bridge and Rixon, 1976).

The supply of oxygen may not be sufficient in deep soils, especially when soil texture is very fine or soils are close to saturation. Metabolism under conditions without oxygen uptake is called anoxic respiration. Anoxic respiration is quite complex compared with oxic respiration with respect to both CO_2 production and its transport through the soil. Generally, the CO_2 efflux is low and some intermediate products, such as methane or soluble carbohydrates, are produced under anoxic conditions (Glínski and Stepniewski, 1985; Gale and Gilmour, 1988; Bridgham and Richardson, 1992). Pure anoxic respiration is unlikely to occur in a soil even if the soil is saturated. In most cases when the soil is close to saturation, oxic and anoxic

respiration coexist and RQ >1 (Linn and Doran, 1984).

The study of soil respiration goes back well over 100 years. The early work was mainly concerned with the measurement of CO_2 evolved from, or O_2 consumed in soil samples or soil cores in laboratory studies (Neller, 1918; Newton, 1923; Heck, 1929). Lundegårdh (1927) developed a technique to measure CO_2 efflux in field situations, in which CO_2 diffusing out of the soil was collected under a tin container and this differs little in operational principle from some methods used today (Nakayama, 1990). Early studies on soil respiration were reviewed by Romell (1932). Since then, various studies on soil respiration in different environmental conditions have been widely reported (Drobnik, 1962; Witkamp, 1966a; Witkamp and Frank, 1969; Wanner, 1970; Garret and Cox, 1973; Chiba, 1977; Doelman and Haanstra, 1979; Salonius, 1983; Raich *et al.*, 1990; Loftfield *et al.*, 1992; Dugas, 1993; Jensen *et al.*, 1996). Some of the studies were reviewed by Singh and Gupta (1977), Schlesinger (1977), Glínsky and Stepniewski (1985), Verma (1990), and Denmead and Raupach (1993).

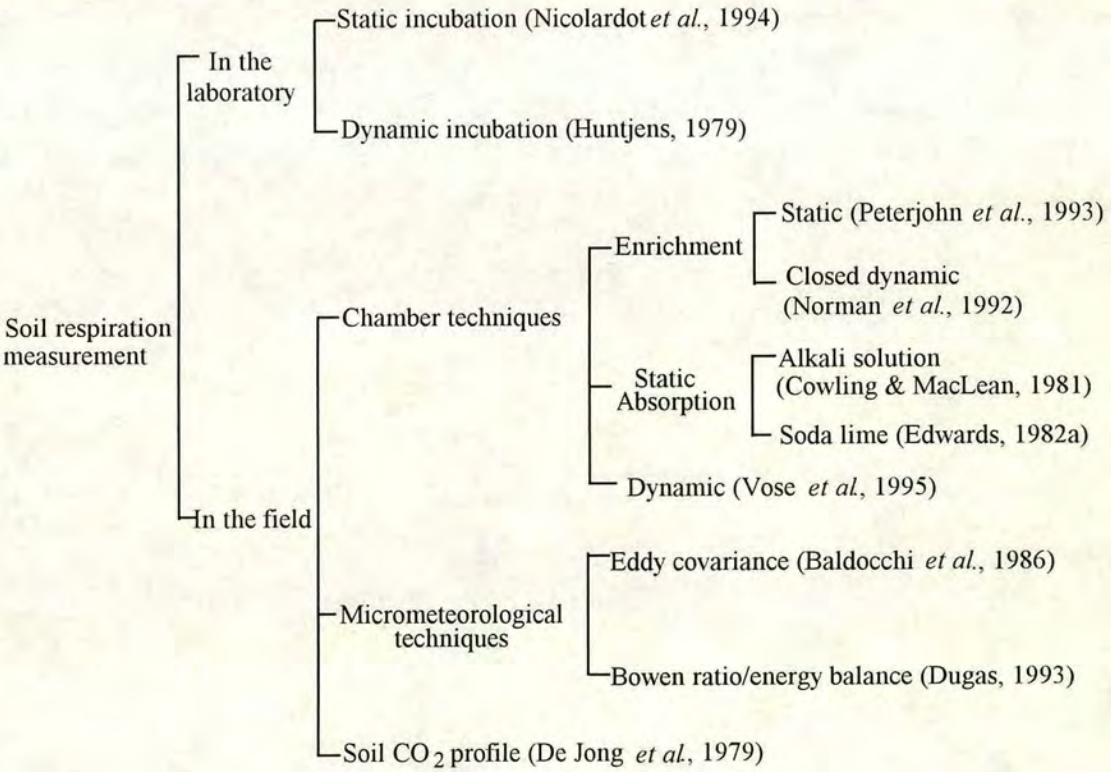


Figure 1.1 Major types of method for measuring soil respiration

Soil respiration or CO_2 efflux can be estimated on the basis of the measurement of oxygen consumption or carbon dioxide efflux in the soil (Glínsky and Stepniewski, 1985). Measurements can be performed both in the laboratory and *in situ* in field conditions. Fig. 1.1 shows examples of methods used in measuring soil respiration rate by different researchers.

1.3.2 Laboratory techniques

Most of the early studies were made in laboratory conditions. A large variety of laboratory techniques have been developed, and all methods involved the measurement of CO_2 released from, or O_2 uptake by, known quantities of soil samples or undisturbed soil cores incubated in controlled conditions (Miller and Johnson, 1964; Anderson and Domsch, 1975; Saito, 1975; Salonius and Mahendrappa, 1979; Billings *et al.*, 1982; Cook *et al.*, 1985). The simplest procedure is that a known quantity of soil sample and alkaline absorbent, which is held in an open container, are enclosed in a container, and soil respiration rate is obtained as the amount of CO_2 trapped in the alkali during a given period.

Neller (1918) used an apparatus in which a flask was covered by a bell-jar. The CO_2 evolved from the soil core contained in the flask diffused into the bell-jar and was then drawn into a bottle where the CO_2 was absorbed by an alkali solution. CO_2 production was determined by titrating the alkali solution at the end of the absorption process. In a slightly different incubation method, CO_2-free air was passed over soil samples (Waksman and Starkey, 1924; Minderman and Vulto, 1973a), or through the soil sample as well as over it (Marsh, 1928). CO_2 in the outgoing air was usually absorbed in an alkali solution (Waksman and Starkey, 1924; Marsh, 1928; Heck, 1929), or determined with an infrared gas analyzer (IRGA) (Wiant, 1967; Huntjens, 1979), or by gas chromatography (GC) (Burford and Bremner, 1972; Brooks and Paul, 1987). The method of passing air through a soil sample may be considered as dynamic incubation when compared with other methods.

The incubation technique is suitable for rapid and routine analysis, particularly for a large number of soil samples. Weaver (1974) developed a device for the

simultaneous collection of CO_2 evolved from 250 soil samples under laboratory conditions. Edwards (1982b) and Brooks and Paul (1987) also described similar sampling systems for the same purpose.

For routine measurement under laboratory conditions, several kinds of respirometers were developed and used, such as the Warburg respirometer (Chase and Gray, 1957; Salonius, 1978), Gilson respirometer (Van Cleve and Sprague, 1971), electrolytic respirometer (Birch and Meville, 1969; Wilson and Griffin, 1975b; Raison and McGarity, 1980), manometric respirometer (Raison and Mcgarity, 1980). All were based on respiration-induced O_2 uptake or CO_2 production, or changes in pH value and air pressure.

Laboratory techniques enable us to study the effects of various factors, such as temperature, moisture content, O_2, CO_2 and other gas concentration, or addition of organic substitutes. Miller and Johnson (1964), and Wilson and Griffin (1975a) studied the effect of soil moisture tension on carbon dioxide efflux. Gilbert and Griebel (1969), Dobson and Wilson (1964), and Salonius and Mahendrappa (1979) reported the effect of different chemical materials on soil respiration. Blet-Charaudeau *et al.* (1990) examined the influence of temperature on soil respiration. Because of the difficulty in controlling some environmental factors in the field, incubation is still used for identifying the influence of some particular environmental factors on soil respiration (Oberbauer *et al.*, 1992; Nicolardot *et al.*, 1994; Amador and Jones, 1995).

The main drawback of the laboratory techniques, however, is that soil conditions are modified in comparison to the field situation. Gas diffusion may be changed in a soil sample as a result of crushing the soil's natural structure and soil settlement; oxygen concentration may be different from the original environment in the field (probably higher in dynamic incubation but lower in the later stage of static incubation). The disturbance caused by sampling, sieving and distributing soil causes a flush of organic matter mineralization (Blet-Charaudeau *et al.*, 1990), and results in an increase in CO_2 emission during the early period of incubation.

1.3.3 Field techniques

Methods for measuring CO_2 efflux from the soil surface in field conditions can be categorized into chamber methods, soil profile methods and micrometeorological methods.

1.3.3.1 Chamber methods

Chamber techniques, whether static or dynamic, all have as their basis that a finite area of soil surface, cleared of green vegetation, is isolated from the atmosphere by a chamber and the CO_2 evolved from the soil covered by this chamber is determined quantitatively. Different chamber techniques were reviewed by Singh and Gupta (1977), Mosier (1989), and Hutchinson and Livingston (1993). Based on the procedure of sampling, Singh and Gupta (1977) grouped the chamber techniques into three types: enrichment, static absorption and dynamic chambers.

1.3.3.1.1 Enrichment chambers

This technique employs an isolation chamber set out on the surface of the soil for a finite period of time, after which a sample of air enriched in CO_2 is removed from it, and the CO_2 content of the sample is determined by alkali absorption (Raich, *et al.* 1990), or by GC (Keller *et al.*, 1986; Crill, 1991; Brumme and Beese, 1992; Peterjohn *et al.*, 1993; Castro *et al.*, 1994), IRGA (Parkinson, 1981, Nakayama and Kimball, 1988) or mass spectrometer (Clymo and Pearce, 1995). The volume of the gas removed may be replaced with CO_2-free air (Parkinson 1981) or by air surrounding the chamber (Desjardins, 1985) or there may be no replacement (Castro *et al.*, 1994). CO_2 production (F) is estimated by repeating the observation after a given time interval.

$$F = (\Delta C / \Delta t) V_{ch} / A \qquad (1.2)$$

where: ΔC is the CO_2 concentration increment in the chamber in the time interval Δt,

V_{ch} is the volume of air within the enclosure of the chamber, and

A is the soil surface area covered by the chamber (Nakayama, 1990).

When a chamber has been placed on the soil surface, the volume enclosed by the chamber, V_{ch}, must be known accurately. The uncertainty in the calculation of the volume is a source of error in estimating CO_2 production with this technique. Parkinson (1981) improved the design of the chamber such that it had a relatively large height, thus diminishing the inaccuracy in calculating the air volume enclosed by the chamber. For most enrichment chambers, gas samples are simply extracted with syringes (Hogg, 1993; Castro *et al.*, 1994; Yavitt *et al.*, 1995). A negative pressure difference between inside and outside the chamber may then result, which draws gas with a high CO_2 concentration from the soil and consequently leads to an error in estimating the soil respiration rate. The magnitude of the error depends on the ratio of total volume of the gas samples removed to the volume of the chamber, as well as on the properties of the soil being measured.

Norman *et al.* (1992) described a closed gas exchange system now frequently referred to as the Li-Cor chamber (Dugas, 1993) or closed dynamic chamber (Rochette *et al.*, 1992). The Li-Cor chamber for measuring soil respiration is actually derived from a Li-Cor photosynthesis system which has a special operating procedure and software to calculate the CO_2 flux (Li-Cor, 1987). In this method, air is withdrawn from the top of a chamber at a rate of about 1.5 $dm^3\ min^{-1}$, passed through a Li-Cor 6200 gas analyzer, and then re-enters the chamber at the bottom. A pressure equilibrium tube is used to balance the pressure inside and outside the chamber. Before flux measurements start, CO_2 concentration inside the chamber is drawn down to about 20 to 30 $cm^3\ m^{-3}$ by scrubbing CO_2 with soda-lime so that flux estimates are obtained from below ambient CO_2 concentration to above ambient concentration. The best estimate of the flux is obtained when the concentration inside the chamber is equal to that outside (Norman *et al.*, 1992). Several recent measurements have been made with this chamber (e.g. Kim and Verma, 1992; Ham *et al.*, 1995; Shurpali *et al.*, 1995), in some cases without the pressure equilibrium tube (Oberbauer *et al.*, 1992) or with a fan for mixing air within the chamber (Hanson *et al.*, 1993). Jensen *et al.*

(1996) and Thierron and Laudelout (1996) also used an enrichment chamber technique which is similar to the Li-Cor chamber but using a different portable IRGA, and both obtained very high estimates of CO_2 efflux. The yearly averaged CO_2 efflux was estimated to be about 0.24 mg CO_2 m^{-2} s^{-1} for the soil of a deciduous forest (Thierron and Laudelout, 1996); the measured CO_2 efflux in an arable soil with this system resulted in an estimation of unreasonably fast turnover of soil organic matter (Jensen *et al.*, 1996).

One of the possible problems with this dynamic enrichment chamber system is the inaccuracy of the volume calculation of the whole gas loop. Nay *et al.* (1994) tested the Li-Cor chamber technique with a laboratory apparatus which provided a stable CO_2 source of known concentration diffusing through a porous medium. They found that the Li-Cor chamber consistently underestimated effluxes by about 15%.

Loftfield *et al.* (1992) described a measuring system comprising 12 chambers with a motor-driven lid connected to a GC by a 16-port valvebank. Chambers were normally open, and were only closed for one hour in every six hours for gas enrichment determination at 30- and 60-min intervals. A 500 to 700 cm^3 gas sample was drawn from each chamber. One complete program cycle lasted six hours. All operations were controlled by computer. In this system two uncertainties in measured efflux may occur because of the long period of enclosure of the soil samples and the large volume of the gas samples withdrawn.

For enrichment techniques, whether using static or dynamic chambers, there is a basic presumption that the accumulation of CO_2 inside the chamber is linearly related to time. This assumption is doubtful in the field as CO_2 accumulated inside the chamber may inhibit further diffusion of CO_2 from the soil. Very different results have been reported on the linearity of CO_2 concentration inside a closed chamber with time. Van Cleve *et al.* (1979) and Svensson (1980) reported a linear accumulation of CO_2 for several hours after enclosure on in a subarctic mire site. Nakayama (1990) examined the accumulation of CO_2 inside a chamber, from which gas samples were taken at 30-second intervals after the chamber was closed, and showed that the rate of increase in CO_2 concentration was essentially linear with time between 0.5 to 3.5 minutes. After that, the CO_2 concentration did not increase much with time. In

practice, the linearity of CO_2 accumulation inside the chamber is dependent on both soil properties and CO_2 efflux (Rochette *et al.*, 1992), as well as on the technique employed, and varies from case to case. The application of a linear model to non-linear chamber concentration data represents a potentially serious source of measurement bias that may influence not only summary statistics for the experiment, but also larger scale budgets based partially or wholly on those data (Anthony *et al.*, 1995). Dugas (1993) reported that the second successive flux estimate was generally lower than the first one with a Li-Cor chamber system in which two fluxes were measured within 4 minutes after the chamber was placed on soil surface. Because little is known about the possible inhibition by high CO_2 concentration of the diffusion of CO_2 from the soil, any enrichment chamber should not be put on the soil surface for a long period of time. It is also clear that continuous monitoring of CO_2 efflux is impossible with the enrichment method.

1.3.3.1.2 Absorption chambers

The absorption technique was first used by Lundegårdh in 1921 (Singh and Gupta, 1977). An alkali solution (KOH or NaOH) of known strength in a vessel is placed within a chamber to absorb the CO_2 evolved over a defined period of time, followed by a titration to determine CO_2 production. Because most absorption measurements have been done with a static chamber, these methods are commonly referred to as *static chambers* in the literature. CO_2 efflux is obtained from the gain of CO_2 trapped in the absorbent, the exposure time and the area beneath the chamber.

Cowling and MacLean (1981) described a typical system for this method. The chamber was made of PVC pipe (152 mm ID), with a clear "plexiglas" top and a reservoir for holding KOH as a CO_2 absorbent. The reservoir was suspended by three columns attached to the chamber top, but was otherwise open to the air within the chamber. A sleeve, also made of PVC pipe, was inserted into the soil below. The respiration chamber fitted snugly onto the top of sleeve, and was sealed with an O-ring gasket. The chamber was covered with aluminum foil to shield it from incoming solar radiation.

Many published studies have used this method, with slight modifications (e.g. Witkamp, 1966b, 1969; Brown and MacFadyen, 1969; Kosonen, 1969, Wanner, 1970; Froment, 1972; Saito, 1975; Yoneda, 1975; De Santo *et al.*, 1976; Vogt *et al.*, 1980; Rout and Gupta, 1989). Wallis and Wilde (1957) designed an apparatus to extract air continuously from a chamber placed on the soil surface, followed by alkali absorption. However, observed soil respiration rates were very high, ranging from about 0.9 to 2.15 mg CO_2 m^{-2} s^{-1} for various forest soils, probably because of reduced pressure within the chamber. Freijer and Bouten (1991), and Hendry *et al.* (1993) used a similar technique but the air was recirculated after CO_2 had been removed by alkali solution.

Piene and Van Cleve (1976) described a system for measuring CO_2 efflux from a forest floor. Forest floor samples were placed inside mesh baskets which were removed from the forest floor and enclosed in a chamber placed on the forest floor for respiration measurement. After each measurement, the baskets were returned to the positions on the forest floor from which the samples were obtained. This method is not very different from laboratory practice, but has the advantage of helping the samples at similar temperature and water content to the undisturbed soil.

Campbell and Frascarelli (1981) reported a simple device to measure CO_2 evolved at different soil depths *in situ* using alkali absorption. Specially designed efflux wells were installed to depths of 10, 20, 40, 60, 80 cm. The upper end of a well protruded from the soil surface and was connected to a flask which contained a solution of NaOH as the absorbent. CO_2 evolved at the specific depths diffused through the efflux well into the flask and was absorbed there. The monitoring interval was one week.

An important improvement in the absorption method is the use of granular soda-lime as the absorbent. The method was thoroughly described and evaluated by Edwards (1982a). A certain amount of soda-lime, pre-dried at 100 °C to constant weight, is placed on a tray enclosed in a chamber on the soil surface. After being exposed to the air inside the chamber for a given period of time, the soda-lime is removed and re-dried at 100 °C to constant weight. CO_2 production is obtained by

multiplying the weight gain of the soda-lime by a factor of 1.41 to allow for loss on drying of the chemical water produced by the absorption of CO_2 by soda-lime. This modification makes field measurement very easy as it eliminates the use of liquids. The absorption period is normally a few hours to a few days and provides an integrated value of CO_2 efflux over that interval (Howard, 1966; De Jong *et al.*, 1979; Edwards and Ross-Todd, 1979, 1983; Weber, 1985; Gordon *et al.*, 1987; Sanhueza and Santana, 1994).

The use of alkali absorption is a simple and easy method and one which enables extensive replication in a variety of habitats. This is important when considering the spatial variability of soil respiration under natural communities (Coleman, 1973a) or when making measurements in remote areas where the supply of electricity is not available. However, many factors affect the accuracy of such a measurement.

Kirita and Hozumi (1966), Kirita (1971a, b, c) examined the method and found that the observed values were affected by:

i) the area of the soil surface enclosed by the chamber;

ii) the height of the chamber;

iii) the amount of absorbent;

iv) the surface area of absorbent;

v) the height of the surface of absorbent above ground; and

vi) the depth of the lower end of the chamber buried in soil.

Gupta and Singh (1977) also found a significant effect of alkali concentration and volume on the measurement of soil respiration. To obtain a reliable estimate of soil respiration, Kirita (1971a) recommended that the apparatus for measuring soil respiration should satisfy the following conditions: the height of chamber $\geq$ 8 cm; the depth of the lower end of chamber into the soil $\geq$ 5 cm; the height of the surface of KOH solution above ground $<$ 2.5 cm. To increase the surface area of absorbent, Kirita (1971c, 1971d) used a disc of plastic sponge soaked with KOH solution as the CO_2 absorber, and claimed that it gave the closest approximation to soil respiration rate under natural conditions. Monteith *et al.* (1964) pointed out that a chamber

should cover at least 400 cm^2 to avoid an edge effect. Edwards (1982a) recommended a 5% minimum ratio of the surface area of absorbent to the area enclosed by chamber. In practice, this ratio has been reported to be more than 5% in most studies (26% in Tate *et al.*, 1993; 16-26% in Jensen *et al.*, 1996; 18% in Marra and Edmonds, 1996).

Besides the above limitations, the observed values of CO_2 efflux with this method are temperature-dependent. Edwards and Sollins (1973) reported that respiration rates with an absorption method were 90% of the values obtained with a dynamic chamber and an IRGA at 12 °C and 63% at 20 °C. Cropper *et al.* (1985) also found that the absorption method produced similar results to a dynamic technique when air temperatures were less than 15 °C, but lower than the dynamic method in warmer months of the year. A probable reason is the decrease in the CO_2 absorption efficiency of alkali at high temperatures. This temperature-dependency is very difficult to correct for in field measurement and no correction has been applied in published results.

In addition, the observed values of CO_2 efflux are related to the length of time the absorbent is exposed to air within the chamber. As absorption proceeds, more and more absorbent is consumed and the overall absorption potential of the absorbent decreases gradually. To prevent this error, an excess amount of absorbent is required. Edwards (1982a) recommended that 30 g soda-lime be used per 500 cm^2 of forest floor and should be replaced as soon as the weight of CO_2 absorbed in the field had reached approximately 7% of the initial weight of soda-lime.

Compared to the dynamic method with an IRGA, the absorption method generally underestimates soil respiration (Ino and Monsi, 1969; Witkamp, 1969; Kucera and Kirham, 1971; Ewel, *et al.*, 1987a). Cowling and MacLean (1981) also pointed out underestimation by the absorption method, compared to the budget of organic matter in the soil. Rochette *et al.* (1992) and Jensen *et al.* (1996) found that the static chamber method consistently produced lower soil respiration rates than closed dynamic chamber, enrichment methods and the difference was larger with higher CO_2 effluxes. The underestimation could be as high as 57% of a total efflux of

0.214 mg CO_2 m^{-2} s^{-1} produced by a laboratory method (Nay *et al.*, 1994). On the other hand, when the magnitude of CO_2 efflux is less then about 0.03 mg CO_2 m^{-2} s^{-1}, the absorption method was found to overestimate CO_2 efflux (Nay *et al.*, 1994; Jensen *et al.*, 1996). Alkali absorption is often considered a method for obtaining a relative measurement of the rate of soil respiration rather than an absolute quantity of CO_2 production (Minderman and Vulto, 1973a; Singh and Gupta, 1977) and any use of this static chamber method ought to be particularly scrutinized (Nay *et al.*, 1994).

1.3.3.1.3 Dynamic chambers

Generally, a chamber with air flowing through it should be regarded as a dynamic chamber but CO_2 flux can be obtained by different methods. The term dynamic chamber or dynamic method is used here with the presumption that a stream of air with a constant flow rate, is passed, rather than circulated, through the chamber. The difference in CO_2 concentration between outside and inside the chamber is constant when the soil CO_2 efflux is in a steady state. CO_2 flux is calculated from the flow rate and the difference in CO_2 concentrations between incoming and outgoing air (Nakayama, 1990):

$$F = \Delta C \cdot f / A \tag{1.3}$$

where: F is the CO_2 efflux;

ΔC is the difference of CO_2 mass fraction in incoming and outgoing air;

f is the gas flow rate through the chamber; and

A is the surface area covered by the chamber.

The CO_2 concentrations in the incoming and outgoing air are commonly measured by an IRGA (Ewel *et al.*, 1987a).

Vose *et al.* (1995) described a dynamic chamber system which automatically measured CO_2 concentration changes among ten chambers. Air was withdrawn from and blown into chambers at a flow rate of 1 to 1.5 dm^3 min^{-1} and each chamber was

sampled for 10 minutes.

The dynamic technique is commonly considered to be a more precise method than static methods. A serious problem with this method, however, is that a possible pressure difference between inside and outside the chamber may significantly influence the observed CO_2 efflux. When air is withdrawn from a chamber, there is a relative negative pressure inside the chamber. On the other hand, a positive pressure difference is established within a chamber when air is blown in. Kanemasu *et al.* (1974) reported that the measured CO_2 efflux was one order of magnitude larger when air was drawn out of a chamber compared to when air was blown in, the pressure difference being –2.5 Pa for withdrawing and +1.0 Pa for blowing in air, respectively. Sign "–" stands for a lower pressure inside the chamber than outside. The absolute magnitude of the negative pressure for withdrawing air was larger than that of positive pressure for blowing in air at the same flow rate. De Jong *et al.* (1979) obtained the lowest CO_2 efflux with a dynamic chamber, operated at a pressure less than +5.0 Pa. A two-pump system for drawing and blowing air synchronously through a chamber is now used routinely when applying the dynamic method (Ewel *et al.*, 1987a; Vose *et al.*, 1995) on the assumption that the effect of drawing air will be offset by blowing air, and *vice versa*.

Fang and Moncrieff (1996) examined the influence of pressure difference and its relation to the air loop for a dynamic chamber system. It was found that the resistance of the whole air circuit is the dominant factor governing the magnitude of pressure difference at a given flow rate. The difference between negative and positive pressure under the same flow rate is mainly caused by the pump used in the measurement rather than by the chamber itself. The absolute magnitude of negative pressure is larger than positive pressure with a small pump, but they are nearly the same when a large pump is used. Blowing air into a chamber alone is inadequate to measure CO_2 efflux under field conditions because the long air circuit of the measuring system induces a large positive pressure difference between inside and outside the chamber. A pressure difference still exists inside a chamber in which air is simultaneously blown in and withdrawn at the same flow rate under both laboratory

and field conditions, as flow rates cannot be made exactly the same. The method fails to give a reasonable estimate of soil respiration when the magnitude of pressure difference exceeds ± 0.5 Pa. To obtain a reliable estimate of soil respiration rate with this technique, a pressure difference held to within ± 0.2 Pa was recommended, although this is very difficult to obtain for most dynamic chamber systems.

Some modifications of the dynamic chamber technique have been reported. Edwards (1974) reported a moving chamber system, in which a chamber was placed on the soil surface for a short time then removed to another sampling point. Schwartzkopf (1978) used an open chamber system to measure CO_2 efflux. The chamber was designed to function much like a wind tunnel. Air was blown in from the enclosed end by a fan and went out the open end. The CO_2 evolved was calculated from the flow rate and the difference of CO_2 concentration between two points within the chamber. Fang and Moncrieff (1996) described an improved dynamic chamber in which air was blown in and drawn out the chamber simultaneously with the same flow rate. It was not difficult to maintain a pressure difference to within ± 0.2 Pa under field conditions for flow rates up to about 4 dm^3 min^{-1} by using flow meters to adjust the rates of incoming and outgoing air. The chamber construction effectively prevented serious error caused by air leakage.

In the dynamic method, the CO_2 concentration inside the chamber may not be significantly changed but turbulence generated in the chamber may cause additional soil air to be withdrawn through the soil pores into the chamber and the natural respiration rate may thus be disturbed (Singh and Gupta, 1977). Golley *et al.* (1962) found that CO_2 production by peat in a mangrove forest increased with increasing flow rates in the chamber up to 15 dm^3 min^{-1}. Schwartzkopf (1978) described a relationship between CO_2 production and air flow, and gave an empirical equation: $F = a\,(f+1)^b$, where F is the measured CO_2 efflux, f is flow rate, and a, b are parameters. One possible explanation for this relationship is that CO_2-enriched air may be pulled out of the soil by air flowing over the soil surface (Witkamp and Frank, 1969; Schwartzkopf, 1978). A second explanation is that an increase in flow rate stimulates the metabolism of the soil biota by increasing the oxygen supply

(Schwartzkopf, 1978). On the other hand, Edwards and Sollins (1973) reported that there was no significant effect of flow rate over a range of about 1 to 6 dm^3 min^{-1} on observed CO_2 efflux. Cropper *et al.* (1985) also pointed out that there was no consistent flow rate effect with flow rates varying between 1 to 8 dm^3 min^{-1}.

For chamber techniques, placing a chamber on the surface of soil disturbs the abiotic as well as the biotic micro-environment of an ecosystem, and there are the so-called "chamber effects" (Edwards 1974). In field measurements, chambers may be fixed in position for several days to a few years (Froment, 1972; Nakane *et al.*, 1983). During the period of enclosure, the chamber is an artificial environment (Schlesinger, 1977). Edwards (1974) showed that both soil moisture and soil temperature are affected by using chambers that are fixed in position, and that CO_2 efflux measured by fixed chambers may exceed those measured by a system with a moving chamber by about 54 to 90%. Leaving a chamber on the soil surface for a long time will definitely decrease root biomass (Gupta and Singh, 1981). Coleman (1973b) reported that root biomass in the enclosed area, after having fixed chambers in position for two years, was only 28% of that in a control area, and litter had been reduced to about 11% of the control amount.

Inserting a chamber too deeply into the soil (e.g., deeper than 7 cm) consistently results in low estimates of soil respiration as it severs surface roots and prevents horizontal root growth into the chamber (Anderson *et al.*, 1983; Raich and Nadelhoffer, 1989). Decreased CO_2 efflux with increasing depth of chamber placement was observed by Wildung *et al.* (1975).

Upward CO_2 diffusion may be stimulated by depletion of CO_2 in a static chamber as it is absorbed by hydroxide (Schlesinger, 1977). Because of the damping of pressure fluctuations inside a chamber, CO_2 diffusion from the soil may be affected (Kimball and Lemon, 1971). Clipping of green shoots could also significantly reduce the root respiration component of the total soil respiration (De Jong *et al.*, 1979) or increase the rate of CO_2 given off (Svensson, 1980). Kosonen (1969) pointed out that when the vegetation was cut away before an experiment, the respiration of the roots decreased considerably or ceased altogether.

To minimize the chamber effect, some precautions have been taken, such as,

insulating the chamber walls (Hutchinson and Mosier, 1981), covering the chamber with aluminium foil (Coleman 1973a) or coloring it white (Raich *et al.*, 1990) to diminish the heating effect of solar radiation; closing the chamber only during the measuring period (Witkamp, 1963, 1966a) or removing the chamber from the soil surface (Raich *et al.*, 1990); using a moving chamber system (Edwards, 1974); not cutting away green parts of plants in the chamber and correcting the observed CO_2 flux with data on dark respiration of the green plants to estimate the soil respiration (Svensson, 1980).

A large number of chambers may be required to get a representative measurement owing to the high spatial variability of CO_2 flux, especially on a forest floor (Nakayama, 1990; Dugas, 1993). Cropper *et al.* (1985) pointed out that even in a relatively uniform pine plantation it would be necessary to increase the number of chambers or sample points to 15 to be within 10% of the mean obtained with 30 sample points 90% of the time. Rochette *et al.* (1991) examined the spatial variability of CO_2 efflux on bare soil and under agricultural crops. They found that, for bare soil, variability occurred at a scale smaller than 0.15 m and that interpolation between measurements was not possible. For soils under crops in the same study, the spatial variability of soil respiration was highest in May and decreased gradually towards the end of the season. The coefficient of variation varied from 25 to 69%. For the estimate of CO_2 efflux to lie within 10 % of its mean value at the 0.05 probability level, the required number of measurements was estimated to be 190 before emergence and decreased to 30 after 70 days. It is operationally difficult to obtain this number, especially with the dynamic technique.

Hutchinson and Livingston (1993) examined the most important sources of error in chamber-based flux measurements. Potential sources of bias were grouped into: (i) physical and biological disturbances associated with the measurement process, and (ii) errors associated with sample handling, sample analysis, and inaccurate models or inappropriate methods for computing flux from measured concentration data. Errors due to (i) can mostly be overcome by using an appropriate chamber design, relatively short sample times, and reasonable care to minimize disturbances to the site.

1.3.3.2 Soil CO_2 profile method

De Jong and Schappert (1972) proposed a method to calculate total CO_2 efflux at the soil surface as well as at different depths in the soil. Under the assumption of steady state, the soil respiration rate is calculated from:

$$F = D_{gs}\, \mathrm{d}c / \mathrm{d}z \tag{1.4}$$

where: F is the CO_2 efflux;

D_{gs} is the effective coefficient of CO_2 diffusion in the soil;

dc/dz is the gradient of CO_2 concentration in the soil.

CO_2 flux of different soil layers is obtained on the assumption that the total soil CO_2 efflux is equal to the surface flux calculated from the CO_2 concentration gradient over the uppermost layer and the diffusion coefficient for that layer.

In field measurements, air samples were drawn from different depths of soil with a diffusion well (De Jong and Schappert, 1972), sampling tube (Buyanovsky and Wagner, 1983; Davidson and Trumbore, 1995) or multilevel sampling probe (Burton and Beauchamp, 1994).

The soil CO_2 profile method involves the uncertainty of quantifying the gas diffusion coefficient, or diffusivity, in the soil, which is affected by soil properties as well as soil moisture content (Parkinson, 1981). Although direct measurement of diffusivity of soil gases can be done *in situ* in the field (Washington *et al.*, 1994), this is difficult and cumbersome (Rolston *et al.*, 1978). Alternatively, gas diffusivity can be calculated from models that require estimates of soil porosity and soil water content (Davidson and Trumbore, 1995). Such models are given by Millington and Shearer (1971), Campbell (1985), and Collin and Rasmuson (1988).

In recent years, the profile of radon (^{222}Rn), a radioactive noble gas produced in the soil by decay of ^{226}Ra, has been used as a tracer for CO_2 transport in the soil (Dörr *et al.*, 1983) or to test gas diffusivity models (Davidson and Trumbore, 1995). ^{222}Rn is distributed rather uniformly in the soil matrix, and its flux at the soil surface

and concentration in soil air are influenced only by soil parameters. The CO_2 efflux is obtained from the CO_2/Rn flux ratio:

$$F / F_{Rn} = (D_{CO_2} / D_{Rn})(\Delta C / \Delta C_{Rn}) \quad (1.5)$$

where F and ΔC are the CO_2 flux and concentration difference, respectively; the ratio of the molecular diffusion coefficients for CO_2 and radon, D_{CO_2} / D_{Rn}, is constant at a given temperature; and F_{Rn} and ΔC_{Rn} are radon flux and concentration difference, respectively, which can be measured directly (Davidson and Trumbore, 1995). The ratio F / F_{Rn} is thought to be independent of soil properties (Dörr and Münnich, 1987).

In general, estimates of the gas diffusivity near the surface limit the accuracy of flux estimates (Rolston *et al.*, 1978). Very low effective diffusivities may be obtained in soils with high moisture content (Collin and Rasmuson, 1988). A large error in the estimated CO_2 efflux may thus arise, although the magnitude of absolute efflux is low in such conditions. De Jong *et al.* (1979) compared the values of CO_2 efflux obtained using five methods. The soil CO_2 profile method gave the highest values and anomalous CO_2 effluxes often occurred immediately following rain. The calculation of CO_2 efflux is based on the assumption of a steady state, i.e. CO_2 concentration in the soil air is constant. Steady state conditions may not be met under field conditions during the whole measuring period, however, and indeed a flush of CO_2 flux has been observed in the field between midnight and dawn (Witkamp, 1969). Little is known about the effect of an unsteady state on the calculation of CO_2 efflux.

Estimating CO_2 production at different depths in the soil is useful for understanding the source of CO_2 and carbon transport in the soil. Although the CO_2-profile method provides a theoretical approach for this purpose, its use is limited by the difficulty in estimating CO_2 diffusivity at different depths (De Jong and Schappert, 1972).

1.3.3.3 Micrometeorological methods

In recent studies, some micrometeorological techniques have been used to estimate CO_2 efflux from the soil. The major advantages of micrometeorological methods are that they cause minimal disturbance to the microenvironment of the ecosystem studied and provide a spatially integrated CO_2 flux measurement (Verma, 1990).

The eddy covariance method provides a direct means of measuring CO_2 efflux from the soil surface, and the method makes no assumption about turbulent diffusivities. In this method, the vertical flux of CO_2 at a point is obtained by correlating the instantaneous fluctuations of CO_2 concentration with the instantaneous fluctuations in vertical wind speed and averaging over a suitable time interval. CO_2 efflux over a horizontally homogeneous surface under "steady state" conditions is given by:

$$F = - < w' \rho_c' > \qquad (1.6)$$

where: F is CO_2 flux, and w' and ρ_c' are fluctuations of vertical wind speed and CO_2 concentration, respectively. The angle bracket denotes time averaging, and fluxes away from the atmosphere are negative in sign by convention (Verma, 1990).

Baldocchi *et al.* (1986) and Baldocchi and Meyers (1991) used an eddy covariance method to study CO_2 efflux from the floor of a deciduous forest. They argued that the technique seems to provide a promising means for measuring CO_2 efflux from a forest or orchard floor, as it imposes minimal impact on the ambient environment and permits the study of the processes that regulate and modulate gas exchange between the soil / litter complex and the atmosphere that can not be probed with chambers.

For other micrometeorological methods, under the assumption of a horizontally homogeneous field, CO_2 efflux is calculated from the gradient of CO_2 in the atmosphere and the estimation of an appropriate transfer coefficient:

$$F = K_c \partial c/\partial z \quad (1.7)$$

where $\partial c/\partial z$ is the vertical gradient of CO_2 concentration and K_c is the transfer coefficient of CO_2 in the boundary layer, which can be estimated by different methods. Dugas (1993) used the Bowen ratio/energy balance method (BREB) to calculate CO_2 flux from bare soil and found that the mean flux from BREB and a chamber method over four days differed by less than 10%. Other micrometeorological methods which may be used in estimating soil respiration are reviewed by Denmead and Raupach (1993).

For a vegetated surface, micrometeorological methods measure the net CO_2 flux above the surface and the calculation of soil CO_2 flux requires estimates of plant photosynthesis and plant respiration (De Jong *et al.*, 1979; Norman *et al.*, 1992) and the storage of CO_2 within the canopy between the eddy covariance sensor and the soil surface (Baldocchi *et al.*, 1997). This will probably cause an error in calculation of soil respiration. For bare soil or within a forest canopy, where the understorey is sparse, micrometeorological methods can be used for direct measurement of the soil CO_2 flux (Baldocchi *et al.*, 1986; Dugas, 1993). However, Baldocchi and Meyers (1991) pointed out that measurements by eddy covariance from a forest floor must be subjected to strict scrutiny and can be accepted only if they meet the requirements on which the technique is based; these include relatively steady conditions over half an hour; negligible sources or sinks between the soil surface and measurement height, and an extensive level and horizontally homogeneous upwind fetch. Data must be rejected when conditions violate the premises on which the technique is based. During sunrise and sunset, when air temperature in the boundary layer varies rapidly, steady state conditions do not exist. Measurement with an eddy covariance method under these conditions will probably result in appreciable errors in the estimation of soil respiration (Verma *et al.*, 1989). So that, the eddy covariance method can not give reliable uninterrupted measurements within a canopy (Baldocchi and Meyers, 1991). Some of the limitations of the eddy covariance method also apply to other micrometeorological methods.

1.4 Estimation of the Root Respiration Fraction

Root respiration is a major component of total soil respiration, ranging from 5% to 90% of total soil respiration (Singh and Gupta, 1977; Chapman, 1979; Thierron and Laudelout, 1996). Most studies show that root respiration accounts for about 30~60% of total soil respiration (Hendrickson and Robinson, 1984; Ewel *et al.*, 1987b) and is often estimated to be 50% of total soil respiration (MacFadyen, 1970). Nakane *et al.* (1983) pointed out that when the cycle of soil organic carbon is nearly in a state of dynamic equilibrium in a forest ecosystem, the proportion of root respiration to soil respiration seems to converge to 50% irrespective of the type of forest ecosystem.

A precise and accurate estimation of the root contribution to total soil respiration is difficult because of the complex nature of the soil sub-system (Behera *et al.*, 1990), but various approaches have been tried to determine root respiration rate *in vitro* or *in situ*.

1.4.1 Laboratory methods

For measurements *in vitro*, the whole root system or a section of root can be extracted from the soil and enclosed in a container. The uptake of O_2 or efflux of CO_2 by incubated roots can be determined by a Gilson differential respirometer (Edwards and Sollins, 1973), by alkali absorption (Harris and Van Bavel, 1957; Crapo and Coleman, 1972), by IRGA (Osman, 1971), or by GC (Holthausen and Caldwell, 1980). Roots can come from cultivated plants (Newton, 1923; Crapo and Bowmer, 1973), from greenhouse experiments (Huck *et al.*, 1962; Holthausen and Caldwell, 1980) or from the forest (Crapo and Coleman, 1972; Walters *et al.*, 1993). Another way to estimate root respiration is to compare the respiration rate of intact soil cores to that of root-free soil samples (Redmann and Abouguendia, 1978). Coleman (1973b) partitioned soil cores into different components, i.e. root, litter and mineral soil for a forest and a broom sedge community. Compared with the total soil

respiration of the intact soil cores, they reported that root activity accounted for 8 to 17% of total soil respiration for the old field samples, and 5.7 to 11.4% for the forest floor samples.

Edwards and Sollins (1973) used a Gilson differential respirometer to measure O_2 uptake by roots at the mean soil temperature measured during the previous 24 hours. They estimated that 22% to 36% of the total CO_2 evolved from the forest floor could be accounted for by roots, together with their rhizosphere flora in the top 15 cm of the soil profile. Redmann and Abouguendia (1978) reported root respiration contributing about 17 to 26% of the CO_2 arising from the soil in a mixed grassland ecosystem.

Chapman (1979) extracted roots from heathland soils. The rates of respiration of different size-fraction of roots were measured in a Gilson respirometer at temperatures of 10 and 20 °C. They showed that specific respiration rate increased with decreasing diameter of the roots. Respiration rates measured with this method, however, seemed to be too high, being 2.4 to 4.7 times that from an indirect method of the actual root respiration from natural heathland soils.

Oberbauer *et al.* (1992) incubated soil samples from which live roots and rhizomes were removed, at constant temperature in the laboratory, and then scaled the observed respiration rate to temperature in the field to estimate the contribution of microbes to the total soil respiration. Their results suggested that microbial respiration accounts for a major portion of measured CO_2 efflux in a tundra soil. A very different estimate using this method was reported by Thierron and Laudelout (1996), who estimated 90% of total soil CO_2 efflux came from root respiration in a deciduous forest soil. However, the CO_2 efflux from the soil surface measured in the field by Thierron and Laudelout (1996) was very high and questionable, and may result in an overestimation of the contribution from root respiration.

There are several reasons why *in vitro* measurements may not reflect the actual root respiration in natural conditions:

1) the root respiration of cultivated plants may be different from that of plants growing in natural conditions (Singh and Gupta, 1977);

2) tissue damage and disturbance by removal of roots from soil and

preparation for measurement; this disturbance will probably stimulate root or soil respiration (Edwards and Harris, 1977; Redmann and Abouguendia, 1978; Chapman, 1979), but on the other hand, the loss of very fine roots may result in an underestimation because of the high metabolic activity of fine roots;

3) fine roots can not be completely removed from root-free soil samples (Oberbauer *et al.*, 1992), and sieving or preparation of root-free soil samples may enhance microbial respiration; and

4) changed environmental condition, e.g. the supply of O_2, which may be deficient in a field soil, especially in deep or compact clay soil, but is probably sufficient during a laboratory incubation.

1.4.2 Field methods

A few approaches have been used to estimate root respiration *in situ* :

1) CO_2 efflux is measured on the surface of planted or cropped soil as well as on bare soil. The difference between the measured CO_2 effluxes is then explained by the contribution of roots (Minderman and Vulto 1973b, De Boois, 1974, Mogensen, 1977).

2) CO_2 efflux is measured at a number of sites, and is related to the amount of root biomass to give an estimate of root respiration (Kucera and Kirham, 1971; Gupta and Singh, 1981; Behera *et al.*, 1990).

3) The decomposition rates of litter, root and soil organic matter are determined separately and root respiration is then obtained by subtracting the CO_2 evolved in decomposition from the CO_2 efflux measured on the soil surface (Phillipson *et al.*, 1975; Edwards and Harris, 1977; Ewel *et al.*, 1987b).

In the experiments of Minderman and Vulto (1973b), CO_2 effluxes were measured from the soil surface of a wooden tub in which birch trees had been growing for ten to twelve years, and from a root-free soil surface. The total CO_2 evolved was 9.2 ± 0.8 mg dm^{-2} h^{-1} and the CO_2 production from root-free soil samples was 1.18 mg dm^{-2} h^{-1}, the difference being taken as the respiration of the roots in the tub.

One of the uncertainties in these experiments is that microbial respiration may be changed by the presence of roots. It is well known that plant roots may improve soil properties such as permeability and hence O_2 supply; some exudates of roots will stimulate or inhibit microbial metabolic activities; and dead roots will add to the soil carbon pool for microbial decomposition. A part of the difference between soils with roots and without roots must have something to do with changes of microbial respiration.

Chapman (1979) measured CO_2 efflux from five sites in heathland over a period of one year. CO_2 efflux was apportioned to different components of soil organic matter by regression equations and root respiration accounted for up to 70% of the total soil respiration. Behera *et al.* (1990) measured CO_2 efflux and root biomass from various positions on the floor of a tropical forest and then related the CO_2 efflux rate to root biomass to estimate the contribution of live root to total soil respiration. They concluded that about 50% of total soil CO_2 came from respiration by live roots in the ecosystem.

Nakane *et al.* (1984) compared the CO_2 effluxes measured on the floor of a mature red pine stand before and after clear felling. The balance of the rates between the two conditions before and after felling was considered roughly to be the contribution of root respiration, as the root system of the pine died and its respiration ceased after felling. Taking into consideration CO_2 efflux resulting from the decomposition of roots that died as a result of the felling and the change of soil organic carbon flows after felling, the proportion of root respiration in the total soil respiration rate was estimated to be about 47 to 54% on an annual basis. Ewel *et al.* (1987b) used similar method to estimate the contribution of root respiration in Florida slash pine plantations. Small plots (3.5 × 2.5 m) were isolated by digging 1m deep trenches around the edges so that there were no live roots in the soil within the plots. Respiration rates from the trenched plots, corrected for the increase of decomposition resulting from the input of fresh dead roots, were compared with rates of control plots to determine root respiration. The contribution from live root respiration was estimated to be 62% of the total soil respiration for a 29-year-old plantation. Bowden *et al.* (1993) estimated that 33% of the total soil respiration in a temperate forest

came from respiration by live roots with this method.

For mature forests it is reasonable to assume that soil organic matter is in a state of dynamic equilibrium, and that root respiration will equal the difference between total soil respiration and the litter inputs. Considering only the leaf litter input, Kawahara (1976) estimated with this method that root respiration contributed 18 to 25% of total soil respiration in oak, pine and larch forests. The difficulty with this method lies in the estimation of the below ground litter production, i.e. the fine root turnover rate (Raich and Nadelhoffer, 1989), and no technique is available at present for accurately estimating root turnover.

Warembough and Paul (1973) used a $^{14}CO_2$ isotope labeling technique to estimate root respiration of potted plants in a growth chamber. Two days after $^{14}CO_2$ was supplied to the foliage, soil air samples were taken by a tube inserted into soil beneath the plants. Root respiration was estimated by the variation of $^{14}CO_2$ concentration in the soil air. A similar approach was reported by Cheng *et al.* (1993) in which an intact plant was incubated in a chamber and labeled with $^{14}CO_2$. The CO_2 released from the root-soil column was measured with an IRGA and the $^{14}CO_2$ fraction in the outgoing gas was measured with a radioactivity counter. Root respiration and rhizo-microbial respiration were estimated to be about 41% and 59%, respectively, of the total soil respiration for an intact wheat plant-soil sample.

