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Minimizing artifacts and biases in chamber-based measurements of soil respiration

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Abstract

Soil respiration is one of the largest and most important fluxes of carbon in terrestrial ecosystems. While eddy covariance methods are becoming widely used to measure nighttime total ecosystem respiration, the use of chambers placed over the soil is the most direct way of measuring respiration occurring within the soil and litter layers. Several decades of experience with chamber-based measurements have revealed most of the potential sources of error with this methodology. The objectives of this paper are to review several recently expressed concerns about uncertainties of chamber-based measurements of CO₂ emissions from soils, to evaluate the direction and magnitude of these potential errors, and explain procedures that minimize these errors and biases. Disturbance of diffusion gradients cause underestimate of fluxes by less than 15% in most cases, and can be partially corrected for with curve fitting and/or can be minimized by using brief measurement periods. Underpressurization or overpressurization of the chamber caused by flow restrictions in air circulating designs can cause large errors, but can also be avoided with properly sized chamber vents and unrestricted flows. We found very small pressure differentials (± 0.1 Pa) and modest ($\sim 15\%$), inconsistent errors in flux estimates using our chamber design. Somewhat larger pressure differentials (± 0.9 Pa) were observed under windy conditions, and the accuracy of chamber-based measurements made under such conditions needs more research. Spatial and temporal heterogeneity can be addressed with appropriate chamber sizes and numbers and frequency of sampling. For example, means of eight randomly chosen flux measurements from a population of 36 measurements made with 300 cm² diameter chambers in tropical forests and pastures were within 25% of the full population mean 98% of the time and were within 10% of the full population mean 70% of the time. Finally, comparisons of chamber-based measurements with tower-based measurements require analysis of the scale of variation within the purported tower footprint. In a forest at Howland, ME, soil respiration rates differed by a factor of 2 between very poorly drained and well drained soils, but these differences were mostly fortuitously cancelled when spatially extrapolated over purported footprints of 600–2100 m length. While all of these potential sources of measurement error and sampling biases must be carefully considered, properly designed and deployed chambers provide a reliable means of accurately measuring soil respiration in terrestrial ecosystems.

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1. Introduction

After photosynthesis, soil respiration is the second largest flux of carbon in most ecosystems. Soil res-

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piration, which includes both root and microbial respiration, has been estimated to be 60–90% of total ecosystem respiration in temperate forests (Goulden et al., 1996a; Longdoz et al., 2000). Variation in net ecosystem productivity (NEP) among sites in a latitudinal gradient (Valentini et al., 2000) and among years at a single forest site (Goulden et al., 1996a) has been attributed largely to variation in respiration. Interannual variation in soil respiration may be large enough to affect interannual anomalies of atmospheric CO₂ concentrations at the global scale (Houghton et al., 1998; Keeling et al., 1995; Trumbore et al., 1996). Allocation of carbon by plants to their roots is difficult to measure by any method, and the difference between soil respiration and aboveground litterfall provides a useful constraint on possible belowground C allocation in many forest ecosystems (Davidson et al., 2002; Raich and Nadelhoffer, 1989). For many reasons, from understanding terrestrial biosphere–atmosphere interactions to constructing C budgets within ecosystems, soil respiration is an important flux that deserves attention.

In forested ecosystems, the effects of photosynthesis and respiration of understory vegetation complicate belowcanopy eddy covariance estimates of soil respiration (Janssens et al., 2000; Law et al., 1999; Norman et al., 1997). Abovecanopy eddy covariance measurements at night are also commonly used to estimate total ecosystem respiration (Goulden et al., 1996a,b; Longdoz et al., 2000), and temperature functions based on these measurements are then applied to daytime temperatures to estimate daytime respiration. However, chamber-based estimates of soil respiration have been reported that were as high or higher than total ecosystem respiration estimated from temperature functions derived from abovecanopy nocturnal eddy covariance measurements (Goulden et al., 1996a; Longdoz et al., 2000). Hence, both eddy covariance and chamber-based methods must be reviewed for possible artifacts, biases, and inaccuracies. Eddy covariance measurements are the subject of other papers in this volume. Chamber-based measurements are the focus of this paper.

Chambers placed over the soil surface have been used to measure soil respiration (Lundegårdh, 1927; Reiners, 1968) and other trace gas emissions from soils (Ryden et al., 1979) for many decades. Excellent reviews of chamber designs and calculations of fluxes

based on chamber methods are available in the literature (Hutchinson and Livingston, 2002; Livingston and Hutchinson, 1995). In the case of soil respiration, the accuracy of methods using alkali traps compared to infrared gas analyzers (IRGAs) for CO₂ quantification has also been extensively reviewed (Bekku et al., 1997; Ewel et al., 1987; Rochette et al., 1997), with the general conclusion that alkali traps often yield overestimates of low fluxes and underestimates of high fluxes, but can sometimes be reliably calibrated for an intermediate range of fluxes. The use of IRGAs is becoming increasingly common and is widely considered the method of choice today for chamber-based soil respiration measurements. The objective of this paper is to review some of the concerns still being discussed in recent years regarding possible artifacts and biases and resulting inaccuracies of soil respiration measurement made with chambers and IRGAs. Specifically, altered soil CO₂ concentration gradients, pressure differentials between chamber and outside air, sampling schemes to address spatial and temporal variation, and comparisons with tower-based eddy covariance measurements are discussed.

Chambers can be used in either of two modes to calculate fluxes (Livingston and Hutchinson, 1995): (1) in steady-state mode, the flux is calculated from the difference in CO₂ concentration between the air flowing at a known rate through the chamber inlet and outlet after the chamber headspace air has come to equilibrium concentration of CO₂; (2) in the non-steady-state mode, the flux is calculated from the rate of increase of CO₂ concentration in the chamber headspace of known volume shortly after the chamber is put over the soil.