Root respiration estimated *in situ* is based on the assumption that respiration rate per unit ground area is linearly related to the root biomass present (Kucera and Kirham, 1971; Crapo and Coleman, 1972; Edwards and Sollins 1973). Chapman (1979) found a non-linear relationship between the total root biomass and respiration rate. The probable explanation is that the specific respiration rate decreases with the increase of structural tissue in roots. Unfortunately, it is very difficult to separate the functional and non-functional root mass in a natural community. Furthermore, the same quantity of root mass may respire at different rates under varying sets of environmental factors (Singh and Gupta, 1977). Another possible source of error in estimating root respiration *in situ* is that the contribution of varying environmental factors, such as soil properties and water content, vary among the sites and may influence the contribution of root respiration.

1.5 Modelling CO_2 Efflux

Soil respiration, including root respiration and microbial respiration, has been reported to be affected by many internal and external environmental factors (Table 1.1). This makes building a model so difficult that no model so far, whether empirical

Table 1.1 Some environmental factors affecting soil respiration

Factors	Reference
soil temperature and moisture	Bridge *et al.* (1983), Rajvanshi and Gupta (1986).
soil physical and chemical properties (e.g., soil porosity, soil pH value)	Bertrand and Kohnke (1957); Jorgensen and Wells (1973); Bridge and Rixon (1976); Raison and McGarity (1980); Groffman and Tiedje (1991).
amount and composition of soil organic matter	Broadfoot and Pierre (1939); Hogg (1993).
composition and size of soil microbial population	Flanagan and Van Cleve (1977).
root biomass	Chapman (1979).
plant productivity	Ellis (1969).
oxygen and CO_2 concentration in soil air	Lemon and Wiegand (1962); MacFadyen (1973).
nutrient availability	Kowalenko *et al.* (1978); Van Cleve and Moore (1978); Amador and Jones (1993).
inhibitors (e.g. antibacterial)	Anderson and Domsch (1975).
concentration of heavy metals (e.g., As, Cd, Cu, Pb)	Komulainen and Mikola (1995); Kuperman and Carreiro (1997).
human practice	De Jong *et al.* (1974); Houghton *et al.* (1991).

or non-empirical, can express adequately all of, or even most of, the major influences of the controlling factors.

1.5.1 Empirical models

Empirical models are mostly obtained by statistical correlation to fit measured field data. CO_2 efflux or concentration in the soil is then estimated from variation in environmental factors. Models in this category can be divided into two groups: single variable and multiple variable model.

1.5.1.1 Single variable models

Soil temperature and moisture content are two dominant factors governing soil respiration (Schlesinger, 1977), and almost all single variable models account for the influence of temperature and moisture on CO_2 efflux.

1.5.1.1.1 Temperature

Linear model

The simplest model is a linear relationship between CO_2 efflux and soil temperature:

$$F = a + bT \tag{1.8}$$

where F is CO_2 efflux; T is soil temperature in °C; and a, b are parameters. This model has been used to fit soil respiration data both in the laboratory and in the field (De Santo *et al.*, 1976; Kowalenko *et al.*, 1978; Boddy, 1983; Buyanovsky *et al.*, 1985; Rochette *et al.*, 1991; Nicolardot *et al.*, 1994). The linear model can be used only under a limited range of temperatures (Rochette *et al.* 1991), but it seems useful and suitable to describe the variation of CO_2 efflux on a large spatial and temporal scale. Fung *et al.* (1987) used a linear model to predict monthly mean soil respiration

with the monthly average air temperature of the soil surface. Raich and Schlesinger (1992) investigated annual temperature-respiration relationships on a global scale, and found a significant linear trend between soil respiration and air temperature in boreal forests and woodlands, temperate coniferous forests, temperate deciduous forests and croplands.

Quadratic model

Edwards (1975) provided a regression model for the dependence of soil respiration on temperature:

$$F = a \cdot T^2 \tag{1.9}$$

where T is the daily average temperature of the litter layer, a is a parameter, equal to about 0.044 for the total soil profile and 0.36 for mineral soil. A good simulation was obtained with this simple model of his observations and 94% of the variability in the CO_2 efflux from a forest floor, and 90% from the mineral soil, were accounted for by the variation in T^2. The annual total CO_2 efflux calculated from measured daily mean rates was less than 3% greater than the total predicted from the mean temperature by the model. However, the author also pointed out that the model overestimates rates of CO_2 efflux from exceptionally wet soil. Holthausen and Caldwell (1980) produced a similar model for root respiration.

Exponential model

The exponential model is based on Van't Hoff's theory, i.e. that the reaction rate increases by a factor (the Q_{10}) for a temperature rise of 10 °C (Glínsky and Stepniewski 1985). The model can be generally expressed as:

$$\ln F = a + bT \tag{1.10a}$$

or: $$F = a\exp(bT) \tag{1.10b}$$

where a, b are parameters and T is the temperature.

This model has been used by many researchers (e.g. Monteith *et al.*, 1964; Anderson, 1973; Kawahara, 1976; Tesarová and Gloser, 1976; Chiba, 1977; Mogensen, 1977; Yakai *et al.*, 1977; Yoneda and Kirita, 1978; Bridge *et al.*, 1983; Nakane *et al.*, 1983; Bridgham and Richardson, 1992; Peterjohn *et al.*, 1994). Kicklighter *et al.* (1994) used this model with aggregated mean monthly and yearly air temperatures to estimate regional soil CO_2 efflux from temperate forests. They found that the model provided good estimates of soil CO_2 effluxes for different sites around the world regardless of forest types.

In this model the parameter b can be related to a common Q_{10} as:

$$b = \ln(Q_{10}) / 10 \tag{1.10c}$$

For soil respiration, the Q_{10} value varies wildly depending on the type of soils or ecosystems and methods used (Table 1.2), and even for the same soil is not constant and decreases with temperature rise (Svensson, 1980; Glínsky and Stepniewski, 1985), i.e. the relationship between soil respiration and temperature is not a simple exponential function over the normal range of temperature (Lloyd and Taylor, 1994). Consequently, use of the Q_{10} approach is limited to a well defined set of conditions.

Table 1.2 Some published Q_{10} values for different ecosystems

Q_{10} value	Application and resource
1.7 ~ 5.3	leaf litter, Howard and Howard (1979).
1.7	wood litter, Yoneda (1975).
1.8~2.7	grass-covered soil, Dörr and Münnich (1987).
1.3 ~ 3.3	soil in a mixed hardwood forest, Crill (1991).
2.4~2.9	incubated soil samples, Crill (1991).
1.3~3.3	soil in various ecosystems, Raich and Schlesinger (1992).

Arrhenius model

An alternative description of the dependence of soil respiration on temperature is given by the equation of Arrhenius:

$$F = a\exp(-E / R\theta) \tag{1.11}$$

where R is the universal gas constant; θ is absolute temperature (K); E is the activation energy for respiration and a is a parameter.

By fitting this model to measured data, Bridgham and Richardson (1992) obtained average E equal to 50.3 kJ mol^{-1} (at 25 °C) but varying between 40.2 and 93.5 kJ mol^{-1} for different communities *in situ*. Lloyd and Taylor (1994), using literature data, compared the linear, exponential and Arrhenius model (with a fixed activation energy E for soil respiration). They found that none of them could provide an unbiased estimation of soil respiration, but an Arrhenius type equation, with an activation energy varying inversely with temperature, could produce an unbiased estimate of respiration rate over a wide range of temperature. The activation energy varied from 37.4 kJ mol^{-1} at 40 °C to 77.5 kJ mol^{-1} at −5 °C. The activation energy is also found to be related to soil water content. Parker *et al.* (1983) reported that activation energy values decreased from 84.9 to 39.5 kJ mol^{-1} when a desert soil was wetted. Thierron and Laudelout (1996) found that the activation energy for soil respiration measured in the field (about 105 kJ mol^{-1}) differed from that in the laboratory (about 63 kJ mol^{-1}).

The Arrhenius equation was initially derived for a chemical reaction from the collision theory of molecules. A possible analogue in a biological process is the existence of the complex of enzyme and substrates. The Arrhenius equation can also be derived more generally from the Gibbs-Helmholtz equation and the variation in enthalpy, rather than the activation energy, of a system can be used to define the temperature dependence of the rate of a process in the system. The relation defined in the Arrhenius equation may be applicable to soil respiration, but the biological explanation of *activation energy* does warrant more work.

1.5.1.1.2 Moisture

The influence of soil moisture content on soil respiration is apparent, but is not as clear as that of temperature (Howard and Howard, 1979; Cowling and MacLean, 1982). A decrease in respiration rate is observed at both low and high moisture content. The reduction in soil respiration at low moisture content is caused by low availability of soil water, and this inhibits the metabolic activity of microbes and roots. At high moisture content, the reduction in soil respiration is caused by poor oxygen accessibility and the accumulation of CO_2 because the soil pore spaces become filled with water (Glínsky and Stepniewski, 1985). Between low and high moisture limits, soil water content has little or no effect on soil respiration (Tesarová and Gloser, 1976). This relationship of soil respiration to soil water content is very difficult to express with a mathematical equation. Furthermore, the respiration rate at a particular moisture content obtained by drying out the wet soil is lower than that at the same moisture content achieved by adding water to dry soil (Glínsky and Stepniewski, 1985).

Orchard and Cook (1983) reported that a linear model fitted well with their data from incubated soil samples, with a range of soil moisture content of about 8% to 36% (water potential −0.05 to −85 MPa). Grahammer *et al.* (1991) provided a polynomial model to represent the relation of soil respiration from a grassland to soil moisture:

$$F = a_0 + a_1\sqrt{W} + a_2 W + a_3 W^2 + a_4 W^3 \qquad (1.12)$$

where a_0~a_4 are parameters and W is soil moisture content. Predicted soil respiration rate agreed well with measured data, with a correlation coefficient $R^2 = 0.85$ and 0.93 for day and night soil respiration rates respectively at 0 - 10 cm depth. The weakness of this multiple-order model is that the parameters have no biological meaning and it provides little information about the relation between biological processes and moisture content.

1.5.1.2 Multiple variable models

1.5.1.2.1 Linear models

Witkamp (1966a) developed a multiple linear model to relate soil CO_2 efflux to environmental conditions:

$$F = 46.5 + 3.22T + 26.86\sqrt{W} + 11.39 \log N - 0.64t \quad (1.13)$$

where F is in μl $g^{-1}h^{-1}$; T is in °C; W is moisture content of litter on a dry mass basis; N is the number of bacterial colonies in 10^{-6} g of air-dry litter; and t is the number of weeks since leaf fall. The correlation coefficient of multiple regression was equal to 0.71. The contribution of temperature (64%), moisture (5%), bacterial colonies (16%), and litter age (5%) were all significant ($p < 0.01$) for data from redbud, oak and pine litter.

Van Cleve and Sprague (1971) developed a high order multiple variable model for litter respiration on a forest floor in Alaska:

$$F = a_0 + a_1 T^{b_1} + a_2 W^{b_2} \quad (1.14)$$

where F is CO_2 efflux per dry litter; T is temperature; W is moisture on a dry mass basis; and a_o, a_1, a_2, b_1, b_2 are fitted parameters. Model analysis indicated that temperature is about 2 to 5 times more important than moisture in explaining variability in respiration rates.

Similar models were built by Svensson (1980), Reinke *et al.* (1981), Gupta and Singh (1981), Rajvanshi and Gupta (1986); and Rout and Gupta (1989). All these models have an inherent assumption that the environmental factors are independent of each other and that their effects are additive. It is clear that this assumption is too simple and inadequate to interpret the influence of environmental factors on soil respiration. For example, it has been reported that the effects of temperature and

moisture are interdependent (Boddy, 1983). At low moisture content, a temperature increase has little effect on soil respiration, but at high moisture content, soil respiration is more responsive to a temperature change. Similarly, soil respiration is more responsive to moisture change at optimal temperature than at a low temperature (Wildung *et al.*, 1975; Howard and Howard, 1979; Schelentner and Van Cleve, 1985).

1.5.1.2.2 Polynomial model

A high-order polynomial model may fit measured data better than the models so far presented here. However, because the form of a polynomial model is completely dependent on data structure rather than ecological meaning it is very difficult to assign biological meaning to the model and its parameters. Examples of this type of model have been presented by Schelentner and Van Cleve (1985) and by Gordon *et al.* (1987). A polynomial model may be more suitable for describing the varying trend of soil respiration on a large scale, where the biological meaning of a model's parameters is less important than interpreting the relationship of soil respiration to environmental factors. Raich and Schlesinger (1992) reviewed the data in the literature and derived a model to predict global variation of soil respiration:

$$F = 9.88T + 0.034P_r + 0.0112T \cdot P_r + 268 \qquad (1.15)$$

where F is the annual CO_2 efflux (g C m^{-2} yr^{-1}); T is the mean annual air temperature (°C) and P_r is the mean annual precipitation (mm), respectively. The model reflected the global trend of annual soil CO_2 efflux with temperature and precipitation and indicated that the global variation of soil respiration is mostly accounted for by the variation of temperature.

1.5.1.2.3 Other models

Semi-empirical model

Models in this group have typically been developed on the basis of some simple theoretical assumptions, such as one factor will influence the others, rather than acting in a simple addictive way. They have a definite ecological basis and are more process based but retain components of a regression model.

Chapman (1979) developed such a model to reflect the relation of soil respiration in heathland to soil temperature, root biomass and organic matter:

$$F = 0.0345 + e^{0.0988T}(0.0457\sqrt{B} + 0.0035M) \tag{1.16}$$

where F is in g CO_2 m^{-2} h^{-1}; B is root biomass and M is root-zone humus in kg dry mass m^{-2}. $\sqrt{B}$ emphases the decrease in relative respiration per unit dry mass with increasing root biomass . The model fitted well the measured data ($R^2 = 0.95$).

Coleman *et al.* (1976) used a model with a complex form to predict CO_2 efflux with soil moisture and temperature:

$$F = \frac{a}{bW^c + 1} e^{-dT_m^2} e^{-dT(T-2T_m)} \tag{1.17}$$

where: F is CO_2 efflux; a is scaling factor; b and c, defining the effect of water, and d are parameters; T_m is the temperature of maximal effect on microbial activity; T and W are soil temperature and soil moisture content, respectively. The form of this model was chosen to represent a qualitatively known relation between soil respiration and limiting conditions. A good simulation was obtained by applying the model in an arid grassland in which soil water content alone accounted for 99% of the abiotic variability.

Oberbauer *et al.* (1992) described a model to predict the CO_2 flux from the soil at a tundra site, incorporating the Arrhenius function for temperature and an

asymptotic function for depth to water table:

$$F = ae^{(-E/R\theta)}e^{bW_d/(W_d+c)} \quad (1.18)$$

where θ is absolute temperature; W_d is the depth to water table below soil surface; E is activation energy and R is the universal gas constant, a, b, c are regression parameters. The soil respiration rate simply increases or decreases with the arise of water table with different values of b and c. This relationship is only suitable for soils where moisture content is always above or below the optimum.

CO_2 concentration model

CO_2 efflux from the soil is closely related to CO_2 concentration in the soil air. Models to determine the relationship of soil CO_2 concentration to environmental conditions may be used to predict CO_2 efflux if gas diffusivity in the soil is known. Buyanovsky and Wagner (1983) evaluated the influence of soil temperature and soil water content on the concentration of CO_2 measured over two years and described a linear model of CO_2 concentration in relation to soil temperature and water content. Brooks *et al.* (1983) found that annual actual evaporation rate was an excellent predictor of CO_2 partial pressure in the soil, after analyzing global relationships between growing season CO_2 concentration in soils and climate. However, it is worth pointing out that evaporation rate may not be a suitable predictor of CO_2 efflux from soils because its influence on CO_2 efflux is different from that on soil CO_2 concentration.

Decomposition model

Many models of decomposition of organic matter or of carbon dynamics in soils include respiration rate as a submodel because CO_2 production is the final product of a decomposition process under most circumstances (Hunt 1977; Golebiowska and Ryszkowski, 1977; Bosatta, 1980; Ewel and Gholz, 1991). The decomposition of organic matter is a complex process in the soil, which is affected by

the quality of organic matter, such as the C/N ratio, content of lignin, etc., as well as by many environmental factors, such as temperature, pH, moisture content, oxygen availability, inorganic nutrients, accessibility, etc.. The decomposition of soil organic matter is also strongly affected by soil texture, for example, a clay soil retains more soil organic matter than a sandy soil. Clay can protect organic matter in a number of ways: by adsorbing otherwise readily available substrates, making them less available to the soil population, by stabilizing the newly formed metabolites, and by increasing the longevity of soil organisms (Jenkinson, 1988). Parton *et al.* (1987) developed the CENTURY model, which includes submodels of C and N cycling and plant growth, to describe the dynamics of soil organic matter. Jenkinson *et al.* (1991) used the Rothamsted model, which combines environmental factors and decomposition rates, to estimate regional CO_2 efflux and to predict the potential response of CO_2 efflux to global warming. A similar approach was adopted by Wang and Polglase (1995) to identify C balance in a tundra ecosystem. However, it should be noted that most of these models accounted for only a part of soil respiration, i.e. microbial respiration, but not the total soil respiration. Furthermore, these models focused on states of decomposition or carbon flow rather than the process of respiration and its relation to controlling factors. They did not provide much information which could be used to predict or interpret CO_2 efflux or soil respiration.

1.5.2 Non-empirical models

CO_2 efflux from soil arises from several complex processes. The soil is a three phase porous, usually unsaturated system with a considerable air-water interface (Rasmuson *et al.*, 1990). The efflux of CO_2 from the soil is generally controlled by the processes of gas transport and the processes of CO_2 production in the soil.

1.5.2.1 CO_2 transport in the soil

Several mechanisms of gas and vapour transport can be distinguished in a porous medium like soil, e.g. Knudsen diffusion, multicomponent molecular diffusion

and pressure flow (Thorstenson and Pollock, 1989; Massmann and Farrier, 1992) and the transport of dissolved gases in the water phase. However, ordinary diffusion and advective flow are considered to be the most important mechanisms (Freijer and Leffelaar, 1996). On the assumption that gas transport only happens in the vertical direction in the soil, one dimensional gaseous transport in both gas phase and aqueous phase can be described by a mass balance equation:

$$\frac{\partial(C_g + C_w)_i}{\partial t} = -\frac{\partial}{\partial z}(F_d + F_a)_{gi} - \frac{\partial}{\partial z}(F_d + F_a)_{wi} + S_i \qquad (1.19)$$

where the subscripts g and w indicate the gas and water phase, respectively; subscripts i, d and a represent the i component, diffusion/dispersion and advective flow, respectively; C, F and S are the mass fraction of CO_2, CO_2 flux and sources/ sinks, respectively.

This mass balance equation has been solved with different assumptions or simplifications and boundary conditions (Wood and Petraitis, 1984; Hendry *et al.*, 1993; Šimunek and Suarez, 1993; Wood *et al.*, 1993; Frejier and Loffelaar, 1996) to characterize CO_2 efflux from or CO_2 concentration in the soil. The simplest derivation from the mass balance equation can be expressed by Fick's first law:

$$F = -D_{gs}\frac{\partial C_g}{\partial z} \qquad (1.20)$$

where D_{gs} and C_g are the effective diffusivity and the mass fraction of CO_2 in the soil gas phase, respectively.

CO_2 is a reactive gas which can be dissolved in soil water and transported by movement of soil water. In wet soils, CO_2 transport in liquid phase may become quantitatively significant (Šimunek and Suarez, 1993). Rasmuson *et al.* (1990) simulated CO_2 transport for acid aggregated soil and Wood *et al.* (1993) described modelling CO_2 transport in calcareous soil.

1.5.2.2 Models for CO_2 production

1.5.2.2.1 Bunnell's model

Based on the assumption that the influence of water on biological activity and on gas diffusion follows Michaelis-Menten relationships independently, and that any one of the major determinants of respiration rate (moisture, O_2, substrate and temperature) can effectively reduce the rate of respiration independently of the other factors, Bunnell *et al.* (1977) developed a model incorporating a Q_{10} relation for temperature to predict the variation of soil respiration:

$$F = \left(\frac{W}{a_1 + W}\right)\left(\frac{a_2}{a_2 + W}\right)a_3 a_4^{(T-10)/10} \tag{1.21}$$

where F is CO_2 efflux; W is percent water content on a dry mass basis; a_1 is the water content at which biological activity is half its optimal value; a_2 is water content at which gas exchange is limited to half its maximal value; and a_3 is the theoretical maximal respiration rate at 10 °C; a_4 is the Q_{10} coefficient.

This model has been applied in different ecosystems by Gordon *et al.* (1987), Kim and Verma (1992) and Shurpali *et al.* (1995). Bonan (1995) also used this model as a submodel for microbial respiration in his land surface process model.

In this model, the influence of soil moisture content on soil respiration at both high and low moisture content are assumed to follow the Michaelis-Menten equation. The assumed relationship between soil respiration and moisture content, $[W/(a_1+W)] \cdot [a_2/(a_2+W)]$, has the form of a rectangular hyperbola (Howard and Howard, 1979). This is better than a linear assumption, but may not reflect the actual response of soil respiration to soil moisture content. There is not a sound theoretical basis for defining the relation between respiratory activity or gas diffusion and soil water content as the Michaelis-Menten equation because the Michaelis-Menten equation relates reaction rate to substrate concentration but not to environmental conditions. As discussed

above, after soil water content reaches a certain amount, the respiration rate does not change with increasing water content until it limits gas diffusion (Tesarová and Gloser, 1976; Piene and Van Cleve, 1976). Bosatta (1980) described the effect of moisture content on soil respiration, which can be expressed as:

$$f(W) = \begin{cases} \text{linearly increase from 0 to 1, when } W1<W<W2 \\ =1, \text{ when } W2<W<W3 \\ \text{linearly decrease from 1 to 0, when } W3<W<W4 \end{cases}$$

It is clear that soil respiration does not stop but maintains at a low rate in a saturated soil. If anaerobic respiration at high moisture content is taken into consideration, this scheme may be more suitable for expressing the response of soil respiration to soil moisture content.

The range of applicability of Bunnell's model is limited, i.e. it is only applicable to aerobic respiration. Furthermore, neither an upper lethal temperature nor a freezing effect is incorporated (Bunnell *et al.* 1977). Schelentner and Van Cleve (1985) modified this model with upper and lower limits for the influence of temperature, but their new model added little to Bunnell's model. Both models were found to be limited in their applicability to moisture-respiration relations because of the lack of model sensitivity to fluctuations in soil moisture when soil moisture content is high.

1.5.2.2.2 Šimunek's model

Šimunek and Suarez (1993) developed a submodel of CO_2 production in the soil for their CO_2 efflux model with a number of assumptions: i) individual CO_2 production processes are additive; ii) CO_2 production is mainly dependent on temperature, soil water content, O_2/CO_2 concentration, time and depth in the soil; iii) individual mechanisms influence the effects of others.

Šimunek's model takes into account more processes and their relations to environmental factors than Bunnell's model, and has a stronger biological/ecological basis. However, some assumptions in the model regarding the reduction of individual

mechanisms are either not clear or are open to question. For example, CO_2 reduction from water content was taken as:

$$f(h) = \frac{\log|h| - \log|h_1|}{\log|h_2| - \log|h_1|} \qquad (h_2<h<h_1) \tag{1.22a}$$

$$f(h) = \frac{\log|h| - \log|h_3|}{\log|h_2| - \log|h_3|} \qquad (h_3<h<h_2) \tag{1.22b}$$

$$f(h) = 0 \qquad (h<h_3) \text{ or } (h>h_1) \tag{1.22c}$$

where h is the water column head, a pressure parameter related to the soil matric potential. Parameters h_1 and h_3 stand for the high and the low water head at which soil respiration stops and h_2 is the water head when $f(h)$ takes its maximum, respectively. The equation gives a response curve of CO_2 efflux to soil moisture similar to that observed in the laboratory (Tesarová and Gloser, 1976) or to those used by other models (Bunnell *et al.* 1977; Bosatta, 1980), but does not explicitly involve any biological process or theory. Furthermore, in Šimunek's model, the influence of water content on gas diffusion was also included in a transport submodel, and $f(h)$ in equation 1.22 is only the effect of water content on CO_2 production, i.e. on soil respiration. In this case, a simple increasing function for $f(h)$ is expected, rather than equation 1.22.

CHAPTER 2: THE OPEN-TOP CHAMBER

2.1 Introduction

Soils are the largest carbon pool and the largest resource of atmospheric CO_2 in global carbon cycling. Accurately and continuously monitoring CO_2 evolution from the soil surface is very important for enhancing our understanding of carbon dynamics at both ecosystem and global scale. The reliability of this measurement is dependent on the technique applied and it is difficult to compare different estimates of CO_2 efflux measured by different techniques. The dynamic chamber method is thought to be one of the more accurate methods relative to other chamber techniques but it is subject to a potentially serious error in that possible pressure differences between inside and outside the chamber can dictate the apparent size of the measured CO_2 efflux. A large error in the estimation of CO_2 efflux may be caused by a small pressure difference. However, the relationship between measured CO_2 efflux to pressure difference is still unknown because of the difficulty in eliminating the pressure difference with existing dynamic chambers.

In dynamic chamber techniques, there are two ways to obtain a representative estimation of the spatial variation of CO_2 efflux: multi-chamber and moving chamber systems. For a multi-chamber system, several chambers are connected in parallel to an IRGA with the CO_2 concentration for each chamber being measured in turn (Vose *et al.*, 1995). Such a system with more than 4 chambers is difficult to implement because of the practicalities of keeping a steady and continuous air flow through each chamber. For a moving chamber system, a fast response chamber is crucial, and one which can be moved quickly between different locations such that the temporal changes of CO_2 efflux between each location will be small.

In published descriptions of other dynamic chambers, which have a common feature of simultaneously drawing air from and blowing air into a chamber placed on the soil surface (Ewel *et al.*, 1987a; Nakayama, 1990; Vose *et al.*, 1995), a pressure difference between inside and outside the chamber is inevitable although it may be

kept small in some chambers (Fang and Moncrieff, 1996). In this chapter, we present a new open-top dynamic chamber technique for continuously monitoring soil CO_2 efflux. The chamber reported here was developed with two objectives: to eliminate the influence of pressure difference on CO_2 efflux measurement and also to develop a sensitive and fast-response chamber which could be moved quickly between different locations in the field.

2.2 Materials and Methods

2.2.1 Chamber description

The chamber (Fig. 2.1) is composed of an outer frame and an inner sampler. The outer frame consists of three brass rings which are soldered together. The lower ring is 3.0 cm high and 13.8 cm in inside diameter and its lower end is sharpened in order to insert into the soil. The middle tapered ring is 13.0 cm ID at its lower end and 18.0 cm ID at the other end, with a height of 3.8 cm. The top ring is 18.0 cm ID and 13.5 cm high. The chamber covers about 150 cm^2 of the soil surface. A ring of brass tubing, 0.6 cm ID, is fixed to the inner wall of the chamber frame, about 2.5 cm away from where the upper and the middle frame ring join. There are many evenly distributed small holes in the tube ring, through which air is sucked into the reference cell of an IRGA. The cone-shaped sampler is suspended inside the chamber frame by an aluminium cross piece. The sampler has an outside diameter of 15.0 cm on the bottom. Many small holes, 0. 2 cm in diameter, are distributed evenly on the bottom of the sampler. A thin wing ring which helps to prevent CO_2 leakage and provides an adequate mixing of evolved CO_2 with air, is attached to the bottom edge of the sampler. The angle of the wing ring, about 60 degrees, is the same as that of the middle frame ring so that the wing ring and frame can fit snugly when the sampler is in its lowest position. The sampler can be moved up and down by screwing a nut on the holding cross.

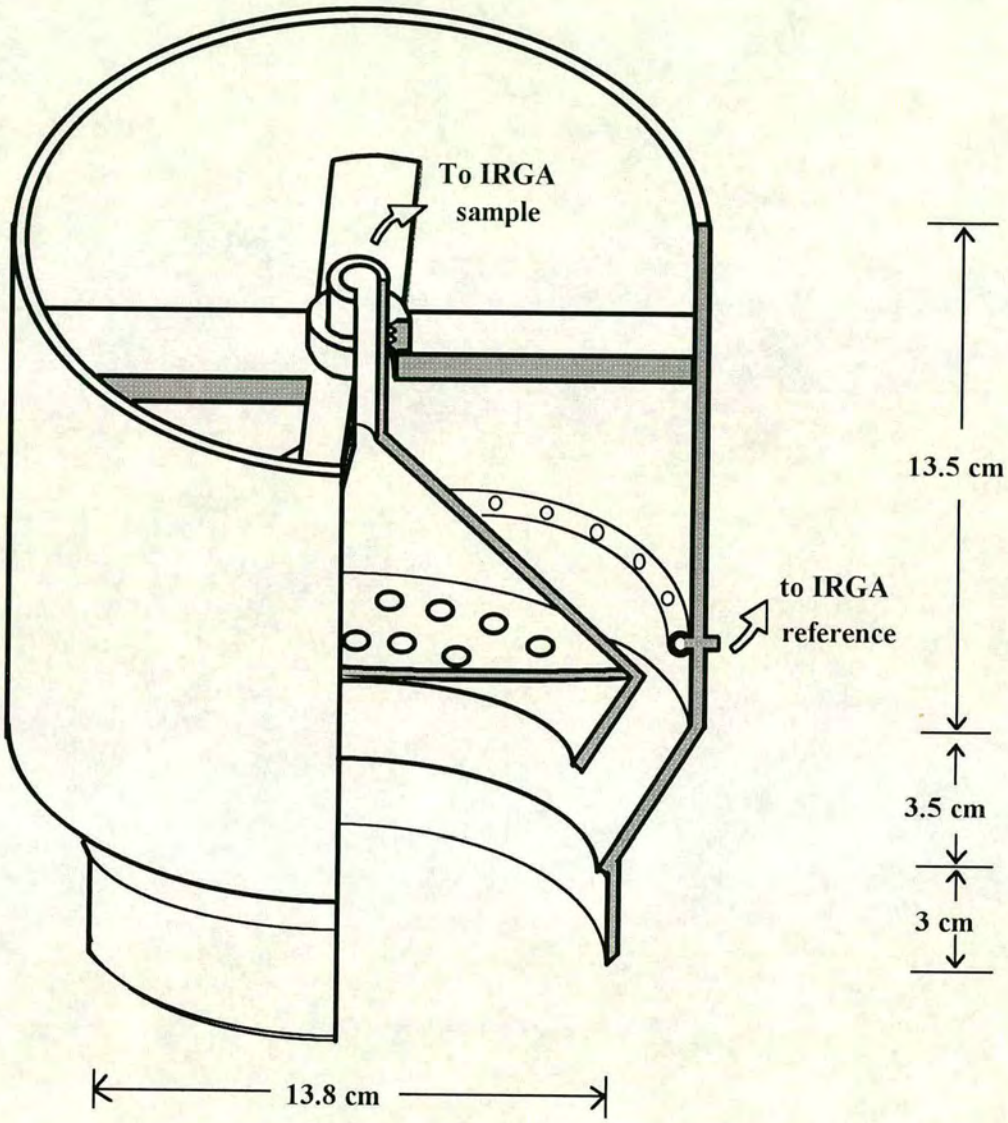


Fig. 2.1 A diagram of the open-top chamber

From the top of the chamber, air goes into the chamber, and then divides into two flows, one going into the reference cell of an IRGA through the tube ring, and the other getting to the lower part of the chamber through the gap between the wing ring and the outer frame. Finally, the air flow, mixed with the CO_2 evolved from the soil underneath the chamber, is drawn through the sampler into the sampling cell of the IRGA (Fig. 2.2). The CO_2 concentration difference between the IRGA sample and reference is only dependent on the amount of CO_2 released from the soil surface covered by the chamber. The gap between the sampler and the frame can be adjusted between 0 and 1.5 cm , depending on the flow rate through the sampler.

A small piece of brass tube was fixed through the wall of the lower frame ring to enable the variation of the pressure difference between inside and outside the chamber to be monitored. Pressure differences were monitored with a micromanometer (Model Mp 30 mb D/u, Air Instrument Resources Ltd., Oxford, England), which has a resolution of 0.1 Pa.

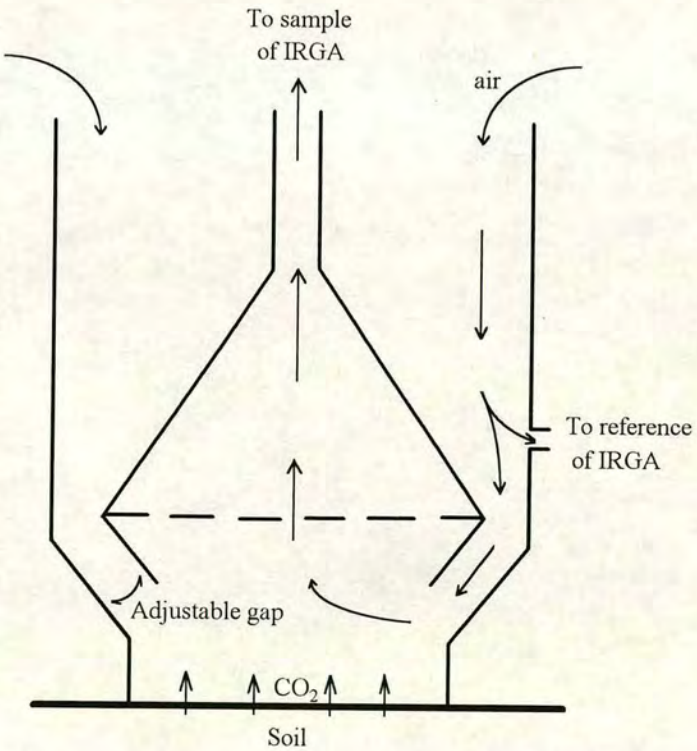


Figure 2.2 The air flow through the chamber

2.2.2 Measurements of CO_2 efflux

Measurement in the field

For measuring CO_2 efflux, the new chamber is placed on a plastic collar. The collar is 5 cm high and 13.3 cm in ID, and is 13.8 cm in OD on the upper 2 cm in order to seal the collar and chamber. No sealing material was applied between the chamber and collar. The lower end of the collar was sharpened and typically, could be pressed about 4 cm into the forest floor or 2 cm into mineral soil, depending on circumstances.

CO_2 effluxes were measured both *in situ* and in the laboratory with a measuring system showed in Fig. 2.3. Field trials were made in a slash pine ecosystem in Florida, USA and on the campus of the University of Edinburgh, during 1995 and

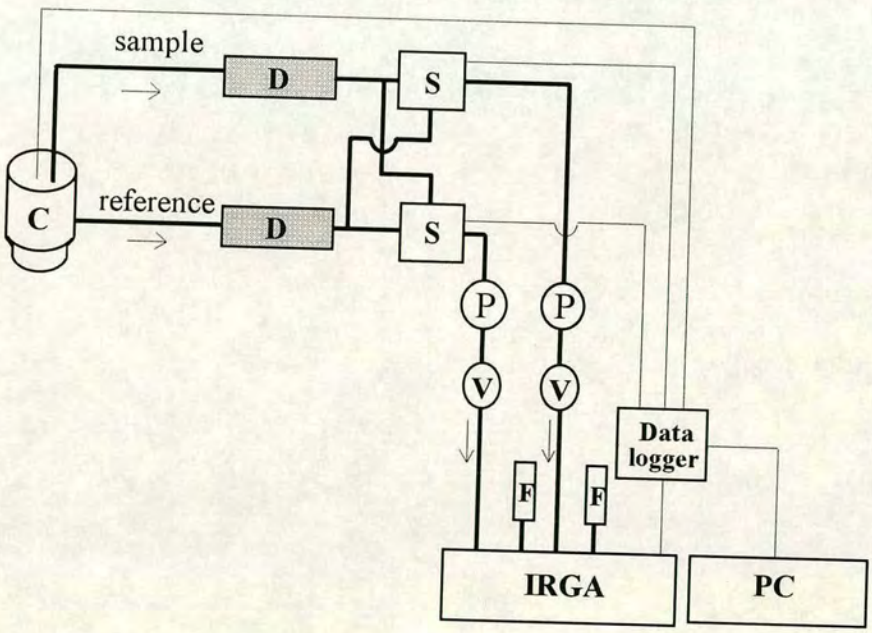


Figure 2.3 The soil CO_2 efflux measuring system
C: chamber; D: dehumidifier; P: pump; V: valve; S: switch; F: flowmeter.

1996. Sample and reference air was continuously drawn from the chamber to an IRGA (Li-Cor 6262/6252, Li-Cor Inc., Lincoln, Nebraska, USA). Flow rates were read and controlled by flowmeters (model A-250-2, Porter Instrument Company, Hatfield, USA). CO_2 concentration difference and efflux were logged at one second intervals during the last three minutes of a six minute sampling period (logger model 21x; Campbell Scientific Instrument Co., Loughborough, UK). After some preliminary trials it was found that more time was needed to allow the system to achieve a new equilibrium when there was a large negative pressure difference between inside and outside the chamber, especially for values exceeding -1.0 Pa.

The whole measuring system, except the chamber and collars, was contained in an environmental enclosure and could be powered by mains electricity as well as by batteries for use in the field (see photos in Appendix).

Measurement in the laboratory

An undisturbed soil core, about 50 cm in diameter and 60 cm deep, was taken and incubated in the laboratory to investigate the influence of flow rate and pressure difference on measured CO_2 efflux. The soil core was put in an open-top plastic container which had the same inside dimension as the soil core. There were several holes in the bottom of the container and the container was immersed, one week before the efflux measurements started, in 3 cm deep water in order to maintain a consistent soil moisture profile and CO_2 concentration gradient inside the soil core. A collar was pushed 2 cm into the soil, in the centre of the soil surface. The measurement of CO_2 efflux in the laboratory was by the same method as in the field.

A previous dynamic chamber (see Fang and Moncrieff (1996) for detail) was used for comparison and for the estimation of CO_2 effluxes under positive pressure differences. The 'old' chamber was modified to fit the collar. Foam tape was applied between the old chamber and collar for sealing.

2.3 Results

2.3.1 Chamber setting and measured CO_2 efflux

With this open-top chamber, the CO_2 efflux measured is mainly dependent on the gap between the sampler and the chamber frame. When the gap is small, a considerable negative pressure difference may be established in the lower part of the chamber, and this will cause some air with a high CO_2 concentration to be sucked from the soil into the chamber and increase the measured CO_2 efflux. On the other

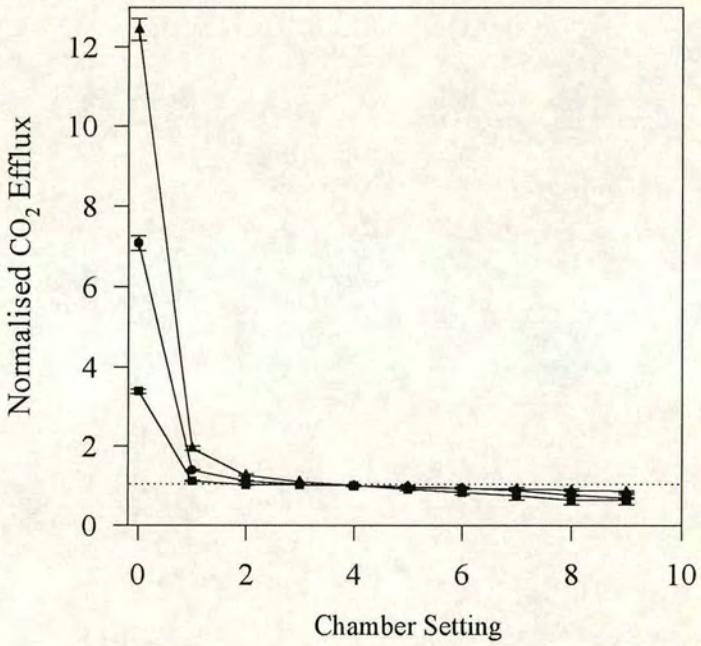


Fig. 2.4 The influence of chamber setting on measured CO_2 efflux: —■—, flow rate 2 dm^3 min^{-1}; —●—, flow rate 4 dm^3 min^{-1}; —▲—, flow rate 8 dm^3 min^{-1}. Error bars indicate ± one standard error of CO_2 efflux (n = 8). Chamber settings 0 and 9 are equivalent to a gap of 0 and 1.5 cm between the sampler and the chamber frame, respectively. The measured CO_2 efflux is normalised such that the efflux at setting 4 is 1.

hand, when the gap is too big, some of the CO_2 evolved from the soil under the chamber will leak from the lower to the upper part of the chamber and then to the atmosphere above resulting in a low efflux.

At a setting such that the effect of pressure difference is negligible and no leakage of CO_2 occurs, the measured CO_2 efflux will be fairly close to the undisturbed one. In a certain range near this setting, the measured CO_2 efflux will be relatively constant.

Figures 2.4, 2.5 show the relation of measured CO_2 efflux to chamber setting

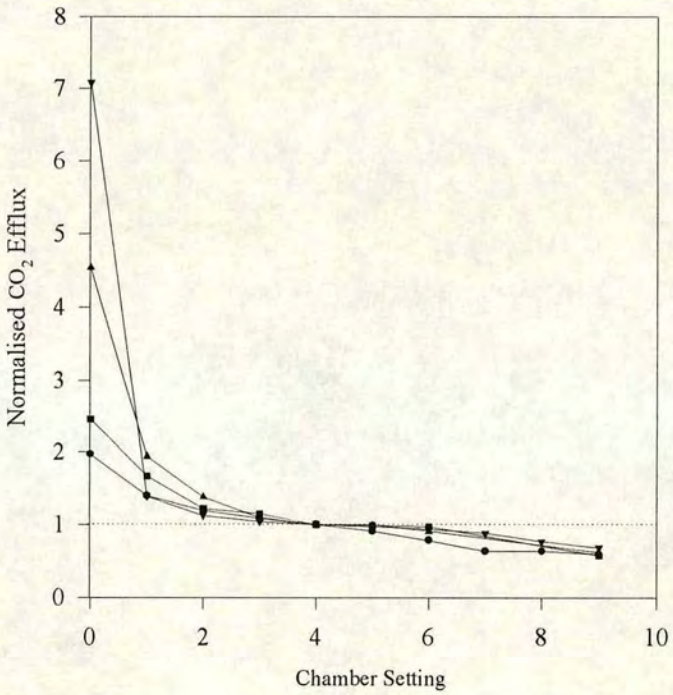


Figure 2.5 The influence of chamber setting on the measured CO_2 efflux:—●—, measured *in situ* in the campus of Edinburgh University with an average CO_2 efflux less than 0.04 mg CO_2 m^{-2} s^{-1}; —■—, *in situ* in a slash pine site in Florida with an average efflux of 0.168; —▲—, *in situ* in the slash pine with an efflux of 0.439; —▼—, in the laboratory with an average efflux of 0.334. Error bars indicate ± one standard error of CO_2 efflux in mg CO_2 m^{-2} s^{-1}(n = 6 for measurements in slash pine site, n = 8 for others). Flow rate was 4 dm^3 min^{-1}.

with different flow rates both in the field and in the laboratory. The unit of chamber setting is one turn of the holding nut. Settings 0 and 9 are equivalent to a gap of 0 and 1.5 cm, respectively. The measured CO_2 efflux is normalised such that the efflux at setting 4 is 1.

No pressure difference between inside and outside the chamber was detected with a chamber setting more than 1 for flow rates of 2 and 4 dm^3 min^{-1} and more than 2 for a flow rate of 8 dm^3 min^{-1}. When the chamber setting was less than 2, a significant increase in measured CO_2 efflux was observed. On the other hand, there was an obvious decrease in measured CO_2 efflux, when the chamber setting was more than 6. At setting 0, the lower part of the chamber was nearly closed and a considerable negative pressure difference arose. In the laboratory, measured CO_2 efflux was 12.4, 7.1 and 3.4 times that at setting 4 for flow rates of 8, 4, and 2 dm^3 min^{-1}, respectively. At setting 9, the corresponding efflux was only 0.84 0.68, and 0.65 times that at setting 4. A very consistent efflux, with a variation less than 5%, was obtained in the range of settings 4 - 5 for flow rate 8 dm^3 min^{-1}, setting 3 - 5 for flow rate 4 dm^3 min^{-1} and setting 2 - 4 for flow rate 2 dm^3 min^{-1}, respectively. Settings 4.5, 4.0 and 3.0 were thus chosen as the equilibrium point for flow rates 8, 4, and 2 dm^3 min^{-1}, respectively.

Paired measurements of the new open top chamber and the previous chamber in the laboratory indicted that the results with these two chambers matched very well. At a flow rate of 4 dm^3 min^{-1}, the average CO_2 efflux (n = 36) was 0.410 mg CO_2 m^{-2} s^{-1} for the new chamber and 0.408 mg CO_2 m^{-2} s^{-1} for the old one in conditions of no detectable pressure difference (less than $\pm$ 0.1 Pa).

The field measurements in a slash pine ecosystem in Florida indicated that this new chamber is reliable for estimating CO_2 efflux. The average CO_2 efflux was estimated to be 0.217 mg CO_2 m^{-2} s^{-1} in September, 1995 and 0.087 mg CO_2 m^{-2} s^{-1} in January, 1996. The results are comparable with previous data from this ecosystem (Ewel *et al.*, 1987a). The daily variation of CO_2 efflux shows a reasonable pattern and is consistent with the daily and seasonal trend of soil temperature (to be discussed later in Chapter 3). The open-top chamber was found to be sensitive enough to detect small fluctuations in CO_2 efflux caused by changes of boundary layer conditions

during dawn and after sunset.

For routine measurements of CO_2 efflux, the system could reach a new equilibrium within about two minutes of the chamber being placed on the soil surface. Most of this time was required for flushing the dead volume of the system and IRGA. The fast response of this system makes it easy to move the chamber amongst different positions within a short period to look at the spatial variation of CO_2 efflux. A good correlation of CO_2 efflux with the spatial distribution of root biomass, organic matter in the soil and understorey features was found in the slash pine system and this will be discussed further in Chapter 3.

2.3.2 Influence of pressure difference on measured CO_2 efflux

The emission of CO_2 from the soil surface was found to be extremely sensitive to the pressure difference between inside and outside the chamber (Fig. 2.6). In the laboratory, a pressure difference of -0.5, -1.0 and -2.0 Pa could cause an increase in measured CO_2 efflux of up to 6, 14 and 21 times that under no pressure difference. Even a very small negative pressure difference, such as -0.1 Pa, could lead to a considerable overestimation of CO_2 efflux (negative indicating pressure inside the chamber was less than outside).

With a pressure difference of 0.2, 0.6, 1.0 and 2.0 Pa, the observed CO_2 effluxes were 0.55, 0.31, 0.19 and 0.13 that with zero pressure difference, respectively. The measured CO_2 emission was relatively less sensitive to a positive pressure difference than to a negative one. The decrease in efflux caused by a positive pressure difference was less than the increase caused by a negative pressure difference of the same magnitude.

With a negative pressure difference between inside and outside of the chamber, some air with a high CO_2 concentration is sucked out from the soil. The influence of pressure difference on the estimated CO_2 efflux rate is related to the type of soil being measured. The increase of measured CO_2 efflux caused by a negative pressure difference from a soil with a high respiratory capacity and high porosity was much more than that from a soil with low respiratory capacity and low porosity (Fig.

2.5). In the floor of the slash pine ecosystem in Florida, a negative pressure difference of -0.6 Pa (0 setting at flow rate of 4 dm^3 min^{-1}) led to an increase of 2.5 times that under zero pressure difference in a position where the average respiration rate was 0.168 mg CO_2 m^{-2} s^{-1} and the soil total porosity was 0.41; the increase was 4.53 times in a position with corresponding values of 0.439 mg CO_2 m^{-2} s^{-1} and 0.55.

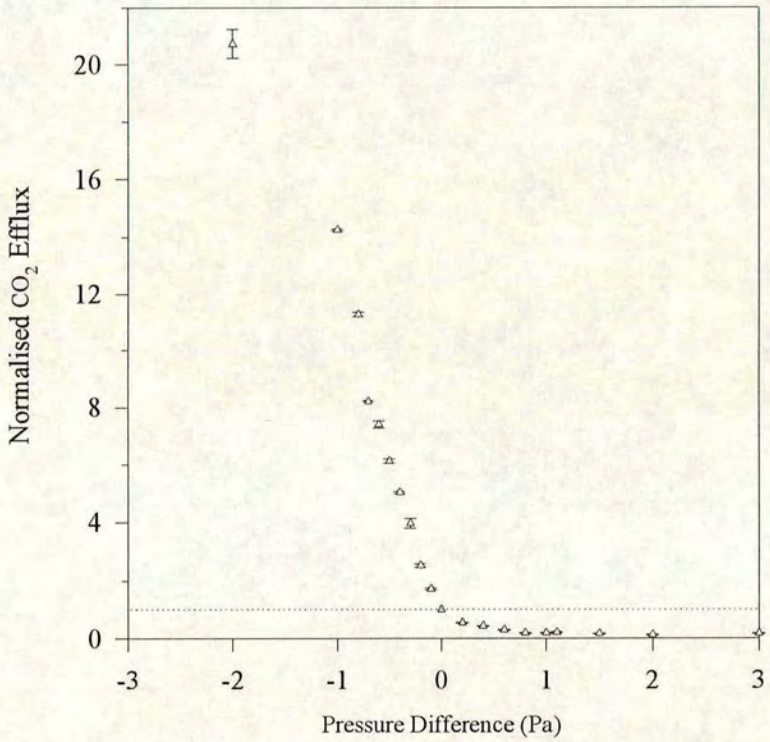


Fig. 2.6 The response of measured CO_2 efflux to pressure difference. Error bars indicate ± one standard error of the CO_2 efflux (n = 8) and fluxes are normalised such that mean flux at 0 pressure difference is 1. Flow rate was 4 dm^3 min^{-1}.

2.3.3 Influence of flow rate on measured CO_2 efflux

No systematically significant variation of measured CO_2 efflux was observed with flow rates ranging from 1 to 8 dm^3 min^{-1} (Fig. 2.7). Corresponding air movements over the soil surface inside the chamber were 7 to 55 cm min^{-1}. The air

movement of 55 cm min^{-1} equates to a flow rate of 11 dm^3 min^{-1} for the old chamber. As the flow rate is unlikely to exceed 8 dm^3 min^{-1} in a routine CO_2 efflux measurement with a dynamic chamber method, its influence on the measured CO_2 efflux can be regarded negligible. The higher measured effluxes with a higher flow rate in Fig. 2.4, mostly visible when the chamber setting was less than 2, were the result of a higher pressure difference caused by the higher flow rate at a giving chamber setting.

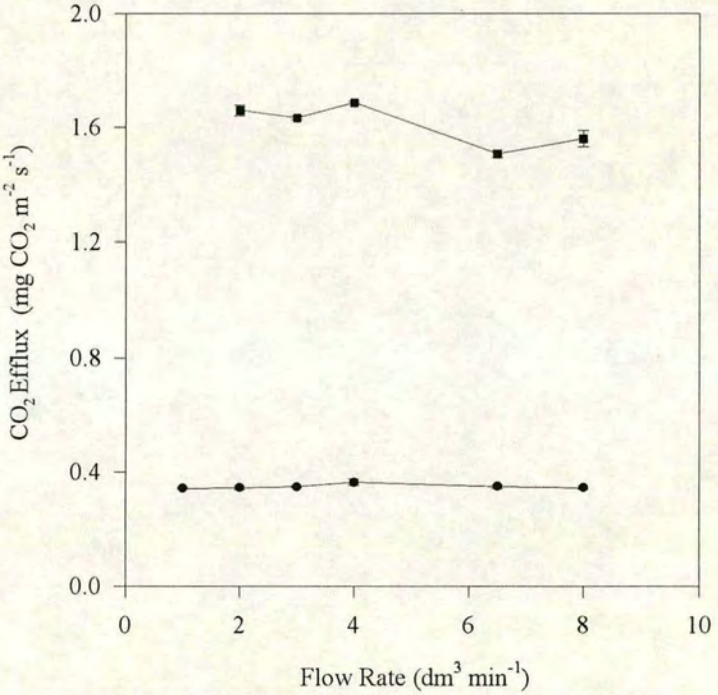


Fig. 2.7 The relation of measured CO_2 efflux to flow rate: —●—, pressure difference 0.0 Pa; —■—, pressure difference -0.4 Pa. The chamber setting was adjusted at high flow rates to ensure that no detectable variations in pressure difference were being caused by the high flow rates. Error bars indicate ± one standard error of measured efflux (n = 6).

2.4 Discussion

A perfect chamber would have no impact on CO_2 evolution and environmental conditions, a fast response, and be able to be used continuously. These characteristics are all desirable yet no published chamber so far meets all of these requirements. Although the closed system Li-Cor chamber that measures the rise in CO_2 concentration has recently been used by several researchers (Norman *et al.*, 1992; Dugas, 1993; Ham *et al.*, 1995; Shurpali *et al.*, 1995), it is not designed for continuous measurement. As discussed by Fang and Moncrieff (1996), the pressure difference in a dynamic chamber system depends on the flow rate through the chamber and the resistance of the system to air movement. In the Li-Cor chamber system, air is circulated in a loop, and flow rates in and out of the chamber are the same. However, a small pressure difference is still possible in the system as a result of the uneven distribution of resistance. The resistance between the pump and inlet of the chamber may be different from that between the pump and the outlet of the chamber. No data so far are available to assess the possible influence of pressure differences on measured CO_2 efflux with the Li-Cor system. Discussion of the pressure difference and its influence on measured CO_2 efflux for other chamber systems passing air through the chamber is not possible as there are no such measurements published with the description of these systems (e.g. Vose *et al.*, 1995; Jensen *et al.*, 1996; Thierron and Laudelout, 1996).

Compared with various published chambers, the new open-top chamber developed here seems to have more of the desired characteristics and has more flexibility for use in different conditions. The system can complete one sample within three minutes, which is much shorter than the sampling interval of 10 minutes used by Vose *et al.* (1995), so this chamber can be moved quickly among many locations over a short period of time during which the temporal variation of CO_2 efflux can be neglected. The system can also be left running unattended for 24 hours or longer.

Kanemasu *et al.* (1974) reported that the measured CO_2 efflux was one order of magnitude larger with a negative pressure difference of about –2.5 Pa than that

with a positive pressure difference of +1.0 Pa. Measurements presented here suggest a variation of about two orders of magnitude of measured efflux within that range of pressure difference. It was previously pointed out that the dynamic method fails to give a reasonable estimate of soil respiration when the magnitude of pressure difference exceeds ± 0.5 Pa, and recommended a pressure difference held to within ± 0.2 Pa or less to get a reliable estimate of CO_2 efflux rate with a dynamic chamber (Fang and Moncrieff, 1996). It seems that the importance of pressure difference and its complexity in dynamic chamber methods were somewhat underestimated in previously published work. In some circumstances, even a very small negative pressure difference (less than -0.1 Pa) may cause an apparent doubling in measured CO_2 efflux (see Fig. 2.5 at chamber setting 1 with a flow rate of 4 dm^3 min^{-1}) and a serious error in the estimation of CO_2 efflux based on such data.

Vose *et al.* (1995) measured CO_2 efflux from the soil surface in an experiment of enriched CO_2 concentration and fertiliser using a dynamic chamber method. Their CO_2 efflux rates were low (maximum rate for a control chamber in June was about 0.02 mg CO_2 m^{-2} s^{-1}) for such an ecosystem and were difficult to explain. A possible reason for that low efflux may be an anomalous pressure difference, but, unfortunately, they did not measure pressure differences.

As discussed by Fang and Moncrieff (1996), in dynamic chamber systems, a high flow rate is always associated with a large pressure difference when air is blown into or drawn out the chamber. When air is blown and drawn simultaneously through the chamber, a higher flow rate will cause a larger pressure fluctuation. A possible explanation for the reported increase of measured CO_2 efflux with flow rate (Golley *et al.*, 1962; Schwartzkopf, 1978) is that the increase was caused by the increasing pressure difference associated with the flow rate but not the flow rate itself. The method used by Golly *et al.* (1962) would definitely create a larger pressure difference with a high flow rate although they did not monitor the change of pressure differences. The wind speed (0 to 0.6 m s^{-1}) generated by a fan in the measurement of Hanson *et al.* (1993) was obviously much larger than the air movement over the soil surface caused by passing air through the chamber. It is possible that the fan may build a negative pressure difference in the lower part but a positive one in the upper

part of the chamber. Additional mass flow may arise from the soil but the actual effect is dependent on the specific chamber structure. For other published dynamic chamber techniques, it is difficult to separate the influence of flow rate from that of pressure difference. Our result for the influence of flow rate is in agreement with the study by Cropper *et al.* (1985).

After the new open-top chamber is correctly set up, the pressure difference will not significantly affect the measured efflux. However, there may be some influence on soil CO_2 evolution as a result of the barometric pressure fluctuations in natural conditions. Massmann and Farrier (1992) pointed out that the fluctuation of atmospheric pressure may cause a significant effect on soil CO_2 efflux when the soil properties are not uniform in an ecosystem. The interaction between pressure difference, soil properties and soil respiratory capacity makes it more complicated to examine the influence of pressure difference on measured CO_2 efflux and more work is needed to identify relations between them. Possible fluctuations of CO_2 efflux from the soil surface resulting from changes in barometric pressure may be damped by a closed chamber system and a bias may thus occur.

Fluctuations in measured CO_2 efflux caused by gusts were found in the field measurements at Edinburgh. As a gust also causes a sudden change of pressure, it is still unclear whether the fluctuation was due to the air movement or the change of pressure or both. More work is needed to address whether a gust can cause a fluctuation in soil CO_2 efflux or only in measured efflux.

A possible modification can be applied to this chamber to get a better performance under some conditions. An open-bottom container, about 21 cm ID and 21 cm high, could overlap the chamber and be fixed to it. The open end of the container should be about 2 cm above the ground. This modification would probably provide a more consistent and steady air flow to the lower part of the chamber and of the reference air flow to the IRGA, and thus reduces possible fluctuations in measured CO_2 efflux caused by gusts. Furthermore, as air is drawn into the chamber from near the soil surface, possible errors in measurement caused by a gas leak from the joint between the chamber and the soil would be negligible. Except for a very loose soil surface, such as a thick fresh litter layer, no base collar would be needed, thus

eliminating this possible source of disturbance.

2.5 Summary and Conclusions

An equilibrium CO_2 efflux can be obtained with this new open-top chamber at different flow rates, with no detectable pressure difference or CO_2 leak in the system. The influence of pressure difference on measured CO_2 efflux is then negligible and the estimated CO_2 efflux is fairly close to the undisturbed CO_2 efflux rate from the soil.

A measuring system with this chamber is simple and easy to use in the field. The system will quickly achieve equilibrium after the chamber is placed on the soil surface, making it suitable to move between different locations to investigate the spatial variation of CO_2 efflux and/or leave unattended at one position for continuously monitoring CO_2 efflux.

The pressure difference between inside and outside the chamber is a dominant factor controlling the measured CO_2 efflux from the soil surface with dynamic chamber methods. A pressure difference change of a few tenths of Pa will cause a several fold variation in the measured CO_2 efflux. Although the measured efflux is less sensitive to a positive pressure difference than to a negative one, a very small positive pressure difference still leads to a considerable underestimation of CO_2 efflux rate.

The influence of a pressure difference on the measured flux is also related to the type of soil being measured. In a soil with a high respiratory capacity and large porosity, a pressure difference will cause a more serious over- or under-estimation of CO_2 efflux rate. The influence of pressure difference on the measured CO_2 efflux and its complexity have been largely overlooked in previous published work.

In the new dynamic chamber method described above, flow rates up to 8 dm^3 min^{-1} or air movement over the soil surface up to 55 cm min^{-1} do not influence CO_2 efflux from the soil beneath the chamber.

CHAPTER 3: SOIL CO_2 EVOLUTION FROM A SLASH PINE PLANTATION

3.1 Introduction

Measurement of carbon dioxide efflux from the soil is an essential component in studies designed to evaluate biological processes in relation to the ecosystem carbon budget. Measurements of forest floor CO_2 efflux have been made previously in various forest ecosystems (Raich and Schlesinger, 1992), but few measurements were continuous because of the limitations inherent in the techniques used. In most studies, sampling of CO_2 efflux was done once per hour or every few hours. Both the rate of CO_2 efflux and the environmental factors affecting soil respiration and CO_2 transport in the soil are likely to have changed during such sampling periods. Discontinuous sampling is less useful when it comes to understanding soil respiration and its relationship with environmental conditions. The spatial variation of soil CO_2 efflux beneath a forest canopy has been studied least so far although it is as important as the magnitude and the temporal variation of the CO_2 efflux. High spatial variability of CO_2 efflux has been reported in some forest ecosystems (Cropper *et al.*, 1985; Raich *et al.*, 1990; Thierron and Laudelout, 1996), and has been related to topographic characteristics, such as slope (Garrett and Cox, 1973; Hanson *et al.*, 1993). However, little is known about the spatial variation of CO_2 efflux and its relationship to environmental factors within an ecosystem.

Slash pine (*Pinus elliottii* Engelm. var. *elliottii*) grows naturally on the Atlantic and Gulf coastal plains in the south-eastern United States and is now planted extensively throughout the region (Fisher and Stone, 1990). At present, 4.3×10^6 ha (11 percent) of the south-eastern states are forested in slash pine and one-half of this total is in plantations. Florida alone contributes about 2.1×10^6 ha to the total and conversions of land to plantations in this state is increasing (Hendry and Gholz, 1986). Because of the importance of these intensively managed forests to the economy and ecology, many studies have been conducted in north Florida slash pine plantations,

such as the structure and productivity, nutrition, above- and below-ground carbon allocation and its dynamics in slash pine plantations (Shoulders and Ralston, 1975; Gholz and Fisher, 1982, 1984; Gholz *et al.*, 1985; Gholz *et al.*, 1986; Gholz *et al.*, 1991b; McMurtrie *et al.*, 1994; Teskey *et al.*, 1994).

Carbon dioxide fluxes from soils under slash pine plantation have also been reported by Cropper *et al.* (1985), and Ewel *et al.* (1987a, b). Most recently, CO_2 fluxes have been sampled during one year before clearcutting on fertilised and unfertilised control stands (Castro *et al.*, 1994) as well as over one year after the clearcutting on the same site (Castro *et al.*, *unpubl.*). Cropper and Gholz (1991) have measured the respiration rates of the needles and fine roots of mature slash pine trees. Published studies did give some estimates of the magnitude of CO_2 efflux from soils in a slash pine plantation, and indicated that soil CO_2 efflux is not affected by fertilisation and only slowly responds to harvesting, soil trenching of plots in intact stands or root severing in small cores. However, in this earlier work the static chamber technique was employed to estimate CO_2 efflux with the use of either the soda-lime absorption method corrected with an IRGA dynamic chamber (Ewel *et al.*, 1987a, b), or the enrichment method (Castro *et al.*, 1994). As discussed in Chapter 1, CO_2 efflux might be underestimated by such static chambers. Furthermore, because a static chamber cannot be left on the soil surface for a long time, no continuous monitoring of CO_2 efflux in the field was possible and it is very difficult to identify the daily pattern of soil respiration and the possible impact of environment factors on soil respiration with such measurements. In addition, the spatial variation of CO_2 efflux on the forest floor and possible reasons for the variation remain unexplored.

The study reported here is part of a wider project entitled "Exchange of Energy and Radiatively-active Gases between Slash Pine and Cypress Ecosystems and the Atmosphere" co-ordinated by the School of Forest Resources and Conservation, The University of Florida, USA. The project aims to measure and to simulate the fluxes of CO_2, H_2O, sensible heat, CH_4 and other non-methane hydrocarbons between these ecosystems and the atmosphere in north-central Florida. The team from the Institute of Ecology and Resource Management, the University of Edinburgh was responsible for measuring CO_2, H_2O, non-methane hydrocarbons and sensible heat

fluxes between the ecosystems and the atmosphere. Part of the University of Edinburgh's role was to provide a reliable estimate of CO_2 efflux and its variation in the slash pine site with the new chamber described in Chapter 2. The collaborative project started in March 1995 and finished in May 1997.

In this chapter, CO_2 effluxes from the soil in the slash pine stand are reported from different seasons with the new open-top chamber. The daily pattern of soil CO_2 efflux and its relation to soil temperature, and the spatiality of CO_2 efflux are also analysed.

3.2 Materials and Methods

3.2.1 Site description

The study site is in Alachua County, 15 km northeast of Gainesville, Florida, USA (29°44' N, 82°9' W), managed by Container Corp. of America for commercial pulpwood production on rotations of about 25 years. The stand is second-rotation slash pine planted after clearcutting (stem-only harvest) the previous stand in 1972. The remaining debris of clearcutting were roller chopped, broadcast and burned, and the site was then bedded. Beds and troughs are still visible, but are not very distinct, on the forest floor. No fertiliser and thinning operations were applied after trees were planted (Gholz, 1996, *pers. comm.*).

A plot of 25 × 25 m was chosen for measuring soil CO_2 efflux and other environmental factors. The plot, more than 100 m from a forest ride, is located in a large uniform plantation of slash pine and has a fetch of several km in all directions. The average tree height at the time of the study (1995) was about 19 m. Understorey shrubs covered about 30% of the forest floor and consisted mainly of clumps of saw palmetto (*Serenoa repens*) and scattered individuals of gallberry (*Ilex glabra*) and wax myrtle (*Myrica cerifera*). There were a few sparsely scattered herbaceous plants.

The mean elevation of the area is about 49 m above sea level and the topography is flat. A thick litter and humus layer which was distinct from the mineral

soil was distributed evenly on the forest floor where it was not covered by the understorey plants. More litter was found under saw palmetto than elsewhere. The soil is classified as ultic haplaquods, being sandy, siliceous, thermic with a subsurface organic accumulation at about 35 cm and an uneven accumulation of kaolinitic clay at about 120 cm. However, the soil profile on the site is not well developed or very distinct because of the bedding when trees were planted. A water table is present in the root zone most of the year at an average depth of about 60 cm, although temporary fluctuations from the surface to a depth over 2 m are possible, depending on rainfall intensity and amounts. The soil has low nutrient availability and is acid with a pH value of 4.5.

The climate of the area is moderately seasonal, with a mean annual precipitation of 133 cm and a mean annual temperature of 21.7 °C (1955 - 1995). There are two generally dry periods from September to November and from February to May (Gholz and Fisher, 1984; Gholz *et al.*, 1991b; Gholz, 1996, *pers. comm.*).

3.2.2 Measurement of CO_2 efflux

For monitoring soil CO_2 efflux, twelve chamber collars (see Chapter 2) were distributed along the diagonal of the plot, taking into account the microtopography resulting from the distribution of beds and troughs and the area covered by understorey plants (Fig. 3.1). Because the litter layer was very porous, collars were pressed into the forest floor at a depth of 3 to 6 cm, depending on the depth of the litter and humus layers, to the mineral soil. Collars were left in place for the whole experimental period of 9 months. The aboveground living vegetation was removed from the area inside the collars.

Soil CO_2 efflux was measured using the method and the system described in Chapter 2. Because of fluctuating environmental conditions and instability of the IRGA itself, there was some variability in the IRGA readings. In the differential measuring mode employed, zero drift is crucial in determining the magnitude of the total error in CO_2 efflux estimation, especially when the efflux is small. A logger-controlled switch unit was introduced to reduce the error caused by possible zero

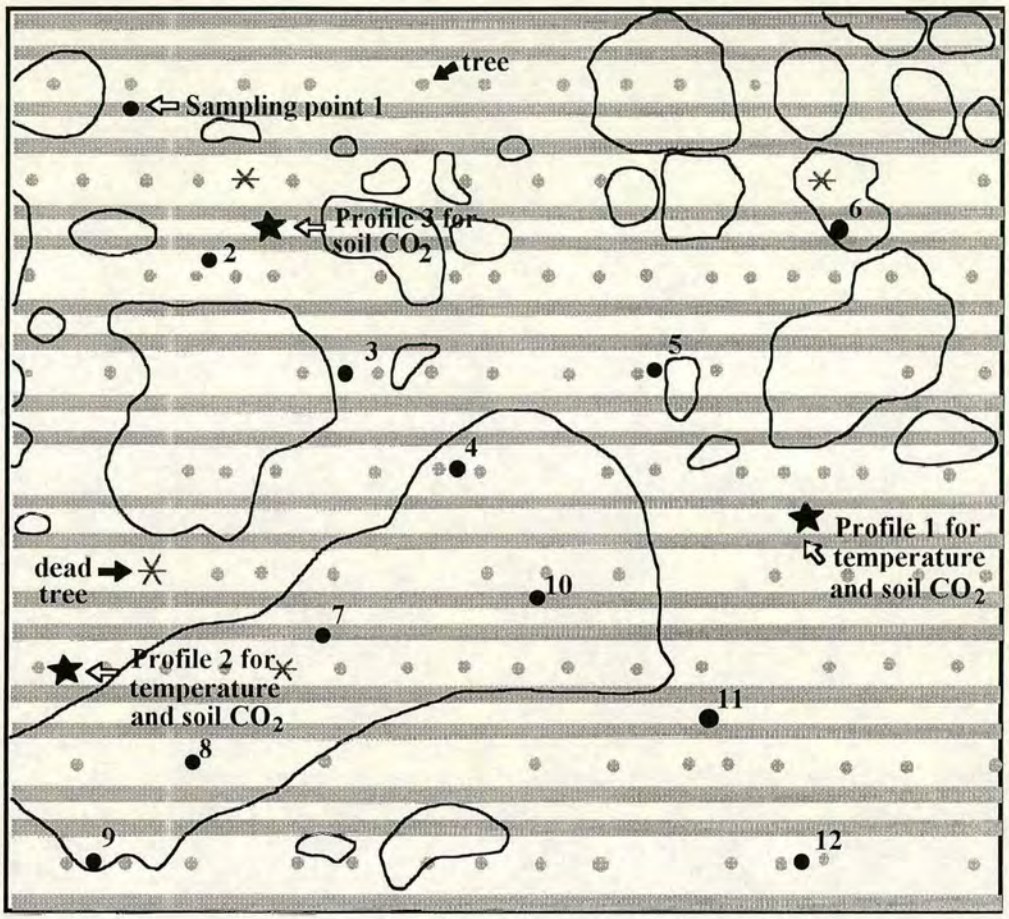


Fig. 3.1 Diagram of the experimental set-up and the projection of understorey plants in the slash pine ecosystem. Plot size is 25 × 25 m; shadow stripes are troughs; white stripes are beds and ridges; irregular line shapes indicate the area covered by understorey plants; the sampling locations for CO_2 efflux are numbered 1-12; and the location of the CO_2 profiles are indicated by a ★.

drift. Coupled 3-way solenoid valves allowed sample gas to pass through the sample and reference cells of the IRGA alternately. To examine this source of error, let the actual concentration difference between sample and reference gas be C_{dif}, and the zero shift of the IRGA be Δx. The IRGA reading is then $C_{dif} + \Delta x$ for subsample one when sample gas passes through the sample cell, and is $-C_{dif} + \Delta x$ for subsample two when sample gas passes through the reference cell. The average of subsample one and two is defined as:

$$C_{dif} = [(C_{dif} + \Delta x) - (-C_{dif} + \Delta x)] / 2 = C_{dif} \qquad (3.1)$$

This method can effectively eliminate the error caused by a zero shift in the IRGA, provided that the CO_2 efflux is relatively steady during the sampling period.

After a preliminary trial, the standard length of the sampling period was set at 6 minutes. When the chamber was placed at a new location, the first 2.5 minutes was required for the system to achieve a new equilibrium, and then the CO_2 difference was read and logged at a frequency of 1 Hz for 1 minute. During the next 1.5 minutes the IRGA reached a new equilibrium after the sample gas was switched from sample cell to reference cell, and the CO_2 difference was read and logged again during the last minute. The chamber setting and the flow rate of 4 dm^3 min^{-1} for pumping air through the chamber and gas analyser were determined during a preliminary trial period in May 1995.

For determining the spatial variation in CO_2 efflux and the relation of this variation to environmental conditions, the chamber was placed on each collar for 6 minutes and then moved to others in sequence. After finishing one sampling round, the chamber was moved in reverse order in the following round. In the slash pine site, the ratios of trough : bed and the area covered by understorey plants : open forest floor were both about 1: 2. The average effluxes for different surface types and the average CO_2 efflux for the plot, weighted by the percentages of surface type, were calculated from the values obtained at all twelve points. The relative efflux for each sampling location was then normalised such that the weighted average CO_2 efflux for the whole plot was unity.

To investigate temporal variation of the CO_2 efflux, the chamber was left on one location unattended for 24 hours. In this case each measurement was made in a 10 minutes interval during which CO_2 efflux was logged every second during minutes 2 - 5, and 7 - 10. The hourly CO_2 efflux for that point was an average of the six samples taken in an hour. This value was then converted to represent the CO_2 efflux from the whole plot using the relative effluxes calculated above.

3.2.3 Soil gas collection and CO_2 concentration analysis

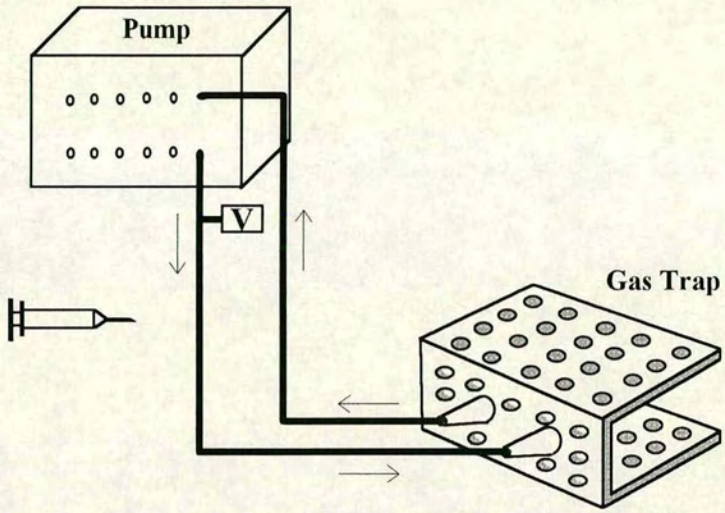
To collect gas samples at different depths in the soil, three sampling positions

were randomly located in the plot (see Fig. 3.1). The position of each point was determined by a pair of random numbers which defined the co-ordinates. Fig. 3.2a shows the gas collecting system employed in the slash pine site. Aluminium gas traps, which are about 5 cm long and have a '⊂ ' type crossection (2.5 × 2.5 cm), were buried at depths of 0, 2, 6, 20, 45 and 60 cm at sampling location one and two, but only at 0, 2, 6, 20, 45 cm at location three. Many small holes were drilled in the walls of the gas traps. Traps were laid in a pattern so that no trap was directly over or under another, and were connected to the soil surface via a pair of plastic tubes, 5 mm ID. The paired tubes from each gas trap were connected on the ground to a mini multi-channel tubing pump with a silicon rubber tube and a plastic three-way valve to create a closed loop. About 10 minutes before collecting the gas sample, the pump system started to circulate gas in every closed loop at a flow rate of about 30 cm^3 min^{-1}. For sampling, a 20 cm^3 syringe was inserted into the silicon rubber tube and a sample of about 21 cm^3 was withdrawn. Syringes were then sealed by insertion into rubber stoppers. After completing the sampling at each location, each closed loop was opened to the atmosphere via the three way valve for a few seconds to equilibrate the pressure and closed again. Soil gas was sampled at each sampling point every two hours during the daytime on each sampling day.

The gas samples were analysed in the field or in the laboratory with an IRGA (Li-Cor 6252, Li-Cor Inc., Lincoln, Nebraska, USA). For rapidly analysing gas samples in the field, the system shown in Figure 3.2b was developed. Dry and CO_2-free air provided by the scrubber, which contained soda-lime and magnesium perchlorate, was circulated in the system at a flow rate of about 1.5 dm^3 min^{-1}. The 20 cm^3 sample of gas was injected into line to the sample cell of the IRGA and could escape to the atmosphere through the valve. The valve opening was adjustable to ensure that there was a constant pressure difference between inside and outside the system during the actual measurement. The reading from the IRGA was logged at an interval of 0.1 second and summed by a data logger. The CO_2 concentration in the gas samples was obtained by comparing the sum with that obtained with calibration gases of known CO_2 concentrations. Calibration of this system with samples of different

known CO_2 concentrations showed agreement within ± 4%.

a:



b:

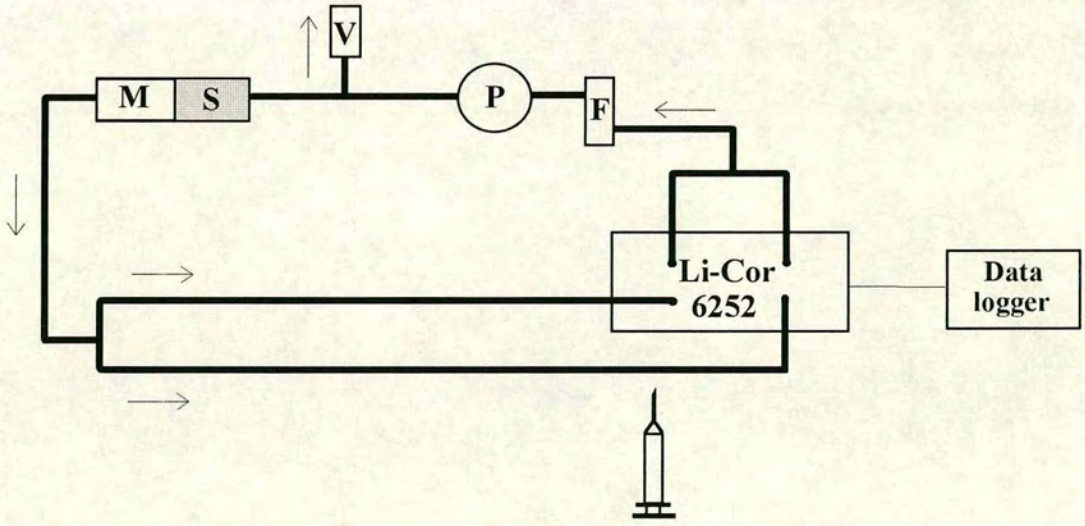


Fig. 3.2 Gas collecting (**a**) and CO_2 concentration analysing (**b**) systems
M: magnesium perchlorate; S: soda-lime; V: valve; P: pump; F: flowmeter.

3.2.4 Measurements of environmental factors

Soil temperature

Soil temperature was measured at 0, 5, 20, 45 and 65 cm by thermocouples in the same location as the soil gas sampling locations 1 and 2. To cover the spatial heterogeneity of temperature in the surface soil, four thermocouples were laid, exposing to the atmosphere, on the soil surface (at least 35 cm apart from each other) and two at 5 cm depth in order to give representative values of soil temperature. Soil temperatures were logged every five minutes and averaged over one hour by a logger (model CR10, Campbell Scientific Instrument Co., Loughborough, UK) during each field trial.

Daily average soil temperature at different depths during the year was estimated by correlating the data from a nearby weather station with the soil temperatures measured at the site.

Soil moisture

During the experimental period, soil moisture at different depths was estimated from gravimetric soil samples, weekly TDR measurement and a continuous soil water table recorder in the plot by co-workers in this project from the Forest Ecosystem Laboratory, Florida University. Daily soil moisture contents at different depths were obtained by fitting a logistic equation with four parameters to the field data. This produced a maximal soil water content when the soil was close to saturation and a minimum when the soil was dry in winter. As pointed out by Ewel *et al.* (1987a), there is little variation in soil moisture during a 24-hour period in slash pine ecosystems in that area, and possible variation of soil water content during the day was not considered.

Soil properties

Four sampling positions for estimating soil density and soil bulk density were randomly chosen in the plot. Two undisturbed soil cores with a given volume (137.5 cm^3) were taken from each position at depths 6 - 20 and 20 - 40 cm. Soil samples

were dried at 100 °C and weighed. The dry soil samples were then put into 200 cm^3 water and were gently stirred. 10 minutes later when there were no visible air bubbles around the soil particles, the volume of soil solid particles was read from the volume increase of the mixture. Soil density and bulk density were then estimated from the dry mass, the undisturbed volume and the volume of solid material of the soil samples. A similar method was used by Crill (1991).

Based on the assumption that the litter has a similar density to wood, litter density was estimated at 500 kg m^{-3} from the wood density of many pine trees (Zobel and Talbert, 1991). The ash percentage, mostly of inorganic sand, in the humus layer was about 20 - 25% (Gholz, 1996, *pers. comm.*). The density of the humus layer was estimated to be 600 kg m^{-3}. The bulk densities of the litter and humus layers were determined by the dry mass of samples and their undisturbed volume (Table 3.1). Similar values of litter density (500 kg m^{-3}) and bulk density (140 kg m^{-3}) for the litter in temperate forest were reported by Crill (1991). The reason for the low soil density under palmetto is not clear; it may partly be caused by a higher root biomass content than that beneath the open floor. Further work is needed in sampling soil in the site and analysing soil composition.

The total and air-filled porosity of soil, litter and humus layers were then calculated from:

$$\phi_T = 1\text{-}(\textit{soil bulk density/soil density}) \tag{3.2}$$

$$\phi_g = \phi_T - V_w \tag{3.3}$$

where ϕ_T and ϕ_g are soil total porosity and air-filled porosity, respectively, and V_w is the volumetric fraction of water in the soil.

Root biomass, soil organic matter and litter

Twelve soil cores, 7.1 cm in diameter, were extracted from the locations close to each of the chamber collars in October, 1995. Two cores were 100 cm long and the rest were 80 cm long. The methods described by Gholz *et al.* (1986) were used for

estimating root biomass. Soil cores were divided as several samples at lengths of 10, 20, 40, 60 or 80 cm and all samples were rinsed with deionized water over a 0.2-mm sieve to loose the material. All root fragments ≥ 3 mm in length were separated and remaining material was spread on a 1 × 1 cm plastic grid sheet and a 10% random sample was sorted for roots. Root fragments were then categorised by species (pine, palmetto and others) and diameter (≤ 1 mm, 1 - 3 mm, ≥ 3mm). All root samples were dried at 70 °C for 24 h and weighted to 1 mg. The organic matter content in the soil samples was determined using the Walkley-Black wet oxidation technique (Gholz and Fisher, 1982). The total dry biomass of fine live roots (< 10 mm in diameter) and soil organic matter in the top 80 cm of the soil were estimated to be 928 g m^{-2} and 13.6 kg m^{-2} (Gholz, 1996, *pers. comm.*). The coarse root (> 10 mm) biomass was estimated as 2.0 kg m^{-2} from earlier works (Gholz and Fisher, 1982; Gholz *et al.*, 1985).

Twelve samples of forest floor litter were taken in February 1996 at locations close to each chamber collar with a sampler. The sampler, with a dimension of 33 × 33 cm, was put on the forest floor, litter and humus were cut along the inner side of the sampler, and then separately sampled and dried. Samples were burned in a muffle furnace to get the ash-free amount of organic matter. The total amount of organic matter in the forest floor for the plot was estimated by averaging that amount from twelve sampling locations.

Some of the field characteristics of the slash pine ecosystem are given in Table 3.1. Annual litterfall from the slash pine trees was measured by collecting litter every two weeks starting in October 1994 from four 1×1 m litter traps randomly distributed on the forest floor in the plot. The total dry leaf biomass of the understorey plants was estimated as about 0.86 kg m^{-2} and annual litterfall was estimated as 25% of the total leaf biomass based on the previous studies under similar conditions in the area.

Sampling and chemical analyses of root biomass, litterfall, litter and humus amount and soil organic matter for this study was done by the team from Florida University (Gholz, 1996, *pers. comm.*).

There were three periods of field observations in May 1995, September-October 1995 and January-February 1996.

Table 3.1 Some features of the slash pine plantation, Florida.

Density (kg m^{-3})	
Litter layer	500*
Humus layer	600***
Mineral soil, 6-25 cm	2400
Mineral soil, > 25 cm	2560
Mineral soil under saw palmetto, 6-35 cm	1740
Bulk Density (kg m^{-3})	
Litter layer	100
Humus layer	170
Mineral soil, 6-25 cm	1220
Mineral soil, > 25 cm	1560
Mineral soil under saw palmetto, 6-35 cm	780
pH Value	
Forest floor and top soil (6-20 cm)	4.0*
Mineral soil , below 20 cm	4.5*
Litterfall (g dry mass m^{-2} yr^{-1})	
Aboveground, litter from slash pine	730**
Aboveground, litter from palmetto and others	218***
Below ground	273***
Organic Matter (g dry mass m^{-2})	
Litter and humus on the forest floor	4787**
Organic matter in the mineral soil (top 80 cm)	13600**
Dead root in the soil	421***
Live Root Biomass (g dry mass m^{-2})	
Fine root (<10 mm)	928**
Coarse root (>10 mm)	2000*

* estimated from literature, see Gholz and Fisher (1982); Gholz *et al.*(1985); Gholz *et al.*(1986); Zobel and Talbert (1991).

** measured by Gholz *et al.* in this study.

*** estimated with measured data and literature.

3.2.5 Spatial variation of CO_2 efflux — theory

Although the spatial variation of CO_2 efflux from the soil has not been well characterised previously, it is reasonable to assume that both the temporal and spatial variation of CO_2 efflux are controlled by the same processes of CO_2 production and transport in the soil. The relationship of spatial variability to environmental factors may be different to that of temporal variation. A brief analysis and a simplified expression for the spatial variation of CO_2 efflux is given below. A more detailed analysis of soil respiration and soil CO_2 efflux in relation to environmental factors will be described later in Chapter 4.

It is an acceptable hypothesis that root respiration, microbial respiration in the surface layer and in the mineral soil are major sources of CO_2 efflux from the soil surface, and that they are additive. For simplicity, we only take account of the spatial heterogeneity of root biomass, the amount of litter and organic matter and soil total porosity. Although soil temperature and soil water content are often dominant factors controlling soil respiration, they are more temporal rather than spatial variables in most relatively uniform ecosystems. We can represent the efflux thus:

$$F = R_r + R_{ml} + R_{ms} \tag{3.4}$$

where F is CO_2 efflux from the soil surface; R_r, R_{ml}, R_{ms} are root respiration, microbial respiration in litter and humus layers and in the mineral soil, respectively.

To define the relation of root respiration rate to root biomass, the simplest assumption is that root respiration is linearly related to root biomass. However, it has been found that the specific rate of root respiration changes with root size: the smaller the root size, the larger is the specific rate (Chapman, 1979). We assume that root respiration rate at different locations is linearly related to total mass of fine roots (< 10 mm size) biomass in the slash pine ecosystem. This simplified assumption will not lead to a serious error given the constraint that the size composition of fine roots at different locations does not change much.

Generally, transport of gases through the soil is easier in a more porous soil than in a less porous soil and will accelerate soil respiration and CO_2 efflux, but the dependence of soil respiration on soil porosity is unlikely to be linear and cannot be expressed explicitly. Linearity is assumed as a first approximation of the relation between root respiration and the soil total porosity at different locations, i.e.

$$R_r \approx bB \cdot \phi_T \tag{3.5}$$

where B is the biomass of live fine roots in the soil, ϕ_T is the soil total porosity, and b is a parameter.

Microbial respiration in both surface layer and mineral soil can be defined by a decomposition equation for organic matter as:

$$\frac{\partial M}{\partial t} = -kM \tag{3.6a}$$

$$M_t = M_0 e^{-kt} \tag{3.6b}$$

where M_t is the amount of material remaining at time t; M_0 is the initial amount; k is a decomposition rate coefficient (Hunt, 1977). In our case, M_t is the present organic pool and M_0 is a variable related to the input of organic matter; k is likely to be a parameter rather than a coefficient, for different locations because the microbial flora and its metabolic activity may change with locations.

In the slash pine plantation, litter from palmetto is decomposed more quickly than pine litter because of the difference in litter quality. This leads to a lower percentage of litter accumulation under palmetto. The greater amount of litter found under palmetto plants suggested, therefore, that the spatial heterogeneity of litter and humus on the forest floor is dominated by the different input rates of litter rather than by spatial variation of the decomposition rate. The litter of slash pine is evenly distributed on the forest floor, but litter from saw palmetto cannot be moved easily by the wind and small animals, so much more litter accumulated under palmetto than on

the open forest floor. It is a reasonable assumption that the annual input rate of litter and consequently the amount of litter and humus at different locations, is the dominant factor controlling the amount of CO_2 released by microbial respiration in the surface layer. The decomposition rate k is less important compared with the amount of litter and humus in determining CO_2 effluxes from different locations. The influence of porosity of the litter layer on microbial respiration is negligible in this case as both oxygen and carbon dioxide diffusion are unlikely to be a limiting factor for microbial respiration in the litter and humus layers. Thus

$$R_{\mathrm{ml}} \approx cM_{\mathrm{lt}} \tag{3.7}$$

where M_{lt} is the present amount of litter and humus of forest floor, and c is a parameter.

Microbial respiration in the mineral soil is much more complicated than that on the forest floor and can only be considered case by case. Firstly, and similarly to root respiration, we also assume microbial respiration in the mineral soil is linearly related to soil porosity. Equation 3.6a can be restated for microbial respiration in the mineral soil as:

$$\frac{\partial M}{\partial t} = -kM\phi_{\mathrm{T}} \tag{3.8a}$$

or

$$k = (\ln M_0 - \ln M_{\mathrm{st}}) / t\phi_{\mathrm{T}} \tag{3.8b}$$

where M_{st} is amount of organic matter in the mineral soil at time t.

In slash pine, a large amount of the remains of the previous stand was buried into the soil during site preparation for the current rotation, and this debris should be evenly distributed. In such a case, M_0 is likely to be somewhat constant between different locations. Thus the present spatial differences in amount of organic matter in the mineral soil is mainly caused by differences in microbial activity (k) and soil porosity (ϕ_{T}), rather than by differences in the input of organic matter. It is the

microbial activity, k, that is the dominant factor controlling the microbial respiration in the mineral soil at different locations. Thus we have:

$$R_{ms} \propto k = a - d\ln(M_{st}) / \phi_T \tag{3.9}$$

where the parameter $a = \ln(M_0)/t\phi_T$ is taken as a constant for simplicity although a variable value for a gave a better fit to field data for the Florida slash pine plantation; and d is a parameter.

In equation 3.9, the microbial respiration changes inversely with the present amount of organic matter; the more organic matter there is in the soil, the smaller the respiration rate is, and *vice versa*. This definition is in contrast to the function for describing the temporal variation of respiration rate in relation to organic matter content in the soil. A more porous soil will accelerate the decomposition of soil organic matter and this will result in less organic matter being left in the soil.

Substituting equation 3.5, 3.7 and 3.9 into 3.4, a simplified equation for characterising the spatial variation of CO_2 efflux from the slash pine site can be developed as:

$$F = a + bB\phi_T + cM_{lt} - d\ln(M_{st}) / \phi_T \tag{3.10}$$

where a, b, c, d are parameters to be determined.

3.3 Results

3.3.1 CO_2 efflux and its temporal variation

Figure 3.3 shows effluxes measured in autumn (October, 1995) and winter (January, 1996) in the slash pine stand. In October, 1995, CO_2 efflux ranged from a minimum of 0.179 mg CO_2 m^{-2} s^{-1} to a maximum of 0.253 mg CO_2 m^{-2} s^{-1}, with a mean of 0.217 mg CO_2 $m^{-2}s^{-1}$. In the winter, the CO_2 efflux could be as low as 0.031

mg CO_2 $m^{-2}s^{-1}$, observed on one of the coldest mornings of the year (28 January, 1996), and the maximum could be as high as 0.146 mg CO_2 $m^{-2}s^{-1}$ in the afternoon. The average value of CO_2 efflux for January was about 0.087 mg CO_2 $m^{-2}s^{-1}$. In the autumn, day-to-day variation in CO_2 effluxes was smaller than in the winter.

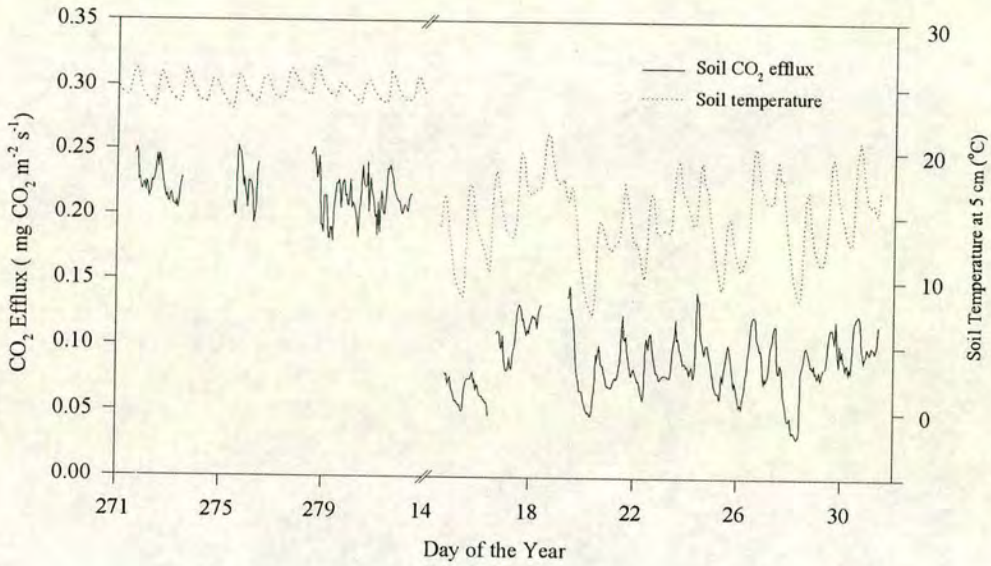


Fig. 3.3 Hourly soil temperature at 5 cm and CO_2 efflux from the soil surface in the slash pine plantation (1995-1996). Soil temperature is an average of obtained, using two thermocouples (about 35 cm apart from each other) at each sampling location. Readings were obtained every five minutes at two locations. CO_2 efflux was continuously monitored at one sampling point, which could be changed from day to day between the 12 sampling locations within the plot. The changeover could take place within a period of 10 minutes and samples were averaged over a hour. Effluxes were then converted using the relative efflux coefficients to the values for the whole plot.

The daily pattern of average CO_2 efflux were similar for October, 1995 and January, 1996 (Fig. 3.4). CO_2 efflux began to increase around 0800 h (local time) and peaked at around 1400-1500 h. Peak average values were 0.238 mg CO_2 m^{-2} s^{-1} for autumn and 0.105 for winter. The efflux decreased until midnight typically and fluctuated around a minimum value until the following morning. However, CO_2 efflux

during the day was more variable in the autumn than in the winter, especially in the evening.

During the daytime, the CO_2 efflux increased quickly and steadily for most of the day in both autumn and winter, but was more variable in the evening. Figure 3.3 shows that fluctuations in the CO_2 efflux often occurred between the time of the peak efflux and midnight. Another period when CO_2 efflux was variable was first thing in the morning.