2. Chamber artifacts

2.1. Altered diffusion gradient

Whenever a chamber is placed over the soil and the concentration of the chamber headspace gas begins to change, then the natural concentration gradient within the soil profile is altered (Conen and Smith, 2000; Healy et al., 1996). Following Fick's first law, the gas flux is dependent on the concentration gradient and the air-filled porosity (diffusivity) of the soil. Therefore, as the CO₂ concentration within the chamber

headspace increases, the diffusion gradient decreases, the flux begins to decline, and the tracing of headspace CO₂ concentration may begin to flatten out. This could result in an underestimation of the flux.

One of the advantages of an IRGA-based system used in non-steady-state mode is that CO₂ fluxes can be measured quickly (≤ 5 min per chamber measurement). Minimizing the time that the chamber is over the soil minimizes the artifact caused by altering the CO₂ concentration gradient within the soil profile and between the soil–atmosphere and the chamber headspace.

The LiCor-6200/6400 soil respiration systems attempt to minimize the error caused accumulating headspace CO₂ concentrations by first scrubbing the headspace CO₂ concentration to slightly below ambient concentrations and then allowing the operator to determine the concentration range near ambient concentrations over which a flux is calculated while the chamber headspace CO₂ concentration increases. The flux is calculated while the chamber CO₂ is near realistic ambient conditions, thus in theory minimizing the alteration of the natural diffusion gradient. On the other hand, if CO₂ concentrations near the forest floor surface are elevated above ambient atmospheric

values, then scrubbing the chamber CO₂ concentration below ambient could cause a significant error in the opposite direction (i.e., overestimating fluxes) by creating an unnaturally large diffusion gradient. Hence, the concentration range over which the flux is calculated must be selected with care.

Another advantage of using IRGAs is that numerous data points of CO₂ concentrations can be logged every minute, yielding a nearly continuous monitoring of increasing CO₂ concentrations that can be used to fit the most appropriate regression function. Frequently, a noisy trace appears shortly after placing the chamber over the soil as a result of small pressure differentials and other disturbances while moving and fixing the chamber in place, and then a nearly linear trace is usually observed (Fig. 1). When the slope of a linear regression is used to calculate the flux in non-steady-state mode, the effect of altering the diffusion gradient is ignored.

It is possible to correct, at least partially, for non-linearity of the non-steady-state CO₂ trace by fitting a nonlinear function and estimating the instantaneous slope (tangent of the curve) at the concentration measured at the beginning of the flux measurement (Healy et al., 1996; Livingston and Hutchinson, 1995).

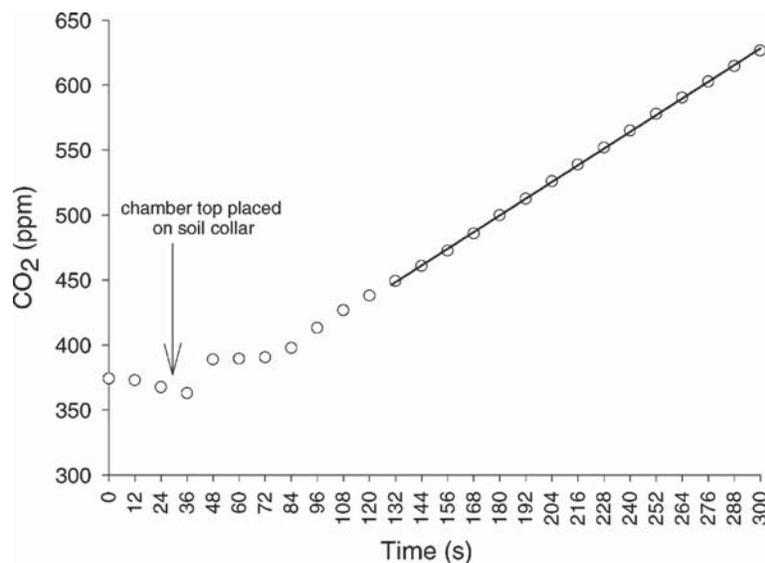


Fig. 1. A typical tracing, using a 12 s interval for logging data, of increasing CO₂ concentration after a chamber is placed over the soil at the Harvard Forest on 17 August 1999. Open circles indicate the recorded CO₂ concentrations. The solid line is the linear regression used to calculate the flux. Note the “noise” in the tracing during the first 1–2 min after chamber placement, which presumably is due to pressure artifacts or other disturbances caused by chamber placement.

However, care must be taken when selecting the correct initial CO₂ concentration where the instantaneous slope is to be calculated. Placement of the chamber over the soil can itself cause a small disturbance that changes chamber concentrations, thus making the choice of initial chamber concentration equivocal. If a “background” ambient concentration of the air outside the chamber is used to estimate the initial chamber concentration, then vertical gradients of ambient air concentrations must be considered. The CO₂ concentration at the forest floor can be several parts-per-million higher than the concentration at shoulder height, and so the height where “background” concentrations are measured can influence the estimated fluxes. Concentrations near the soil surface tend to vary rapidly, depending on the presence or absence of small currents of air.