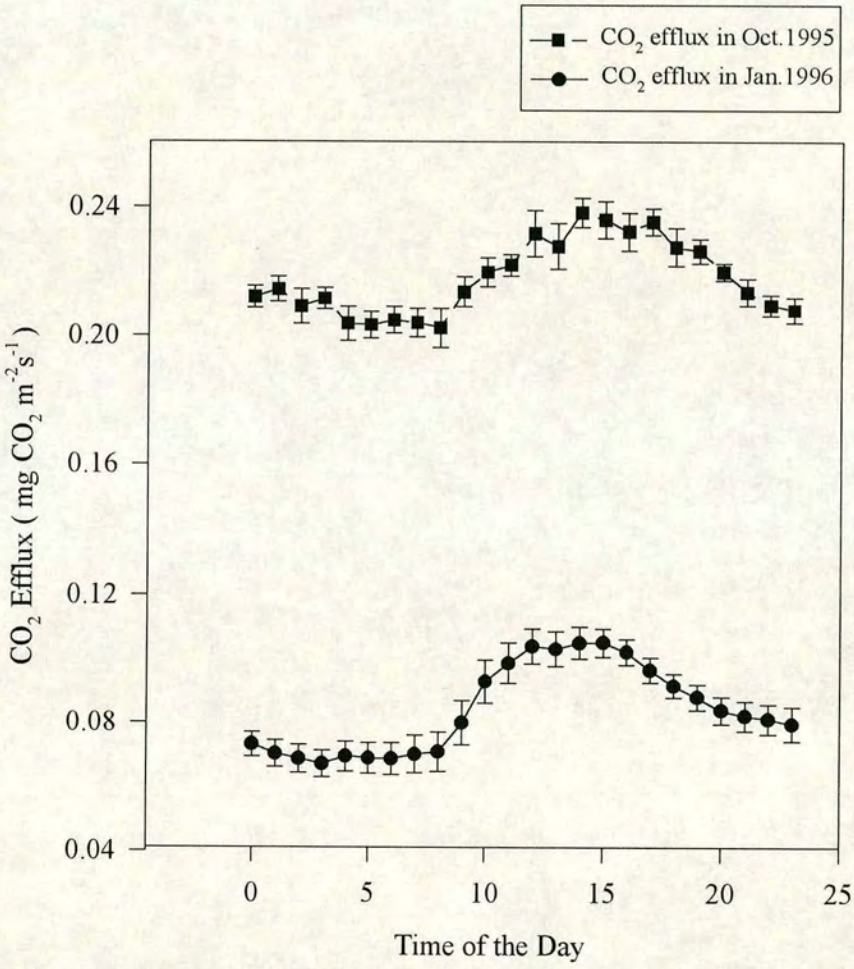


Fig. 3.4 The daily pattern of soil CO_2 efflux in different seasons. Error bars indicate ± one stand error of CO_2 efflux. Effluxes are averages over 5 and 16 days for October 1995 and January 1996, respectively.

3.3.2 Relation of CO_2 efflux to soil temperature

Soil CO_2 efflux in the field was affected by a number of environmental variables but was dominated by temperature when soil water was not limiting. Parallel changes in the daily pattern of CO_2 efflux and soil temperature are shown in Fig. 3.3. Variations in CO_2 efflux during the day or between days in both autumn and winter followed the variation in soil temperature.

The logarithm of hourly soil CO_2 effluxes measured in October 1995 and January 1996 in the slash pine site is plotted in Fig. 3.5 against the average soil temperatures at 5 cm depth. Logarithmic CO_2 efflux has a closely linear relation to soil temperature on most sampling days except in the evening of 27 and in the morning of 28, January 1996. The CO_2 efflux from the soil in the morning of 28, January 1996 was very low (average of 0.059 mg CO_2 m^{-2} s^{-1} with a minimum of 0.031 mg CO_2 m^{-2} s^{-1}) and deviated from the data observed on other days. Two cold

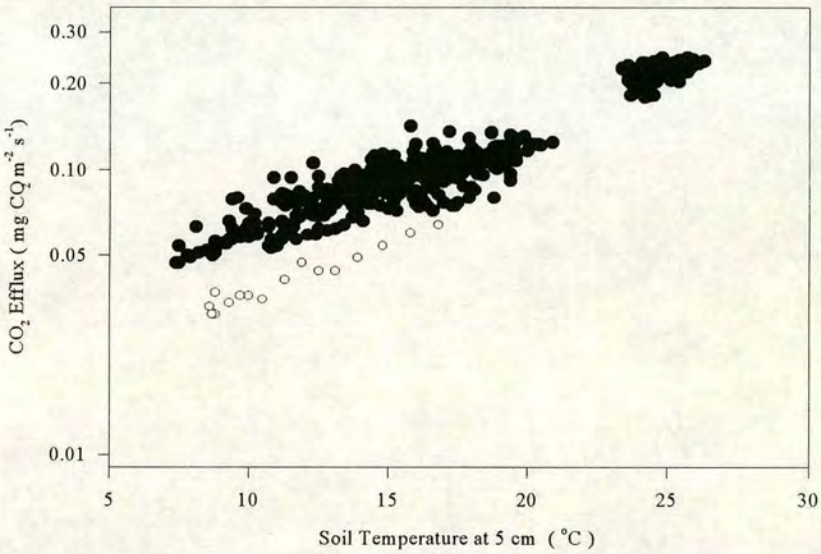


Fig. 3.5 Relationship of measured CO_2 efflux to soil temperature. Open circles indicate the data measured between 1800 h, on 27 January and 0900 h, on 28 January, 1996. Solid circles are for other data measured in October 1995 and January 1996.

days, 20 and 28 January, were recorded but only the CO_2 effluxes from 1800 h, on 27 January to 0900 h, on 28 January showed an significant deviation. However, the logarithm of CO_2 efflux plotted against the temperature was still linear for the data in that period. The low values of CO_2 efflux suggested that there were some other factors affecting soil respiration or CO_2 diffusion in the soil on the evening of 27 and the morning of 28 January, 1996.

The mean temperature at 5 cm was 24.7 °C for autumn and 19.5 °C for winter. The Q_{10} value for the response of hourly CO_2 efflux to soil temperature at 5 cm was 2.5. The activation energy of soil respiration, obtained by fitting the field data to the Arrhenius equation, was estimated to be 56.9 kJ mol^{-1}. About 90% of the variability in CO_2 efflux was accounted by the variation in soil temperature alone fitted with both Q_{10} and Arrhenius model. Soil temperature was by far the most important factor controlling the rate of soil respiration.

3.3.3 Spatial variation of soil respiration

The spatial variability of soil respiration rates between the twelve sampling locations in the plot was relatively high, with a coefficient of variation of 55% in CO_2 efflux. The deviation among these sampling points ranged from 38% to 173%. No significant variation in relative effluxes was found between October 1995 and January 1996.

Beds and troughs, although they are recognisable, did not contribute significantly to the spatial heterogeneity of CO_2 efflux in the slash pine site (*t*-test; $P > 0.05$). CO_2 effluxes were large from the locations under palmetto plants, with an average relative CO_2 efflux rate of 1.57 times that for the whole plot, or about 3 times larger than that on the open forest floor where the average relative CO_2 rate was 0.59. The difference between CO_2 effluxes from the soil under palmetto and from the open floor is significant (*t*-test; $P < 0.001$). Although only about a third of forest floor was covered by understorey plants, mostly palmetto, it contributed more than a half of the total CO_2 released.

The amounts of litter and humus in the surface layer and fine root biomass

were found higher under palmetto plants, by about 30% for both, than on the open forest floor. Palmetto plants did not only increase litterfall to the forest floor around them but also changed the property of the soil underneath. Soil under palmetto plants was more porous with a total porosity of 0.55 in the top 30 cm of the mineral soil compared to the soil on the open forest floor where total porosity was 0.46 for the top 30 cm of soil. The difference between air-filled porosities under palmetto and open floor may be even greater because that a larger portion of rain water was detained by the thick litter layer and that soil water drains downward more easily under palmetto. A high porosity facilitates oxygen transport into the soil, where respiration takes place, and CO_2 escape from the soil, and thus increases the CO_2 efflux from the soil surface.

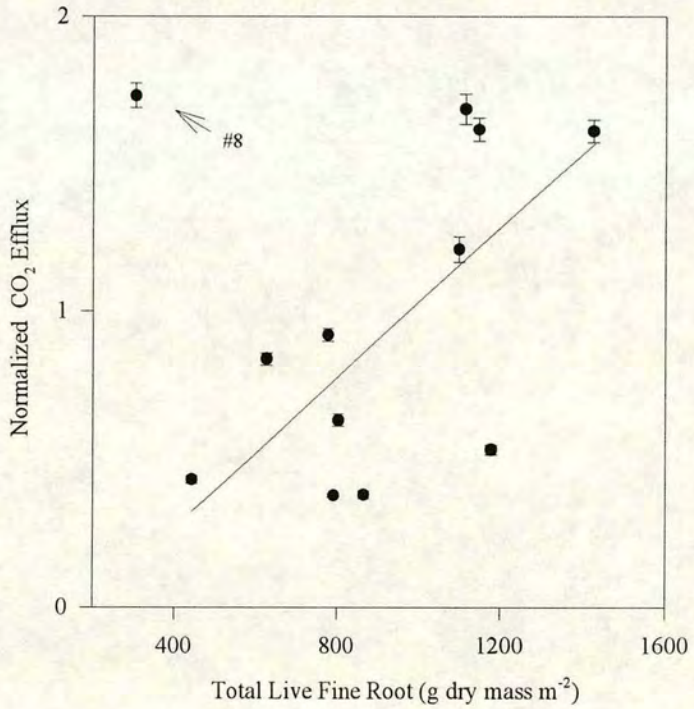


Fig. 3.6 The relation of soil CO_2 efflux to fine root (< 10 mm in diameter) biomass. The error bars indicate ± one standard error of the CO_2 efflux (n = 22). The line represents a linear regression (R^2 = 0.46, ignoring data from point 8).

Figure 3.6 shows soil efflux at different sampling locations plotted against the fine root biomass (0 - 10 mm in diameter) in the top 80 cm of soil. The efflux is normalised such that the average efflux for the plot is one. CO_2 efflux increased with increasing fine root mass at these sampling points except point 8 where root biomass seemed to be abnormally low. Ignoring the data from point 8, a significant but not close linear relationship exists between CO_2 efflux and fine root biomass ($R^2 = 0.46$, $P < 0.05$). A similar relation was found between soil CO_2 efflux and the amount of litter and humus in the surface layer (Fig. 3.7), but again, the relation is only reasonable ($R^2 = 0.45$, $P < 0.05$), with some evident scatter. Location 6 and 9 had lower litter amount than expected. More scatter is evident in Fig. 3.8 showing the relationship between CO_2 efflux and organic matter in the mineral soil, with a significant but low correlation coefficient ($R^2 = 0.4$ for a linear regression, $P < 0.05$). Generally, high CO_2

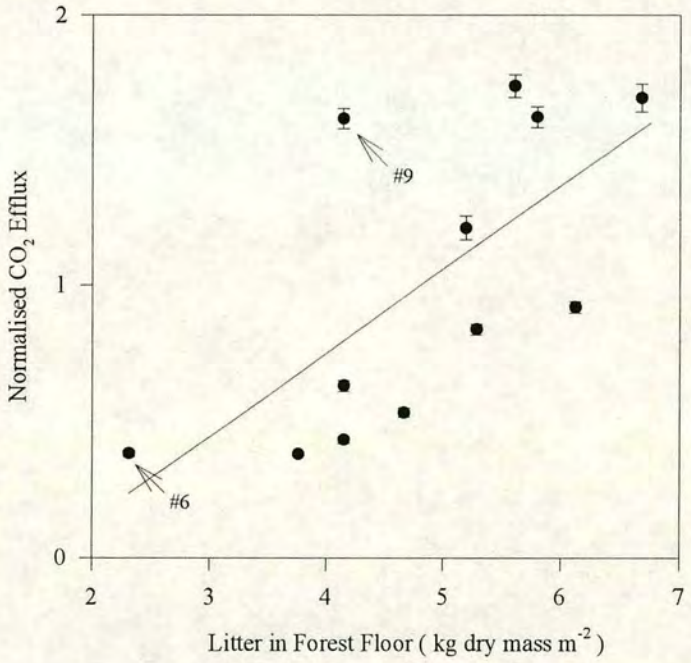


Fig. 3.7 The relation of CO_2 efflux to litter amount in the surface layer. The error bars indicate ± one standard error of the CO_2 efflux ($n = 22$). The line indicates a linear regression with a correlation coefficient $R^2 = 0.45$.

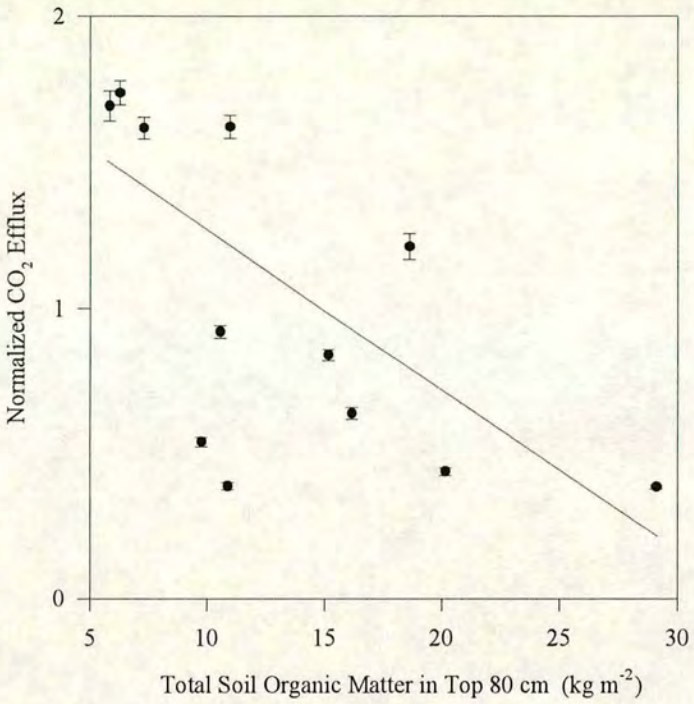


Fig. 3.8 The relation of CO_2 efflux to total organic matter in the top 80 cm of soil. The error bars indicate ± one standard error of the CO_2 efflux (n = 22). The line represents a linear regression (R^2 = 0.40).

effluxes were associated with a low amount of organic matter in the mineral soil, and *vice versa*. However, sampling points 5 and 6 had very low organic matter content with a very low CO_2 efflux.

From Figs. 3.6 to 3.8, it is clear that root biomass, the amount of litter and humus on the forest floor and the organic matter concentration in the mineral soil, all affected soil respiration but no single factor could explain adequately or dominate the spatial heterogeneity of CO_2 efflux. In other words, root respiration, and the decomposition of litter and organic matter all contributed considerably to the total CO_2 released from the soil surface but none of them dominate the efflux of CO_2.

Fitting the field data to equation 3.10 gives good agreement between measured and estimated CO_2 efflux from different sampling locations (Fig. 3.9), with a correlation coefficient R^2 = 0.96. Most of the spatial variability in CO_2 efflux could

be explained by variations in live and dead biomass and associated soil total porosity by relations defined in equation 3.10.

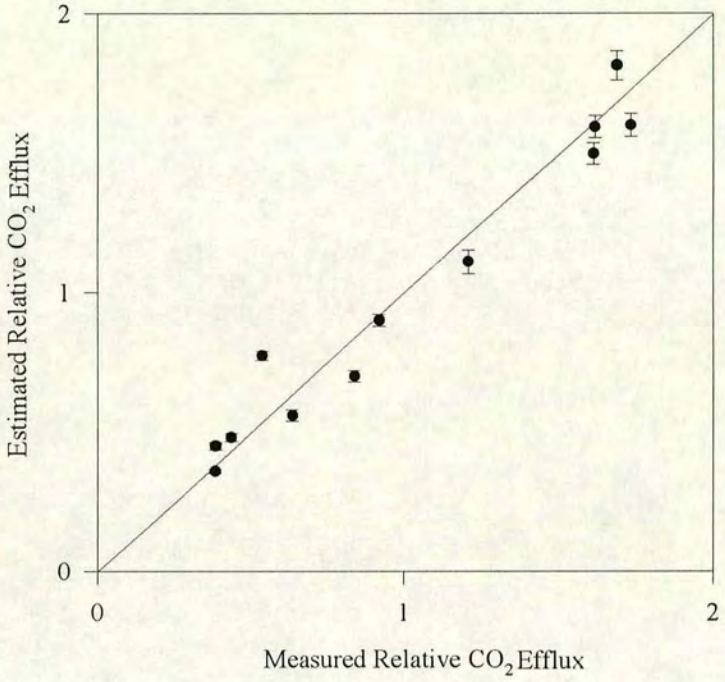


Fig. 3.9 Comparison of measured and estimated relative CO_2 efflux rate, The error bars indicates ± one standard error of the measured CO_2 efflux (n = 22). Estimated CO_2 effluxes were calculated using equation 3.10 fitted to the field data: $F = 2.52 + 0.000152\ B\ \phi_\Gamma + 0.000117 M_{lt} - 0.1005 \ln(M_{st})/\ \phi_\Gamma$.

3.3.4 CO_2 concentration in the soil

The CO_2 concentration generally increased with increasing depth. Figure 3.10a shows the variation of CO_2 concentration in the soil gas with depth in autumn. CO_2 concentration in soil gas was as high as 1% at 60 cm in October 1995 when the soil water table was around that depth and decreased linearly to the soil surface where it was 600-763 $cm^3\ m^{-3}$ at 2 cm. In winter, the CO_2 production rate in the soil was reduced because of the low soil temperature but gas transport through the soil was

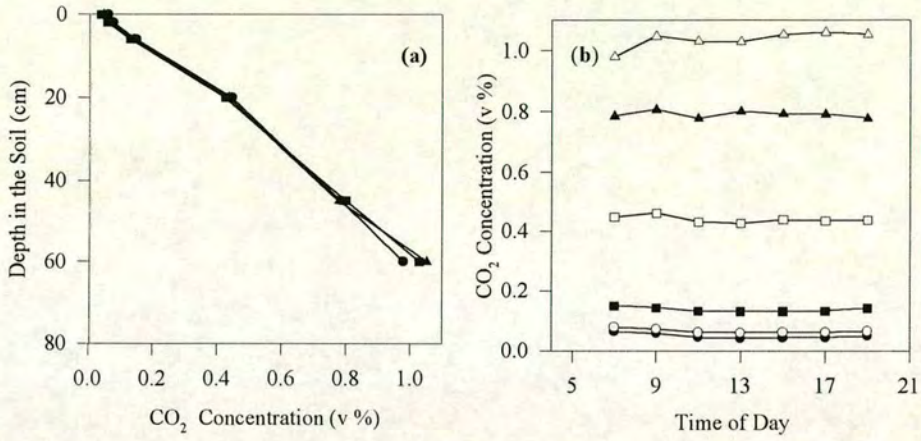


Fig. 3.10 The variation of CO_2 concentration in the soil gas (8/10/95): (**a**). CO_2 concentration at different depths (–●– at time 0700, –■–1300, –▲–1900); (**b**). variation in CO_2 concentration during daytime (–●– 0 cm, –○– 2 cm, –■– 6 cm, –□–20 cm, –▲– 45 cm, –Δ– 60 cm).

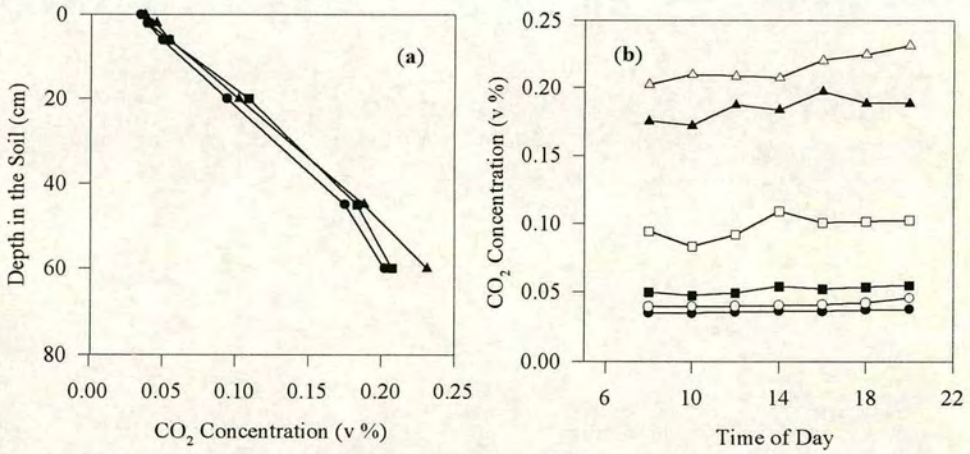


Fig. 3.11 The variation of CO_2 concentration in the soil gas (20/1/96): (**a**). CO_2 concentration at different depths (–●– at time 0800, –■–1400, –▲–2000); (**b**). variation in CO_2 concentration during daytime (–●– 0 cm, –○– 2 cm, –■– 6 cm, –□– 20 cm, –▲– 45 cm, –Δ– 60 cm).

accelerated because of the drier soil. The combination of these two changes made soil CO_2 concentrations in winter much lower than in autumn (Fig. 3.11a). The highest soil CO_2 concentration was less than 2500 $cm^3 m^{-3}$ at 60 cm and less than 500 $cm^3 m^{-3}$ at 2 cm. The CO_2 concentration increases linearly with soil depth. The lower CO_2 concentration in the winter was the result of a lower respiration rate and a higher diffusivity caused by a reduced temperature and moisture content in the winter. The linear CO_2 profile reflects the combined influence of the vertical distribution of respiration rate and gas diffusivity in the soil. If the ratio of CO_2 flux : effective diffusion coefficient is nearly constant with depth in the soil, a linear CO_2 profile is expected.

Temporal variation of CO_2 concentration at different depths in the soil during the daytime was quite small (Figure 3.10b, 3.11b). CO_2 concentrations did not show a clear relation with soil temperature or the CO_2 efflux from the soil.

3.4 Discussion

3.4.1 Magnitude of CO_2 efflux

Because we were able to make field measurements of CO_2 efflux only in the autumn and the winter, data were insufficient to estimate the average annual CO_2 efflux from the soil surface in the slash pine plantation. However, the typical range of CO_2 efflux rates, 0.035-0.292 mg CO_2 $m^{-2} s^{-1}$, in this study are comparable with those observed in *Pinus roxburghii* (Rout and Gupta, 1989) and *Pinus radiata* (Carlyle and Than, 1988) (0.03 - 0.25 mg CO_2 $m^{-2} s^{-1}$) and those in other forest ecosystems in similar climatic conditions (0.025 - 0.31 mg CO_2 $m^{-2} s^{-1}$) (Rajvanshi and Gupta, 1986; Behera *et al.*, 1990).

Ewel *et al.* (1987a) measured soil respiration rate with a dynamic chamber in a 29-year-old slash pine plantation, which was similar to the site in this study. The CO_2 efflux rate was about 0.19 mg CO_2 $m^{-2} s^{-1}$ between October and November, and about 0.06 mg CO_2 $m^{-2} s^{-1}$ between January to February, similar to the rates found in this

study (0.217 mg CO_2 m^{-2} s^{-1} for October and 0.087 mg CO_2 m^{-2} s^{-1} for January). Castro *et al.* (1994) reported measurements using an enrichment static chamber in a slash pine plantation in the same area. CO_2 efflux, ranged from 0.053 to 0.083 mg CO_2 m^{-2} s^{-1}, were significantly lower than the values reported here. Sampling with this same static chamber in November, 1995 on our study site also gave lower estimates of CO_2 efflux (about 0.1 mg CO_2 m^{-2} s^{-1}) during the daytime (Castro, *unpubl.*) than we obtained. The use of such a different methodology as well as the high spatial heterogeneity of CO_2 efflux from the slash pine floor is most likely the reason for the different CO_2 effluxes.

3.4.2 Temperature dependence of CO_2 efflux

Soil temperature dominated soil respiration and the diurnal pattern in CO_2 efflux was largely explained by changes in soil temperature. The observation of a high correlation between soil respiration and soil temperature is in general agreement with many previous reports (Oberbauer *et al.*, 1992; Bridgham and Richardson, 1992). When soil moisture is limiting, however, soil CO_2 efflux may not be sensitive to temperature (Carlyle and Than, 1988; Rout and Gupta, 1989). The proportion of the variation in CO_2 efflux that can be accounted for by temperature depends on the environmental conditions (Rajvanshi and Gupta, 1986). In this study, the diurnal change of CO_2 efflux was most strongly related to temperature at 5 cm depth rather than at the soil surface or at greater depths, and this indicates that most of the CO_2 released came from metabolic activity in the surface layers of litter and organic matter in the top soil layer. One reason for the high correlation between CO_2 efflux and soil temperature (R^2 = 0.9) is that soil moisture was never a limiting factor during the measuring periods. In October, 1995, average soil volumetric moisture content was about 25% for the mineral soil and 14% for the litter. Corresponding values for January, 1996 were 20% and 12%, respectively. January is the driest season in Florida and soil moisture was fairly constant with some changes in the litter layer and top soil as a result of occasional rainfall. Average mineral soil moisture was 53% of saturation. Soil respiration did not show a clear relationship with changes in soil

moisture. A similar result was reported by Ewel *et al.* (1987a) in both a young and a mature slash pine plantation.

The reason for the extremely low CO_2 efflux measured in the morning of 28 January 1996 is not yet clear. Other environmental factors might have contributed to the low rates, such as a possible variation of barometric pressure. Massmann and Ferrier (1992) pointed out that the daily trend of atmospheric pressure may influence the efflux of CO_2 from the soil to the atmosphere if the soil is not uniform. It was cloudy with occasionally showers on 26 - 27 January, but skies became clear on the evening of 27th and lasted until the 30 January. A rapid change in barometric pressure was possible in the evening of 27th and the morning of 28th, and may have depressed gas transport through the soil. The variation of moisture content in the top soil may also help to explain the variation in CO_2 efflux, but the possible change in soil moisture caused by showers on 26-27 January were not reflected in water table height which we used to indicate changes in soil moisture content.

The value of Q_{10}, an important parameter in the relation of soil respiration to temperature, has been reported in the range 1.9 to 3.7 (Yoneda and Kirita, 1978; Carlyle and Than, 1988; Crill, 1991; Kim and Verma, 1992; Hanson *et al.*, 1993; Howard and Howard, 1993; Peterjohn *et al.*, 1994). Our Q_{10} values of 2.5 lie in this range.

The activation energy (E) in the Arrhenius equation, which quantifies the temperature dependence of soil respiration on temperature, was thought to be a better indicator of the response to temperature than the Q_{10} value. Published E values for soil respiration vary from 29 kJ mol^{-1} (Oberbauer *et al.*, 1992) to 93.5 kJ mol^{-1} (Crill, 1991; Bridgham and Richardson, 1992) in different ecosystems or under different environmental conditions. Our E value, of 56.9 kJ mol^{-1}, is comparable. The E value of CO_2 efflux is also related to the soil depth at which the temperature used is measured. The temperature at the soil surface is the most changeable and CO_2 efflux had the smallest E value using the temperature on the surface compared to the temperature at greater depths. E ranged from 51.5 kJ mol^{-1} using the surface temperature to 90 kJ mol^{-1} using the temperature at 60 cm in this study. The most relevant estimate of E should come from the layer in which most of the CO_2 is

produced by respiration. The comparability of E between different ecosystems is complicated by the vertical distribution of CO_2 production in the soil and the depth at which soil temperature is measured.

3.4.3 Spatial variation of CO_2 efflux

High spatial variability of soil CO_2 efflux has been routinely reported. A representative estimate of CO_2 efflux from the soil surface is dependent on our understanding of the spatial variability of CO_2 efflux within an ecosystem where the measurements have been made. Although the coefficient of variation in CO_2 effluxes from different locations within an ecosystem is useful to specify the spatial variability of CO_2 efflux or soil respiration, the lack of a standard design of experiments, such as the size of plot, the number of sampling positions and their arrangement, makes it very difficult to compare spatial variabilities of CO_2 efflux between different studies. Dugas (1993) reported a coefficient of variation of 40% in the CO_2 effluxes from nine positions in a 9 × 9 m block during the day, indicating the need for a large number of chamber measurements to obtain a representative CO_2 flux measurement. Raich *et al.*(1990) arranged chambers, 0.5 m apart, along a 20 m transect and found no spatial autocorrelation in soil CO_2 efflux, and suggested that 13 chambers were necessary to estimate the mean CO_2 efflux within 10% of that measured by 41 chambers 90% of the time. However, their data did indicate a trend in the CO_2 efflux along the transect (Fig. 2 in Raich *et al.*, 1990), which suggested that the distribution of CO_2 efflux along the transect was not random but determined by some other factors which the authors did not identify. In this study, the coefficient of variation in CO_2 efflux was 55% for 12 locations in a 25 × 25 m plot. This is not excessive, but a large number of sampling positions is still required to get a representative estimate of CO_2 efflux rate if sampling positions are randomly arranged. Cropper *et al.* (1985) pointed out that, although a slash pine plantation was a relatively uniform ecosystem, it would be necessary to increase the number of chambers or sample points to 15 to be within 10% of the mean obtained with 30 sample points for 90% of the time. Involving such

a large number of chambers is practically difficult, especially using the dynamic chamber technique. The arrangement of sampling locations in this study was not fully random being along the diagonal of the plot, and weighted by the percentage covered by the understorey plants which dominated the forest floor heterogeneity at the site. This distribution of sampling locations may cover more spatial heterogeneity of the forest floor and give a more reliable estimate of average efflux for the plot than a random or a stratified random sampling when the number of sampling position is probably insufficient.

Another way to get a representative average value of CO_2 efflux is to determine the relation between CO_2 efflux and the governing factors and then to estimate average CO_2 efflux from these environmental factors. Generally, the distribution of CO_2 efflux within an ecosystem may be influenced by the distribution of some environmental factors which affect soil respiration or gas transport in the soil. Hanson *et al.* (1993) found a significant topographic effect on the CO_2 effluxes from different locations, with lower CO_2 effluxes in valley bottoms in the summer time. Actually, soil CO_2 efflux is not directly related to topographic characteristics but to other factors which are influenced by topographic features, such as soil temperature, moisture and re-allocation of organic matter. In the slash pine site in this study, the topography should not be a significant factor controlling the distribution of environmental factors because of the flat topography in the site. The trough and bed arrangement may contribute some variability in CO_2 efflux in a young but not in a mature stand (Ewel *et al.*, 1987a). Our consideration that the live and dead biomass dominated the distribution of CO_2 efflux from the soil surface in the slash pine plantation is supported by the good agreement between estimated and measured relative CO_2 efflux in Fig. 3.9.

It is difficult to determine the relative importance of different independent variables in equation 3.10 because these variables are correlated with each other and the equation is not linear. The model is linearised by considering root respiration, microbial respiration in the surface layer and in the mineral soil as new predictor variables and the results of a path analysis are presented in Table 3.2. The direct path coefficient represents the direct contribution of a predictor variable to CO_2 efflux and

the indirect path coefficient indicates the influence of a predictor variable on CO_2 efflux via other correlated predictor variables. The negative sign of a path coefficient of a predictor variable indicates the negative influence of the variable on the CO_2 efflux (Sokal and Rohlf (1995) discuss the detail of the path analysis method). The largest direct path coefficient (-0.763), is for the microbial respiration in the mineral soil, indicating that this respiration rate is most closely correlated with the CO_2 efflux from the soil surface in the site in this study. This high correlation is understandable because the amount of soil organic matter does not change temporally or spatially as

Table 3.2 The path analysis of equation 3.10 regarding the spatial variability of CO_2 efflux (F) with respect to root respiration (X_1), microbial respiration in litter layer (X_2) and in the mineral soil (X_3) in the slash pine site. Direct path coefficient determines the relative direct influence of a predictor variable on CO_2 efflux. Indirect path coefficient represents the relative influence of a predictor variable via other correlated predictor variables. R^2 indicates the percentage of variation in CO_2 efflux which can be accounted for by the variation in a predictor variable via its direct and indirect influences.

Predictor variables	Direct path coefficient	Indirect path coefficient	Correlation coefficient between X_i and F (R^2)
$X_1=B\ \phi_T$	0.055	via X_2 0.049 via X_3 0.697	0.64
$X_2=M_{lt}$	0.258	via X_1 0.010 via X_3 0.334	0.36
$X_3=\ln(M_{st})/\phi_T$	-0.763	via X_1 -0.050 via X_2 -0.113	0.86
Unknown	0.2		0.04

much as that of fine root biomass and litter in the surface layer. Although the fine root respiration has the smallest direct path coefficient (0.05), its indirect path coefficient through its relation with microbial respiration in the mineral soil is about 0.7,

indicating that the contribution of root respiration to the spatial variation of CO_2 efflux is mainly through its interaction with the microbial respiration in the mineral soil. The fine root respiration is significantly related to the microbial respiration in the mineral soil, with a coefficient of about 0.9 (ignoring data from point 8). The contribution from the microbial respiration in the surface layer somewhat splits between direct and indirect influence (mainly via the microbial respiration in the mineral soil), with values of 0.258 and 0.344 for direct and indirect path coefficients, respectively. The percentages of the variation in CO_2 efflux which can be accounted for by the variation in a predictor variable and associated variation in other variables are 64%, 36% and 86% for fine root respiration, the microbial respiration in the surface layer and in the mineral soil, respectively. The path analysis indicates that these three respiration components are all important in relation to the spatial variation in CO_2 efflux, although root respiration has a small direct contribution to the spatial variation in CO_2 efflux.

Equation 3.10 may be also suitable for use in other ecosystems, such as other mature plantations, or relatively uniform natural forests developed after a sudden strong disturbance. However, it is the principle underpinning equation 3.10 rather than the equation itself that is particularly useful. In the application of equation 3.10, it was assumed that microbial respiration in the litter layer increases with the increase in surface litter amount but that mineral soil respiration is inversely related to the amount of deeper soil organic matter. This is true in the slash pine plantation, but may be not true in other ecosystems or conditions. The organic matter on the forest floor increased linearly with plantation age but the mineral soil organic matter decreased with age before year 26 in the slash pine plantation (Gholz and Fisher, 1982). If there was not an input of large amounts of organic matter or the organic matter were introduced unevenly into the soil in the history of an ecosystem, then the appropriate form of equation 3.10 may differ from that proposed here.

Separating microbial from root derived CO_2 remains a challenging yet critical area for future research on the mechanisms governing soil CO_2 production (Fernandez *et al.*, 1993). Some methods relating CO_2 efflux to associated root biomass or to the amount of organic matter to estimate the contribution from root or microbial

respiration to the total soil respiration have been reported. For example, Behera *et al.* (1990) estimated the relative root and microbial contributions to the total soil respiration in a mixed deciduous tropical forest from linear relationships between large, fine and total root biomass and total soil respiration. The linear regression yielded a y-intercept value which was thought to be the contribution of microbial respiration in the absence of roots.

With Behera's method, an unreasonably low contribution from the microbial respiration to total CO_2 efflux can be obtained, using the relationship between CO_2 efflux and fine root biomass (Fig. 3.6), in the site in this study. Although equation 3.10 includes more details about root and microbial respiration than the kind of simple regression model used by Behera *et al.*(1990), it is still impossible to separate root respiration from microbial respiration, or *vice versa*. Because that root biomass, the amounts of litter and organic matter in the mineral soil are significantly correlated, the CO_2 efflux from the soil surface can not be portioned into different components by simply relating this efflux to root biomass or organic matter. Behera's method may only be adequate in an ecosystem with an extremely even structure, where randomness is the common feature of most mechanisms or processes controlling the spatial distribution of CO_2 efflux. However, in most ecosystems, the complete independence between environmental factors governing soil respiration and gas transport in the soil is unlikely to be true. Caution is thus required when attempting to use simple regression methods to estimate the root contribution to total soil respiration.

3.4.4 CO_2 profile in the soil

Reported CO_2 concentrations in soil gas at different depths range from 314 cm^3 m^{-3} to 3.5% but mostly lie within the range of 1000 cm^3 m^{-3} to 2% (Yavitt *et al.*, 1995; Cosby *et al.*, 1985; Fernandez *et al.*, 1993; Castelle and Galloway, 1990; Crill, 1991). Fernandez and Kosian (1987) reported soil air CO_2 concentrations ranging from 0.1 to 0.35 %, 0.1 to 1.25% and 0.2 to 1.2% at depths of 5, 10, 40 cm, respectively, in a Maine forest during the growing season. Higher concentrations,

ranging from 1 to 3.5% at 30 cm and 2.5 to 5.5% at 80 cm, were measured by Hesterberg and Seigenthaler (1991) in a grass-covered soil. The CO_2 concentrations in soil gas measured in this study are comparable with those in the literature. The results in this study indicate that the seasonal variation of soil CO_2 concentration was related to variations in both soil temperature and soil moisture, but the daily pattern of the soil CO_2 profile did not show a clear relation with the daily variation in soil temperature. A couple of reasons were possibly responsible for the daily variation in soil CO_2 concentration. Firstly, the gas diffusivity in the soil during the period was sufficient to let the CO_2 produced by respiration diffuse out of the soil quickly, such that the CO_2 concentration was not closely related to the production rate, which is mainly temperature dependent. Secondly, the decrease in atmospheric CO_2 concentration within the canopy during the daytime, as a result of the canopy photosynthesis, partly offsets the influence of an increase in soil respiration rate during the same period on the CO_2 concentration in the soil gas. The daily pattern of CO_2 production, which is mainly related to soil temperature, did not cause an obvious change in the soil CO_2 profile. The seasonal difference of CO_2 concentration in the soil gas may reflect an accumulative effect of the variation in soil respiration rate and in gas diffusivity through the soil.

3.5 Summary and Conclusions

Carbon dioxide efflux from the soil surface was measured during 1995 and 1996 in a slash pine plantation in Florida. The daily average efflux in the autumn of 1995 ranged from 0.179 to 0.253 mg CO_2 m^{-2} s^{-1} with an average of 0.217 mg CO_2 m^{-2} s^{-1}. In the winter, the CO_2 efflux rate was much lower than in the autumn, and ranged from 0.031 to 0.146 mg CO_2 m^{-2} s^{-1} with an average of 0.087 mg CO_2 m^{-2} s^{-1}. The daily pattern of CO_2 effluxes was similar in both autumn and winter. Maximum CO_2 effluxes were observed in the afternoon around 1400-1500 h local time and minimum values occurred in the evening between midnight and sunrise. CO_2 effluxes during the day were more variable in autumn than in winter but the day-to-day effluxes were

very changeable in the winter.

Soil temperature was by far the most influential factor controlling the rate of soil respiration. The trend of CO_2 effluxes, whether during the day or between days, clearly followed the variation in soil temperature in both autumn and winter. The logarithmic value of hourly CO_2 efflux were closely related to the soil temperature at 5 cm, and about 90% of the variability in CO_2 efflux could be accounted for by the variation in soil temperature alone when fitting the field data to the Q_{10} model or the Arrhenius model. The Q_{10} value for the response of total CO_2 efflux to soil temperature measured at 5 cm was 2.5 and the activation energy of soil respiration had a value of 56.9 kJ mol^{-1}.

A large amount of CO_2 was released from soils under palmetto plants in the site. Although only about a third of the forest floor was covered by palmetto plants, it contributed more than a half of total CO_2 released from the soil surface. Palmetto is an important factor governing C cycle in a mature slash pine plantation in the area.

The CO_2 efflux from the soil surface in the slash pine plantation is highly heterogeneous spatially although the topography is uniform. Beds and troughs which were built in site preparation, although visually distinct on the forest floor, did not contribute significantly to the spatial heterogeneity of CO_2 efflux. The spatial variability in CO_2 efflux can be well characterised using a model, which is based on a simplified relationship between soil respiration and environmental factors and incorporates live and dead biomass and associated soil total porosity as predictor variables of CO_2 efflux. Among different locations in the site, CO_2 efflux generally increased with increase in soil fine root biomass, litter and humus amounts and soil total porosity but was inversely related to the amount of organic matter in the mineral soil. Understorey plants, mostly palmetto, were a major contributor to the spatial pattern of CO_2 efflux because of their large input of litter and consequent change in soil properties.

The CO_2 concentration in the soil gas increased with increasing depth, ranging from 0.25 % to 1% at 60 cm and 600-763 cm^3 m^{-3} at 2 cm during autumn and winter.

CHAPTER 4: MODELLING SOIL RESPIRATION

4.1 Introduction

Modelling the spatial and temporal variation of CO_2 efflux from the soil and the spatial distribution of CO_2 in the soil helps us to understand soil respiration and its governing processes. As noted in Chapter one, simulation of soil respiration or CO_2 efflux has mostly been attempted by statistical correlation. Such regression models are limited in the extent to which they can be applied to the conditions encountered during the investigation. Extrapolation of a regression model in both time and space may be of dubious value.

It is difficult to describe adequately the CO_2 efflux from soil and its response to various controlling environmental factors in a non-empirical model. The transport of trace gases within the soil has been studied previously, however, and a sound theoretical base has been developed, and this can be used in modelling soil CO_2 efflux (Thorstenson and Pollock, 1989; Massmann and Ferrier, 1992; Freijer and Leffelaar, 1996). A number of CO_2 mass balance models have been reported (Hendry *et al.*, 1993; Šimunek and Suarez, 1993, Suarez and Šimunek, 1993; Wood *et al.*, 1993). In a process-based model used to predict CO_2 efflux from the soil, the greatest uncertainty arises in describing CO_2 production and its dependence on soil conditions and no existing model is wholly appropriate. Although Šimunek's model includes a larger number of biological processes than other previous models (Šimunek and Suarez, 1993), some of the hypothesised mechanisms in the model remain uncertain, e.g. the dependence of soil respiration on soil moisture content or the response to soil oxygen concentration.

In this chapter, a process-based CO_2 efflux model is described and is used to predict the production, transport and vertical distribution of CO_2 in the soil. The model is validated with data obtained from the field experiment in a Florida slash pine plantation.

4.2 Model Description

CO_2 emission from the soil is considered to be the combined result of two main processes: the production of CO_2 (mainly respiration by plant roots and microbes) and gas transport out of the soil (controlling the movement of CO_2 from the soil to the atmosphere and of O_2 in the opposite direction). Some processes other than biological ones, are generally of relatively minor importance for the CO_2 balance in the soil, and are not taken into account in this model. Both of the primary processes are affected by many environmental factors, such as soil temperature, soil moisture content, etc..

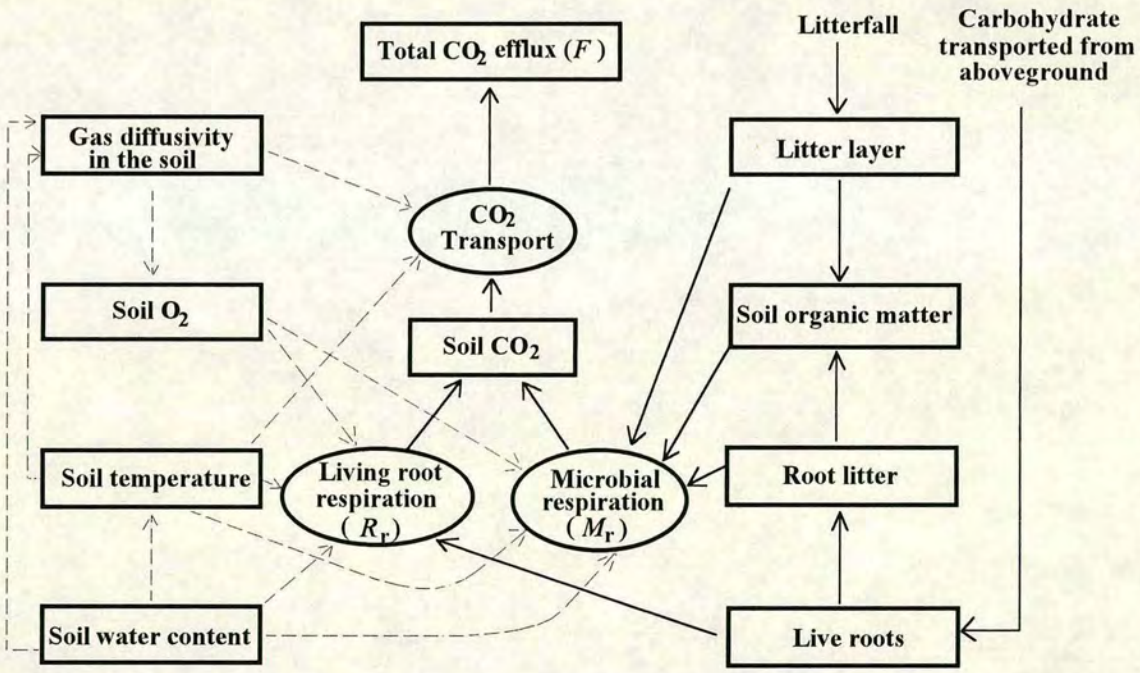


Fig. 4.1 Diagram of CO_2 efflux model. Solid lines and arrows indicate carbon flows; dashed lines and arrows represent the influence of environmental factors on respiration or gas transport; rectangles indicate state variables and ellipses indicate processes.

Figure 4.1 is a diagram of carbon flows, environmental factors and their interactions in the model. The major input of soil carbon is in the form of detritus (leaf and root litter) and carbohydrates transported from leaves above ground to the roots below. The loss of soil carbon is assumed only to be as CO_2 released from the soil to the atmosphere through respiration by roots and microbes. Some minor sinks or sources of soil carbon, such as the CO_2 arising from chemical reactions in the soil (Bunt and Rovira, 1954), the influence of soil animals (Berg *et al.*, 1980), the loss of carbohydrates to underground water (Edwards and Harris, 1977), etc., are not included in the model partly for model simplicity and partly because of their assumed minor importance.

Both CO_2 production and CO_2 transport in the soil are influenced by many environmental factors. As noted before, many previous studies have indicated that temperature, soil moisture content, soil properties such as porosity and organic matter content are probably the most important ones. Other factors, such as type and quantity of the microbial flora, pH, C/N ratio of the decomposing organic matter, presence of inhibitors or stimulants such as heavy metals and antibiotics, may also affect soil respiration and CO_2 transport. However, the influence of some of these factors are quite qualitative and are difficult to quantify exactly in a model. We do not consider these factors explicitly but include their influence indirectly through some of the parameters.

4.2.1 CO_2 mass balance and transport in the soil

Under the assumption of horizontal homogeneity, where the horizontal loss or gain of CO_2 is negligible, one-dimensional CO_2 transport in both the gas phase and liquid phase in the soil can be expressed by a mass balance equation (Wood *et al.*, 1993; Šimunek and Suarez, 1993). The CO_2 mass balance of an arbitrary volume below the surface can be written as:

$$\frac{\partial C_T}{\partial t} = -\nabla(F_{dg} + F_{ag} + F_{dw} + F_{aw}) + S \qquad (4.1)$$

where ∇ is a differential operator; F_{dg}, and F_{dw} are CO_2 fluxes caused by diffusion/dispersion in the gaseous and liquid phases of the soil, respectively; F_{ag} and F_{aw} are the fluxes resulting from gas convection and water vertical movement, respectively; S is the strength of sources /sinks of CO_2 and its magnitude changes with depth in the soil; C_T is the total concentration of CO_2 in both the gas and liquid phases, defined by equation 4.2:

$$C_T = C_g V_g + C_w V_w \tag{4.2}$$

where C_g, and C_w (mg CO_2 m^{-3}) are CO_2 concentrations in the gas and liquid phase, respectively; and V_g and V_w (m^3 m^{-3}) are the volumetric fractions of air and water in the soil, respectively. Because changes in soil water volume are always matched by changes in gas volume in the opposite direction:

$$V_g + V_w = \phi_T \tag{4.3}$$

ϕ_T is the soil total porosity as defined in equation 3.2.

When CO_2 dissolves in water, only a small fraction of the total dissolved CO_2 is actually present as carbonic acid, H_2CO_3 (*ca.* 1%, Moeller, 1952). Despite this fact, it is convenient to treat all dissolved CO_2 as H_2CO_3 (Lindsay, 1979). Taking account of the magnitude of the variation in CO_2 production and water movement in the soil, the assumption of an instantaneous equilibrium between dissolved CO_2 and H_2CO_3 is always reasonable. The dissolution of CO_2 in soil water can be then described by the following reactions and equilibrium constants for acid soils (Lindsay, 1979; Rasmuson *et al.*, 1990):

$$CO_2(g) + H_2O(l) \Leftrightarrow H_2CO_3(aq) \qquad K_1 = \frac{[H_2CO_3]}{p_{CO_2}} \tag{4.4a}$$

$$H_2CO_3 \Leftrightarrow H^+ + HCO_3^- \qquad K_2 = \frac{[H^+][HCO_3^-]}{[H_2CO_3]} \tag{4.4b}$$

$$HCO_3^- \Leftrightarrow H^+ + CO_3^{2-} \qquad K_3 = \frac{[H^+][CO_3^{2-}]}{[HCO_3^-]} \tag{4.4c}$$

The CO_2 concentration in the liquid phase (C_w), defined as the sum of all C species resulting from CO_2 dissolution, can be then obtained from equation 4.4 as:

$$\begin{aligned} C_w &= [H_2CO_3] + [HCO_3^-] + [CO_3^{2-}] \\ &= 4.34 \times 10^2 \{K_1 + \frac{K_1 K_2}{[H^+]} + \frac{K_1 K_2 K_3}{[H^+]^2}\} P_{CO_2} \end{aligned} \tag{4.5}$$

where P_{CO_2} is the partial pressure of CO_2 in the soil air (Pa); the value of 4.34×10^2 is a coefficient for converting C_w from the unit of mol dm^{-3} to mg CO_2 m^{-3} and P_{CO_2} from the unit of atmosphere to Pa; K_1 is the Henry's law constant, which can be calculated from:

$$\log K_1 = 2385.73 / T - 14.0184 + 0.01526T \tag{4.6}$$

where T is temperature (K) (Harned and Davis, 1943).