Even where the tracing of increasing concentration appears very linear, there can still be an underestimation of the flux. Hutchinson et al. (2000) argue that nearly instantaneous alteration of gas exchange at the soil–atmosphere interface causes an underestimation of the flux. Conen and Smith (2000) show that an apparent linear increase in headspace chamber gas in non-steady-state measurements can occur while the concentration of the gas within the soil also increases, causing an underestimation of the flux. The use of relatively tall chamber tops minimizes these disturbances and hence minimizes the errors. However, increasing the chamber height also reduces sensitivity of the system to measure small fluxes, and so a balance must be struck where the chamber volume-to-area ratio is small enough to permit measurement of the smallest flux of interest, but large enough to minimize chamber disturbance effects.

To measure the magnitude of this error, Nay et al. (1994) made chamber flux measurements in a controlled laboratory design where a known flux was imposed by establishing a known diffusion gradient over a polyurethane foam medium of known diffusivity. They estimated that calculating the flux from a linear regression of the increasing CO₂ concentration tracing during a chamber measurement made over the foam caused an underestimation of about 15%. This foam medium had a high diffusivity, and the error would be less when the medium has a lower diffusivity (lower air-filled porosity), as is the case for soil. Similar experiments over dry sand columns have indicated that

chamber estimates were consistently about 5–15% too low compared to the experimentally imposed known flux (Eric Sundquist, USGS, pers. commun.). This error should be still smaller for loamy or clayey or wet soil, because diffusivity declines as the soil texture becomes finer (although aggregation of particles is a confounding factor) and diffusivity also decreases with increasing water content (Conen and Smith, 2000; Davidson and Trumbore, 1995; Healy et al., 1996; Hutchinson et al., 2000). When the soil diffusivity is lower, the diffusion gradient is altered more slowly by the increasing chamber headspace concentration, resulting in smaller underestimation of the flux.

Rayment (2000) interprets this problem from a different perspective. He argues that non-steady-state chambers systematically underestimate fluxes because the “effective volume” of the chamber is larger than the chamber itself and includes some of the pore spaces within the soil. The volume of the chamber must be known to convert the slope of the increase in CO₂ concentration (Fig. 1) to a flux per unit area. However, this is really the same source of bias as described by Nay et al. (1994), Healy et al. (1996), and Livingston and Hutchinson (1995). These authors showed through measurements and simulations based on diffusion theory that the CO₂ concentration within the soil increases at the same time that the chamber headspace concentration increases. Hence, the changing diffusion gradient described by Nay et al. (1994) and the larger effective chamber volume described by Rayment (2000) are manifestations of the same process of CO₂ accumulation within the upper part of the soil profile due to an altered diffusion gradient while CO₂ is accumulating in the chamber headspace. Not surprisingly, the average error of 10% underestimation estimated by Rayment (2000) for a spruce forest sandy soil, was somewhat smaller than the average error of 15% measured by Nay et al. (1994) over more porous polyurethane in the laboratory. Because they are manifestations of the same phenomenon, these errors are not additive. Moreover, large within-site spatial heterogeneity of surface soil porosity would preclude the practical application of the concept of an effective chamber volume to empirically correct flux underestimates obtained by linear regression (Hutchinson and Livingston, 2001).

Taking together the results of the modeling, laboratory, and field studies cited in this section, we

can generalize that non-steady-state chambers of 10–20 cm height will usually produce an artifact ranging from negligible to 15% underestimation, depending on the soil texture and water content. Although the magnitude of this error is small relative to the spatial and temporal heterogeneity that often contributes to uncertainty of mean flux estimates, it should be recognized that this chamber artifact is generally a bias towards underestimation.

Opinions vary as to how and if this underestimation should be corrected when calculating fluxes. We have chosen to use a linear fit of data acquired after the disturbance effect of chamber placement has passed (e.g., Fig. 1). Although this linear fit may cause a biased underestimation of fluxes by a few percent in moist soil, identifying the initial concentration that would be needed for nonlinear modeling of the instantaneous slope is difficult because of the noisy part of the tracing immediately after chamber placement.

Determining fluxes using a steady-state mode of chamber deployment is also subject to errors caused by altered diffusion gradients. First, Hutchinson et al. (2000) question whether a true steady-state is actually achieved within a reasonable deployment time due to delayed recovery from the initial perturbation of the diffusion gradient during chamber placement. Secondly, once constant concentrations are achieved during the steady-state measurements, altered diffusion gradients with the soil profile may cause CO₂ to diffuse laterally and escape out of the soil outside of the chamber base (Hutchinson and Livingston, 2001; Livingston and Hutchinson, 1995). Simulations show that the altered CO₂ gradients extend beyond the outer perimeter of the chamber base, and so some of the CO₂ produced below the chamber base is likely diffusing laterally as well as vertically under both steady-state and non-steady-state chambers. Increasing the flow rate of gas through the steady-state chambers will lower the equilibrium concentration, thus perhaps minimizing this error, but the tradeoff is that higher flow rates create a greater risk of pressure differentials, which can cause a larger error (discussed below). There is little published literature about the ideal flow rates for steady-state chamber systems, and opinions vary widely. Hutchinson et al. (2000) show that selection of the optimal flow rate is very difficult, but that large artifacts causing either overestimation or underestimation of the flux can result from inappro-

priate flow rates and concentrations of flush gas. We recommend testing the effects of varying flow rates on both pressure differences and measured fluxes.

Inserting chamber bases deeply into the soil can minimize lateral diffusion of CO₂, but this advantage must be weighed against the perturbation effect of severing more roots and altering soil structure when chambers penetrated deeply into the soil. The depth to which chamber bases should be inserted into the soil to minimize lateral diffusion of CO₂ depends upon soil porosity, which in turn depends upon soil texture and water content. For short term (<10 min) deployments, Hutchinson and Livingston (2001) showed that 2.5 cm insertion depth is sufficient to limit this source of error to 1% in simulated fluxes from soils of low to moderate porosity (such as most wet soils and/or fine and medium textured soils), but that 9 cm was required for highly porous soils (such as most dry, highly aggregated, or coarse textured soils).