Constants K_2, K_3 can be estimated from the relation:

$$\frac{\mathrm{d} \log K_{(2,3)}}{\mathrm{d}T} = \frac{\Delta H_{(2,3)}}{2.303RT^2} \tag{4.7}$$

where R is the universal gas constant; ΔH is the enthalpy of the ionising reaction of hydrogen carbonates. At a temperature of 25 °C, log K_2 = -6.35 and log K_3 = -10.33, with corresponding ΔH values of -2.0 and -3.5 kJ mol^{-1} (Smith and Martell, 1976).

Because diffusion is the dominant process of CO_2 transport in the gaseous phase in the soil and dispersion in the gas phase can be neglected (Šimunek and Suarez, 1993), F_{dg} is given by Fick's first law :

$$F_{dg} = -D_{gs}\frac{\partial C_g}{\partial z}$$

$$= -D_g \varepsilon(\phi_g)\frac{\partial C_g}{\partial z} \tag{4.8}$$

where D_{gs} and D_g are the CO_2 gaseous diffusion coefficients in the soil gas and in the atmosphere, respectively; and $\varepsilon(\phi_g)$ (defined in equations 4.13 and 4.15) is the tortuosity factor of gas diffusion through the soil as a function of the air-filled porosity, ϕ_g.

Equation 4.8 assumes that Fick's law adequately describes the diffusive gas flux. For gases such as CO_2, which have sources or sinks in the system and constitute a small fraction of the total system pressure, this appears to be true (Thorstenson and Pollock, 1989). Šimunek and Suarez (1993) also pointed out that Fick's law is adequate when soils are not close to saturation.

The CO_2 diffusive coefficient in the air is taken from Campbell (1985):

$$D_g = D_{g0}(T/T_0)^n(P_0/P) \tag{4.9}$$

where T_0 =273.2 K and P_0=101.3 kPa; D_{g0} is the diffusion coefficient of CO_2 in the atmosphere at θ_0 and P_0; P is air pressure. For CO_2 , D_{g0} is 1.39×10^{-5} m^2 s^{-1} and n=1.75. Corresponding values for O_2 are 1.77×10^{-5} m^2 s^{-1} and n = 2.

In equation 4.1, F_{dw}, F_{ag} and F_{aw} are defined below:

$$F_{dw} = \left[-D_w\varepsilon(\phi_w) + \lambda_w\left|\frac{q_w}{V_w}\right|\right]\frac{\partial C_w}{\partial z} \tag{4.10}$$

$$F_{ag} = q_g C_g \tag{4.11}$$

$$F_{aw} = q_w C_w \tag{4.12}$$

where D_w and λ_w are the CO_2 diffusion coefficient and dispersion coefficient in soil water, respectively; $\varepsilon(\phi_w)$ is the tortuosity factor for CO_2 diffusion in the water phase;

and q_g and q_w are gas and water fluxes, respectively.

For a wet porous medium such as soil, the tortuosity factor for CO_2 gaseous diffusion, $\varepsilon(\phi_g)$, can be estimated from:

$$\varepsilon(\phi_g) = \phi_g^{2a}(\phi_g / \phi_T)^2 \tag{4.13}$$

where a is determined from the relation (Collin and Rasmuson, 1988):

$$\phi_g^{2a} + (1-\phi_g)^a = 1 \tag{4.14}$$

However, most soils have an aggregated structure with an intra-aggregate pore space and an inter-aggregate pore space. Equation 4.13 may not apply in these soils Millington and Shearer (1971) suggested a model for estimating air diffusivity through aggregated soils:

$$\varepsilon(\phi_g) = \left[\frac{(\frac{\phi_{g_1}}{\phi_{T_1}})^2 (\frac{\phi_{g_1}}{1-\phi_{T_2}})^{2a} (1-\phi_{T_2}{}^{2b})(\phi_{g_2} - \phi_{g_2}{}^{2c})}{(\frac{\phi_{g_1}}{\phi_{T_1}})^2 (\frac{\phi_{g_1}}{1-\phi_{T_2}})^{2a} (1-\phi_{T_2}{}^{2b}) + (\phi_{g_2} - \phi_{g_2}{}^{2c})} \right] + \left[\phi_{g_2}{}^{2c} (\frac{\phi_{g_2}}{\phi_{T_2}})^2 \right] \tag{4.15}$$

where ϕ_{g_1}, ϕ_{T_1} are intra-aggregate air-filled pore space and total pore space; ϕ_{g_2}, ϕ_{T_2} are inter-aggregate air-filled and total pore space, respectively; a, b, c are parameters calculated from relations below:

$$(\frac{\phi_{g_1}}{1-\phi_{T_2}})^{2a} + (1 - \frac{\phi_{g_1}}{1-\phi_{T_2}})^a = 1 \tag{4.16}$$

$$\phi_{T_2}^{2b} + (1-\phi_{T_2})^b = 1 \tag{4.17}$$

$$\phi_{g_2}^{2c} + (1-\phi_{g_2})^c = 1 \tag{4.18}$$

One approach for estimating the total intra- and inter-aggregate porosities is to assume that all intra-aggregate spaces ϕ_{T_1}, and no others, are entirely water-filled at field capacity and hence can be estimated from the volumetric water content at field capacity. The inter-aggregate pore space is assumed to be the macropores that are air-filled at field capacity, and are water-filled only when the soil is saturated. Hence, the total inter-aggregate porosity, ϕ_{T_2}, is estimated from the difference between total porosity and volumetric water content at field capacity (Davidson and Trumbore, 1995).

There is no effective method to estimate the tortuosity factor for CO_2 liquid diffusion ($\varepsilon(\phi_w)$ in equation 4.10). Šimunek and Suarez (1993) assumed that the relation between $\varepsilon(\phi_w)$ and water-filled porosity is the same as that between $\varepsilon(\phi_g)$ and air-filled porosity. However, because the diffusivity of CO_2 in the liquid phase, D_w, is about 10,000 times lower than that in the gas phase, CO_2 diffusion in the liquid phase is usually negligible.

The water dispersion coefficient, λ_w, typically ranges from about 0.005 m or less at the laboratory scale to about 0.1 m or more for field scale experiments (Nielsen *et al.*, 1986) and is assumed to be 0.1 m here. The flux term for CO_2 resulting from air movement in the soil (eq. 4.12) is unlikely to be important for total CO_2 efflux and is ignored here because of the slow movement of soil gas and the low viscosity of air.

4.2.2 CO_2 production in the soil

The total CO_2 output from the soil is mainly from the respiration of living roots and heterotrophic microbial respiration. If we assume that any possible CO_2 sink in the soil is negligible compared with the CO_2 production in soil respiration, the source/sink term in equation 4.1, S, is simply dependent on soil respiration rate. We can further assume that root and microbial respiration are additive and that there is no direct interaction between them. The indirect interaction between root and microbial respiration can be specified by their relationship to environmental factors and corresponding carbon pools in the soil. Thus we have:

$$S = R_r + R_m \tag{4.19}$$

where R_r and R_m are the rates of root and microbial respiration, respectively.

The heterotrophic microbial respiration is actually the process of decomposition of soil organic matter by microbes. In this process, the decomposition rate for constant environmental conditions is:

$$\frac{dM}{dt} = -kM \tag{4.20}$$

where k is the decomposition rate coefficient and M is the amount of effective decomposing substance. However, equation 4.20 does not always fit well in the field because soil organic matter is a mixture of different substances which have different decomposition rates in the same environmental conditions. In most cases, soil organic matter can be divided into labile and resistant fractions (Hunt, 1977; Hogg, 1993). Let the ratio of labile to total amount of organic matter be λ, and decomposition rates for labile and resistant organic matter be k_{lab} and k_{ris}, respectively, then:

$$\frac{dM}{dt} = -k_{lab}\lambda M - k_{ris}(1-\lambda)M = -k_{lab}M' \tag{4.21}$$

where $M' = \lambda M + k_{ris}(1-\lambda)M / k_{lab}$ can be considered as the equivalent amount of labile organic matter, to which microbial respiration is directly related. In a given ecosystem, k_{lab} can be presumed to be constant in constant conditions, but k_{ris} may vary with the age of organic matter, and consequently with depth in the soil. λ is also related to the depth of soil.

Assuming that all the C in decomposing soil organic matter is finally transformed into CO_2, the microbial respiration rate can be obtained from:

$$R_m = \alpha\frac{dM}{dt} = \gamma_m M' \tag{4.22}$$

where α is a coefficient representing the amount of CO_2 arising from the decomposition per unit of dry organic matter; $\gamma_m = \alpha k_{lab}$ is then the microbial respiration rate parameter. α varies between 1.5 and 1.7 (Larcher, 1995).

The production of CO_2 from root respiration is related to the specific rate of root respiration and the root biomass. Usually, root respiration is not linearly related to the total root biomass as respiration rates per unit dry mass of root vary with root diameter, or size-class: the bigger the root, the less is the respiration rate per unit dry mass. However, assumption of a linear relation between respiration rate and root biomass for each size class is reasonable (Chapman, 1979). The total root respiration can be written as:

$$R_r = \sum \gamma_{r_i} B_i \tag{4.23}$$

where γ_{r_i} is the respiration rate parameter of root size class *i*; and B_i is the root biomass of size class *i*. Similarly, if the respiration rate of the finest root be γ_r, the equivalent root biomass B' is given by:

$$B' = \sum \gamma_{ri} / \gamma_r B_i \tag{4.24}$$

and equation 4.23 becomes

$$R_r = \gamma_r B' . \tag{4.25}$$

Substituting equations 4.22 and 4.25 into equation 4.19, soil respiration is then:

$$S = \gamma_r B' + \gamma_m M' . \tag{4.26}$$

The total CO_2 production rate, S_T, can be obtained by integrating equation

4.26 through the whole soil profile:

$$S_T = \int_0^{Z_l} S\mathrm{d}z = \int_0^{Z_l} \gamma_r B' \mathrm{d}z + \int_0^{Z_l} \gamma_m M' \mathrm{d}z \tag{4.27}$$

where Z_l is the depth of the lower boundary in the soil.

4.2.3 Influences of environmental factors on soil respiration

Root and microbial respiration may have different sensitivities to environmental factors, for example, the responses of root and microbial respiration rate to O_2 concentration and water content in the soil are expected to be different because of the different size of roots and microbes. However, an assumption that environmental factors have similar influences on both root and microbial respiration is reasonable and necessary for model simplicity and solvability. On the assumption that any factor can act effectively on any others, we have:

$$\gamma_r = \gamma_{r0} f(T) f(W) f(O_2) \tag{4.28}$$

$$\gamma_m = \gamma_{m0} f(T) f(W) f(O_2) \tag{4.29}$$

where γ_{r0} and γ_{m0} represent the maximum respiration rates of roots and micororganisms under optimal conditions, respectively, at a given temperature T_0; $f(T)$, $f(W)$, $f(O_2)$ are scaling factors for temperature, water content and O_2 concentration in the soil, respectively. $f(W)$ and $f(O_2)$ have a value between 0 and 1.

An equation of the Arrhenius type is used to describe the response of soil respiration to soil temperature:

$$f(T) = \exp(-E/R\theta) \tag{4.30}$$

where E is the activation energy for respiration, in kJ mol^{-1}; R is the universal gas

constant and θ is absolute temperature. Although an Arrhenius type equation with a constant value of E has been successfully used by many authors, Lloyd and Taylor (1994) pointed out that only when E varied with temperature could an equation of the Arrhenius type give an unbiased estimate of the relationship between soil respiration and temperature. E is assumed to be a variable parameter in our model, having a larger value at low temperature than at high temperature. Assuming that $f(T)$=1 at temperature $T_{10} = 283.15$ K, then the temperature dependence of respiration can be expressed as:

$$f(T) = \exp(\frac{E}{RT}\frac{T - T_{10}}{T_{10}}) \tag{4.31}$$

Generally, soil moisture content restricts soil respiration when low or high. The reduction in soil respiration at low moisture content is thought to be caused by lack of soil water which inhibits the metabolic activity of microbes and roots. At high moisture content, the reduction in soil respiration is caused by lack of oxygen and the accumulation of CO_2 as a result of the soil pore spaces becoming filled with water (Glínsky and Stepniewski, 1985). Between the low and high moisture limits, the change in soil moisture content has little or no obvious effect on soil respiration (Tesarová and Gloser, 1976). The effect of soil moisture content can thus be separated into a direct and an indirect effect. The direct effect concerns the influence of water on the metabolic activity of microbes and roots, and the indirect effect affects gas diffusion.

Any soil system has an inherent metabolic or respiratory potential with respect to soil moisture content, but this potential cannot be fully realised when the soil is dry. With other conditions constant, adding water to the soil will increase soil respiration. However, the increasing rate of soil respiration will slow down with a further increase in soil moisture. Assuming that the increasing of soil respiration is linearly related to the unrealised portion of the respiratory potential, the direct effect of soil moisture content on soil respiration can expressed as:

$$\frac{df(W)}{dW} = a[f(W)_{max} - f(W)] \tag{4.32}$$

where W is soil moisture content; a is a parameter, representing the maximal increase in rate of soil respiration with soil moisture. $f(W)_{max}$=1 is the maximum value of $f(W)$, when soil moisture content does not limit respiration.

Integrating equation 4.32:

$$f(W) = 1 - \exp(-aW + c) \tag{4.33}$$

where c is an integration constant.

Respiration rates of plant tissues or organs have been observed to increase linearly with increasing ambient O_2 concentration when O_2 concentration is low. The increase in respiration rate will slow down, till a maximum, with further increase in O_2 concentration (Berry and Norris, 1949; Forward, 1965; Yemm, 1965). Assuming this relationship is also applicable to microbial respiration, the dependence of soil respiration rate on ambient oxygen concentration can be described by the Michaelis-Menten equation:

$$V = \frac{V_{max}[O_2]}{[O_2] + K_M} \tag{4.34}$$

where V and V_{max} are the reaction rate and maximal rate, respectively; K_M is the Michaelis-Menten constant, representing the concentration of oxygen at which the reaction rate is half maximum; $[O_2]$ is oxygen concentration in the soil gas (Glínsky and Stepniewski, 1985). The scaling factor for soil respiration in relation to oxygen concentration in the soil air is then given by:

$$f(O_2) = \frac{1}{1 + K_M / [O_2]} \tag{4.35}$$

$f(O_2)$ is supposed varying between 0 and 1. Because oxygen concentration in soil air is unlikely to exceed 21% (the oxygen concentration in the atmosphere), the upper limit of $f(O_2)$ is dependent on the value of K_M. Some studies have shown that a decrease in soil respiration rate to half its maximal value takes place below 2% of oxygen in the soil gas (Glínsky and Stepniewski, 1985). $f(O_2)$ is then about 0.9 of that in the atmosphere and that is a disadvantage of using the Michaelis-Menten equation to describe the dependence of soil respiration on oxygen concentration. It is worth pointing out that the Michaelis-Menten equation describes only the relationship between respiration rate and O_2 concentration but does not provide any explanation about the relation. The constant, K_M, is not tied to any individual process which affects respiration or O_2 concentration in soil gas but may be related to all of them.

When the soil is dry or fairly wet, O_2 concentration is fairly high in soil gas and the diffusion of O_2 to microbes or fine roots where respiration take places should not be a limiting factor to soil respiration. In a wet soil, microbes or fine roots may be surrounded by soil water. The slow diffusion of oxygen through soil water to microbes or roots may limit respiratory activity, and the respiration rate is likely to be linearly related to the oxygen concentration in the soil gas. However, a linear relationship can also be obtained from the Michaelis-Menten equation because the O_2 concentration in the soil gas is low in this case. Generally, the Michaelis-Menten equation can approximately describe the relationship of soil respiration rate to ambient oxygen concentration over a wide range of moisture content, when K_M is assumed to include the influence of O_2 diffusion through soil water and of O_2 concentration on respiratory activities. K_M is likely to be a variable dependent on soil conditions, such as moisture content, temperature, etc. However, a constant K_M is a reasonable assumption for the purpose of simulation in the field.

In the model it is assumed that the respiratory quotient equals unity and that all oxygen entering the soil is consumed only by soil respiration. Given a boundary condition that the volumetric concentration of oxygen in the atmosphere is 21% and that there is no O_2 flux through the bottom of soil, oxygen concentrations in soil air at different depths are estimated with the method described by Campbell (1985).

4.2.4 Dynamics of soil litter and organic matter

The dynamics of litter, including litter from above and below ground, or soil organic matter in the model are expressed as:

$$L_t = L_0 + \int_0^D L(t)_l \, dt - \frac{1}{\alpha}\int_0^{D-1}\int_0^H R_{ml} \, dt dt + \int_0^D M_{tranl} \, dt \qquad (4.36a)$$

$$M_t = M_0 + \int_0^D L(t)_s \, dt - \frac{1}{\alpha}\int_0^{D-1}\int_0^H R_{ms} \, dt dt + \int_0^D M_{trans} \, dt \qquad (4.36b)$$

where L_0, L_t, M_0 and M_t are the litter and organic matter amounts at time *0* and time *t*, respectively; $L(t)_l$ is the dynamics of litterfall for the surface layer and $L(t)_s$ is the input of root debris in the mineral soil; D is the Julian day of the year; H is the hour of day; α is as in equation 4.22; R_{ml} and R_{ms} are the microbial respiration rate in the litter layer and mineral soil, respectively; M_{tranl} and M_{trans} are the exchange rate of organic matter with other soil layers in litter layer and mineral soil, respectively, defined as negative for net mass moving out of the layer.

It is difficult to estimate M_{tranl} and M_{trans}. Two assumptions can be made to solve equation 4.36. Firstly, the amount of soil organic matter can be assumed to be in dynamic equilibrium, i.e. there is no change in the soil dead carbon pool between years, when an ecosystem approaches a steady state. The soil organic matter consumed through the microbial respiration would be fully compensated by the inputs of above- and below-ground litter, although small year-to-year variations may exist. Alternately, the transport of organic matter between soil layers can be considered to be negligible, i.e. $M_{tranl} = M_{trans} = 0$. The balance between below-ground litterfall and the organic matter consumed by microbial respiration is compensated by the change in soil organic matter pool.

The dynamics of litterfall are dependent on the type of ecosystem and the climate. In most cases, litterfall takes place at a particular time of year. The seasonal pattern of litterfall for leaf, wood and root may be different, but they are assumed to be the same here for model simplicity.

4.3 Application in Slash Pine Plantation

4.3.1 Initial conditions in the slash pine site

For simulating soil respiration at different depths and determining the spatial distribution of soil CO_2, the forest floor and soil in the slash pine site are divided into five layers, depending on the soil properties and their relationship to respiration and CO_2 transport:

- Layer 1: 0-2 cm, consisting of fresh undecomposed litter sparsely distributed on the ground; the water content in this layer will affect CO_2 production rate but not gas diffusivity through it; no roots occur.
- Layer 2: 2-6 cm, broken or semi-decomposed litter and humus; CO_2 diffusion will not be significantly influenced by a moderate moisture content but may be impeded at high moisture content; some fine roots are present.
- Layer 3: 6-20 cm, A horizon of the mineral soil with a relatively porous and recognisable aggregated structure, especially under the palmetto plants; however, the aggregated structure is not well developed in this slash pine plantation because of the sandy soil texture and previous site preparation for tree planting; many fine roots present.
- Layer 4: 20-45 cm, a transition layer to the deep soil; aggregated structure was only recognisable under palmetto plants; many roots occur.
- Layer 5: 45-100 cm, B horizon with a sandy texture and less organic matter and root biomass.

The soil deeper than 100 cm is assumed for model purposes not to be a significant source/sink of soil CO_2 although in reality some CO_2 may be produced there and transported to the soil above.

Based on the difference in decomposability from previous work in slash pine

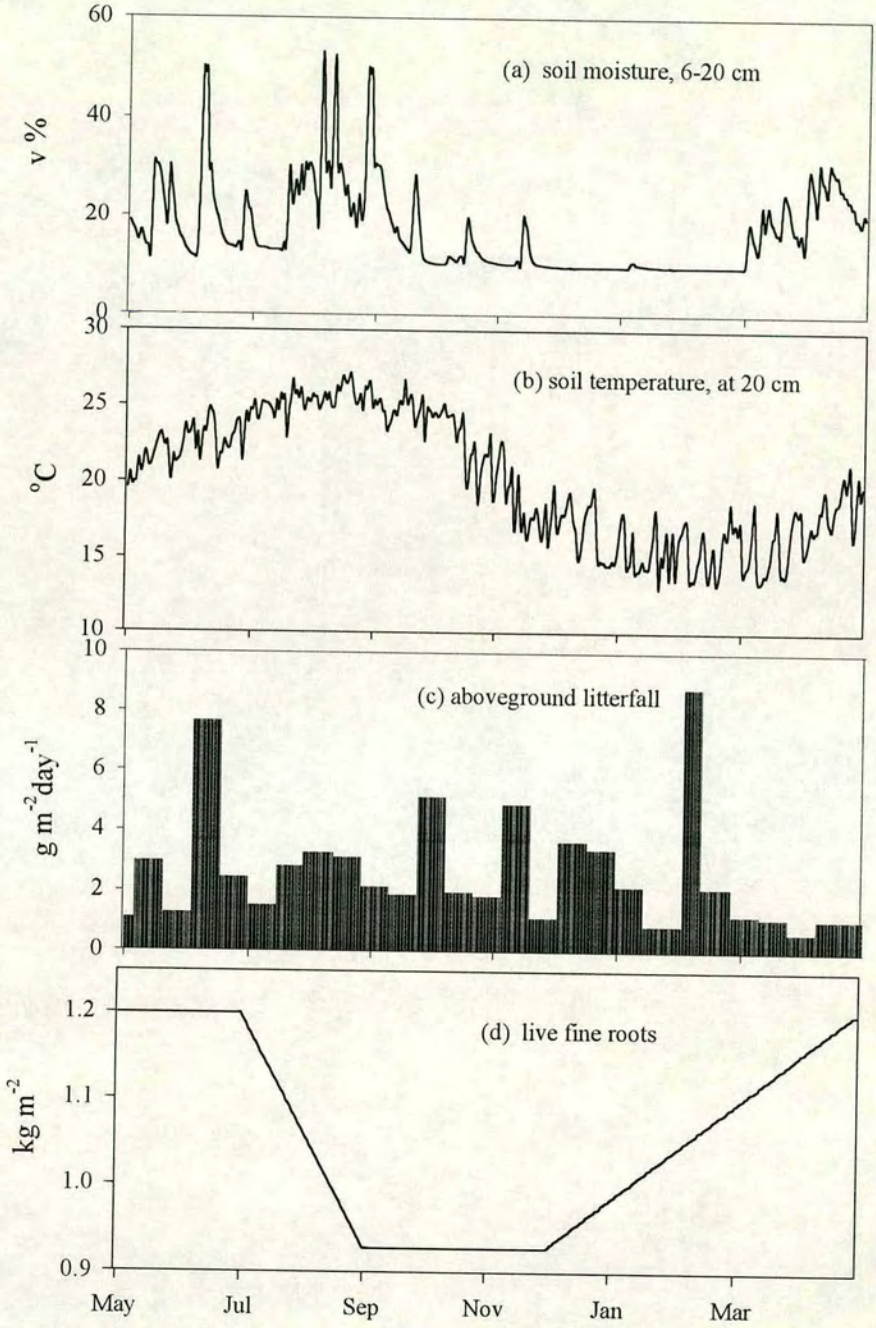


Fig. 4.2 Variation of environmental factors and aboveground litterfall during the year measured or estimated in a slash pine plantation, Florida, 1995-1996.

plantations (Ewel *et al.*, 1985b, Cropper and Gholz, 1991), three categories of organic matter were used as model input: above ground litter, root detritus and resistant organic matter in the mineral soil. Root biomass was put into in three groups according to diameter: small fine roots (< 3 mm), fine roots (3~10 mm) and coarse roots (> 10 mm). All data for model input on root biomass, litter amount in the surface layer and organic matter content in the mineral soil were measured or estimated as discussed before in Chapter 3. The derivation of parameters for decomposition and root specific respiration rates is to be discussed later in 4.3.3.

Figure 4.2 shows the magnitude and seasonal pattern of some variables used as model inputs. Soil moisture, estimated from the variation of the water table height, was more variable in summer than in winter (Fig. 4.2a). Between June and September there were a few occasions of saturation which may suppress soil respiration or CO_2 transport from the soil to the atmosphere. On the other hand, soil moisture was moderate and stable during the winter season. North Florida typically experiences mild, dry winters and hot, wet summers (Hendry and Gholz, 1986). The seasonal pattern of soil temperature was sinusoidal, with a maximum between August and September and a minimum in February.

Because the dynamics of litterfall and root biomass are not explicit in the model, the measured litterfall rate and estimated root biomass were used as inputs to the model. Litterfall did not show a consistent seasonal trend during the experimental period in 1995-1996, and occasionally a high input of litterfall was the result of particular weather conditions, such as hurricanes in June 1995 (Fig. 4.2c). Fine live roots increased in the spring to a peak in midsummer and then declined to a minimum in the late autumn (Gholz *et al.*, 1986) in slash pine. It was assumed that the yearly trend and variability between maximum and minimum of fine live roots observed by Gholz *et al.* (1985) was also applicable to the site in this study. The estimated yearly trend of fine live roots biomass is showed in Fig. 4.2d.

4.3.2 Boundary conditions for model solution

Equation 4.1 can be solved numerically, hourly or daily, with the following

boundary conditions and assumptions.

(1) There is no convective flux of CO_2 or O_2 in the gaseous phase at the lower boundary of the soil.

(2) The compressibility of soil air is negligible. This assumption seems to be reasonable except in the case of saturation. When soil is saturated (typically at the soil surface) air cannot escape and is probably compressed under the wetting front (Šimunek and Suarez, 1993) .

(3) Liquid phase CO_2 in the soil is always in equilibrium with the ambient gaseous CO_2 concentration. This assumption may not be correct when soils are close to saturation. A considerable error may thus arise in a soil CO_2 profile if this model is used for soils which are nearly saturated.

(4) The respiratory quotient is unity and the CO_2 production rate from soil respiration is zero when the soil is saturated (assumed equivalent to an air-filled porosity of 1% of total bulk soil or less).

(5) The oxygen volumetric concentration in the air above ground is constant at 21%; and the CO_2 concentration at 360 $cm^3 m^{-3}$. For simulating CO_2 concentrations at different soil depths during the day, the CO_2 concentration in the air above ground is assumed to have a minimum of 300 $cm^3 m^{-3}$ at 1700 h in the afternoon and a maximum of 400 $cm^3 m^{-3}$ at 0600 h in the morning.

4.3.3 Determination of parameters

The transpiration rate in the slash pine site was assumed to be 5 mm day^{-1} from the beginning of July to the end of September and 2.5 mm day^{-1} at other times, following Ewel and Gholz (1991) who simulated daily transpiration rates between 2 to 3 mm day^{-1} with a maximum at 6.7 mm day^{-1} for a slash pine plantation. It was further assumed that this water was split into the evaporation from the soil surface and the transpiration from the surface of the plants, and that water uptake rate by roots is related to fine root biomass in different layers. The upward water flux through each soil layer can then be estimated with these assumptions and soil moisture data. On rainy days, the vertical water flux was estimated from rainfall, interception

capacity of the canopy, evaporation from the soil surface, uptake by roots and the change in soil moisture content. The interception loss was set at 12% of the precipitation (Ewel and Gholz, 1991). For calculating gas diffusivity in the soil with eq. 4.15, the field capacity was estimated as the water content at a matric potential of -30 kPa.

Fifteen periods in which CO_2 efflux was measured from 0100 h to 2400 h were used, with other relevant data, to derive model parameters. The remaining data (about a third of the total data measured in the field) were used to validate the model. A multidimensional optimisation method, the Downhill Simplex Method (Press *et al.*, 1992), was used to determine the value of model parameters. The Downhill Simplex Method takes the parameters to be determined as a multidimensional simplex and uses the sum of squares of residual between estimated and measured CO_2 effluxes as an indicator to find parameter values which produce the best estimate of CO_2 efflux with a pre-set convergence criteria. The parameter values, obtained with a convergence criteria of 0.001, are listed in Table 4.1. The standardised residual between the estimated and the measured CO_2 effluxes fairly distributes along the estimated CO_2 efflux, indicating that the CO_2 efflux estimated with the model is generally unbiased over this range, although may be somewhat higher than measured efflux when the efflux is high (Fig. 4.3).

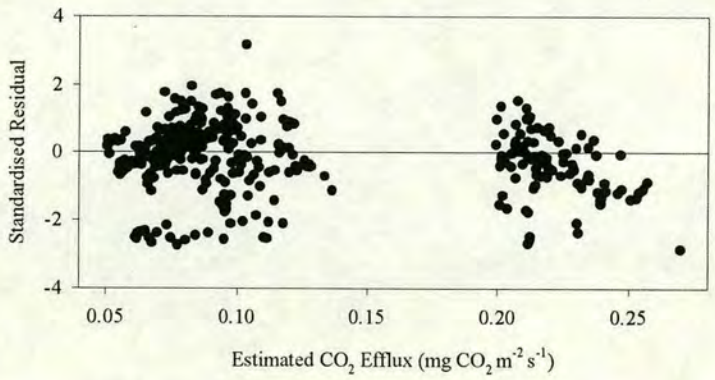


Fig. 4.3 The standardised residual over the range of the estimated CO_2 efflux. A negative residual indicates a higher efflux estimated than measured.

4.4 Model Validation

4.4.1 CO_2 efflux

Simulated *hourly* CO_2 effluxes from the soil surface are compared with a set of efflux data, different from that used in deriving model parameters, measured during September - October, 1995 and January, 1996 in Fig. 4.4. The average hourly CO_2 effluxes measured during the two field measurements were 0.205 and 0.095 mg CO_2 m^{-2} s^{-1}, and corresponding simulated values were 0.200 and 0.09 mg CO_2 m^{-2} s^{-1}, respectively. Simulated CO_2 effluxes agreed closely ($R^2 = 0.96$) with measured values both in the magnitude and daily pattern.

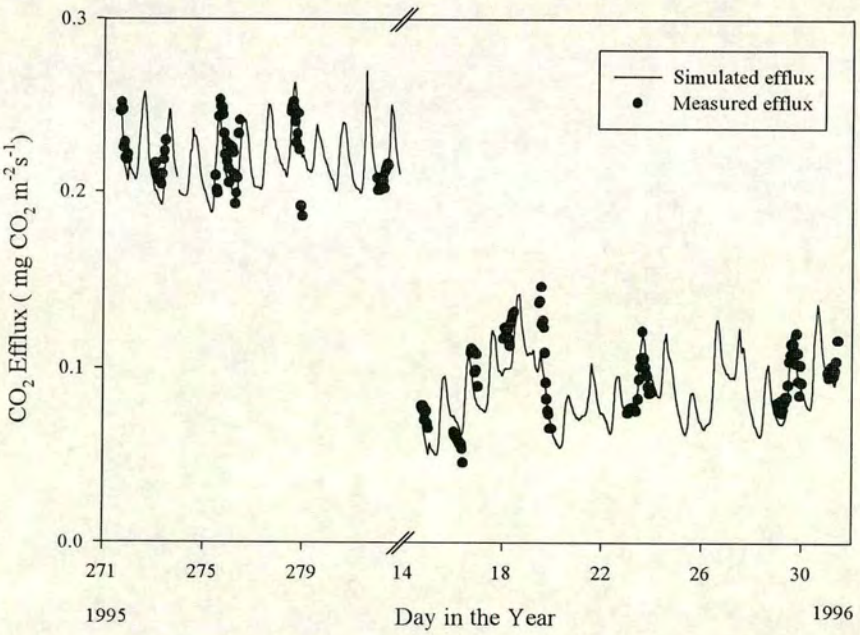


Fig. 4.4 Comparison between simulated and measured hourly CO_2 efflux in slash pine plantation, Florida.

Daily CO_2 efflux simulated using estimated daily soil temperatures and the parameters derived for hourly simulation also showed a good agreement with the daily effluxes estimated from the measured data (Fig. 4.5). The average simulated daily effluxes were 0.213 and 0.085 mg CO_2 m^{-2} s^{-1} for the autumn and the winter, and corresponding measured values were 0.217 and 0.087 mg CO_2 m^{-2} s^{-1}, respectively.

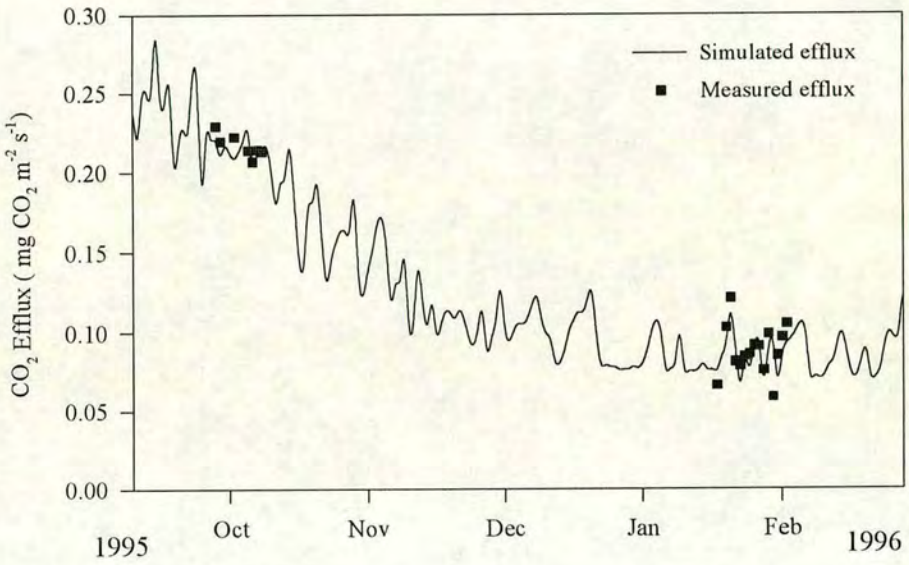


Fig. 4.5 Comparison between simulated and measured daily average CO_2 efflux from the soil in slash pine ecosystem, Florida, 1995-1996.

4.4.2 CO_2 concentration

The simulated daytime soil CO_2 profile matched the measured ones well (Fig. 4.6). It is noticeable that when soil is wet the model produces a slightly lower soil CO_2 concentration than the independently measured values. On the other hand, when soil is dry, the simulation gives a higher soil CO_2 concentration profile. In the simulation, equation 4.15 was used for the aggregated soil layer (6 to 20 cm) and equation 4.13 for the surface layer and other soil layers to define the relation of soil

diffusivity to soil moisture content. The comparisons in Fig. 4.6 indicate that these equations are suitable for the soil in the slash pine site but slightly overestimate the soil diffusivity of wet soil and underestimate it when the soil is dry.

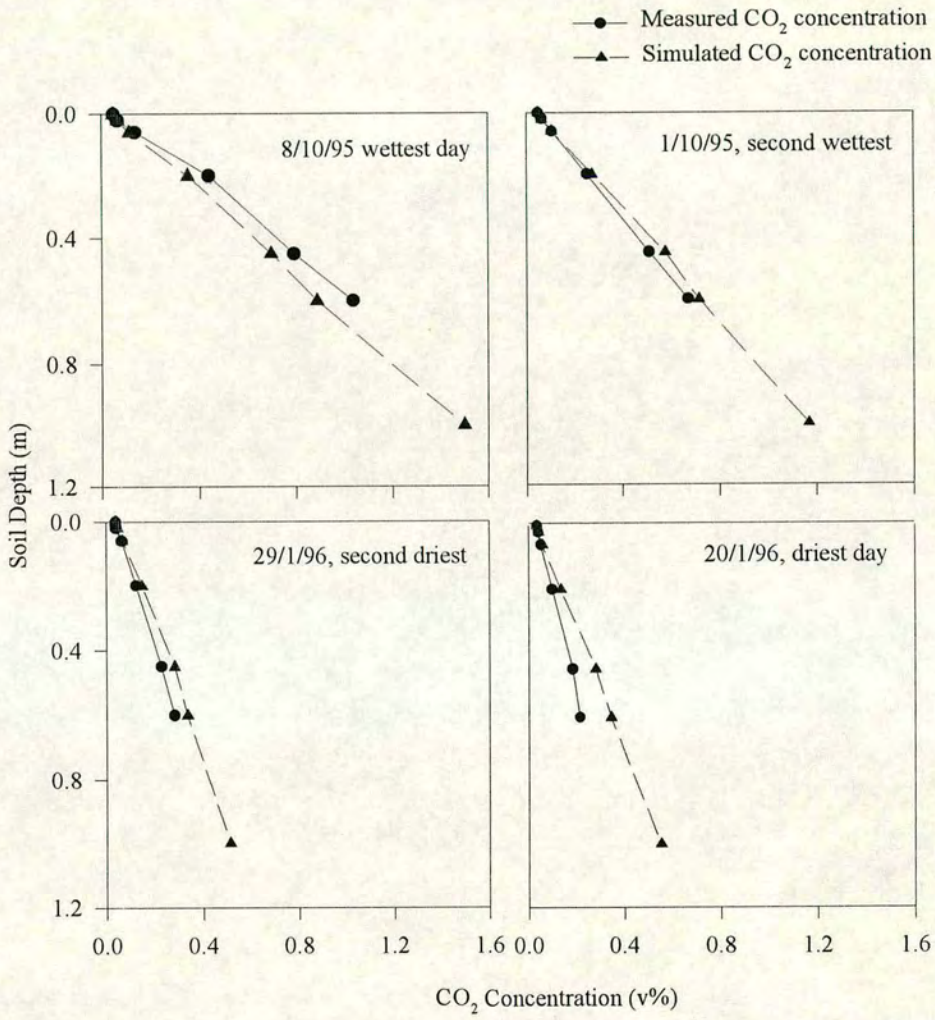


Fig. 4.6 Comparison between simulated and measured soil CO_2 profile. The CO_2 concentration is a daytime average (n = 7).

4.5 Sensitivity Analysis

A sensitivity analysis provides information about the response of a model output with respect to perturbations in its input or changes in individual parameters under given conditions. This information is used to evaluate the potential errors associated with parameter uncertainties as well as to determine which parameter or input variable needs to be more accurately quantified. The response of CO_2 efflux to a change in a parameter or model input presented in this section represents changes made under the actual conditions in Florida slash pine plantation. The sensitivity, or the importance, of model parameters and variables may differ in other ecosystems because of the different ranges of variation in variables and associated parameters.

4.5.1 Sensitivity of annual CO_2 efflux to model parameters

Table 4.1 presents the sensitivity of the annual CO_2 efflux to an increase in the model parameters equal to 5% of their value and applied from 1 May, 1995 when the simulation starts. The parameters are ranked in order of decreasing importance of their influence on the annual CO_2 efflux from the soil. The parameter with the largest influence on annual CO_2 efflux is the activation energy for soil temperatures > 20 °C. A 5% change in the parameter produces a 5.4% increase in annual CO_2 efflux. However, the output of the model is much less sensitive to activation energy for other temperature ranges. The reason for the largest response of annual CO_2 efflux to activation energy for temperatures over 20 °C is that soil temperature was a dominant factor governing soil CO_2 efflux and soil temperature was over 20 °C for most of the year.

The sensitivity of model output to a perturbation varies with time of the year. Figure 4.7 shows the yearly pattern of sensitivity of CO_2 efflux to activation energy, expressed as the percentage of the average efflux for the year. The figure indicates that CO_2 efflux is more sensitive to activation energy E_1 (i.e. for temperatures > 20 °C) then to E_2 (i.e. for temperatures 10 to 20 °C) during summer and autumn months,

Table 4.1 Sensitivity of the annual CO_2 efflux to the model parameters

Parameter, α	Parameter Nominal Value	δ(Annual CO_2 Efflux), %, Induced by $\delta\alpha$= 5 %α
Activation energy, E_1, > 20 °C (eq. 4.30)	78.2 kJ mol^{-1}	5.4
total porosity in mineral soil		3.5
optimal root respiration rate,< 3 mm*	4.30×10^{-5} mg CO_2 $g^{-1}s^{-1}$	3.1
optimal litter decay rate*	3.85×10^{-6} mg CO_2 $g^{-1}s^{-1}$	1.5
Activation energy, E_2,10 to 20 °C (eq. 4.30)	79.3 kJ mol^{-1}	1.2
Michaelis-Menten constant for O_2 (eq. 4.34)	4.88×10^{4} mg O_2 m^{-3}	-0.7
optimal organic matter decay rate*	3.73×10^{-7} mg CO_2 $g^{-1}s^{-1}$	0.5
parameter *a* for litter (eq. 4.33)	7.5	0.4
optimal root respiration rate, 3 to 10 mm*	5.07×10^{-6} mg CO_2 $g^{-1}s^{-1}$	0.2
optimal dead root decay rate, < 3 mm*	6.21×10^{-6} mg CO_2 $g^{-1}s^{-1}$	0.2
optimal root respiration rate, > 10 mm*	6.75×10^{-7} mg CO_2 $g^{-1}s^{-1}$	0.2
pH value in mineral soil	4.5	0.1
pH value in litter layer	4.0	0.1
water dispersion coefficient	0.1 m	0.1
Activation energy, E_3, < 10 °C	94.9 kJ mol^{-1}	0.1
transpiration rate in winter	2.5 mm day^{-1}	0.1
transpiration rate in summer	5 mm day^{-1}	0.1
total porosity in humus layer	0.72 m^3 m^{-3}	0.1
parameter *a* for mineral soil (eq. 4.33)	22.6	0.0
parameter *c* for mineral soil (eq. 4.33)	0.11	0.0
parameter *c* for litter layer	0.15	-0.0

* at temperature 10 °C.

but less sensitive in winter and spring. This pattern of sensitivity to activation energy is largely the result of the seasonal variation in soil temperature. During summer and autumn, daily soil temperatures were almost always above 20 °C (Fig. 4.2b) at different depths except in deep soil layers in early summer. In late autumn, temperature at the soil surface and in the top soil fell below 20 °C but the deep soil temperature was still above 20 °C for a period of time. The high daily sensitivity of CO_2 efflux to E_1 in July indicates that efflux is most temperature dependent at this time, when moderate soil moisture and high temperature were observed at the slash pine site. The decline in sensitivity between August and September is the result of high soil moisture hindering CO_2 efflux during the period.

Note that the sensitivity of CO_2 efflux to E_1 has a small negative value during the winter. This does not imply that an increase in E_1 will reduce soil respiration or CO_2 efflux but represents the accumulated effect of increasing E_1 during the preceding summer and autumn. An increase in microbial respiration resulting from increase in E_1 in the summer and autumn will reduce the organic matter pool in the soil, and thus

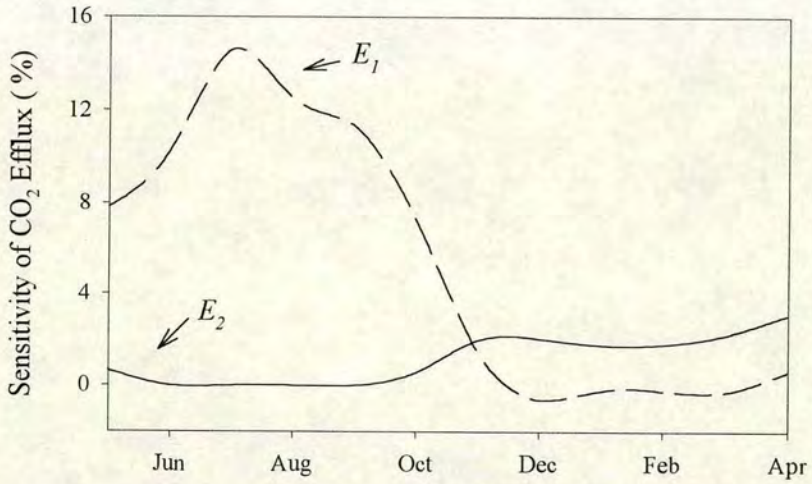


Fig. 4.7 Sensitivity of CO_2 efflux to activation energy in Arrehnius equation. E_1 is the activation energy for soil temperatures > 20 °C and E_2 for temperatures 10 to 20 °C. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

leads to a slight decline in the consequent sensitivity. This phenomenon also applies to variations in other parameters that changes the microbial respiration rate.

The sensitivity of CO_2 efflux to root respiration rate and soil organic matter decomposition rate is shown in Fig. 4.8a. CO_2 efflux is always more sensitive to root respiration rate than to microbial respiration rate, suggesting a larger contribution from root respiration than from organic matter decomposition, and thus can be attributed to differences in spatial distribution of root and organic matter in the soil, the seasonal variation of soil moisture and the yearly pattern of root biomass. In the slash pine plantation, most microbial respiration takes place in the surface layer but root respiration largely occurs in the mineral soil (top 45 cm). When the water table was high, as observed in the field during some summer days, the high soil moisture seriously hindered root respiration in the mineral soil, because of increasing resistance to O_2 and CO_2 transport through the soil, but this was not the case for microbial respiration in the surface layer. On the other hand, higher fine root biomass in the summer months (Fig. 4.2d) increased the sensitivity to root biomass. From September to the end of the year, sensitivities of CO_2 efflux to root and microbial respiration rates show a similar pattern and magnitude, suggesting that there were similar environmental effects on both the litter layer and the mineral soil.

Figure 4.8b shows the sensitivity of CO_2 efflux to soil porosity and the Michaelis-Menten coefficient for O_2 (eq. 4.34). Increasing soil porosity generally increases CO_2 efflux from the soil. The high value of sensitivity of efflux to soil porosity on summer days suggests that the percentage of air-filled soil pore space is a crucial factor controlling soil respiration or CO_2 efflux when the soil is wet. During winter and spring, CO_2 efflux is insensitive to soil porosity.

A 0.7% decrease in annual CO_2 efflux caused by a 5% increase in the Michaelis-Menten constant is quite stable through the year, indicating that the Michaelis-Menten coefficient acts differently from other model parameters and variables, and has a minor impact on CO_2 efflux. This pattern suggests that oxygen concentration in the soil gas is unlikely to be a significant factor limiting soil respiration except when soil moisture content is high.