Fans are sometimes used to mix chamber air in both steady-state and non-steady-state designs, but they can also create artifacts by altering concentration gradients. Le Dantec et al. (1999) attribute higher estimates of soil respiration by the PP commercial system compared to the LiCor system to differences in wind speed within the chambers. The LiCor system obtains mixing of chamber air by returning air through a manifold at the bottom of the chamber while withdrawing air from the top, whereas the PP system has both air ports at the top of the chamber and relies upon a fan for mixing chamber air. Le Dantec et al. (1999) measured 0.9 m s⁻¹ wind speed within the PP chamber and only 0.4 m s⁻¹ windspeed within the LiCor chamber. They argue that the excessive air movement caused by the PP fan disrupts the high laminar boundary layer over the forest floor, thus increasing the CO₂ concentration gradient from the soil and overestimating the flux. They found that reducing the fan speed in the PP system reduced the measured flux. Fans are usually unnecessary for mixing of air within the chamber and may also create undesirable pressure differentials within the chamber headspace (Hutchinson et al., 2000).

2.2. Pressure artifacts

In our opinion, all chambers should have vents to equalize pressure between the inside and outside of

the chamber. Unvented designs can result in development of pressure differentials caused by circulating gases or by cooling or warming of chamber air. A small amount of gas exchange will occur through the vent, thus diluting chamber air with ambient air. The resulting error, which depends upon the dimensions of the vent and the headspace concentration of CO₂, should be very small. Longdoz et al. (2000) estimated the error due to CO₂ leaking out their vented chamber design to be 0.07 μmol m⁻² s⁻¹, which was <3% of their reported mean flux. A much larger error can result when an overpressurized chamber impedes diffusion of CO₂ out of the soil or when underpressurization sucks CO₂ out of the soil. The differences in CO₂ concentration between the soil and the chamber are much larger than the differences between the chamber and the ambient air, so it is best to relieve pressure differentials by allowing a small exchange of air between the chamber and the outside air. Hutchinson and Mosier (1981) calculated the ideal lengths and diameters of vent tubes based on chamber volume and the expected wind speeds under operating conditions.

Conen and Smith (1998) argue that the vent they used for non-steady-state static chamber measurements of N₂O fluxes caused an overestimation of the flux, because wind blowing across the vent opening presumably caused a Venturi effect that pulled air out of the chamber (and hence also pulled N₂O-enriched air out of the soil). While this effect is entirely possible, it is also possible that increases in headspace air temperature that may have developed within their non-vented aluminum chambers could have caused a pressure increase that would have depressed fluxes (Hutchinson and Livingston, 2001). Even when chambers are vented, placement of the chamber over the soil can trap air in such a way as to elevate pressure within the chamber headspace for several seconds (Fig. 2a), which could alter concentration gradients and reduce the measured flux. Without a vent, this effect is likely to be larger and persist longer. With possible errors in both directions for the vented and non-vented chambers used by Conen and Smith (1998), it is difficult to say which yielded the “true” flux, and perhaps both were somewhat in error. Furthermore, this study of N₂O fluxes in static chambers may not be applicable to measurements of CO₂ fluxes with gas circulating between an IRGA and the chamber. In the next few paragraphs, we discuss how pressure differences

caused by the air circulation could create a much larger error if not relieved by a vent.

Lund et al. (1999) demonstrated the large errors that can result from overpressurization. They placed a vented LiCor-6200 soil chamber inside a larger chamber that could be experimentally manipulated to yield above ambient pressures. Therefore, even though the soil flux chamber itself was properly vented, it was making measurements within an overpressurized environment. Pressure increases of only 0.5 Pa reduced measured fluxes by 20–70%, with the biggest errors encountered in dry soil. Fluxes were reduced by 70–90% as the pressure was increased by 6 Pa. These results are relevant to chamber measurements under normal operating conditions if the system of air circulation forces air through the chamber by pushing pressurized air into the chamber inlet. For example, some steady-state mode chamber systems pass pressurized gas through the chamber and measure the difference between CO₂ concentrations at the inlet and outlet of the chamber once an equilibrium concentration has been reached (Livingston and Hutchinson, 1995). Similarly if the chamber outlet is restricted relative to the inlet in any sort of pass-through or circulating airflow system, then the pressure within the chamber could be elevated. These design flaws could cause underestimation of the flux if the pressure within the chamber is a few tenths of a Pascal above ambient.

Fang and Moncrieff (1996, 1998) demonstrated that underpressurization of the chamber can result in overestimation of fluxes. In this case, if air is being pumped from a chamber for steady-state-based flux measurements, or if the chamber inlet is restricted relative to the outlet in a non-steady-state circulating system, then the pressure within the chamber headspace may decrease, causing CO₂-rich air to be sucked out of the soil. By restricting the chamber inlet relative to the outlet in an otherwise unvented chamber, Fang and Moncrieff (1998) demonstrated that a difference of only a few tenths of a Pascal caused a factor of 2 overestimation of flux in their steady-state mode chamber design using flow rates of 4 l min⁻¹. As the underpressurization increased to 2 Pa, the flux was overestimated by a factor of about 20. Smaller but substantial errors due to chamber underpressurization were observed in a similar experiment by Longdoz et al. (2000) using a 2.7 l min⁻¹ flow rate in an open steady-state chamber design. Although large errors caused by over-

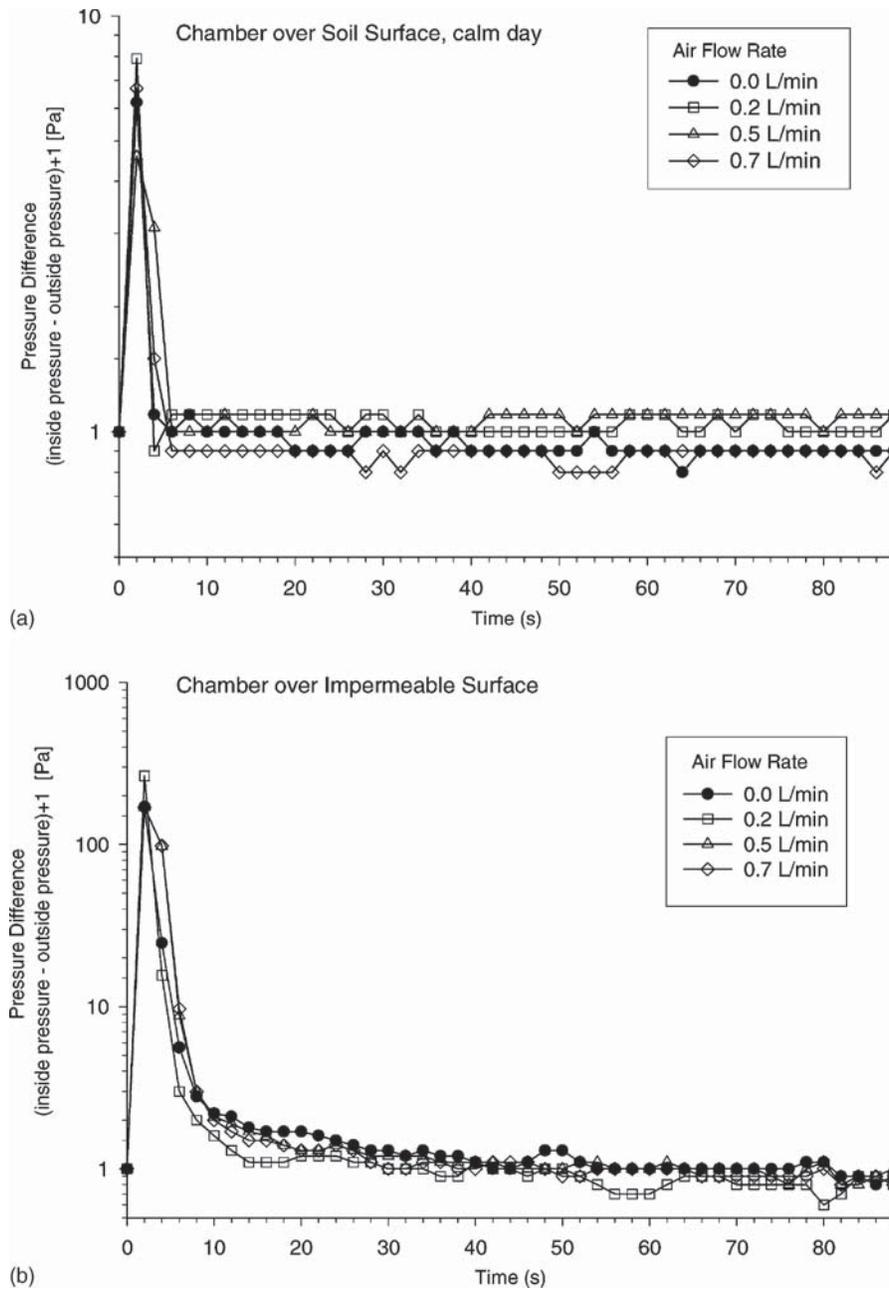


Fig. 2. Effects of chamber placement and airflow rate on internal chamber headspace pressure. To express pressures on a log scale, 1 was added to all values to make them positive. Hence, a plotted value of 1 is really 0 Pa, and a plotted value of 0.9 is really -0.1 Pa. Measurements made over a soil surface are shown in (a) and measurements over an impermeable surface are shown in (b).

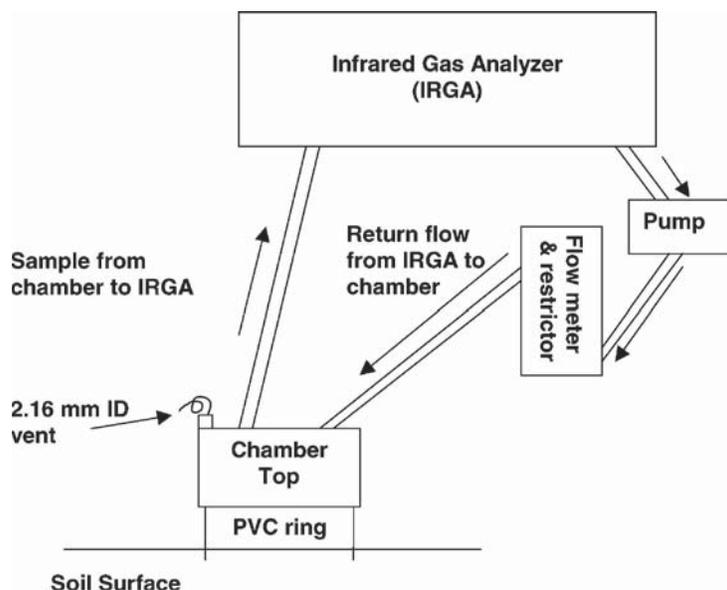


Fig. 3. Diagram of CO₂ chamber flux system. The chamber diameter is 25 cm.

underpressurization of the chamber are striking, they can be avoided by balancing flows or by the use of a properly sized vent and a proper flow rate.