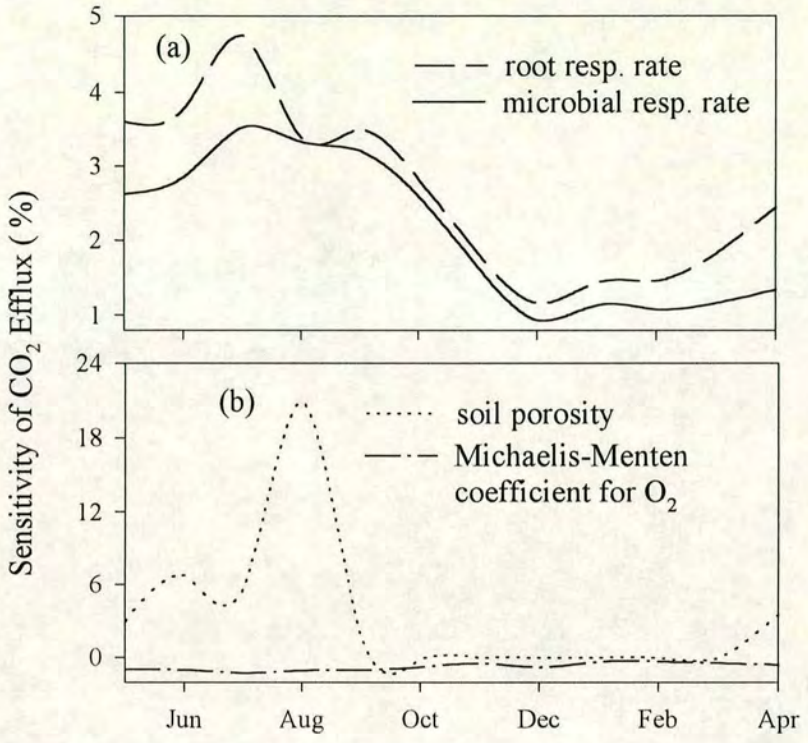


Fig. 4.8 Sensitivity of CO_2 efflux to a 5% increase in some model parameters. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

4.5.2 Sensitivity of annual CO_2 efflux to initial conditions

Table 4.2 lists the sensitivity of soil CO_2 efflux to initial conditions. The highest sensitivity arises from the amount of litter and humus on the forest floor, although only a 1.6% change in CO_2 efflux is induced by a 5% increase in litter amount.

The sensitivity of efflux to the initial amount of organic matter increases during the summer, achieving a maximum in July (Fig. 4.9) when a moderate soil moisture content and high temperature were observed in the field. From August, soil organic matter becomes less important, as reflected by the consistent decrease in the sensitivity.

Table 4.2 Sensitivity of the annual CO_2 efflux to initial conditions

Variable	Initial Value X	δ(Annual CO_2 Efflux), %, Induced by δX= 5%X
mass of organic matter:		
in surface layer	4.79 kg m^{-2}	1.6
in mineral soil *	13.6 kg m^{-2}	0.5
mass of dead root in soil **	421 g m^{-2}	0.2

* in mineral soil of the top 80 cm. ** in both surface layer and mineral soil of the top 80 cm.

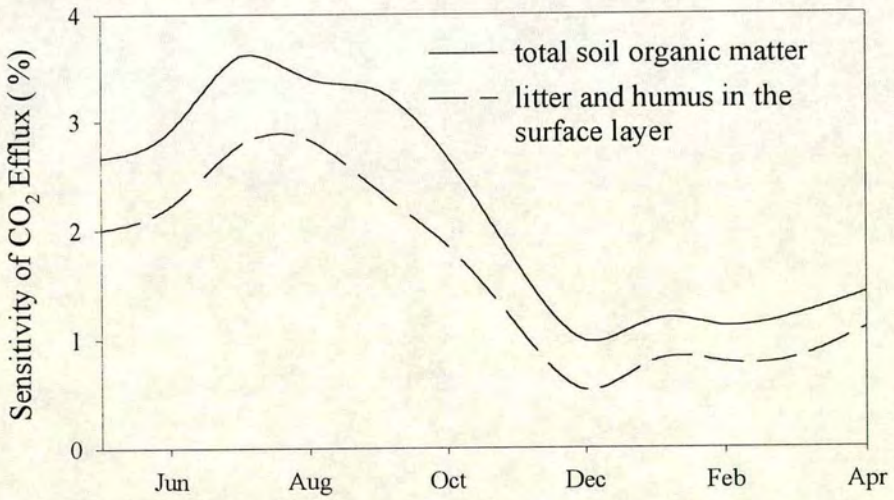


Fig. 4.9 Sensitivity of CO_2 efflux to a 5% increase in soil organic matter content. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

4.5.3 Sensitivity of CO_2 efflux to model inputs

Table 4.3 lists, in order of decreasing importance, the response of CO_2 efflux to increases in soil variables, of 5% of their yearly average, every day from 1 May. CO_2 efflux shows the highest sensitivity to changes in temperature of the surface layer and mineral soil. Temperature on the soil surface has a minor impact on CO_2 efflux. The day-to-day variation of sensitivity to the litter temperature (Fig. 4.10) differs from sensitivity to the mineral soil temperature between March and August, suggesting that something other than temperature is limiting CO_2 efflux. The explanation for this is likely to be similar to that proposed for different sensitivity of the root and microbial

Table 4.3 Sensitivity of the annual CO_2 efflux to a 5% increase in model inputs

Variable X	δ(Annual CO_2 Efflux), %, Induced by $\delta X = 5\%X$
temperature of surface layer (°C)	6.3
temperature of mineral soil (°C)	5.0
moisture in mineral soil	-2.6
live root biomass,< 3 mm	2.4
temperature on the surface (0 cm)	0.6
live root biomass, 3 to 10 mm	0.2
above ground litterfall	0.2
live root biomass , >10 mm	0.2
dead root input	0.2
moisture in forest floor	0.1

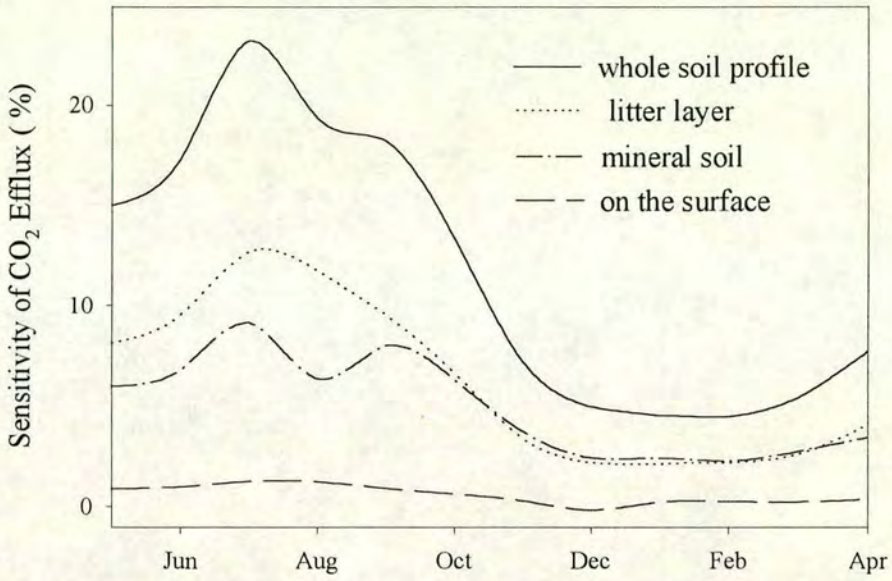


Fig. 4.10 Sensitivity of CO_2 efflux to a 5% increase in soil temperature. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

respiration rates. From May to August, the high soil moisture content hindered respiration in the mineral soil so higher mineral soil temperature is not as effective as higher temperature of litter layer in enhancing CO_2 efflux. From September to March, the temperature sensitivities of forest floor and mineral soil are nearly the same in both magnitude and trend, indicating that environmental differences, affecting CO_2 production and transport, between litter layer and mineral soil have been reduced.

Increasing the moisture content of the mineral soil generally decreases annual CO_2 efflux. There are two different patterns in the yearly sensitivity to mineral soil moisture content (Fig. 4.11). The negative response of CO_2 efflux, from February to September, indicates that soil moisture is higher than optimum for CO_2 transport through the soil. The largest negative sensitivity of efflux in August coincides with the highest water table in the slash pine plantation. During late autumn and winter, the small increase in output of CO_2 from the soil caused by an increase in soil moisture

suggests that soil moisture in winter may be a factor limiting root and microbial respiration.

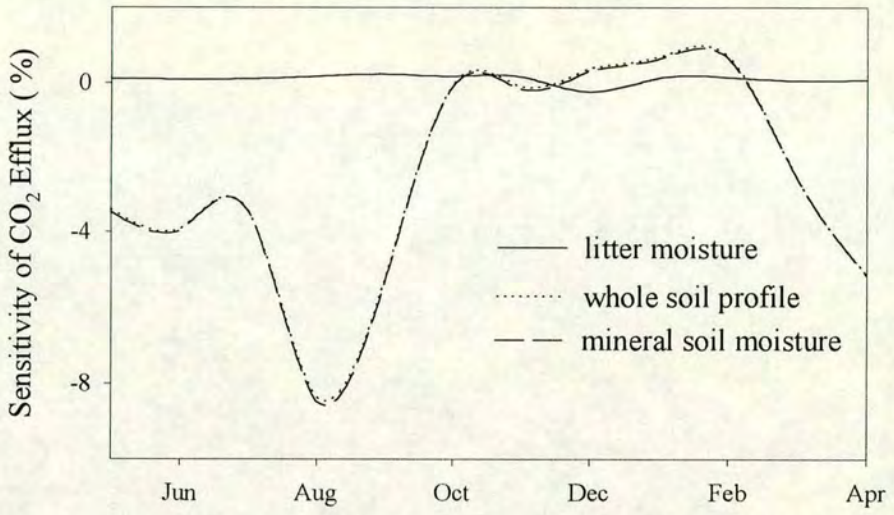


Fig. 4.11 Sensitivity of CO_2 efflux to a 5% increase in soil moisture content. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

Although the surface layer is an important source of CO_2, CO_2 efflux seems to be insensitive to litter moisture through the year, even in winter when relatively low soil moisture may slow down respiration in the mineral soil. Moisture content of the litter layer is unlikely to limit CO_2 diffusion and the lack of sensitivity indicates that the range of moisture contents of litter and humus does not significantly limit soil respiration through the year (Fig. 4.11).

Figure 4.12 illustrates that most of sensitivity of CO_2 efflux to root biomass comes from the contribution of small fine roots (< 3 mm). Compared with the sensitivity to initial organic matter, both have a similar yearly trend but sensitivity to root biomass is more variable during summertime.

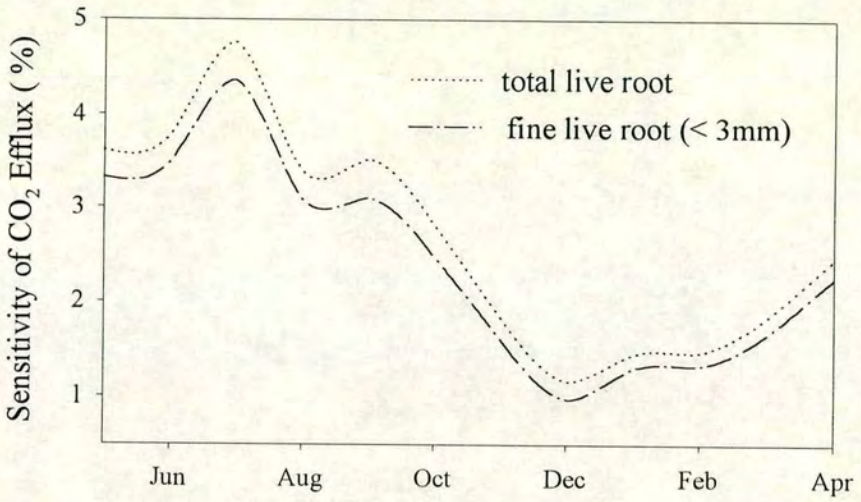


Fig. 4.12 Sensitivity of CO_2 efflux to a 5% increase in root biomass. The sensitivity is expressed as the percentage of yearly average CO_2 efflux.

4.6 Results of Simulation

4.6.1 Seasonal pattern of total CO_2 efflux and soil respiration

Simulated total CO_2 efflux from the soil surface in the slash pine plantation ranges from 0.066 (day 62) to 0.321 mg CO_2 m^{-2} s^{-1} (day 227). Efflux increases from a minimum in March and achieves a maximum between July and September. Two dramatic reductions in CO_2 efflux occur in June and August when a high water table, nearly reaching the soil surface, was observed (Fig. 4.13). The total annual CO_2 efflux is 5136 g CO_2 m^{-2} yr^{-1} or 14.0 ton C ha^{-1} yr^{-1}.

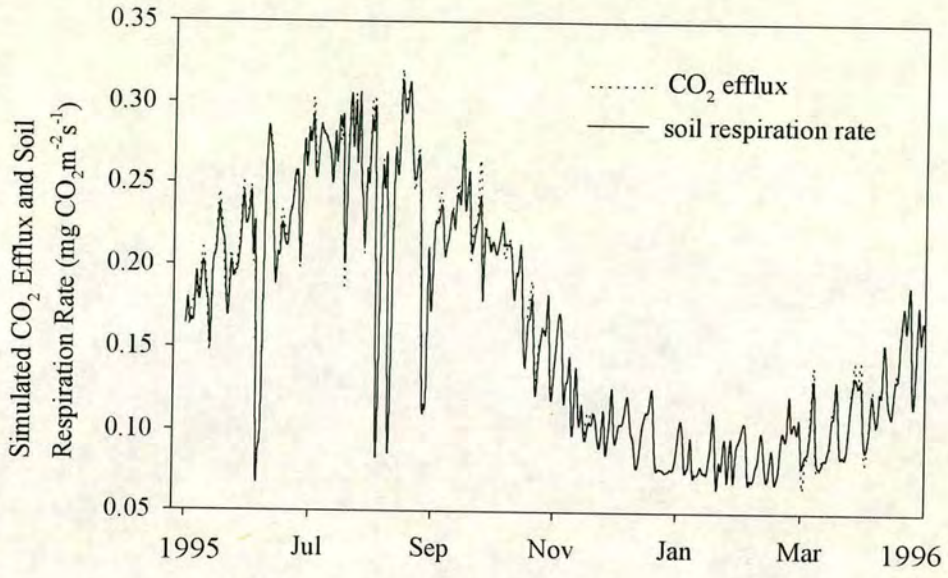


Fig. 4.13 Simulated daily CO_2 efflux from the soil surface and soil respiration rate.

The simulated soil respiration rate, including root and microbial respiration, has a range of 0.066 (day 20) to 0.312 mg CO_2 m^{-2} s^{-1} (day 231) and is very close to the range of CO_2 efflux, with small differences only when sudden day-to-day changes occur. The total CO_2 produced by soil respiration is 5098 g CO_2 m^{-2} yr^{-1} or 13.9 ton C ha^{-1} y^{-1}. The contribution from soil water movement and CO_2 release/absorption by soil water and soil gas is a negligible component of the annual total efflux.

4.6.2 Soil respiration at different depths

Figure 4.14 shows the yearly variation of soil respiration, averaged monthly, at different depths. Most CO_2 is produced in the humus layer (2 - 6 cm) and the top soil (7 - 20 cm), both of which contribute about 32% to the annual efflux. CO_2 fluxes from the litter layer and mineral soil at the lower depths of 21 - 45 and 46 - 100 cm contribute about 10%, 17% and 9%, respectively.

The yearly patterns of respiration in the litter and humus layers are in good

agreement with the variations in soil temperature. During the summer months, most variation in soil respiration occurs in the top mineral soil (7 - 20 cm), and with increase in soil depth the variation in respiration rate is damped. Reductions in CO_2 efflux in June and August are the result of reduced respiration in the mineral soil.

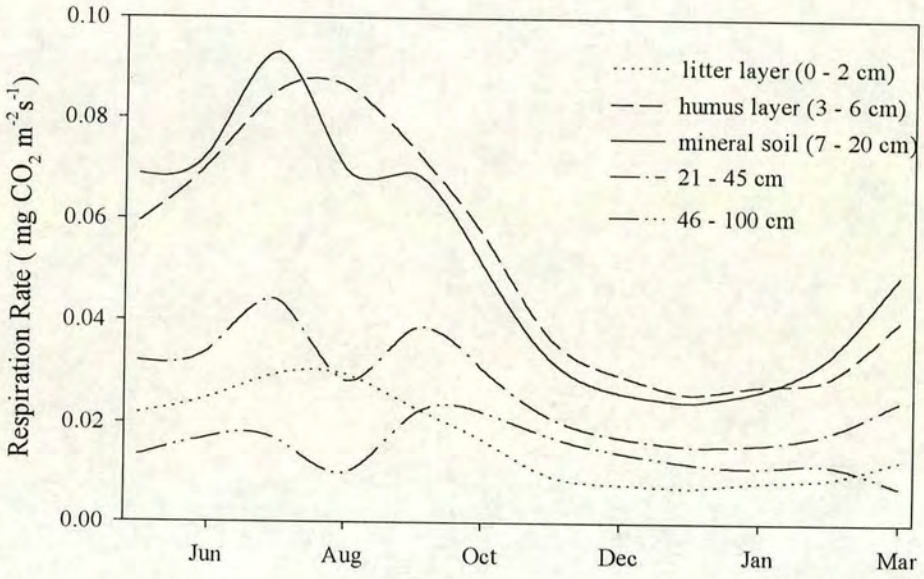


Fig. 4.14 Yearly pattern of soil respiration rate at different depths.

4.6.3 Contribution of roots and microbes to soil respiration

During spring and summer months, root respiration is consistently higher than microbial respiration. When soil saturation takes place in August, root respiration is affected more by the high water content and falls below the rate for microbial respiration. With the soil get drier from September to January, when live root biomass is at its minimum for the year, total soil respiration is evenly split between root and microbial respiration (Fig. 4.15).

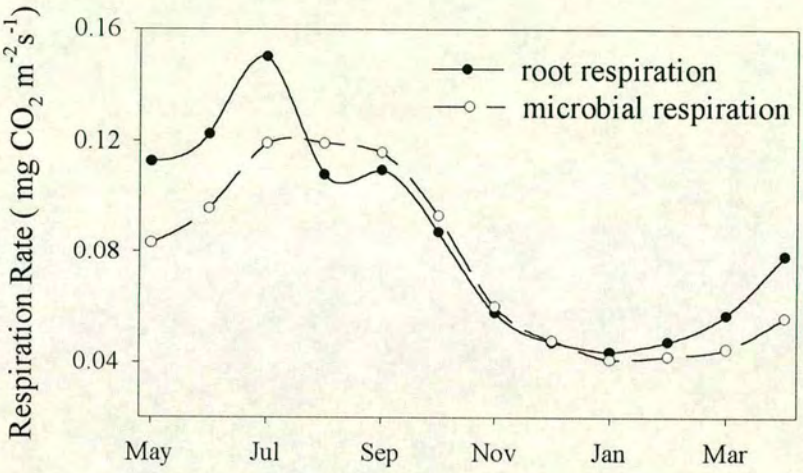


Fig. 4.15 Yearly pattern of contributions from root and microbial respiration.

Table 4.4 Contribution of root and microbial respiration to total soil respiration

Depth in the soil	Root respiration (%)	Microbial respiration (%)
0 - 2 cm	0	10.4
3 - 6 cm	8.3	23.8
7 - 20 cm	27.9	4.0
21 - 45 cm	12.7	3.8
46 - 100 cm	3.8	5.3
Total	52.7	47.3

Integrating the different components of soil respiration at different depths through the year, about 53% of total annual CO_2 produced by soil respiration is attributable to root respiration and the remaining 47% to microbial respiration (Table 4.4). Most of the microbial respiration occurs in the humus layer. Despite the large amount of dead organic matter there in the mineral soil (about 72% of the total soil dead organic matter pool), its decomposition contributes only about 28% to total microbial respiration. The top layer of mineral soil (7 - 20 cm) is the most important layer for root respiration and about 53% of total root respiration takes place there.

4.6.4 CO_2 concentration in soil gas

Simulated CO_2 concentrations in the soil gas at different depths reach maximum values between August and September when daily soil respiration and soil moisture are also at a maximum (Fig. 4.16). During the winter and spring months, CO_2 concentrations at different depths in the soil gas are low and relatively stable.

The CO_2 concentration in the soil increases with depth. The deepest soil always has the highest CO_2 concentration throughout the year and is most variable during summer months. The yearly range of CO_2 concentration is 0.42 to 4.6% by volume at 100 cm but only 0.04 to 0.06% at 2 cm. Although most CO_2 was produced in the upper soil layers (top 20 cm), the CO_2 concentration below 20 cm increased rapidly with depth, as a result of the low effective gas diffusion coefficients in lower soil layers caused by higher moisture contents in those layers.

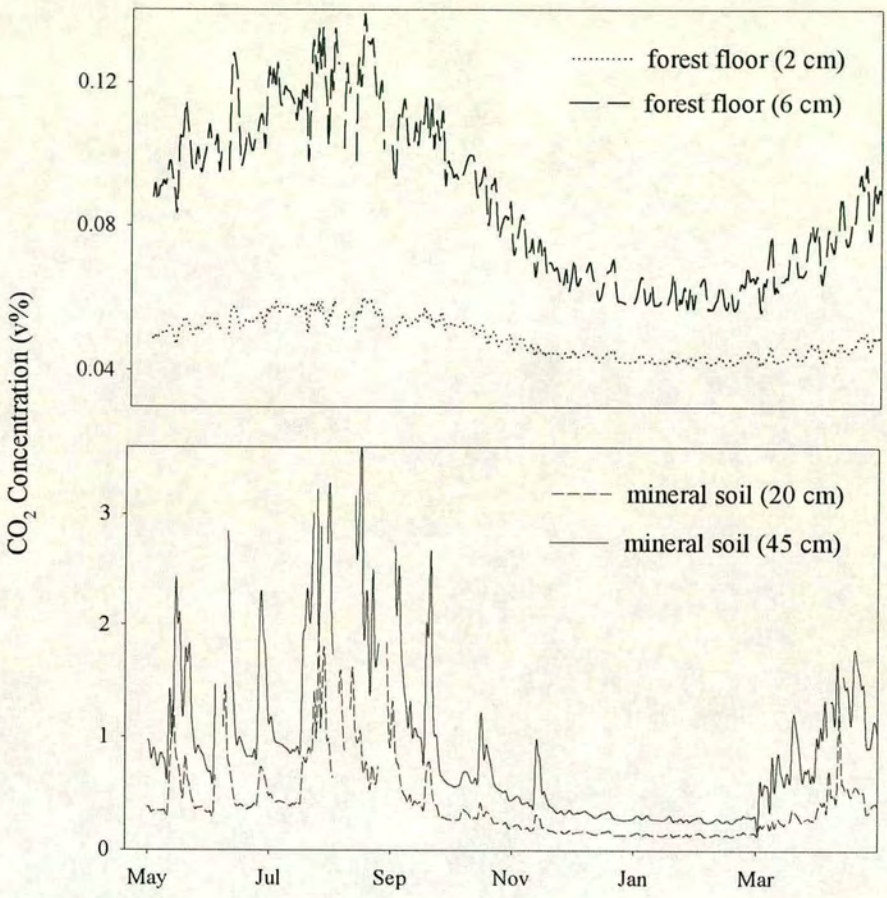


Fig. 4.16 Variation of simulated daily average soil CO_2 concentration at different depths.

4.7 Discussion

4.7.1 The influence of soil moisture on CO_2 efflux

The complexity of the influence of soil moisture on CO_2 efflux has been reported and discussed in many studies (Howard and Howard, 1979; Naganawa *et al.*, 1989). Although it is widely accepted that soil respiration increases with increasing moisture until an optimal moisture content is reached and then decreases with further increase in soil moisture, how to express the response of CO_2 efflux to soil moisture on a sound theoretical basis remains a challenge. In this model, the influence of soil moisture content is considered separately through its limitation on metabolic activity at the low end (eq. 4.33) and on the supply of oxygen affecting gas diffusion (eqs. 4.13 - 4.18 and 4.35) at the high end. In an actual soil profile, the moisture content varies with depth. The limitation on soil metabolic activity can be simply analysed with equation 4.33 and suitable parameters derived for any particular soil layer in which it is assumed there is a uniform moisture content. However, no theory is available which describes the influence of high moisture content on the CO_2 flux from each soil layer as such an influence is dependent on several other factors, such as temperature, soil respiration rate, and environmental conditions in neighbouring layers, etc.. The overall response of CO_2 efflux to soil moisture on one day in Autumn (1/10/1995) is shown in Fig. 4.17 where soil volumetric moisture content is assumed to be constant with depth. CO_2 efflux from the soil surface does not change significantly over the range 15 to 35% and reaches an optimum between 20 to 35%. Soil moisture contents lower than 15% reduce soil respiration rate; soil moisture contents larger than 35% reduce the supply of oxygen to the soil. The shape of the response curve of CO_2 efflux to soil moisture matches with previously accepted theory (Tesaraová and Gloser, 1976; Bosatta, 1980; Schelentner and Van Cleve, 1985; Howard and Howard, 1993; Waelbroeck and Louis, 1995). The optimal range of soil moisture for CO_2 efflux is also in good agreement with other studies (Naganawa *et al.*, 1989; Goto *et al.*, 1994). Linn and Doran (1984) observed that soil,

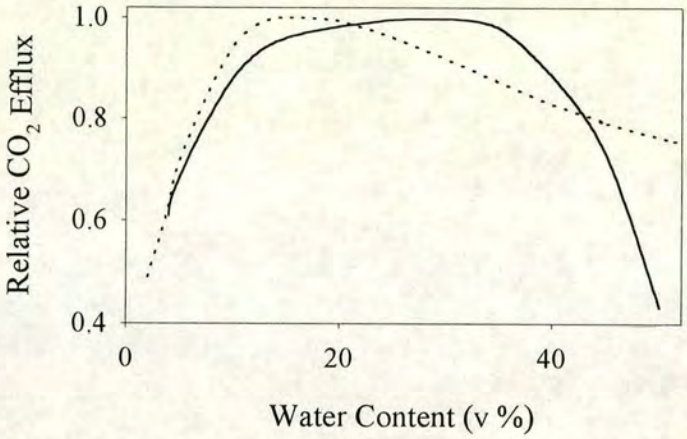


Fig. 4.17 The influence of soil water content on simulated CO_2 efflux from the soil surface: —— this model, ····· from Bunnell's model

incubated in the laboratory with 60% soil pore space filled with water, supported maximum aerobic microbial activities. Below a value of 60%, water limits microbial activity, and above 60% aerobic microbial activity decreases, apparently as a result of reduced aeration. The corresponding value for the slash pine plantation is between 23% and 30% for different layers in the mineral soil. The wider range of optimal soil moisture simulated by this model is understandable given that high soil moisture has little effect on gas diffusion through the litter and humus layers which contribute 42.5% of total annual CO_2 efflux at the slash pine site.

In Bunnell's model, which has used in some recent studies (Kim and Verma, 1992; Bonan, 1995), the influence of water on soil CO_2 efflux was expressed as $\frac{W}{a_1+W}\ \frac{a_2}{a_2+W}$, where W is soil moisture content, a_1, a_2 are parameters with values of half field capacity and half the optimal water content, respectively (following Schlentner and Van Cleve, 1985). A simulation of the influence of soil moisture for the slash pine site at the soil depth of 21 - 45 cm (a_1 = 0.155, a_2 = 0.175) is also

shown in Fig. 4.17. The slow decline of the influence of water content at the high end on CO_2 efflux may not suit most mineral soils. When soil moisture reaches 40% at this depth (when almost all the pore space is filled with water), CO_2 efflux is expected to be significantly reduced but Bunnell's model shows it to be 83% of its optimum. The insensitivity of Bunnell's model to high soil moisture content was also pointed out by Schlentner and Van Cleve (1985). It is also doubtful that the influence of water declines at a moisture content of about 15% when two-thirds of the soil pores are air-filled. As discussed in Chapter one, the reduction in CO_2 efflux by high soil moisture was doubly accounted in Šimunek's model (Šimunek and Suarez, 1993), all this leads to an underestimation of CO_2 efflux in wet soils. The influence of water content on CO_2 efflux (see eq. 1.18) given by Oberbauer *et al.* (1992) is described by a simple shape with different parameters, and may be used in wet soils where soil moisture is always greater than optimum.

A comparison of the parameters used in equation 4.33 with other studies is not possible as no such data have been published. However, the overall response of CO_2 efflux to low soil moisture, which is largely determined by these constants, does suggest that the parameter values chosen for the slash pine plantation give a reasonable estimation of CO_2 efflux dependence on moisture content. The reduction in CO_2 efflux at high soil moisture content is solely the result of the reduced gas diffusion as the value given by equation 4.33 is close to 1 for each soil layer.

4.7.2 Response of soil respiration to O_2 concentration

In the process of soil respiration, oxygen is used both as a terminal electron acceptor and as material in the oxidation of soil organic matter (Glínski and Stepniewski, 1985). The amount of O_2 in the cell where respiration takes place is in equilibrium with the ambient O_2 concentration in the soil gas. The Michaelis-Menten equation is a suitable description for the response of respiration rate to O_2 concentration in soil gas. Šimunek and Suarez (1993) assumed that the decrease in O_2 concentration was compensated for by the increase in CO_2 concentration and used the Michaelis-Menten equation to express the relationship between soil respiration and

CO_2 concentration in the soil gas. The diffusivity of oxygen in the gas phase is about 25% higher than that of CO_2 in standard atmospheric conditions of 273.2 K and 1.013 $\times$ 10^5 Pa (Campbell, 1985), that means the decrease in O_2 concentration does not match the increase in CO_2 concentration. Furthermore, CO_2 is the product of the respiration process rather than a substrate (unlike O_2), so that the Michaelis-Menten equation may not be a proper description for limitation of the respiration rate by CO_2 concentration.

The parameter for O_2 in the Michaelis-Menten equation at which respiration rate is half its maximum is 0.037 m^3 m^{-3} for the whole soil profile in the slash pine plantation, a larger value than the 0.02 m^3 m^{-3} suggested by Glínski and Stepniewski (1985). A higher value of the Michaelis-Menten parameter for the whole soil profile is reasonable given that in bulk soil, because of heterogeneity, the O_2 concentration may be high in some parts whilst low in others.

4.7.3 Diffusion in liquid phase

The contribution from diffusion in the liquid phase to effective gas transport through the soil in this model is assumed to be negligible because of the low diffusivity of CO_2 in water (four orders of magnitude smaller than in the gas phase). This assumption will not cause significant error in the simulation of CO_2 efflux or in the soil CO_2 concentration profile in most conditions of soil moisture. When soil is close to saturation, CO_2 diffusion in the water phase may be important compared with diffusion in the gas phase. Šimunek and Suarez (1993) pointed out that the effective CO_2 diffusivities in both phases are equal when the volumetric air fraction is about 6% of the total porosity. Because the solubility of O_2 in water is low compared with that of CO_2, with a volumetric solubility of 3.16% at 25 °C (CRC, 1992), O_2 diffusion in the water phase will not significantly improve O_2 supply in the soil when it is nearly saturated. Ignoring liquid phase diffusion will not result in any serious error in soil respiration or CO_2 efflux but may lead to overestimation of CO_2 concentration in the soil gas. However, CO_2 concentration was not simulated here for the air-filled soil pore space of less than 6% of the total porosity because the simulated CO_2

concentration is extremely variable because of the very small effective diffusivity.

4.7.4 Relation between respiration of different soil layers

There may be some interaction in respiration between soil layers. A change in respiration rate in one soil layer may cause a change in a neighbouring layer. In this model, it is assumed this interaction is mostly the result of O_2 uptake in the different layers. An increase in respiration in the upper layer consumes more O_2 and results in less O_2 being available for respiration in lower layers. On the other hand, if soil respiration in a lower layer is accelerated, a steeper O_2 gradient through the soil profile will occur in order to supply sufficient O_2 to the soil layer, and thus leads to a lower O_2 concentration and consequent decrease in soil respiration in the upper soil layers. The inter-dependence of soil respiration rates between layers was simulated through a procedure of progressive iteration. Soil respiration in the uppermost layer was simulated firstly using an initial O_2 concentration of 21% at the upper boundary and 0% at the lower boundary. Simulated O_2 concentration at the bottom of the layer was used as an upper boundary condition for next layer, and so on. O_2 concentrations in each layer were then re-evaluated using the first solution and the model was solved again until a satisfactory degree of convergence was obtained for each layer. The simulation for the slash pine site shows that the interaction among different soil layers is not significant when the soil is moderately wet during the winter because soil respiration rates are low and O_2 concentration is unlikely to be a limiting factor then. On the other hand, variation in soil respiration in the upper layers may significantly reduce respiration in the lower layers for a wet soil during the summer when the soil respiratory potential is high because of high soil temperature and O_2 may be insufficient to maintain a maximal respiration in the deep mineral soil.

4.7.5 Temporal variation in CO_2 efflux

Simulated annual CO_2 efflux from the soil surface in the slash pine plantation is 14.0 ton C ha^{-1} yr^{-1}, which is in an agreement with but a little higher than the value

of 13.0 ton C ha^{-1} yr^{-1} estimated by Ewel *et al.* (1987a), using soda-lime absorption corrected with dynamic chamber method through the year, in a similar mature Florida slash pine plantation.

The seasonal pattern of observed CO_2 efflux in Ewel's 29-year-old stand was very similar to the simulation presented here, with two reductions in CO_2 efflux between June/July, and August/September resulting from a temporary high water table following rain. Ewel *et al.* (1987a) pointed out that the decrease in CO_2 efflux during flooded conditions is most likely attributable to the roots, because decomposition rates of litter and the soil organic matter are not likely to respond rapidly, and root respiration is the largest component of the soil CO_2 respiration. This agrees with the simulation in this study (Fig. 4.8a and 4.13). A similar yearly pattern was simulated by Cropper and Gholz (1993) but the decline of CO_2 efflux in summer months did not occur because soil moisture was not included in their simulation.

In other forest ecosystems at a similar latitude (30 to 35° N), soil CO_2 efflux was reported to be 9.9 to 12.6 ton C ha^{-1} yr^{-1} in *Pinus densiflora* (Nakane *et al.* 1984); 5.1 in *Pinus palustris* (Reinke *et al.*, 1981); 11.3 in mixed *Quercus* forest (Yoneda and Kirita, 1978); and 5.2 in *Pinus Roxburghii* (Rout and Gupta, 1989). The simulated value of annual CO_2 efflux in the slash pine plantation reported here seems higher than these measured values in other ecosystems. Ewel *et al.* (1987a) also pointed out that CO_2 efflux in slash pine plantations is rapid compared with both measured and predicted values for other temperate forests. Raich and Schlesinger (1992) compiled much published data for CO_2 efflux and these also indicated that the soil under slash pine has a high respiration rate. It is an interesting question as to the causes responsible for the high soil respiration rate in slash pine plantations. Rapid efflux is thought unlikely to be caused by large amounts of soil organic matter (Ewel *et al.*, 1987a), as this is in the range summarised globally by Schlesinger (1977), or by a high decomposition rate of soil organic matter, as this is slower in Florida slash pine plantations compared with other ecosystems (Gholz *et al.*, 1985). The root respiration rate is also in the range reported for various ecosystems (see Cropper and Gholz, 1991). Some explanation for the high CO_2 efflux measured in Florida slash pine plantations may be: 1) different techniques used which may overestimate or

underestimate the CO_2 efflux; 2) mild temperature and moderate soil moisture in winter in Florida, which could maintain a considerable respiration rate; 3) roots of palmetto may have a an exceptionally higher respiration rate, which has not been measured. The high soil CO_2 efflux in the Florida slash pine ecosystem does warrant further investigation.

Residual analysis shows a larger discrepancy between simulated and measured CO_2 effluxes in the slash pine site at midday and midnight, but the magnitude of the discrepancy is small and there is no consistent trend. However, this larger discrepancy at midday and midnight suggests that there may be a daily course of root and microbial activity which was not included in the model. Huck *et al.* (1962) reported that the respiration rate of intact roots was 25 to 50% higher in daytime than during the night under conditions of constant temperature and humidity in the laboratory. When light was also constant, no consistently higher respiration rate was found in daytime. Holthausen and Caldwell (1980) also found higher root respiration rates during summer and lower rates at other times. Such evidence suggests that the variation in plant photosynthetic rate, and consequent transfer of carbohydrate from above ground parts to roots, may be a factor affecting the temporal pattern of root respiration. It is not yet clear whether there is a time-dependence of microbial respiration although no such dependence was found in incubations by Huntjens (1979). Time-dependence of soil respiration is not included in the model on the assumption that such dependence for trees is not likely to be as significant as for herbaceous plants because large parts of a tree are structural tissues rather than functional tissues as in herbaceous plants. The small residual between simulated and measured CO_2 effluxes in the slash pine site suggests that this assumption is reasonable.

4.7.6 Turnover rate of soil organic matter

Optimal decomposition rates, defining the decomposition potential of organic matter at 10 °C, are simulated to be 3.85×10^{-6}, 3.73×10^{-7}, 6.22×10^{-6} mg CO_2 g (dry mass) s^{-1} for litter and humus on the forest floor, resistant organic matter in the

mineral soil and dead fine roots (< 3 mm), respectively. Direct comparison of these values with other studies is difficult as they are a decomposition potential rather than the actual observed decomposition rates of soil organic matter.

The simulated annual turnover rate is 21% per year for litter and humus in the surface layer. Observed dry mass loss of needle litter of slash pine was reported to be 15% per year measured *in situ* with a litter bag technique (Gholz *et al.*, 1985 ; Gholz *et al.*, 1986), although this is relatively slow compared with other ecosystems in a warm temperate climate with plentiful rainfall (Gholz and Fisher, 1984; Gholz *et al.*, 1985). The decomposition rate of conifer needles varies between 15 to 70% per year (see Enríquez *et al.*, 1993). Loss of litter and humus in the surface layer was simulated to be between 954 to 1027 g (dry mass) m^{-2} yr^{-1}, assuming a C portion of 0.47 to 0.5. The simulated value agrees with measured annual input of litterfall, of 989 g m^{-2}, estimated from collected pine litter, above ground biomass of palmetto and herbs (Gholz, 1996, *pers. comm.*) and the fine root detritus in the humus layer. Because of the lack of litterfall data over a longer period at the site, it could not be confidently argued that the organic matter in the surface layer had reached dynamic equilibrium. Observations on litterfall (Gholz *et al.*, 1985) and soil respiration in the surface layer (Ewel *et al.*, 1987b) do suggest that a steady state was reached about 30 years after the trees were planted, but Gholz and Fisher (1982) reported that the forest floor was still accumulating organic matter after about 35 years.

Simulated organic matter turnover rates in the mineral soil were about 2.3% per year and lie in the middle of the range of other estimated values of 1.9-2.8% per year for mature stands (Gholz *et al.*, 1986). Annual loss of organic matter in the mineral soil is 367-390 g m^{-2} yr^{-1} and total below ground detritus in the mineral soil is estimated at 230 g m^{-2} yr^{-1}. On the assumption that the transport of organic matter from the forest floor to the mineral soil is negligible, the mineral soil at this stage is still losing mass which was buried in previous clear-cutting, and this is supported by observations of soil organic matter dynamics with stand age: mineral soil in a Florida slash pine plantation consistently lost organic matter up to and over 26 years (Gholz and Fisher, 1982).

To simulate the decomposition of dead roots, it was assumed that the

decomposition rate of dead roots (> 3 mm) equalled that for litter and humus on the forest floor. Dead fine roots of 2 to 5 mm diameter were found to have a turnover rate of 15.8 ± 0.4% per year (Gholz *et al.*, 1986), close to that for pine wood (15% per year, Gholz *et al.*, 1991a) and needle litter, coheres small fine roots (< 2 mm) were reported to have a higher decay rate of 20.0 ± 0.9% per year. The ratio of decay rates of small fine root detritus to needle litter was then 1.33 from these measured values. A higher ratio, 1.61, was simulated here.

4.7.7 Root respiration rate

Simulated fine root (< 3 mm) optimal respiration rate at 10 °C is 4.30×10^{-5} mg CO_2 g^{-1} s^{-1} for slash pine. The respiration rate of fine roots (most less than 2 mm in diameter) extracted from the forest floor in a Florida slash pine plantation was 1.08×10^{-4} mg CO_2 g^{-1} s^{-1} at 20 °C with a Q_{10} of 1.94 (Cropper and Gholz, 1991). Thus, the measured value was about 25% higher than the simulated respiration rate in this study but the values are close given that tissue can be damaged by removing and preparing fine root samples and thus probably have increased root respiration, especially in short-duration measurements (Edwards and Harris, 1977; Chapman, 1979).

Using the values of optimal root respiration rate listed in Table 4.1, the simulated respiration rate is 1.92 g (dry mass) g^{-1} (dry mass) yr^{-1} for fine root (< 3 mm) in litter and humus layer, and 0.36 for all roots in the mineral soil. Based on litter removal and trenched plot experiments in a similar slash pine plantation in Florida, Ewel *et al.* (1987b) estimated fine root (< 10 mm) respiration at about 1.7 g (dry mass) g^{-1} (dry mass) yr^{-1} for the surface layer and averaged all root respiration at 0.34 for the mineral soil. The higher simulated root respiration rate in the surface layer may be because of the different root size categories used: smaller roots are expected to have high metabolic activity (Chapman, 1979).

4.7.8 Root : microbial contribution

In a 29-year-old slash pine plantation, Ewel *et al.* (1987b) estimated that 62% of the annual CO_2 efflux from the soil surface could be attributed to root respiration and the remaining 38% to microbial decomposition of organic matter; corresponding values were 51% and 49% for a 9-year-old plantation. The simulated values (53% root respiration, 47% microbial respiration) give more weight to microbial respiration and are closer to the measured values for the younger stand. The relative contributions from root and microbial respiration are influenced by many factors and vary from stand to stand and with different measuring methods. The ratio of root respiration to total soil respiration has been reported to vary from 22 to 50% for various forests in different climates (Edwards and Harris, 1977; Nakane, 1980; Nakane *et al.*, 1983; Behera, 1990; Bowden *et al.*, 1993). Nakane *et al.* (1983) pointed out that when a forest ecosystem is in equilibrium, root respiration will contribute about 50% of total soil respiration regardless of forest type, and this agrees with the simulated value presented here. Ewel's estimate for the root contribution is actually higher than most reported values for other forest ecosystems, except for the large contributions of root respiration reported in heathland (70%, Chapman, 1979) and in a deciduous forest (90%, Thierron and Laudelout, 1996).

4.7.9 CO_2 concentration in soil gas

The simulated soil CO_2 profile matches most measured and predicted soil CO_2 concentrations published elsewhere. The CO_2 concentration in forest soils was reported to have a maximum of 0.55% at depths below 8 cm (Crill, 1991); 0.6% at 10 cm (Castelle and Galloway, 1990); 3% (Cosby *et al.*, 1985); 1.2% at 10 cm (Fernandez and Kosina, 1987) and 1.95% at 20 cm in a northern hardwood ecosystem (Yavitt *et al.* 1995). In other soils, CO_2 concentration was reported to vary between 0.5 to 7% (Buyanovsky and Warner, 1983) or 0.1 to 0.7% (Nakayama and Kimball, 1988, Osozawa and Hasegawa, 1995) for agricultural soils at 20 cm.

The modelled soil CO_2 concentration was controlled both by soil temperature

and moisture. The yearly pattern of soil CO_2 concentration (Fig. 4.16) follows that of soil temperature, indicating that temperature is the dominant factor governing soil CO_2 through the year. This is in agreement with field observations (Buyanovsky and Wagner, 1983; Fernandez *et al.*, 1993; Nakayama *et al.*, 1994).

The simulation indicates that CO_2 concentration in the soil gas increases with depth through the year, the highest concentration being at 100 cm. A different pattern was simulated by Suarez and Šimunek (1993), and Wood *et al.* (1993), with a maximum at a certain depth in the soil following by a decrease with further increase in depth. More complex CO_2 profiles are possible when there is a sink or a locally strong source of CO_2 in the soil as has been observed in some farmland soils (De Jong and Schappert, 1972; Buyanovsky and Wagner, 1983) or grassland soils (Wood *et al.*, 1993). A rapid increase in respiration in the upper soil, as a result of rising temperature and seasonal variation of root metabolic activity, may result in an inverted CO_2 profile for a short period. A temporary inverted CO_2 profile may also caused by heavy rainfall (Osozawa and Hasegawa, 1995) or by a very low CO_2 production rate in the lower layers (Hendry *et al.*, 1993; Wood *et al.*, 1993). At the site used here, a dramatic increase in root metabolic activity is unlikely and soil temperature is mild in winter. However, a low CO_2 concentration is possible deep in the soil where CO_2 production rate is nearly zero but this was not simulated in this study. The influence of rainfall on soil CO_2 concentration was not included in the simulation because the water table height cannot respond quickly to changes in moisture in the upper soil. Our simulated soil CO_2 profile is supported by most field measurements in various forests (Yoneda and Kirita, 1978; Fernandez and Kosina, 1987; Castelle and Galloway, 1990; Crill, 1991). Even in an agricultural soil, CO_2 has been observed always to increase with depth through the year (Nakayama and Kimball, 1988, Osozawa and Hasegawa, 1995).

It is assumed in the model that the CO_2 concentration in soil water is always in equilibrium with the ambient soil gas. This is an acceptable hypothesis except in very wet soils where the equilibration between a small volume of gas phase and a large volume of water phase takes an appreciable time because of the small diffusion coefficient of CO_2 in water. A downward flux of water will bring water with a low

CO_2 concentration from the upper to the lower soil layers, whereas an upward water movement will take CO_2 to shallower soil layers. A flux of water, whether upward or downward, will increase CO_2 transport from lower soil layers to upper soil layers. If we do not consider the locally high soil moisture in upper soil layers associated with a downward water flux, a reversed CO_2 profile is unlikely to be caused by water movement as suggested by Suarez and Šimunek (1993).

4.7.10 Response of CO_2 efflux to climate change

Global climate models predict an average annual mean increase in global air temperature of 1.3 to 2.3 °C for a doubling of atmospheric CO_2 (IPCC, 1995). If the increase in air temperature is translated into higher soil temperature, CO_2 efflux from the soil can be expected an increase as a response of the ecosystem to increased temperature and associated climate changes. To estimate this response, one needs to know the likely variations in other climate factors as well as biological inputs governing soil respiration and transport through the soil. However, sensitivity analysis of the model with respect to soil temperature is helpful for us to understand the potential impact of global warming. The response of annual soil CO_2 efflux in slash pine ecosystem to a 1.3 °C increase in soil temperature applied every day during the year for 10 years is shown in Fig. 4.18b. Annual CO_2 efflux increases by 14% at the beginning and declines eventually, because of the consumption of the soil organic pool, to 8.6% above that in current conditions (Fig. 4.18a) in the tenth year. The average increase in CO_2 efflux is 10.4% over 10 years and the soil organic matter pool is reduced by about 6 ton C ha^{-1} by the end of the period.

It is reasonable to expect some changes in the net primary production of an ecosystem as a response to CO_2 doubling, and this is supported by a number of short term experiments on the influence of elevated CO_2 concentration on trees. Root biomass was found to increase by about 30% (Conroy *et al.*, 1990; Vose *et al.*, 1995) to 65% (Morgan *et al.*, 1994) with doubling CO_2 treatments. Total biomass increased from about 14% (Mousseau and Sangier, 1992), 20% (Conroy *et al.*, 1990; Jones *et al.*, 1996) to 35% (Morgan *et al.*, 1994) as a result of doubling CO_2 concentration.