We tested for pressure differentials in our vented non-steady-state chamber system (Fig. 3) both over an impermeable plastic surface and over a soil surface. A micro-manometer pressure meter (Infiltec model DM1) that displays pressure differences in increments of 0.1 Pa was connected to a chamber port through which we normally attach a temperature probe. To test the effects of the rate of airflow on the chamber air pressure, we placed a needle valve flow restrictor on either the inlet or outlet side of the chamber.

When measured over a soil surface, the pressure within the chamber increased by several Pascals within the first 2 s after putting the chamber in place, and then returned to ± 0.1 Pa of ambient pressure within 4–6 s (Fig. 2a). Thereafter, the pressure within the chamber remained within 0.1 Pa of ambient pressure (which is within the measurement error of our pressure meter), regardless of the circulating airflow rate of the pump. Similarly, Longdoz et al. (2000) report that their closed non-steady-state chamber and their open steady-state chamber were underpressurized relative to the ambient atmosphere by only 0.01 and 0.15 Pa, respectively, under normal operating conditions.

When we repeated the same procedure over an impermeable surface, the initial increase in chamber pressure was about 10 times higher, and returned to near ambient conditions only after 10–20 s (Fig. 2b). When no air was circulating through the chamber, the re-equilibration period was longer, but there were no differences in pressure re-equilibration among the different nonzero airflow rates. Apparently, our vent was too small to instantaneously relieve all of the initial pressure effect of chamber placement. Hence, some pressure equilibration probably occurs through the soil surface in our system, causing some unnatural mixing as CO₂-poor chamber air is forced into the soil. Whether this placement artifact is as ephemeral as implied in Fig. 2a, or whether the forcing of some air into the soil surface affects the subsequent flux measured over the entire 5 min period deserves further study.

The relatively large pressure differences reported by Lund et al. (1999) and Fang and Moncrieff (1998) were measured while the chamber was over the soil, and so they were continuously exceeding the capacity of air exchange across the soil surface to relieve the experimentally imposed pressure difference. Therefore, the large flux errors that Fang and Moncrieff (1998) documented were the result of significant flow restrictions at very high flow rates that sucked

significant amounts of CO₂-rich air out of the soil. This artifact can be easily avoided with a properly designed chamber vent and minimally restricted airflows. For example, Longdoz et al. (2000) calculated that slight underpressurization of their non-steady-state chamber during normal operation caused an overestimation of the CO₂ flux by only 0.4%, and the slightly larger underpressurization of their open steady-state chamber caused a flux overestimation by 6.3%.

We also tested the effects of flow restriction, which could cause pressure differences, on measured CO₂

fluxes. In all of our tests except one, we did not observe a significant effect of flow restriction on measured fluxes (Fig. 4). In one test, the flux was inversely related to flow rate (Fig. 4a), which would be consistent with CO₂-rich air being sucked out of the soil when the return flow to the chamber was restricted at low flow rates (i.e., the restrictor was upstream of the chamber inlet; Fig. 3). In the past, we have routinely slightly restricted the flow so that we would always have a consistent flow of 0.5 l air min⁻¹ regardless of the degree of discharge of the battery operating the

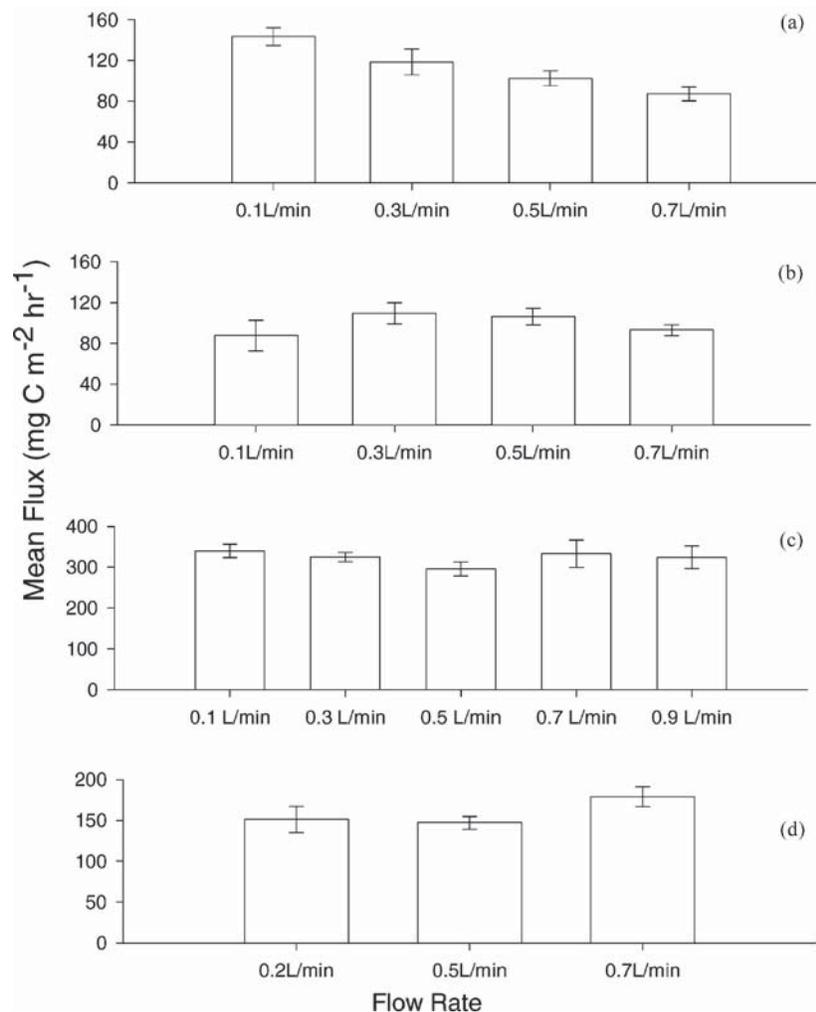


Fig. 4. Effects of flow rate on measured CO₂ fluxes of a single non-steady-state chamber measured repeatedly at (a) the Harvard Forest on 12 July 1999, (b) a second chamber in the Harvard Forest on 12 July 1999, (c) the Howland Forest on 1 July 1999, and (d) the Woods Hole Research Center on 28 April 2000. For each date and location, a flux measurement was made at each flow rate, and this process was repeated three times, with the order of the flow rates randomized each time. Means and standard errors of three measurements are presented.

pump. The data in Fig. 4 indicate that this restriction has not caused a detectable error in CO₂ fluxes most of the time, but it could have occasionally caused an overestimation of flux by about 15% (compare the fluxes measured at 0.5 and 0.71 air min⁻¹ in Fig. 4a). We can eliminate this potential error by either allowing the pump to always operate without flow restriction and/or by using a slightly larger vent.

Moving the needle valve flow restrictor to the outlet side of the chamber (the opposite side as that shown in Fig. 3) caused the buildup of a slight positive pressure (0.3–0.5 Pa) within the chamber for flow rates between 0.2 and 0.71 min⁻¹. Apparently, the air pump was returning slightly more air to the chamber than the needle valve was permitting to be withdrawn from the chamber, and the excess was not exiting via the vent rapidly enough. An underestimate of CO₂ fluxes might be expected under these conditions. This result indicates the need to directly measure pressure differences for any configuration or change in configuration of a chamber plumbing design.

Another potential problem arises from pressure differentials caused by wind. Kimball and Lemon (1971) demonstrated that wind affected the flux of water vapor through coarse mulch and shallow soil, although they also concluded that diffusion is probably the dominant process affecting soil aeration (i.e., flux of oxygen, and by extension, CO₂). Because recent studies have demonstrated the potentially large effects of small pressure changes within chambers on CO₂ flux measurements, the accuracy of flux measurements made under windy conditions probably deserves renewed attention. We observed variation of chamber pressure between -0.7 and +0.9 Pa during a moderately windy day, with an average of about -0.2 Pa (Fig. 5). Conen and Smith (1998) reported consistently reduced chamber headspace pressures when a vented static chamber was exposed to wind. In general, the chamber pressure should be allowed to vary as gusts of wind cause the pressure within the surface soils to vary, but the effects of this variation can be very complex, and the topic merits more systematic study.

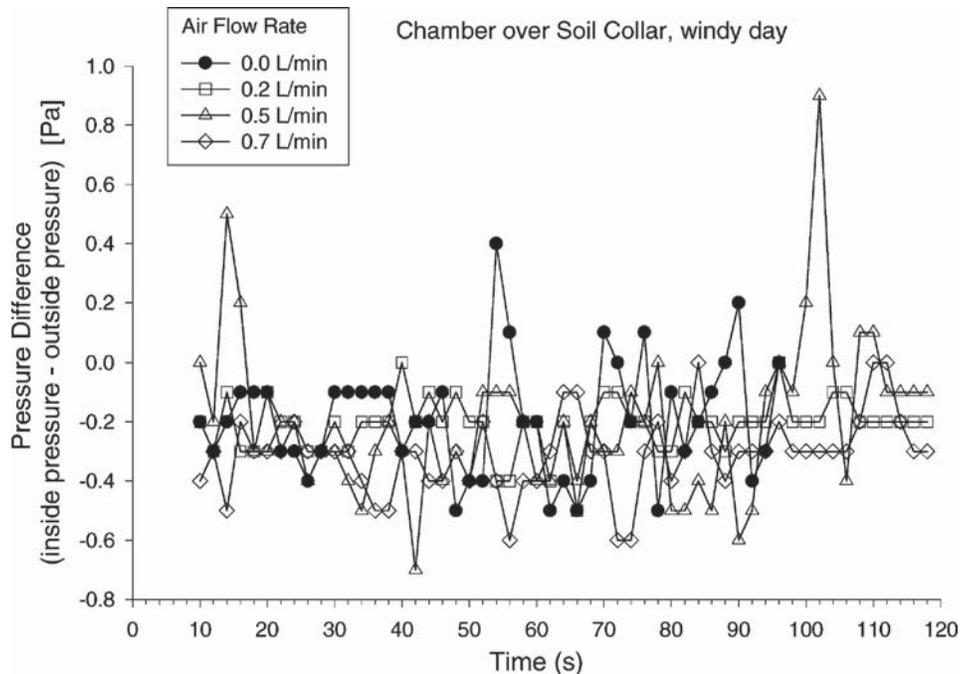


Fig. 5. Internal chamber headspace pressure measured on a moderately windy day while the chamber was over a soil surface. In this case, the initial increase in pressure shown in Fig. 1a was not recorded, so measurements began at 8 s after chamber placement. Measurements were repeated at the four different airflow rates indicated.

In summary, pressure differences can cause large errors in flux measurements, especially when the pressure differences persist even when the chamber is over a soil surface where gas can exchange freely. A rapid change in pressure occurs during chamber placement, but is dissipated to ≤ 0.1 Pa within seconds over a soil surface, perhaps resulting in small and inconsistent errors. Differences in wind could also influence the magnitude of this error, but the effects of wind are poorly understood. Moreover, errors due to chamber pressure artifacts can be minimized, and perhaps almost eliminated, with an appropriately sized vent. Testing a chamber design for these pressure differences and their effects on flux measurements is recommended for any new or modified chamber and flux system design.