We assume that an increase of 20% in net primary production and 30% in root biomass are appropriate for forest ecosystems in doubled atmospheric CO_2 concentration, and that the increase in net primary production will include a similar

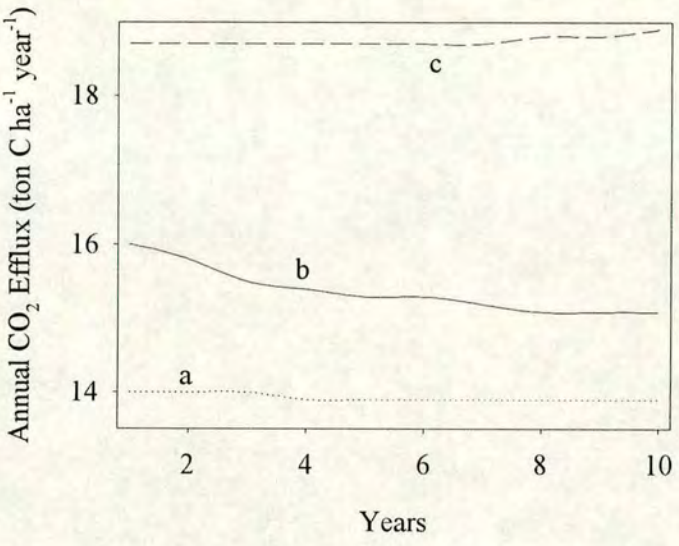


Fig. 4.18 Modelled potential response of annual CO_2 efflux from the soil in a slash pine plantation to global warming caused by CO_2 doubling: **a)** present conditions; **b)** + 1.3 °C only, evenly applied to different depths during the year; **c)** +1.3 °C, +20% increase in litterfall and +30% increase in root biomass, and evenly applied.

proportional increase in annual litterfall, e.g. a 20% increase over the current litterfall rate on each day during the year. On the basis of these assumptions, the annual soil CO_2 efflux in the Florida slash pine plantation will increase by about 35%, to *ca* 18.8 ton C ha^{-1} yr^{-1} (Fig. 4.18c). It is interesting that in this case, the soil organic matter pool will not change significantly in the future conditions, although CO_2 efflux increases greatly. However, because little is known about the potential response of tree growth and C allocation with respect to climate change, rather than merely to elevated CO_2 concentration as in most current field experiments, any further

speculation is not warranted. More and longer field experiments and large scale simulation for various climate conditions are needed to determine the potential response of soil respiration and the carbon pool to future climate change.

4.7.11 Model limitation and applicability

Although application of the model to a nearly saturated soil was reasonable, there is limited confidence in the accuracy of the simulated CO_2 efflux when the soil is very wet. The respiratory quotient (RQ) was set to equal unity in the numerical solution. This assumption is doubtful when soil is very wet. Bridge and Rixon (1976) reported that the RQ is greater than unity when the soil air-filled pore space is less than 0.1 cm^3 cm^{-3} and suggested 0.1 cm^3 cm^{-3} as an index for aerobic and anaerobic conditions in the soil. Linn and Doran (1984) found the soil respiration rate was at a maximum when the percentage of soil pores filled by water (WFP) was 60% and decreased with further increase in moisture; the rate of oxygen uptake in the soil was higher than that of CO_2 release at 70% WFP. According to their measurements, the respiratory quotient will be larger than unity when soil volumetric moisture is 0.34 - 0.40 for the 7 to 20 cm layer and 0.29 for the 21 to 45 cm layer in the slash pine plantation. When soil moisture is higher than these critical values the assumption of RQ =1 leads to an error in estimating the CO_2 efflux.

Another source of error when applying this model to wet soil is the assumption that soil respiration rate is zero when the soil is saturated (i.e. the air-filled soil pore space < 1% of the volume of bulk soil). However, CO_2 production does not completely stop under anaerobic conditions although the absolute magnitude of the respiration rate is small. The anoxic respiration rate (as CO_2 production) was constant at about 10% to 40% of aerobic respiration when measured in the laboratory (Gale and Gilmour, 1988; Bridgham and Richardson, 1992; Magnusson, 1993).

In the simulation, the input of soil moisture was estimated by water table height through the year. It is easy to monitor the water table continuously in the field and it did provide a reasonable estimate of soil moisture for most of the year. The disadvantages of this approach are several: moisture content in the litter layer is not

closely related to the water table height; the change of moisture in the upper soil layer from rain cannot alter quickly, and may not be reflected by a change in water table height; and when the soil is dry, the water table may be too deep to be recorded. Although these inaccuracies in estimation of soil moisture content did not produce a serious error in the annual CO_2 efflux in the slash pine plantation, as shown by the sensitivity analysis, they restrict model performance when soil moisture is changing during rain.

The inhibition effect of CO_2 concentration on soil respiration is not included in this model. Carbon dioxide has an inhibitory effect on the respiration of plant tissues, but this is only pronounced at high CO_2 concentration (Glínski and Stepniewski, 1985). MacFadyen (1973) found an inhibitory effect at concentrations below 1% CO_2 in a sandy soil but he also pointed out that such inhibition did not occur below a concentration of 10% CO_2 in soils from other sources. Qi *et al.* (1994) recently reported that soil basal and root respiration rates are exponentially related to CO_2 concentration when soil CO_2 concentration varied from about 100 to 7000 cm^3 m^{-3}. This implies that soil respiration rate is only sensitive to CO_2 concentration when CO_2 concentration is low, e.g. less than 2000 cm^3 m^{-3}. It remains unclear how root and microbial respiration rates relate to CO_2 concentration and just what the mechanism of this inhibition is. Generally, soil respiration rate in the slash pine site may have been somewhat overestimated as a result of neglecting the inhibitory effect of CO_2 concentration during summer days when very high CO_2 concentrations occurred in the deep soil layers (45 to 100 cm) (Fig. 4. 16).

It is recommended that the model presented here is not used for very dry or very wet soils. This is a common feature of other published soil respiration models.

4.8 Future Work

— Incorporating a detailed submodel for water movement in the soil.

In the model, water movement in the soil is simplified, using fixed rates of water transpiration for summer and on other days, splitting the total transpired water

between root uptake and soil evaporation, with soil evaporation only occurring at the soil surface. These simplifications will not have significant effects on the simulation of annual CO_2 efflux, but may result in errors under some conditions, e.g. a lower transpiration rate is expected when the soil is dry and the error in estimating soil moisture content from a fixed transpiration rate may cause a considerable error in the estimation of CO_2 efflux. A more sophisticated submodel which accounts for soil water movement and variation in moisture content may improve model performance in some weather conditions.

— Model scaling up

The model in this study has a time step of one hour or one day and assumes a spatial scale of a stand with a uniform structure. Scaling up this model to larger spatial and longer temporal scales will not change the major processes which control CO_2 production and transport in the soil. However, some properties of the model are expected to change at larger scales. For example, the respiration rate of roots and microorganisms and their inter-relationships may be different at different developmental stages of an ecosystem. A change in the contribution of root respiration to total soil respiration with stand age has been observed in some forest ecosystems (Nakane *et al.*, 1984; Ewel *et al.* 1887a), possibly caused by changes in the microflora, accumulation of the soil C pool, and variation of root metabolic activity. Other difficulties include linking climate variables evaluated for longer time scales, such as a month or a year, with the processes governing CO_2 efflux, and finding the most important processes and variables controlling soil respiration and CO_2 transport at ecosystem or regional scale. Kicklighter *et al.* (1994), for example, used mean monthly air temperature to simulate regional CO_2 effluxes from temperate forest soils. It is a challenge to scale up the model with no loss of its theoretical rigour.

— Combining the model with an aboveground model to give an overall estimation of CO_2 exchange between an ecosystem and atmosphere.

There are many models for estimating above ground gas and water vapour exchange, production and C dynamics within a terrestrial ecosystem. For example, the MAESTRO model, developed by Wang and Jarvis (1990), identified the significant properties of crown structure and predicted hourly and daily radiation absorption, photosynthesis and transpiration by an individual tree or by a stand. Primary production and carbon allocation among above-ground and below-ground components for a slash pine plantation were simulated by Ewel and Gholz (1991). Canopy photosynthesis has been linked to the Rothamsted soil carbon model to estimate carbon balance of terrestrial ecosystems (Wang and Polglase, 1995). However, most of such models deal with carbon assimilation, allocation and transition above-ground but do not deal with all the processes of CO_2 exchange between atmosphere, above ground canopy and the below ground component of the system..

It is the ecosystem as a whole, not merely the above-ground or below-ground parts that we are interested in. Combining the soil CO_2 efflux model presented here with above-ground models will enhance our understanding of carbon dynamics in an ecosystem and the function of an ecosystem as a whole in the global C cycle and climate change. In this model, CO_2 and O_2 concentration in the air and at the soil surface, litterfall and carbohydrate transferred from above ground to roots, rainfall, soil moisture and temperature were used as model inputs or boundary conditions, and these can be provided or simulated by some above-ground models. The output of this model, CO_2 efflux, also acts as an input for an above-ground model. Although there are some uncertainties, such as fine root turnover, the transport of carbohydrate from leaves to roots, building an integrated atmosphere-canopy-soil model for gas exchange and carbon dynamics is possible.

4.9 Summary and Conclusions

Based on processes of root and microbial respiration and CO_2 transport through the soil, a one-dimensional model was developed to predict CO_2 efflux from the soil surface and the spatial distribution of CO_2 in the soil. In this model, gaseous

diffusion and liquid phase dispersion were taken as major mechanisms governing the transport of CO_2. The submodel for CO_2 production in the soil was built on a number of assumptions:

- there is no direct interaction between root and microbial respiration;
- any environmental factor works on the effects of other factors;
- soil temperature, moisture and O_2 concentration in soil gas are considered as the most important environmental factors which influence equally on root and microbial respiration;
- the influence of soil moisture content on CO_2 efflux is considered separately through its limitation on biological activity at the low end and its restriction on gas diffusion at the high end;
- the interactions between root and microbial respiration in different soil layers are determined by their relation to oxygen concentration in the soil gas, whose influence on respiration is described by the Michaelis-Menten equation.

The model was validated with data collected in a mature slash pine plantation in Florida. Model sensitivity analysis showed that CO_2 efflux in the slash pine plantation is most sensitive to soil temperature and associated parameters. Moisture content in the mineral soil had a large negative effect on CO_2 efflux in summer and autumn but a small positive one in winter. The sensitivity of CO_2 efflux to root biomass was generally larger than to the amount of soil organic matter.

The model successfully simulated CO_2 efflux from the soil and its temporal variation over the period May, 1995-April, 1996. Annual CO_2 efflux was simulated to be 5136 g CO_2 m^{-2} yr^{-1} or 14 ton C ha^{-1} y^{r-1}. The CO_2 efflux varied between 0.066 to 0.321 mg CO_2 $m^{-2}s^{-1}$ during the year. Soil respiration, including root and microbial respiration, was simulated annually producing 5098 g CO_2 m^{-2} yr^{-1} or 13.9 ton C ha^{-1} y^{r-1} with a range of 0. 0.066 to 0.312 mg CO_2 m^{-2} s^{-1}. Of the total CO_2 released from the soil surface, about 53% come from live root respiration and 47% from decomposition of organic matter. Most CO_2 is produced in the surface layer on the forest floor and the top 15 cm of mineral soil, with contributions of about 43% and 32% of the total annual efflux, respectively. In the simulated slash pine ecosystem,

most microbial respiration takes place in the litter and humus layers, with a contribution of 72% to the total microbial respiration.

Simulated CO_2 concentrations in the soil gas varied with depth and from time to time. The soil CO_2 concentration reached maximal values in summer when soil respiration was its maximum and soil moisture at its yearly peak, with a range of 0.42 to 4.6% at a depth of 100 cm, and 0.04 to 0.06% at 2 cm through the year.

CHAPTER 5: SUMMARY AND FINAL CONCLUSIONS

The method to measure CO_2 efflux

An open-top dynamic chamber was developed to measure CO_2 efflux, and the influence of pressure difference on measured CO_2 efflux is negligible with this new chamber. The quick and sensitive response of the measuring system with this chamber allows it to be used to investigate both temporal and spatial variations in CO_2 efflux.

For a dynamic chamber technique, the measured CO_2 efflux is extremely sensitive to the pressure difference between inside and outside the chamber, as even a change in the pressure difference of a few tenths of a Pa causes a several fold variation in measured efflux. This error is also related to the type of soil being measured, as a pressure difference will cause a serious over- or under-estimation of the CO_2 efflux in a soil with a high respiration rate and large porosity.

Flow rates up to 8 $dm^3\ min^{-1}$ in this chamber do not influence the measured CO_2 efflux provided the pressure difference is constant.

The CO_2 efflux in the slash pine plantation—temporal and spatial variation

The daily average CO_2 efflux in a slash pine plantation in Florida was found to be 0.217 mg $CO_2\ m^{-2}\ s^{-1}$ (varying between 0.179 to 0.253) in the autumn of 1995, and 0.087 mg $CO_2\ m^{-2}\ s^{-1}$ (varying between 0.031 to 0.146) during the winter.

Soil temperature is by far the most influential factor controlling the CO_2 efflux. About 90% of the variability in hourly values of CO_2 efflux could be accounted for by the variation in soil temperature alone when the field data are fitted to a Q_{10} or an Arrhenius model.

The CO_2 efflux in the slash pine plantation was highly heterogeneous spatially. Understorey plants, mostly palmetto, were a major contributor to the spatial pattern of CO_2 efflux in the plantation as they increased the litterfall input and thus changed the soil properties.

The spatial variation in CO_2 efflux can be determined by the variation in the environmental factors to which soil respiration is directly related. In the slash pine

site, CO_2 efflux generally increases with increase in soil fine root biomass, litter and humus amount in the surface layer on the forest floor but is inversely related to the amount of organic matter in the mineral soil. Most of the spatial variability in CO_2 efflux can be explained well by a simple model which incorporates live and dead biomass and associated soil total porosity.

Process-based model for CO_2 efflux and soil respiration—model structure

Based on processes of root and microbial respiration and CO_2 transport through the soil, a one-dimensional model was developed to predict CO_2 efflux from soil surfaces, microbial and root respiration and the spatial distribution of CO_2 in soils. In this model, gaseous diffusion and liquid phase dispersion were taken as major mechanisms governing the transport of CO_2. The submodel for CO_2 production in the soil was built on some assumptions which differ from those in previous published models:

- besides soil temperature and moisture content, O_2 concentration in the gas phase is also one of the most important environmental factors;
- soil moisture content affects CO_2 evolution through its limitation of metabolic activity at the low end and its restriction of gas transport through the soil at the high end;
- the interactions between root and microbial respiration in different soil layers are determined by their relations to the oxygen concentration in the soil gas, the influence of which can be described by the Michaelis-Menten equation

Sensitivity analysis of the model and simulation in the slash pine plantation

Sensitivity analysis of the model showed that CO_2 evolution in the slash pine plantation is most sensitive to soil temperature and associated model parameters. Increase in moisture content in the mineral soil will inhibit both CO_2 production and transport in the soil during summer and autumn when soil is wet, and will enhance soil respiratory activity in the winter when the soil has a moderate to low moisture content.

Annual CO_2 efflux in the slash pine plantation was simulated to be about 5.1 kg CO_2 m^{-2} yr^{-1} and the efflux varied between 0.066 to 0.321 mg CO_2 m^{-2} s^{-1} during the year. Soil respiration, including root and microbial respiration, was simulated to be about 5.1 kg CO_2 m^{-2} yr^{-1} with a range of 0. 0.066 to 0.312 mg CO_2 m^{-2} s^{-1}.

Of the total CO_2 released from the soil surface, about 53% comes from live root respiration and 47% from decomposition of organic matter. Most CO_2 is produced in the litter and humus surface layer and the top 15 cm of the soil, with contributions of 43% and 32% of the total annual efflux, respectively.

CO_2 concentrations in the soil gas were simulated to increase with depth, with ranges of 0.42% to 4.6% by volume at 100 cm, and 0.04% to 0.06% at 2 cm through the year.

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APPENDIX

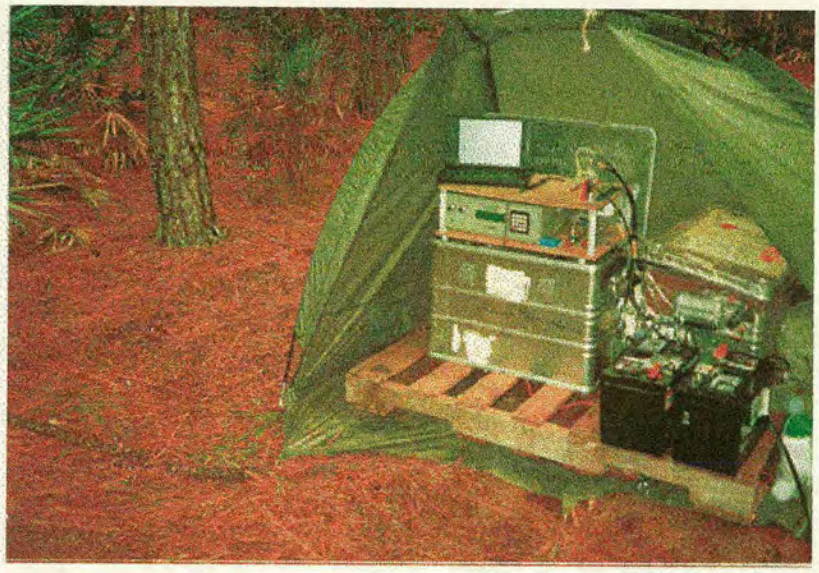
A.1 Photographs about Florida slash pine site and the equipment used in the field.

Picture 1: A thick layer of litter and humus evenly distributes on the forest floor in the slash pine plantation, Florida and the open floor is relative uniform.

Picture 2: Palmetto (*Serenoa repens*) plants under the canopy of slash pine. Palmetto is the most common understory plant in a mature slash pine plantation in Florida, and much more litter and humus is accumulated under this plant than on open floor.

Picture 3: One of twelve PVC collars inserted into the forest floor, commonly 3-6 cm, to the mineral soil. The collar has a ID of about 13.2 cm.

Picture 4: The top-open dynamic chamber placed on a collar in the site.



Picture 5: The CO_2 efflux measuring system with every equipment inside the box at left side. The Li-Cor can be also enclosed in the box when it is raining if the air temperature is not high. Two car batteries on right hand bottom continuously powered the system for 24-36 hours.

Picture 6: A multi-channel mini pump system is inside the larger water proof box on left side, and it is connected to gas traps buried in the soil at different depths via plastic tubes for sampling soil gas. The small box at right side is a connecting box for soil temperature sensors.

A.2 Publications:

1. Fang, C. and Moncrieff, J. B., 1997 An open-top chamber for measuring soil respiration and the influence of pressure difference on CO_2 efflux measurement. *Functional Ecology*, in press.

2. Fang, C. and Moncrieff, J. B., 1996, An improved dynamic chamber technique for measuring CO_2 evolution from the surface of soil. *Functional Ecology* **10**: 297-305.

AN OPEN-TOP CHAMBER FOR MEASURING SOIL RESPIRATION AND THE INFLUENCE OF PRESSURE DIFFERENCE ON CO_2 EFFLUX MEASUREMENT

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Summary

A new open-top chamber for measuring CO_2 efflux from the soil is reported here. The equilibrium CO_2 efflux, when there is no detectable pressure difference between the chamber and outside nor leakage of CO_2 into or out of the chamber, can be obtained with the new design. In previous dynamic chamber techniques, the measured CO_2 efflux is mainly dependent on the pressure difference between inside and outside the chamber. A negative pressure difference of -1 Pa may cause an order of magnitude increase in measured CO_2 efflux. Although the measured CO_2 efflux is less sensitive to a positive pressure difference than to a negative one, a positive pressure difference of a few tenths of a Pa will lead to a considerable underestimation in soil CO_2 evolution. The influence of pressure difference on measured CO_2 efflux is negligible in this new design and the estimated CO_2 efflux is close to the undisturbed soil respiration rate. Flow rates up to 8 dm^3 min^{-1}, or air movement over the soil surface up to 55 cm min^{-1}, will not affect CO_2 evolution from the soil. The influence of pressure difference is related to the type of soil being measured and this has also been reported here for the new design.

key- words: dynamic chamber, CO_2 efflux, soil respiration.

Introduction

The measurement of the emission of trace gases from the soil to the atmosphere on a small scale is normally made by some kind of chamber-based technique. Although the dynamic technique is considered to be a more precise method than the static method (Nakayama, 1990) and given that several different types of dynamic chamber methods have been developed (Edwards, 1974; Schwartzkopf, 1978; Fang and Moncrieff, 1996), there are still some uncertainties and limitations associated with this particular technique.

It is well established that the most serious problem with the dynamic method is the influence of pressure differences between inside and outside the chamber on measured CO_2 efflux. Kanemasu *et al.* (1974) reported that the CO_2 efflux measured with a pressure difference of -2.5 Pa was an order of magnitude larger than that with a

pressure difference of 1.0 Pa. De Jong *et al.* (1979) obtained the lowest CO_2 efflux with a dynamic chamber method, operated at a positive pressure difference less than +5 Pa, when compared to a static chamber, a soil CO_2 profile and two micrometeorological methods. Fang and Moncrieff (1996) pointed out that the method fails to give a reasonable estimate of soil respiration when the magnitude of negative pressure is greater than −0.5 Pa and a pressure difference within ± 0.2 Pa was recommended for getting reliable estimates of soil respiration rate with a dynamic chamber. Several issues remain unclear, however, about the relationship between measured CO_2 efflux and pressure difference: what is the relationship between measured efflux and pressure difference?; does the measured efflux respond similarly to a negative pressure difference as to a positive one?; is there an interaction between the pressure difference and some other environmental factors, such as soil properties ?

In the dynamic chamber technique, when a stream of air moves over the soil surface covered by the chamber, turbulence generated in the chamber may cause additional soil air to be withdrawn through the soil pores into the chamber and the undisturbed respiration rate may thus be disturbed or accelerated (Singh and Gupta, 1977; Hanson *et al.*, 1993). Golley *et al.* (1962) found that CO_2 production by peat in a mangrove forest increased with increasing flow rates up to 15 dm^3 min^{-1} using a method similar to that of a dynamic chamber. Schwartzkopf (1978) pointed out that there is a relationship between CO_2 production and air flow velocity, and expressed this by an empirical equation: $y = a\,(x+1)^b$, where y is the measured CO_2 efflux, x is flow rate, a, b are constants. On the other hand, Edwards and Sollins (1973) reported that there was no significant effect of flow rate (over a range of 56~340 l/hr) on observed CO_2 evolution. Cropper *et al.* (1985) also pointed out that there was no consistent flow rate effect with flow rates varying between 1-8 dm^3 min^{-1}. Hanson *et al.* (1993) included a fan in a chamber to generate a wind speed from 0 to 0.6 m s^{-1} within the chamber and found that the measured CO_2 efflux increased with the wind speed. The question whether flow rate affects the result of CO_2 efflux measurement thus remains unclear and needs to be addressed for the dynamic chamber technique.

In actual field measurements, being able to monitor continuously the CO_2 efflux at one location is as important as measuring CO_2 efflux simultaneously at a number of different positions. A large number of chambers may be required to obtain a representative estimate given the high spatial variability which has been observed for the efflux of CO_2 (Nakayama, 1990; Rochette *et al.*, 1992; Dugas, 1993). Cropper *et al.* (1985) pointed out that even in a relatively uniform pine plantation it would be necessary to increase the number of chambers or sample points to 15 to be within 10% of the mean obtained with 30 sample points for 90% of the time. This would be operationally difficult for the dynamic technique when chambers are in fixed positions.

A fast response chamber which can be moved between different positions within a short period of time is a possible alternative way to deal with this problem.

Hutchinson and Livingston (1993) pointed out that potential sources of bias for chamber-based flux measurements could be grouped into: (i) physical and biological disturbances associated with the measurement process, and (ii) errors associated with sample handling, sample analysis, and inaccurate models or inappropriate methods for computing flux from measured concentration data. Errors due to (i) can mostly be overcome by using an appropriate chamber design, relatively short sample times, and by taking reasonable care to minimise site disturbances. However, no chamber so far described can effectively eliminate these errors. A chamber, available commercially, was recently used to estimate CO_2 efflux (Norman *et al.*, 1992; Dugas 1993; Hanson *et al.*, 1993; Ham *et al.*, 1995; Shurpali *et al.*, 1995). This chamber consists of a cylinder fitted with a Li-Cor sensor housing (Part No. 9960-035, Li-Cor Inc., Lincoln, Nebraska, USA) and must be used with a Li-Cor 6200 system. A small (3 mm ID) pressure equilibrium tubing was attached to the chamber by some researchers (Norman *et al.*, 1992). The calculation of CO_2 efflux with the Li-Cor chamber is based on the increase of CO_2 concentration in the system during a known period , clearly a feature which makes it unsuitable for continuously monitoring soil CO_2 emission. Even for this system little is known about the possible influence of pressure difference, the calculation method, and the actual volume of the whole measuring system, on the estimation of soil respiration.

The chamber reported here was developed with the twin desires to eliminate the influence of pressure difference on CO_2 efflux measurement and to have a fast and sensitive response to environmental variation in order for it to be moved quickly among different positions in the field. With the new chamber, a further objective was to find the influence of pressure differences and flow rates on the measured CO_2 efflux.

Materials and methods

Chamber description

In all dynamic chambers, the degree to which the chamber is open to the atmosphere is one of the dominant factors controlling the pressure difference between inside and outside the chamber. The new open-top chamber has been developed with the design criteria that the chamber opening to the atmosphere should be at a maximum without inducing a significant CO_2 leakage from the chamber. The chamber consists of an outer frame and an inner sampler (Fig. 1). The outer frame, consists of three brass rings, the last of which is sharpened at its base in order to insert into the soil. A ring of brass tubing, 0.6 cm ID, is fixed to the inner wall of the chamber frame at about 9 cm from the lower end. Many small holes are evenly distributed in the tube

such that air can be sampled into the reference cell of an infra-red gas analyser (IRGA). A cone-shaped sampler, with an outside diameter of 15.0 cm on its bottom edge, is suspended inside the chamber and its height can be adjusted up and down. A number of small holes, 0. 2 cm in diameter, are drilled evenly on the bottom of the sampler. A thin wing ring, helping to prevent CO_2 leakage and providing an adequate mixing of evolved CO_2 with air, is attached to the bottom edge of the sampler. The angle of the wing ring is the same as that of the middle frame ring. The chamber covers about 150 cm^2 of the soil surface. Figure 2 shows a cross-section of the new chamber and illustrates how the air flows through the chamber. From the top of the chamber, air goes into the chamber, and then divides into two flows, one goes into the reference cell of an IRGA through the tube ring, and the other gets to the lower part of the chamber through the gap between the wing ring and the outer frame. Finally, the air mixed with the CO_2 evolved from the soil is drawn through the sampler into the sampling cell of the IRGA. The gap between the sampler and the frame can be adjusted between 0 and 1.5 cm by moving the sampler up and down, depending on the air flow rate used. A small piece of brass tube was fixed through the wall of the lower frame ring to monitor the variation of the pressure difference between inside and outside the chamber.

Measurements of CO_2 flux

For measuring CO_2 efflux, the new chamber is placed on a plastic collar. The collar, 13.3 cm ID and 5 cm high, has an outside diameter of 13.8 cm on the upper 2 cm in order to seal the collar and chamber. No sealing material was applied between the chamber and collar. The lower end of the collar was sharpened and typically, could be pressed about 4 cm into forest floor or 2 cm into mineral soil, depending on circumstances.

CO_2 effluxes were measured both *in situ* and in the laboratory. Field trials were made in a slash pine ecosystem in Florida, USA and in the campus of the University of Edinburgh, UK during 1995 and 1996. Sample and reference air was continuously drawn from the new chamber to an IRGA (Li-Cor 6262, Li-Cor Inc., Lincoln, Nebraska, USA). Flow rates were read and controlled by flowmeters (model A-250-2, Porter Instrument Company, Hatfield, USA). Pressure differences were monitored with a micromanometer (Model Mp 30 mb D/u, Air Instrument Resources Ltd., Oxford, England), which has a resolution of 0.1 Pa. CO_2 concentration difference and efflux were logged at 1 second intervals during the last 3 minutes of a 6 minute sampling period. More time was needed to allow the system to achieve a new equilibrium when the pressure difference between inside and outside the chamber was negative, especially if it exceeded -1.0 Pa.

The whole measuring system (Figure 2a), except the chamber and collars, was assembled in an environmental enclosure and powered by mains electricity as well as batteries for use in the field.

An undisturbed soil core, about 50 cm in diameter and 60 cm deep, was extracted and maintained in the laboratory to investigate the influence of flow rate and pressure difference on measured CO_2 efflux. The soil core was put in an open-top plastic container which had the same inside dimension as the soil core. There were several holes on the bottom of the container and the container was immersed in 3 cm deep water in order to obtain a consistent soil moisture and CO_2 concentration gradient inside the soil core. A collar was placed 2.0 cm into the soil, in the centre of the soil surface. The measurement of CO_2 efflux in the laboratory was by the same method as in the field.

A previous dynamic chamber (Fang and Moncrieff, 1996) was used for comparison and for the estimation of CO_2 effluxes under positive pressure differences. Figure 3 shows schematically the main differences between the chambers discussed here. This previous chamber is referred to hereafter as the 'old' chamber for comparison with the present design. The old chamber was modified to fit the collar. Foam tape was applied between the old chamber and collar for sealing.

Result and discussion

Chamber setting and measured efflux

With this open-top chamber, measured CO_2 efflux is mainly dependent on the gap between the sampler and the chamber frame. When the gap is small, a considerable negative pressure difference may be established in the lower part of the chamber, which will suck some air with a high CO_2 concentration from the soil and increase the measured CO_2 efflux. On the other hand, when the gap is too big, some of the CO_2 evolved from the soil under the chamber will leak from the lower to the upper part of the chamber and then to the atmosphere and a low efflux will be observed. When an equilibrium is achieved such that the pressure difference is negligible and no leakage of CO_2 occurs, the measured CO_2 efflux will be fairly close to the real one. In a certain range near the equilibrium point, the measured CO_2 efflux will be nearly constant with gap change.

Figures 4 and 5 show the relation of measured CO_2 efflux to chamber setting with different flow rates both in the field and in the laboratory. The unit of chamber setting is one turn of the holding nut. Settings 0 and 9 are equivalent to a gap of 0 and 1.5 cm, respectively. The measured CO_2 efflux is normalised such that the efflux at setting 4 is 1.

No pressure difference between inside and outside the chamber was detected with a chamber setting more than 1 for flow rates of 2 and 4 dm^3 $min^{-1}$and more than 2 for a flow rate of 8 dm^3 min^{-1}. When the chamber setting is less than 2 or more than 6, there is an obvious increase or decrease in measured CO_2 efflux, respectively. At setting 0, the lower part of the chamber was nearly closed and a considerable negative pressure difference arose. In the laboratory, measured CO_2 efflux was 12.4, 7.1, and 3.4 times of that at setting 4 for flow rate of 8, 4, and 2 dm^3 min^{-1}, respectively. At setting 9, the corresponding efflux was only 0.84 0.68, and 0.65 times of that at setting 4. A consistent efflux, with a variation less than 5%, was obtained in the range of settings 4 -5 for a flow rate of 8 dm^3 min^{-1}, setting 3-5 for flow rate 4 dm^3 min^{-1} and setting 2 - 4 for flow rate 2 dm^3 min^{-1}, respectively. Setting 4.5, 4.0 and 3.0 were thus chosen as equilibrium point for flow rates 8, 4, and 2 dm^3 min^{-1}, respectively.

Paired measurements of the open top chamber and the previous chamber in the laboratory indicted that the results with these two chambers matched very well. At a flow rate of 4 dm^3 min^{-1}, the averaged CO_2 efflux (n = 36) was 0.410 $\pm$ 0.0057 mg CO_2 m^{-2} s^{-1} for the new chamber and 0.408 $\pm$ 0.0065 mg CO_2 m^{-2} s^{-1} for the old one which was carefully maintained under no detectable pressure difference (less than $\pm$ 0.1 Pa).

The field measurements in a slash pine ecosystem in Florida (to be discussed in another paper) indicated that this new chamber is reliable in estimating soil respiration. Averaged soil respiration rate was estimated to be 0.217 mg CO_2 m^{-2} s^{-1} in September, 1995 and 0.087 mg CO_2 m^{-2} s^{-1} in January, 1996. The results are comparable with previous data from this ecosystem (Ewel *et al.*, 1987). The daily variation of CO_2 efflux showed a reasonable pattern and good agreement with the daily and seasonal trend of soil temperature.

For routine measurement of soil respiration, the system could reach a new equilibrium within 2 minutes of the chamber being placed on the soil surface. Most of this time was required for the flushing of the dead volume of the system and IRGA. The fast response of this system makes it easy to move the chamber between different positions within a short period to look at the spatial variation of soil respiration. A good correlation of soil respiration with the spatial distribution of root biomass, organic matter amount in the soil and understory feature was found in the slash pine ecosystem.

Influence of pressure difference on measured CO_2 efflux

The emission of CO_2 from the soil surface is extremely sensitive to pressure differences between inside and outside the chamber (Figure 6). In the laboratory, a pressure difference of -0.5, -1.0 and -2.0 Pa could cause an increase of measured CO_2 efflux up to 6.1, 14.2 and 20.7 times that under no pressure difference. Even a very

small negative pressure difference, such as -0.1 Pa, could lead to a considerable overestimation of soil respiration.

With a pressure difference of 0.2, 0.6, 1.0 and 2.0 Pa, the observed CO_2 efflux were 0.55, 0.31, 0.19 and 0.13 of that under zero pressure difference, respectively. As noted by Fang and Moncrieff (1996), the evolution of CO_2 is relatively less sensitive to a positive pressure difference than to a negative one. The decrease in efflux caused by a positive pressure difference will be less than the increase caused by a negative pressure difference of the same magnitude.

With a negative pressure difference between the inside and outside of the chamber, some air with a high CO_2 concentration will be sucked out from the soil. The influence of pressure difference on estimated soil respiration is obviously related to the type of soil being measured. The increase of measured CO_2 efflux caused by a negative pressure difference from a soil with a high respiratory capacity and high porosity will be much more than that from the soil with low respiratory capacity and low porosity. In the floor of the slash pine ecosystem in Florida, a negative pressure difference of -0.6 Pa (Figure 4, at 0 setting) caused the apparent efflux to be 2.45 times greater than that under zero pressure difference. This was in a position where the averaged respiration rate was 0.168 mg CO_2 m^{-2} $s^{-1}$and the ratio of soil bulk density / soil density was 0.6. An overestimate by a factor of 4.53 occurred in this position with corresponding values of 0.439 mg CO_2 m^{-2} s^{-1} for soil respiration and 0.45 for the ratio of soil bulk density /soil density.

It seems that the importance of pressure difference, either negative or positive, in dynamic chamber methods and its complexity were somehow underestimated in previously published work. In some circumstances, a very small negative pressure difference (less than -0.1 Pa) may cause a doubling in measured CO_2 efflux and a serious error in the estimation of soil respiration based on that data. For a dynamic chamber system, examining *in situ* the influence of pressure difference on the measured flux and continuously monitoring the pressure difference is a possible way to reduce this influence.

The influence of flow rate on measured CO_2 efflux

No obvious variation of measured CO_2 efflux was observed when flow rates were varied in the range from 1 to 8 dm^3 min^{-1} (Figure 6), a result which has appeared earlier (Cropper *et al.*, 1985). Corresponding air movements over the soil surface inside the chamber were 7 to 55 cm min^{-1}. The air movement of 55 cm min^{-1} equates to a flow rate of 11 dm^3 min^{-1} for the previous chamber. As the flow rate is unlikely to exceed 8 dm^3 min^{-1} in a routine soil respiration measurement with a dynamic chamber method, its influence on measured CO_2 efflux is negligible.

As discussed by Fang and Moncrieff (1996), a high flow rate is always associated with a large pressure difference when air is blown into or drawn out of a chamber system. When air is blown and drawn simultaneously through a chamber, a higher flow rate will cause a larger pressure fluctuation. A possible explanation for the reported increase of measured CO_2 efflux with flow rate (Golley *et al.*, 1962; Schwartzkopf, 1978) is that the increase was caused by the increasing pressure difference associated with the flow rate but not the flow rate itself. The method used by Golley *et al.* (1962) would definitely create a larger pressure difference with a higher flow rate. The wind speed (0 - 0.6 m s^{-1}) reported by Hanson *et al.* (1993) is obviously much larger than the air movement over the soil surface caused by passing air through the chamber. Additional mass flow may have arisen from the soil. It is also possible that the fan built a negative pressure difference in the lower part but a positive one in the upper part of the chamber.

Large fluctuations in measured CO_2 efflux caused by gusts were found in the field measurements in Edinburgh. As a gust also causes a sudden change of pressure, it is still unclear whether the fluctuation was due to the air movement or the change of pressure or both of them.

A possible modification can be applied to this chamber. An open-bottom container, about 21 cm ID and 21 cm high, can overlap the chamber and be fixed to it. The open end of the container should be about 2 cm above the ground. This modification will probably provide a steadier and balanced air flow to the lower part of the chamber and to the reference line of the IRGA, and reduce the possible fluctuations caused by gusts. Furthermore, as air is drawn into the chamber from the boundary layer near the soil surface, a possible error in measurement caused by any gas leakage from the joint between chamber and the soil will be negligible. Except for a very lose soil surface, such as a thick fresh litter layer, no base collar is needed in the field measurement, thus eliminating this possible source of disturbance.

Conclusion

Equilibrium CO_2 efflux, with no detectable pressure difference nor CO_2 leak, can be obtained in this new open top chamber with different flow rates. The influence of pressure difference on measured CO_2 efflux is then negligible and the estimated CO_2 efflux is fairly close to the undisturbed soil respiration rate.

A measuring system with this chamber is simple and easy to use in the field. The system will quickly achieve equilibrium after the chamber is placed on the soil surface, making it suitable to move between different positions to investigate the spatial variation of soil respiration It can also be left in one position to monitor continuously soil respiration.

The pressure difference between inside and outside the chamber is a dominant factor controlling the measured CO_2 efflux from the soil surface with any dynamic chamber method. A pressure difference of a few tenths Pa will cause several fold variation in measured CO_2 efflux. Although the measured efflux is less sensitive to a positive pressure difference than to a negative one, a very small positive pressure difference still leads to a considerable underestimation of soil respiration rate. The influence of pressure difference is also related to the type of soil being measured. In a soil with a high respiratory capacity and large porosity, pressure differences will cause more serious over- or under-estimation of soil respiration rate. The influence of pressure differences on measured CO_2 efflux and its complexity have been largely underestimated in previous published work.

In the new dynamic chamber method, flow rates up to 8 dm^3 min^{-1} or air movement over the soil surface up to 55 cm min^{-1} will not influence CO_2 evolution from the soil.

Acknowledgements

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List Of Figures

Fig. 1 A schematic of the new open-top chamber.

Fig. 2 Diagram of chamber longitudinal section and the air flow through the chamber

Fig. 3 Schematic diagram of measuring system and their configuration. (**a**) for new open-top chamber, (**b**) for previous dynamic chamber, C: chamber; F: flowmeter; P: pump.

Fig. 4 The influence of chamber setting on measured CO_2 efflux in the laboratory. (—■— : flow rate 2 dm^3 min^{-1}; —●— : flow rate 4 dm^3 min^{-1}; —▲— : flow rate 8 dm^3 min^{-1}).

Fig. 5 The influence of chamber setting on the measured CO_2 efflux. (—●— : measured *in situ* in the campus of the University of Edinburgh with an average CO_2 efflux less than 0.04 mg CO_2 m^{-2} s^{-1}; —■— : *in situ* in a slash pine site in Florida with an average efflux of 0.168 mg CO_2 m^{-2} s^{-1}; —▲— : *in situ* in the slash pine with an efflux of 0.439 mg CO_2 m^{-2} s^{-1}; —▼— : in the laboratory with an average efflux of 0.334 mg CO_2 m^{-2} s^{-1}. Flow rate was 4 dm^3 min^{-1}).

Fig. 6 The response of measured CO_2 efflux to pressure difference between inside and outside chamber. Measured in the laboratory with an average CO_2 efflux of 0.334 mg CO_2 m^{-2} s^{-1} under zero pressure difference and a flow rate of 4 dm^3 min^{-1}.

Fig. 7 The relation of measured CO_2 efflux to flow rate. (—●— : pressure difference is 0.0 Pa; —■— : pressure difference -0.4 Pa.)

Fig. 1

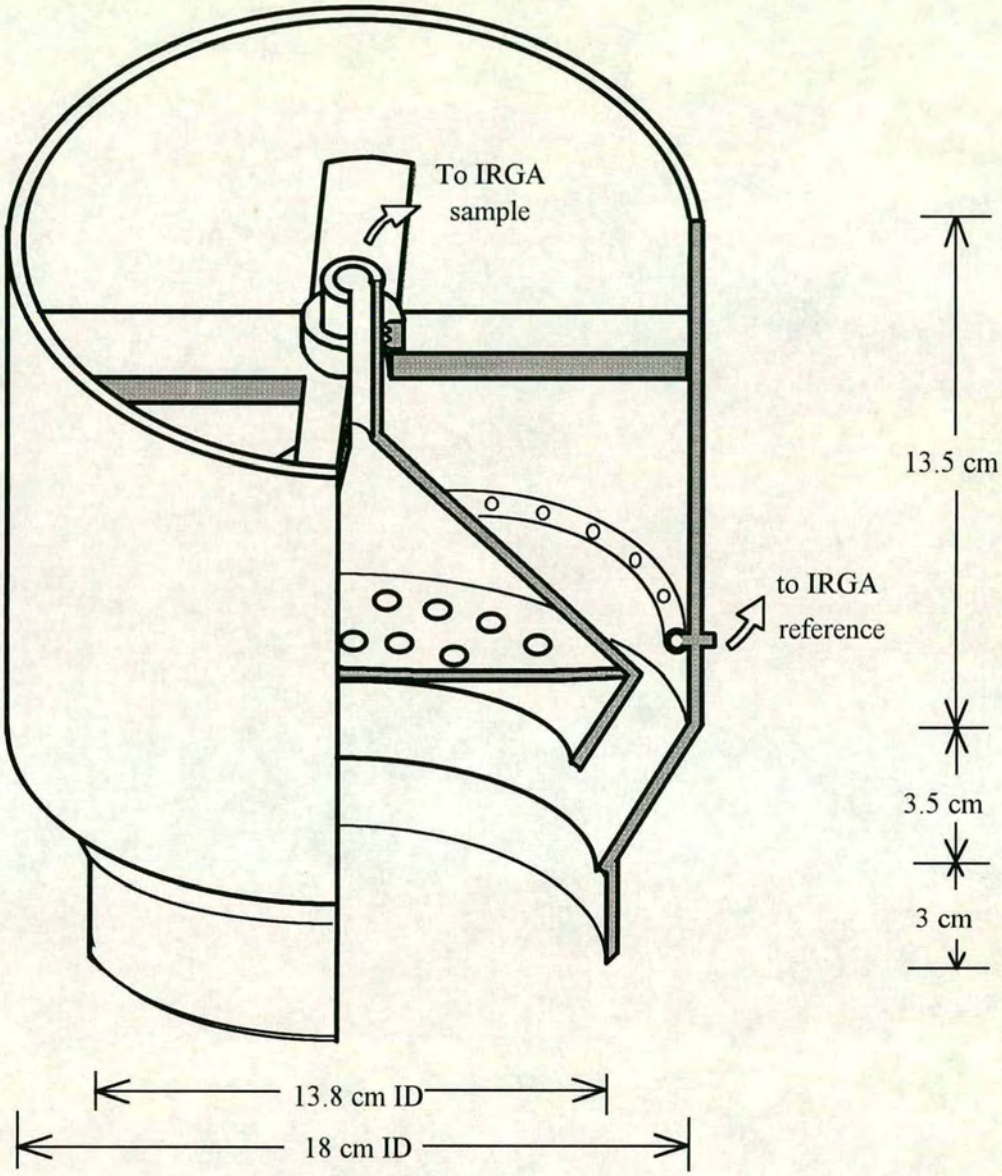

To IRGA
sample
to IRGA
reference
13.5 cm
3.5 cm
3 cm
13.8 cm ID
18 cm ID

Fig. 2

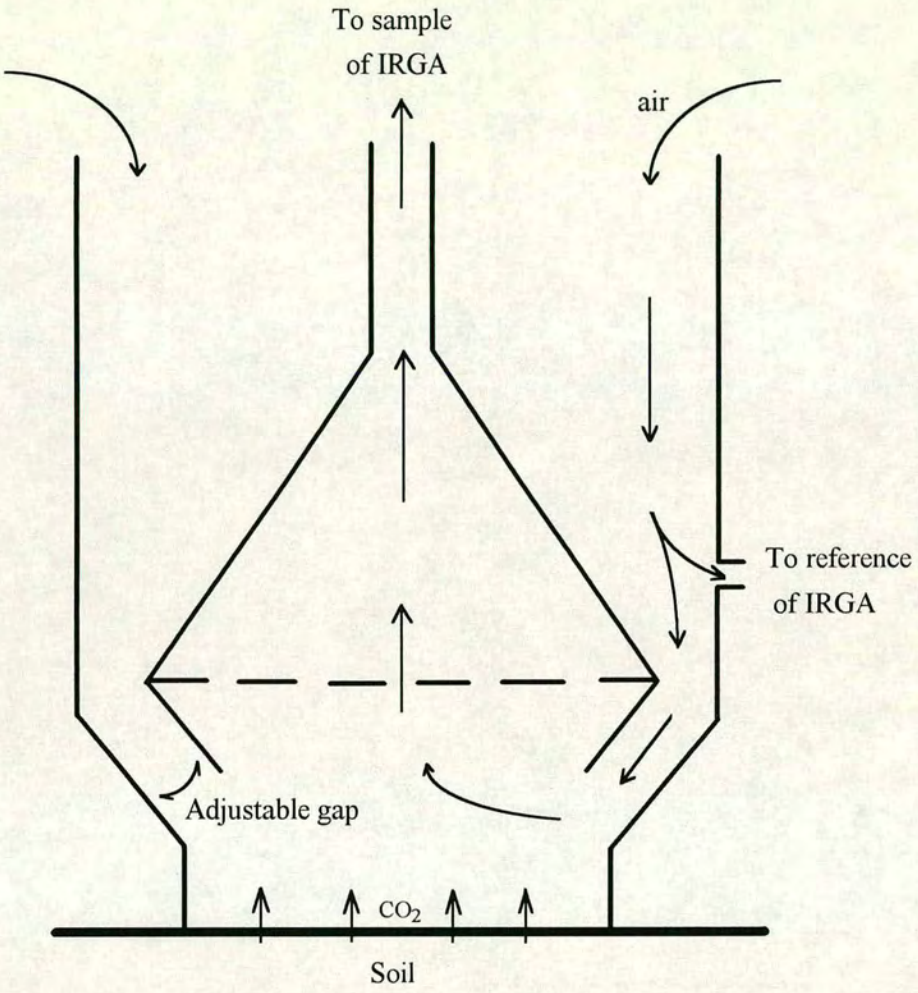
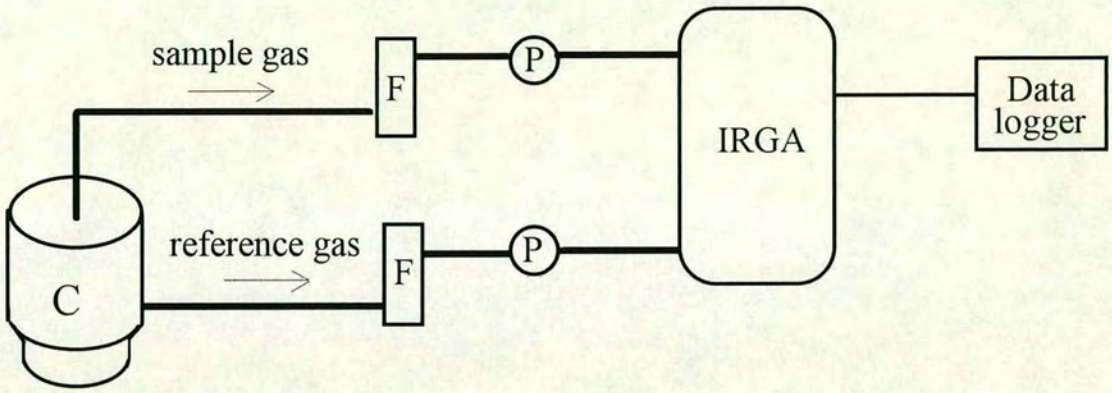
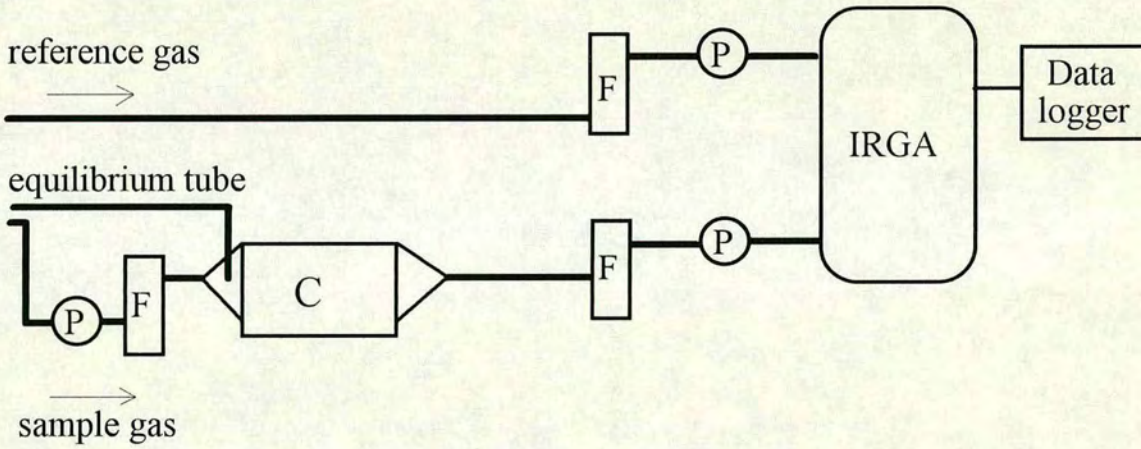

To sample
of IRGA
air
To reference
of IRGA
Adjustable gap
CO_2
Soil

Fig. 3

a.


sample gas
F
P
IRGA
Data logger
reference gas
F
P
C

b.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P
IRGA
Data logger
equilibrium tube
P
F
C
F
P
sample gas

Fig. 4

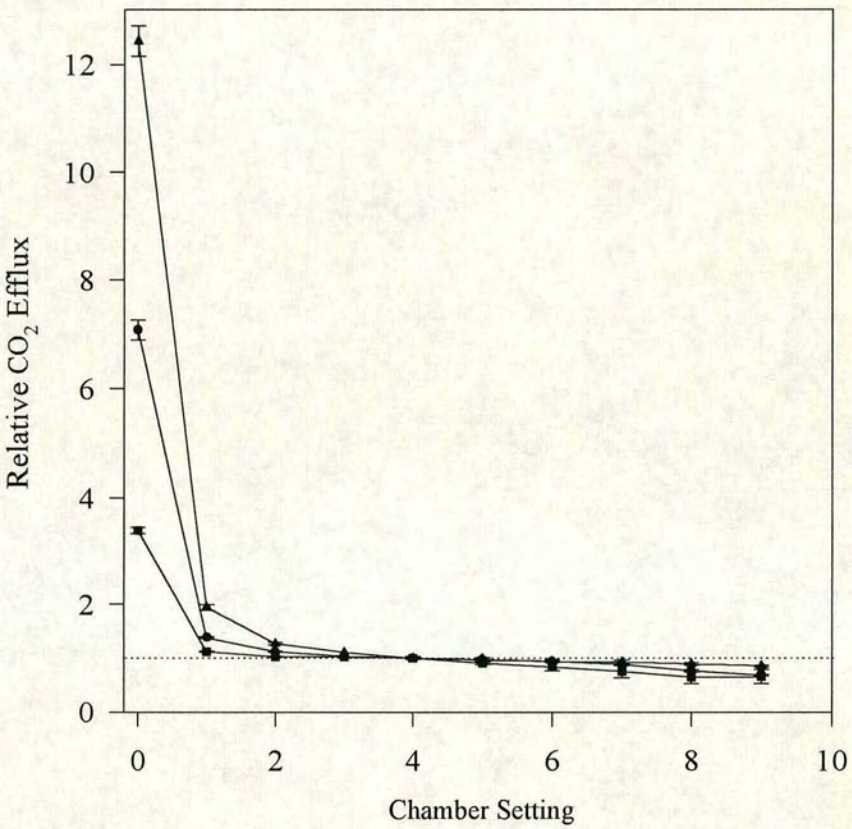


Fig.5

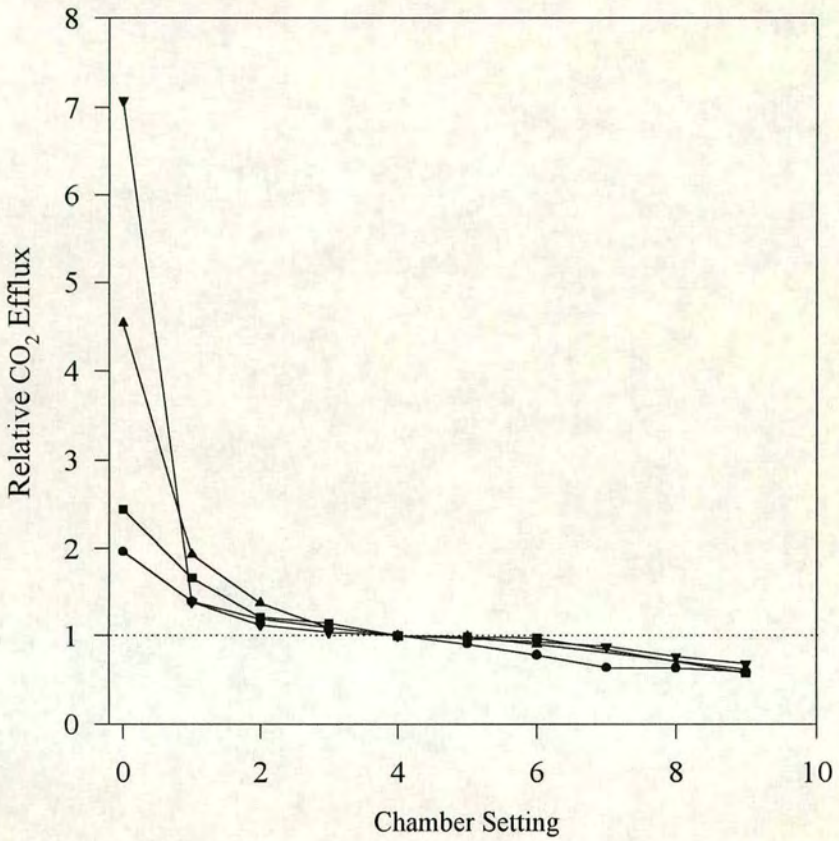


Fig.6

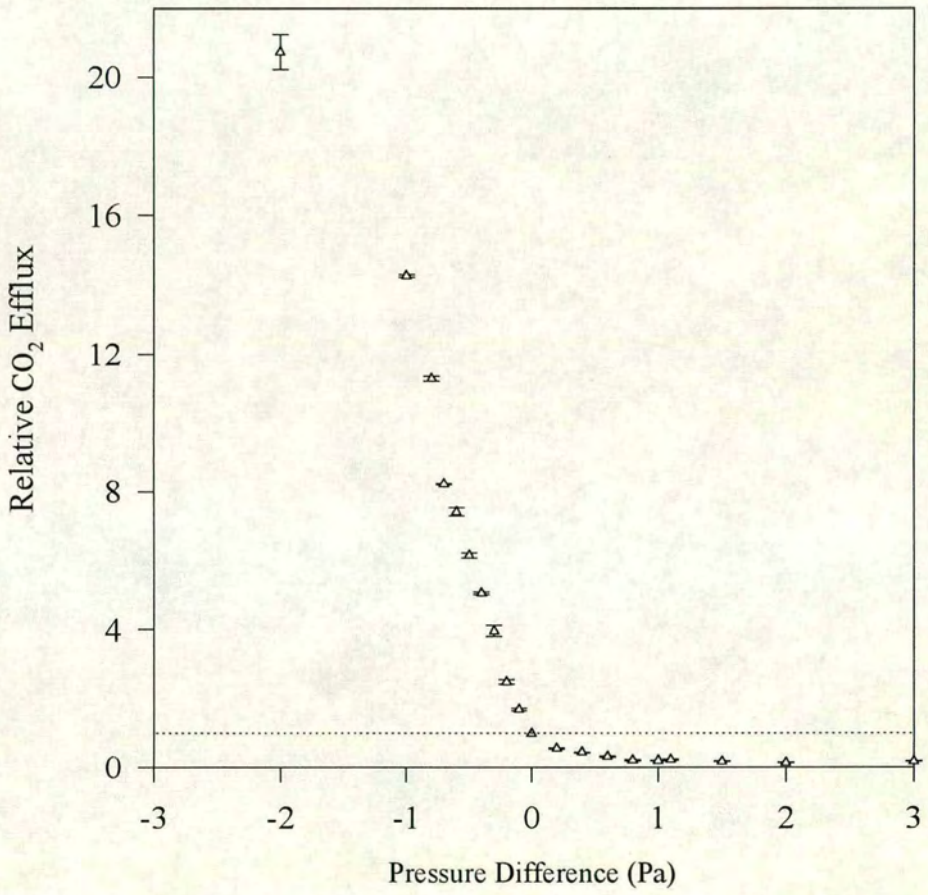
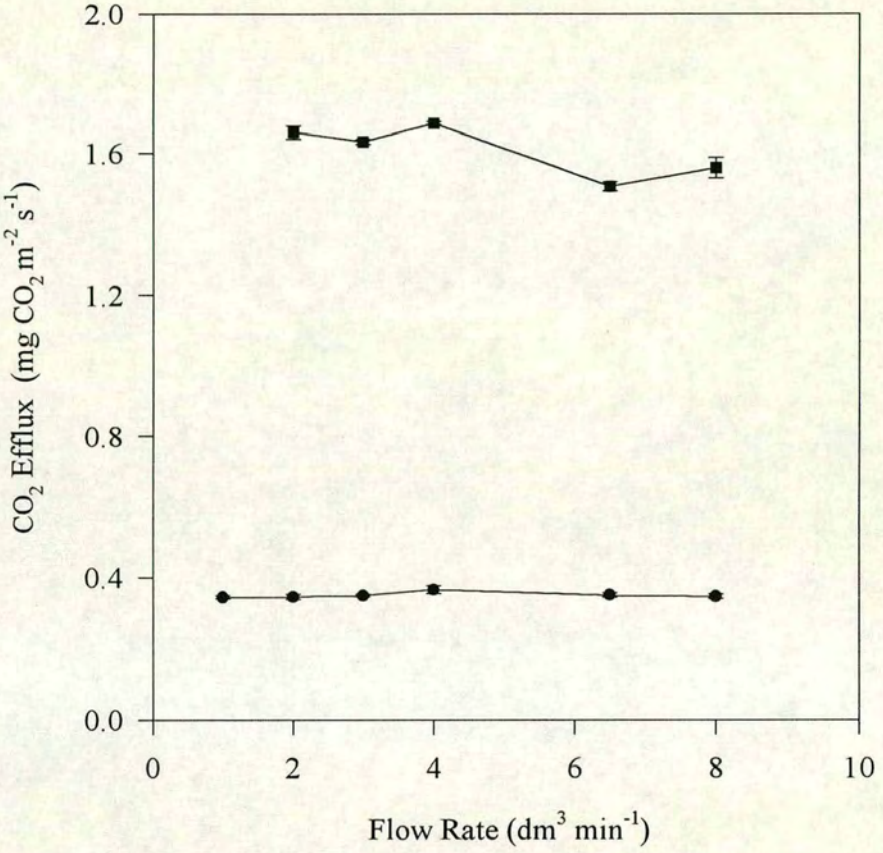

Relative CO_2 Efflux
20
16
12
8
4
0
-3
-2
-1
0
1
2
3
Pressure Difference (Pa)

Fig. 7


2.0
1.6
1.2
0.8
0.4
0.0
0
2
4
6
8
10
CO_2 Efflux (mg CO_2 m^{-2} s^{-1})
Flow Rate (dm^3 min^{-1})

Functional Ecology 1996
10, 297–305

TECHNICAL REPORT

An improved dynamic chamber technique for measuring CO_2 efflux from the surface of soil

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Summary

1. A new dynamic chamber has been developed with the aim of improving the performance of existing techniques for measuring CO_2 efflux from the soil surface. It has been shown that differences in the flow rates of incoming and outgoing air can be balanced quickly with this new chamber, consequently reducing the pressure difference between the inside and outside of the chamber. In the new chamber, the pressure difference varied within ± 0·2 Pa at flow rates of up to 4 litres min^{-1} when placed on the soil surface, whereas the corresponding value for an earlier design of chamber was about ± 1·0 Pa. The improved chamber can give a better and a more reliable estimation of CO_2 evolution from the soil surface compared to existing dynamic chambers, as demonstrated by either the magnitude or the trend of daily variation of measured CO_2 effluxes.

2. In a dynamic chamber technique, the pressure difference depends mainly upon the flow rate of sample air and the length and diameter of inlet or outlet tubing through which air passes into or out of the chamber. It is difficult to obtain a steady and negligible pressure difference with a normal dynamic chamber, especially if the method employs simultaneously blowing and drawing air, as the pressure difference is very changeable.

Key-words: CO_2, dynamic chamber, soil respiration

Functional Ecology (1996) **10,** 297–305

Introduction

The efflux of CO_2 from the soil of the terrestrial biosphere is an important component of the global carbon balance (Baldocchi *et al.* 1986). Many previous studies have measured CO_2 evolution and demonstrated the relationship between CO_2 evolution and environmental factors (Anderson 1973; Weber 1985; Gordon, Schlentner & van Cleve 1987). Although several techniques, including static and dynamic chambers and micrometeorological techniques such as eddy covariance, have been used with varying degrees of success in estimating CO_2 efflux, all of them have some shortcomings which have either prevented them from giving an adequate estimation of CO_2 emission or restricted them to use under limited conditions.

In recent years, eddy covariance has been used to measure CO_2 efflux above the surface (Baldocchi *et al.* 1986; Verma, Kim & Clement 1989; Baldocchi & Meyers 1991) and is considered to have great potential for directly measuring CO_2 efflux at the floor of a forest canopy. Eddy covariance can give an areally averaged estimation of CO_2 efflux with minimal impact on the local environment, but there are strict requirements which must be met for the technique to be applicable, e.g. steady-state conditions, no sources and sinks between soil surface and measurement height, and an extended level and horizontal homogeneous upwind fetch (Baldocchi & Meyers 1991). The requirement of steady-state conditions is not always met in field measurements, especially in early morning and late afternoon. Baldocchi & Meyers (1991) have reported that near sunset the thermal stability of the overlying atmosphere often changes rapidly from an unstable to a near-neutral or stable regime. Under such non-steady conditions, CO_2 efflux measurements are not constant with height and should be discarded. Nocturnal efflux rates, less than 0·02 mg m^{-2} s^{-1}, were below the detection limit of the eddy flux measuring system.

Biogeochemical cycling studies on the biogenic emission of carbon dioxide from the soil under plant canopies have relied heavily upon static and dynamic chamber techniques. The static chamber method is based on the absorption of CO_2 by KOH or $Ba(OH)_2$ inside a small chamber placed on the soil surface

(Edwards & Ross-Todd 1979; Vogt *et al.* 1980; Cowling & MacLean 1981; Gordon *et al.* 1987). Although the method is easy to use and inexpensive, most studies have shown that it underestimates CO_2 efflux (Ewel, Cropper & Gholz 1987), especially when effluxes are large (Kucera & Kirkham 1971; Norman, Garcia & Verma 1992). Raich & Nadelhoffer (1989) have pointed out that low estimates of soil-CO_2 efflux are consistently obtained with the method when alkali absorbent is placed inside a vial that has an opening less than 6% of the area covered by the chamber. Furthermore, this underestimation is temperature dependent, which makes the correction very difficult to apply. Edwards & Sollins (1973) reported that CO_2 efflux estimated with the static method was 63% of that with a dynamic method at 20 °C and 90% at 12 °C.

There are some closed chamber techniques in which there is no replacement of air in the chamber system and gas concentration increases continuously (Denmead & Raupach 1993). These chambers are examples of the enrichment method (Singh & Gupta 1977). In these methods, whether taking a gas sample (Hutchinson & Mosier 1981; Desjardins 1985; Peterjohn *et al.* 1993) or measuring CO_2 concentration with an infrared gas analyser (IRGA) *in situ* (Parkinson 1981; Norman *et al.* 1992), CO_2 efflux is estimated by the difference of CO_2 concentration at the beginning and the end of the measuring period. Underestimation is still likely because of the non-linear change of CO_2 concentration in the chamber (Hutchinson & Livingston 1993; Dugas 1993). Nakayama (1990) examined the accumulation of CO_2 inside a chamber and showed that the rate of increase in CO_2 concentration was essentially linear with time within 3·5 min of the chamber being closed. The CO_2 concentration did not increase much after that. Another probable error in estimating CO_2 evolution by this method is from the estimation of the actual enclosed space by the chamber and the base collar, which does not always equal the volume of the chamber.

The dynamic chamber technique passes air at a known flow rate through a chamber and measures the change of CO_2 density over time (Edwards & Harris 1977; Ewel *et al.* 1987). The most serious problem with this method is that the results are affected by whether the air is drawn or blown through the chamber. When air is drawn out of a chamber there is a pressure deficit inside the chamber, whereas positive pressure will be established when air is blown in. Large errors in CO_2 efflux rates arise from an extremely small pressure difference (on the order of 1 Pa of total pressure). Kanemasu *et al.* (1974) reported that the measurement of CO_2 efflux was an order of magnitude larger when air was drawn out of a chamber than when air was blown into the chamber, with pressure differences of $-2{\cdot}5$ Pa when air was drawn out and 1·0 Pa for blowing air in, respectively. The absolute value of negative pressure difference for drawing air was larger than the positive pressure when air was blown in at the same flow rate. De Jong, Redmann & Ripley (1979) obtained the lowest CO_2 efflux with a dynamic chamber method, operated at a pressure difference less than + 5 Pa, compared to four other methods. To diminish the influence of pressure difference on the measurement, it has been common practice to blow and draw air through a chamber at the same time (Kucera & Kirkham 1971; Ewel *et al.* 1987).

In this paper, we report some studies on an improved dynamic chamber, which was designed to reduce the possible pressure difference and to be easier to use in the field. The role of the pressure differential and factors governing it in the dynamic chamber method are also reported here. We sought to answer questions such as 'Does it really reduce the pressure difference to blow air in and to draw out simultaneously' and 'What factors control the pressure difference and its variation in a dynamic chamber'? These questions have not been systematically examined before and reducing the pressure difference is still the key to using the dynamic chamber technique.

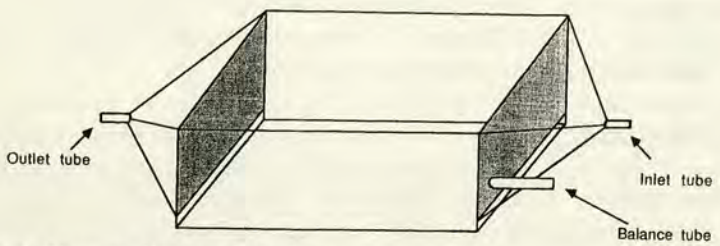

Fig. 1. Diagram of improved chamber.

Materials and methods

CHAMBER DESCRIPTION

A new dynamic chamber (Fig. 1) has been developed. It consists of a cube-shaped box made of Perspex®, with no base, similar to existing dynamic chambers, and with an inside dimension of 26 × 17 × 12 cm. Two pyramid sections are attached to each end of the box. The dimensions of the pyramid pieces are 16·5-cm long, 9-cm wide and 7-cm high. There are many small holes, 0·4 cm in diameter, arranged regularly on the walls at each end of the box. The space inside each end pyramid acts as a buffer to prevent the pressure from changing suddenly when air is blown in and drawn out and, consequently, provides a smooth and effective mixing of the air sample. Equilibration of pressure between the inside and outside of the chamber is mainly achieved by a balance tube, which has a length of 100 cm and an inside diameter of 0·8 cm. The tube is connected to one end-pyramid through which air is blown in. The opening of the balance tube is in the same place as the sample inlet. Air is blown in

through one pyramid and drawn out through the other at the same flow rate. When the flow rate of the air blown in is more than that drawn out, the excess gas leaks out through the balance tube before mixing with CO_2 emitted from the soil. On the other hand, any pressure deficit will be compensated for by the air passing in through the balance tube with the same CO_2 concentration as that blown in. The diameter of the balance tube is much larger than that used by Norman *et al.* (1992) in their closed gas-exchange system. A large tube can quickly balance the pressure difference between the inside and the outside of the chamber but may introduce serious errors in the estimation of CO_2 efflux because of the leakage through it. The structure of this new chamber can effectively minimize this error. At any time, the pressure in the buffer section through which air is blown in is slightly higher than that inside the chamber. This slight pressure excess prevents CO_2 emitted from the soil surface leaking into the atmosphere through the balance tube.

Two other chambers were made using a more traditional design and with the same dimension as the new chamber for comparison.

MEASUREMENT OF PRESSURE DIFFERENCE

Measurement of the pressure difference between the inside and outside of the chamber was conducted both in the laboratory and on the soil surface. In the laboratory, chambers were placed on a wooden base with a gutter 1-cm deep. Water was used to provide a complete sealing between the chamber and the base at a pressure of up to about ±100 Pa. Experiments performed included blowing air in only, drawing air out only, and then blowing in and drawing out simultaneously, with different flow rates. Two types of pumps were used, one with a capacity of 16 litres min^{-1} (model DA7.S/E; Charles Austen Pumps Ltd, Weybridge, UK), and the other about 8 litres min^{-1} (model Capex 2d; Charles Austen Pumps Ltd). The inlet and outlet tubes of the chamber were changed in diameter and length. Flow rates were monitored and adjusted by flowmeter (model 1100-V-A-A-300; GEC-Elliott Process Instruments Ltd, Croydon, UK) (full scale 10 litres min^{-1}; accuracy ± 2% indicated flow, ± 0·2% full-scale reading). Pressure differences were monitored with a micromanometer (model Mp 30 mb D/u; Air Instrument Resources Ltd, Oxford, UK), which has a resolution of 0·1 Pa. After checking the pressure at different points inside the chamber, the sampling tube of the micromanometer was placed in the middle of the chamber. The reference tube was put in a small box, which had a hole open to the atmosphere. The hole was covered by a sponge to prevent a sudden change in reference pressure.

Steel collars, of outside dimension 26 × 17 × 10 cm, were made for the measurement on the surface of the soil. The top ends of the collars were V-shaped and collars were set 4 cm into the soil, 2 weeks before the beginning of measurements, in order to allow the surface layer of soil to recover from disturbance. Chambers were put on the collars and water was added as a sealant. The measurement of pressure differences on the soil surface was by the same method as in the laboratory.

CO_2 EFFLUX MEASUREMENT

CO_2 efflux from the soil surface was measured on a grassland shaded by large trees. All green plant parts were removed from the measuring area. Four collars were inserted, 30-cm apart from each other, in a 1 × 1 m plot. Air, from 40 cm above the ground, was blown or drawn through the chambers. The CO_2 concentration in the air was analysed by an IRGA (model ADC 225 MK3; The Analytical Development Co. Ltd, Hoddesdon, UK). A micrologger (model CR-10; Campbell Scientific Instrument Co., Loughborough, UK) was used to collect data at a frequency of 0·5 Hz. Measurements reported here were made in June 1991.

Results and discussion

PRESSURE DIFFERENCE

Pressure differences for blowing or drawing air only

Figure 2 shows the pressure difference and its variation with flow rate when air was either blown or drawn through a chamber. At a flow rate of 1 litre min^{-1}; pressure differences were 2·8 Pa and –2·6 Pa for blowing air and drawing air, respectively. As the flow rate increased, the pressure difference increased rapidly, increasing to 94·9 Pa and –89·7 Pa at a flow rate of 8 litres min^{-1} for blowing and drawing air, respectively. The relationship between the pressure difference and flow rate was not linear and pressure differences increased faster at a higher flow rate.

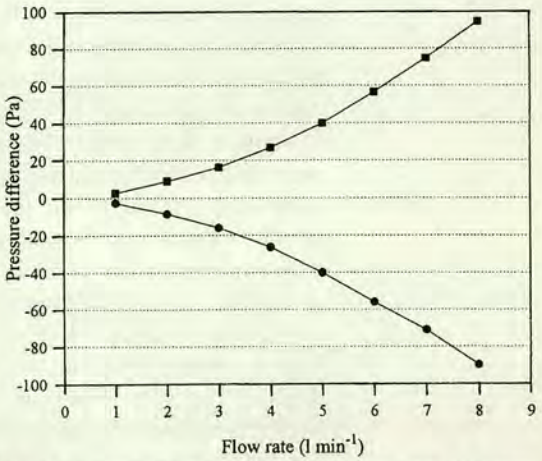

Fig. 2. Pressure difference at different flow rates; (●) drawing air from the chamber only, inlet 0·5-cm internal diameter (ID), 10-cm length; (■) blowing air into the chamber only, outlet 0·5-cm ID, 10-cm length.

Table 1. Pressure difference at different flow rates

Flow rate (litres min^{-1})	Pressure difference (Pa)	
	Drawing	Blowing
1	–1·1	1·3
2	–4·1	4·6
3	–7·9	8·7
4	–13·0	14·5
5	–19·5	21·7
6	–27·8	30·7
7	–36·5	40·2
8	–45·4	50·9

*The outlets for blowing air in and inlet for drawing air out were 5 cm in length with a 0·55 cm inside diameter. The pump used had a capacity of 16 litres min^{-1}.

Kanemasu *et al.* (1974) reported that the absolute value of the negative pressure difference for drawing air was larger than that of the positive pressure difference for blowing air at the same flow rate. Results reported here suggest tha t this is not a feature of the chamber itself, but is related to the pump used in the measurements. The magnitude of negative pressure difference will be larger than that of the positive difference when a small pump (8 litres min^{-1}) is used. However, it will be nearly the same as or even slightly smaller than that of the positive pressure difference for a larger pump (16 litres min^{-1}) (Table 1). It is interesting that the pump influences only the magnitude of the negative pressure difference when air is drawn out of the chamber. When a small or a large pump is used to blow air into the chamber, there is no obvious differences in the positive pressure provided flow rates are the same. There is no evidence to suggest any significant difference in pressure at different points inside the chamber. While the influence of the chamber volume on pressure difference was not significant, the resistance of the inlet or outlet tube was a dominant factor governing the pressure in a chamber. The resistance was related only to the diameter and length of inlet or outlet tubing in the experiments, and a long and thin inlet or outlet tube caused a large pressure difference (Figs 3 and 4).

Because of the extremely significant influence of pressure difference on the measurement of CO_2 efflux (Kanemasu *et al.* 1974), the pressure difference should be maintained as small as possible during the measuring period. For example, if a range of ± 0·2 Pa is required for a reliable estimation of CO_2 evolution, as shown by Figs 3 and 4, it is met only at a flow rate of no more than 1 litre min^{-1} and with an inlet or outlet tube of 20 cm in length and 1·2 cm in diameter. Measurements should thus be conducted with extreme care when using the method of blowing or drawing air only through a chamber.

On the soil surface, pressure differences between the inside and outside of the chamber varied from 0·55 Pa for blowing air and – 0·8 Pa for drawing air at a flow rate of 1 litre min^{-1}, to 11·0 Pa and –10·6 Pa at a flow rate of 7 litres min^{-1}. Differences were smaller than those obtained in the laboratory at the same flow rates. The reason is that a complete sealing could not be achieved on the soil surface, and some air leaked in or out of the chamber through the underlying soil. The characteristics of the soil to be measured therefore is one of the factors influencing the pressure inside the chamber. Pressure differences will be smaller on a

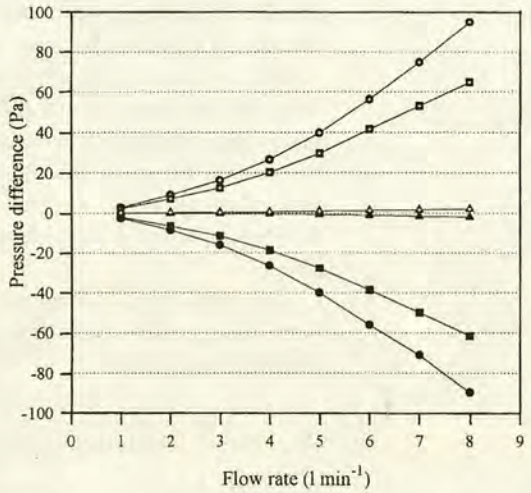

Fig. 3. Pressure difference at different flow rates; (●) drawing air out of the chamber, inlet tube 0·5 cm ID, (■) drawing air, 0·55 cm ID; (▲) drawing air, 1·2 cm ID; (○) blowing air into the chamber, outlet tube 0·5 cm ID; (□) blowing air, 0·55 cm ID; (△) blowing air, 1·2 cm ID. All outlet and inlet tubes were 10 cm long.

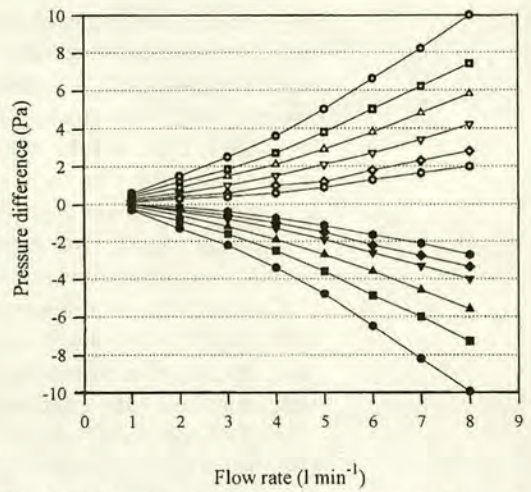

Fig. 4. The influence of tube length on pressure difference at different flow rates. (●) Drawing air; (○) blowing air, inlet and outlet tube 1·2 cm ID, 100 cm length; (■) drawing air; (□) blowing air, inlet and outlet tube 1·2 cm ID, 80 cm length; (▲) drawing air; (△) blowing air, inlet and outlet tube 1·2 cm ID, 60 cm length; (▼) drawing air; (▽) blowing air, inlet and outlet tube 1·2 cm ID, 40 cm length; (◆) drawing air; (◇) blowing air, inlet and outlet tube 1·2 cm ID, 20 cm length; (●) drawing air; (○) blowing air, inlet and outlet tube 1·2 cm ID, 10 cm length.

sandy, loose and dry soil than on a fine, compact and wet soil.

In an actual measuring system, the outlet of a chamber is connected to the analysing system by tubing. The pressure inside the chamber is related to the resistance of the whole measuring system when air is blown into the chamber. In that case, the resistance is much larger than that which occurs when the measurement is conducted in the laboratory. As a result of this, pressure differences will increase. In our system, the pressure difference was 3·9 Pa at a flow rate of 1 litre min^{-1} and 33·5 Pa at 7 litre min^{-1}. It was apparent that the method of blowing air through a chamber alone is inadequate for measuring CO_2 effluxes from the soil surface.

Pressure differences for blowing and drawing air simultaneously

In the laboratory, the magnitude of the pressure difference for the improved chamber was no more than ±0·5 Pa at flow rates of up to 7 litres min^{-1}, when flow rates in and out were nearly equal. When flow rates were up to 17 litres min^{-1}, the pressure differences could still be maintained within the range of ±0·5 Pa by adjusting flow rates with the micromanometer. By contrast, it was impossible to adjust flow rates in and out of the traditional chamber to obtain a pressure difference as small as that in the improved chamber. A difference in pressure was inevitable because flow rates in and out cannot be regulated to be exactly the same, even with a micromanometer. No matter how small the difference is, it will become large enough to cause a significant pressure difference in a normal chamber after a period of time. This problem is common to all such chambers.

On the soil surface, the pressure differences between the inside and outside of the improved chamber were in the range of ± 0·2 Pa at a flow rate of 4 litres min^{-1}, using a flow meter only to adjust flow rates. At that flow rate, the pressure difference varied within ± 0·5 Pa with a difference between observed rates of about ± 0·2 litres min^{-1}. For actual field measurements, it would be possible to achieve that goal with most types of flow meter after careful calibration. With an accurate flow meter and the necessary condition that flow rates should be adjusted, it is not difficult to keep the pressure difference within ± 0·2 Pa. For a normal dynamic chamber, the leakage of air through the underlying soil acted in a similar way to the balance tube of the improved chamber. Problems caused by pressure differences were not as serious as in the laboratory. However, because of the large resistance to air leaking through the soil, air could not pass through the soil quickly and efficiently. Pressure differences were much larger and more changeable than in the improved chamber, corresponding values being ± 1·0 Pa when flow rates were equal for incoming and outgoing air, and ± 2·0 Pa for a difference of 5% between flow rates in and out.

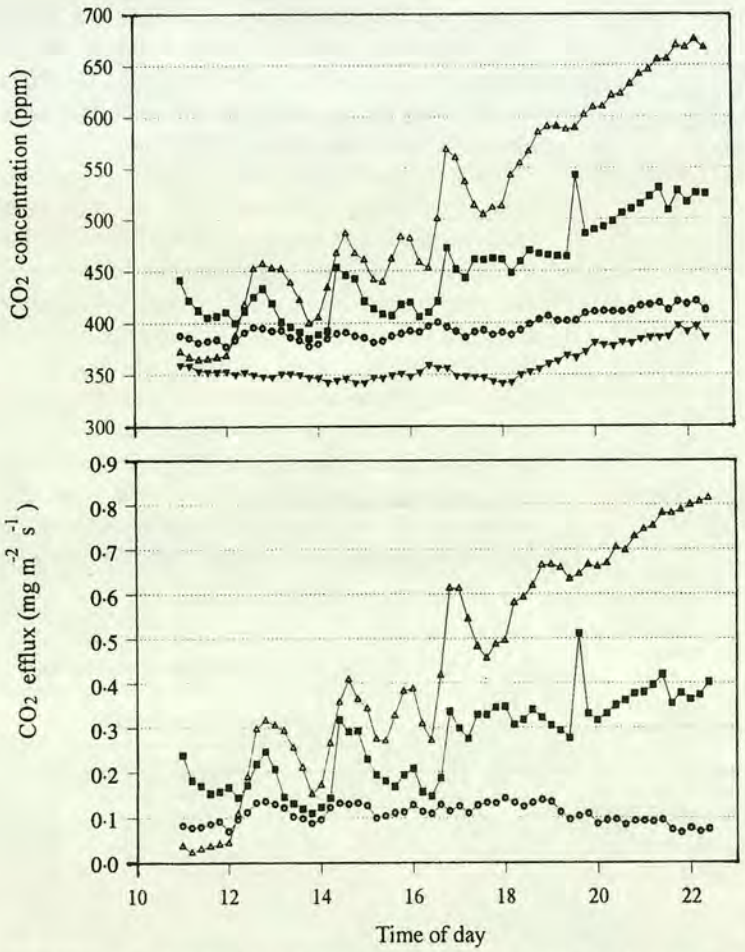

Fig. 5. CO_2 concentration and efflux from soil surface during daytime; (▼) reference; (■) chamber 1; (△) chamber 2; (○) chamber 3 (improved). Flow rates were 4 litres min^{-1}.

CO_2 EFFLUX

Figure 5 shows the result of the experiment in which air was blown in and drawn out of chambers simultaneously at a rate of 4 litres min^{-1}. Incoming and outgoing flow rates were adjusted to be nearly the same. A large difference in CO_2 efflux rate existed between data from the improved chamber (chamber 3) and normal chambers (chambers 1 and 2). It was unlikely to have been caused by differences between the sites. After interchanging chambers among four sites, there was no significant difference among positions. The only reason was pressure differences having developed in each chamber.

For chambers 1, 2 and 3 (being the improved chamber), pressure differences were – 0·3 Pa, + 0·6 Pa and – 0·1 Pa at the beginning of the experiment and – 0·6 Pa, – 0·8 Pa and – 0·1 Pa at the end, respectively. For chamber 3, CO_2 fluxes varied within a range of 0·07–0·14 mg $m^{-2} s^{-1}$ during the period 11.00–22.00 GMT. CO_2 evolution increased before 13.00, fluctuated within a narrow range from 13.00 to 19.00, and

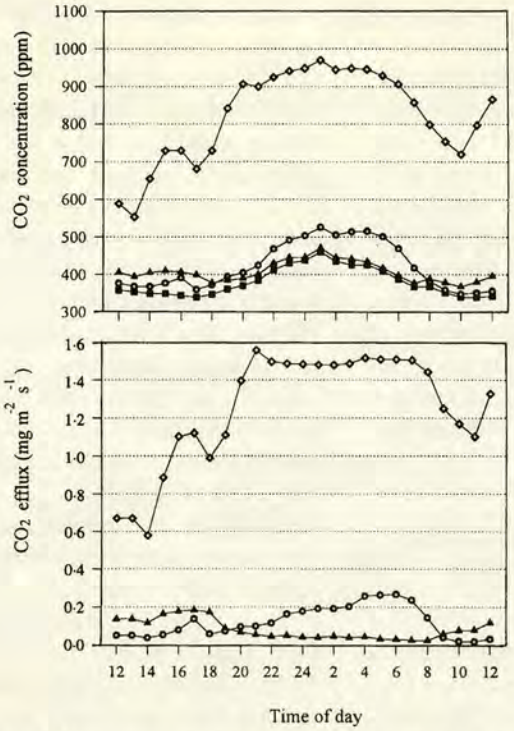

Fig. 6. Comparison of CO_2 concentration and efflux from soil surface between chambers (19–20 June 1991); (■) reference; (◇) chamber 1; (○) chamber 2; (▲) chamber 3 (improved). Flow rates were 4 litres min^{-1}.

Table 2. Daily variation of CO_2 effluxes (mg m^{-2} s^{-1}) reported as the mean value over the hour. Chambers 1 and 2 are normal dynamic chambers, drawing air out of the chamber only at a flow rate of 4 litres min^{-1}. Chamber 3 is the improved one, simultaneously drawing and blowing air through the chamber with a flow rate of 4 litres min^{-1}

Time	Chamber 1	Chamber 2	Chamber 3
19 June			
12.00	0·669	0·053	0·138
14.00	0·887	0·056	0·164
16.00	1·121	0·139	0·184
18.00	1·112	0·075	0·090
20.00	1·558	0·101	0·057
22.00	1·488	0·163	0·052
24.00	1·481	0·192	0·041
20 June			
2.00	1·488	0·203	0·042
4.00	1·510	0·262	0·035
6.00	1·506	0·237	0·028
8.00	1·251	0·042	0·060
10·00	1·102	0·021	0·080
12·00	1·521	0·039	0·156

then declined slowly. For chambers 1 and 2, CO_2 effluxes rose rapidly, with some large fluctuations, from 0·24 and 0·04 mg $m^{-2}s^{-1}$ at 11.00 to 0·4 and 0·83 mg $m^{-2}s^{-1}$ at 22.00, respectively.

Figure 6 and Table 2 show results obtained on 19–20 June 1991. Flow rates for drawing air out were adjusted to 4 litres min^{-1} with flow meters. Rates for blowing air in were regulated with a micromanometer to obtain pressure differences of –1·0 Pa, +0·3 Pa and 0 Pa in chambers 1, 2, and 3, respectively, in order to examine the influence of pressure differences on CO_2 efflux. There was no apparent difference in observed flow rates. Variations in pressure differences are shown in Table 3.

The pressure difference in chamber 3 was much more stable than that in chambers 1 and 2. A variable and large negative pressure difference in chamber 1 resulted in a high CO_2 efflux. In chamber 2, a positive pressure difference caused low CO_2 efflux, but this was not the reason for the high efflux during the night. A more likely reason is that the pressure difference changed from positive to negative during the night, but we did not make pressure measurements at night to confirm this.

For chamber 3, hourly averaged CO_2 effluxes varied from 0·028 to 0·184 mg $m^{-2}s^{-1}$, and the daily average was 0·084 mg $m^{-2}s^{-1}$. CO_2 evolution began to rise in the morning (about 8.00), and rose to a maximum between 16.00 and 18.00. During the night, CO_2 efflux remained stable and the diurnal cycle of CO_2 evolution was regular. For chamber 1, the smallest CO_2 efflux was 0·578 mg $m^{-2}s^{-1}$ (at 13.00) and the peak CO_2 emission occurred at 20.00, with a value of 1·55 mg $m^{-2}s^{-1}$. The daily average was 1·28 mg $m^{-2}s^{-1}$. The CO_2 efflux during the night was larger than that in the daytime, with an unlikely diurnal rhythm. For chamber 2, daily averaged CO_2 efflux was 0·123 mg $m^{-2}s^{-1}$ and again the night-time value was much higher than that in the daytime.

Figure 7 shows the results obtained from the improved chamber and those from the method in which air was drawn out only. Air was drawn out at a rate of 4 litres min^{-1} through a hole that was 1·5 cm in diameter, on the wall of a normal chamber. Pressure differences were 0·1 Pa and – 0·2 Pa for the improved chamber (chamber 1) and a normal one (chamber 2), respectively. There was no obvious variation in pressure differences in both chambers during the measuring period. The estimation of CO_2 efflux obtained with chamber 2 was always larger than that with chamber 1. The magnitude of CO_2 efflux for both fell in the normal range and, averaged over the day, were

Table 3. The variation of pressure difference in chambers

	Pressure difference (Pa)		
Time	Chamber 1	Chamber 2	Chamber 3
19 June			
11.00	–1·0	093	0
17.00	–1·6	0·2	0
20 June			
8.30	–2·0	0·7	<0·1
10.30	–1·8	2·0	<0·1

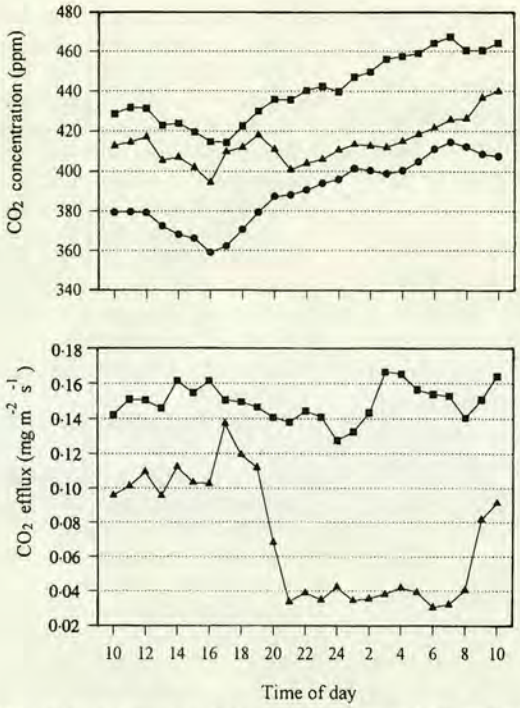

Fig. 7. Daily course of CO_2 concentration and efflux from soil surface (24–25 June 1991); (●) reference; (▲) chamber 1 (improved); (■) chamber 2. Flow rates were 4 litres min^{-1}.

0·071 mg m^{-2}s^{-1} and 0·149 mg m^{-2}s^{-1}, respectively. However, it is not easy to explain the high efflux in the evening for chamber 2.

From Figs 5, 6 and 7, the magnitude of the CO_2 efflux obtained with the improved chamber was reasonable and consistent with results from other investigators. Gordon *et al.* (1987) obtained CO_2 effluxes ranging from about 0·7 g CO_2 m^{-2}h^{-1} (about 0·2 mg m^{-2}s^{-1}) in midsummer to 0·2–0·3 g CO_2 m^{-2}h^{-1} (about 0·06–0·08 mg CO_2 m^{-1}s^{-1}) later in the season on a forest floor after harvesting. This seems to be the normal range of CO_2 evolution from most types of soil (Edwards 1974; Yoneda & Kirita 1978; Desjardins 1985; Weber 1985; Ewel *et al.* 1987). Schulze (1967) reported a high value of CO_2 efflux of up to 2556 mg m^{-2}h^{-1} but it was for soil under tropical forests. For temperate soil, Romell (1932) reported that all European soil respiration rates were in the range of 200–700 mg m^{-2}h^{-1} (about 0·06–0·19 mg m^{-2}s^{-1}). Data obtained with the improved chamber were typically low in the morning, rose to a maximum in mid-afternoon and then decreased. The daily pattern agreed well with the typical pattern found by Schlesinger (1977) and the investigation of Baldocchi *et al.* (1986) and Dugas (1993). It is obvious that the improved chamber can give a better estimation of CO_2 efflux from the soil surface compared to the normal dynamic chamber when one considers either the magnitude or the daily course of CO_2 evolution. For the method of drawing air only, an adequate result might only be obtained if the requirement of low flow rate and low incoming resistance of the air sample is met. For simultaneously blowing and drawing air through a normal chamber, it is difficult to control the pressure in the chamber. As discussed above, it is very difficult to maintain an extremely small and stable pressure during a measuring period with a normal dynamic chamber. It is noticeable that little previous work has been done on the daily course of CO_2 evolution with the dynamic chamber technique so far, and most reported results are for daily averages. The main reason for this may be the difficulty of controlling the pressure difference between the inside and outside of the chamber and thus of obtaining a realistic daily trend of CO_2 efflux.

Two types of pressure disturbances can be generated by using chamber systems – those that reduce pressure fluctuations associated with air turbulence over the soil surface, and those that result in a difference between mean air pressure inside and outside the chamber (Hutchinson & Livingston 1993). The exchange of any trace gas between the soil surface and atmosphere is enhanced by pressure fluctuations (Kimball & Lemon 1971, 1972). The dynamic chamber technique, with blowing and drawing air simultaneously, might dampen the pressure fluctuations, especially the fluctuations with high frequency, which will reduce trace gas exchange. The mean pressure difference induced by the chamber is believed to cause mass flow from or into the soil (Schwartzkopf 1978; Cropper, Ewel & Raich 1985). Little is known about the amount of mass flow due to this pressure difference, which is also related to the properties of the soil, such as permeability, water content, etc. What is clear now is that very small pressure differences will cause a significant variation in trace gas efflux. Denmead (1979) found that a pressure deficit of about 100 Pa produced a flux of N_2O into the chamber approximately 10 times that from diffusion alone. From the results reported here the impact of pressure differences on CO_2 emission is still significant even if it is as small as ±0·5 Pa. For any practical use of a dynamic chamber, it seems adequate to maintain the pressure difference within ±0·2 Pa in order to get a reliable estimation of CO_2 efflux, but it may not be easy for most dynamic chamber systems. An interesting point is that the variation in CO_2 efflux is much more sensitive to negative pressure differences than to positive ones, as calculated by Kanemasu *et al.* (1974). It means that a negative pressure will cause a larger change in CO_2 efflux than a positive pressure of the same absolute magnitude. If the pressure difference cannot be controlled within an adequate range, it would be better to maintain a small positive pressure rather than a negative one.

Conclusions

The pressure difference in the dynamic chamber technique is governed by several factors. For blowing air

into or drawing air out of a chamber only, it will depend mainly upon the flow rate at which air is passed through and the length and diameter of inlet and outlet tubing. Only under limited conditions will it be possible to get a small pressure difference, and only in that case will an adequate estimation of CO_2 evolution be obtained.

For the method of drawing and blowing air through a chamber simultaneously, the pressure difference between the inside and outside of the chamber is related to the difference of air flow rates in and out. On the soil surface, the sealing between the chamber and soil and the characteristic of the soil also affects the magnitude of the pressure difference. It is very difficult to maintain an extremely small pressure difference in a chamber and obtain a reliable result with this method.

The new chamber developed here is easier to operate for field measurements of CO_2 efflux than existing normal dynamic chambers. On the soil surface, pressure differences were in the range of $\pm 0{\cdot}2$ Pa at flow rates of up to 4 litres min^{-1}. Compared with results of CO_2 effluxes reported elsewhere, the estimation obtained with the new chamber is better and more reliable than those with a normal dynamic chamber, whether measured by the magnitude or the daily pattern of measured CO_2 effluxes.

The influence of pressure difference on CO_2 emission is extremely significant. A pressure difference as small as a few tenths of 1 Pa will cause large errors in CO_2 efflux measurement. CO_2 emission is more sensitive to negative pressure than to a positive one in the chamber.

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