3. Sampling uncertainties

3.1. Spatial heterogeneity

Chambers offer both advantages and disadvantages for dealing with spatial heterogeneity of fluxes. Where variation within the landscape is recognizable, chamber deployment can be stratified to measure the importance of that variability. At the Harvard Forest of central Massachusetts, for example, stratifying the area by soil drainage class within the footprint of a micrometeorological tower revealed that the very poorly drained areas had CO₂ emissions about 40% lower than better drained soils (Davidson et al., 1998). On the other hand, heterogeneity also exists within sites that appear mostly homogeneous to the investigator's eye. Hence the investigator is always faced with the question of how many chambers are needed to adequately estimate the mean and variance of CO₂ fluxes within a site that is considered relatively homogeneous.

The area covered by a chamber influences the number of chambers needed. In our experience in forested ecosystems, the difference in fluxes measured 1 m apart or less can be as large as differences measured tens of meters apart within an area of similar soil drainage class and vegetation type. Hence, the variation that is relevant to chamber measurements is often at the scale of centimeters, reflecting the sizes of rocks, disturbances by soil fauna, pockets of fine root proliferation, and remnants of decaying organic matter. In row-crop agriculture, the spacing of rows

is obviously important. The variance among flux measurements made by chambers that measure fluxes over only a few square centimeters will probably be larger than the variance among measurements made by larger chambers, because the larger is the chamber, the greater the area will be over which it integrates centimeter-scale variability. A disadvantage of the LiCor-6200/6400 chamber design is that it is only 72 cm², whereas chambers of 300–700 cm² are not difficult to make from PVC or other types of tubing and to deploy and to use (e.g., Fig. 3). Measuring fluxes over the course of a few hours with chambers of 300–500 cm² distributed over a plots of a few hundred square meters, we have found that the coefficient of variation (CV) is usually on the order of about 30% for CO₂ fluxes (Davidson et al., 1998, 2000). Production of N₂O and CH₄ tends to be localized in “hot spots” to a greater extent than CO₂, and so CVs tend to be higher for measurements of these gases with the same sized chambers (Verchot et al., 1999, 2000).

In a study of tropical forests and cattle pastures, we used a chamber of about 300 cm² (which was the largest size of thin-walled PVC pipe that we could find in northern Brazil; Davidson et al., 2000). We made 36 CO₂ chamber flux measurements in relatively homogeneous plots of each land use type. The measurements were repeated in wet and dry seasons. We compared the mean of the population of 36 measurements to means of randomly selecting groups of eight fluxes from the population of 36. At both sites and seasons, 100% of the 1000 randomly selected groups of eight fluxes had means within 50% of the full population mean (Table 1). About 98% of the means of groups of eight fluxes were within 25% of the full population mean, and about 70% were within 10% of the full population mean. We obtained similar results at the Harvard Forest with 500 cm² chambers, where 100, 97 and 61% of randomly selected means of six fluxes fell within 50, 25, and 10% of the full population mean of 36 flux measurements, respectively.

Another approach to estimate confidence in the estimate of the mean flux is to use the mean and standard deviation from a large sampling, such as our 36 measurements made in a single day, to estimate the number of individual flux measurements needed for various degrees of precision at various confidence levels (Folorunso and Rolston, 1984). First, the distribution of 36 measurements was tested for normality;

Table 1

The percentage of the means of subsets of eight chamber flux measurements that fall within an interval of the mean of the full population of 36 measurements. The subsets of eight flux measurements were selected randomly, with replacement, from the full population of 36 flux measurements^a

Interval about the full population mean (%)	Forest		Pasture	
	Wet season	Dry season	Wet season	Dry season
±50	100	100	100	100
±25	97.4	99.3	98.3	98.4
±10	63.3	71.3	71.9	68.4

^a From unpublished data of Louis Verchot for primary forest and cattle pastures of the eastern Amazon, Brazil (Davidson et al., 2000; Verchot et al., 1999, 2000).

a non-normal distribution would require transformation, which was not the case here. Then the following equation was applied (Folorunso and Rolston, 1984):

$$n = \left[\frac{ts}{\text{range}/2} \right]^2$$

where n is the sample number requirement, t the t -statistic for a given confidence level and degrees of freedom, s the standard deviation of the full population of measurements, and range the width of the desired interval about the full population mean in which a smaller sample mean is expected to fall (i.e., ±20% of the full population mean). The results in Table 2 demonstrate that a mean based on the six flux measurements that we typically make per date and drainage class area at the Harvard Forest will fall within ±20% of the full population mean with 80–90% confidence, within ±30% with 95% confidence, and within ±40% with 99% confidence. This type of intensive study can help guide researchers to determine how many flux measurements are routinely needed per site and date, depending upon what tem-

poral or spatial differences that the study is attempting to identify and at what level of statistical confidence.

Clearly, large numbers of flux measurements are ideal, but logistical constraints of labor and time often limit the number of measurements that are feasible. By characterizing a relatively homogeneous site with about 6–8 flux measurements performed within an hour, 4–8 such sites can be measured within a day.

3.2. Temporal biases

Diel and seasonal variation are important considerations in sampling designs. Diel variation is somewhat less important in heavily shaded forested areas than in agricultural fields (Davidson et al., 2000), but it is still important in many temperate forests. By characterizing the diel variation, which ranged ±25% of the daily mean, we found that mid-morning fluxes closely approximated the 24 h mean flux at the Harvard Forest of Massachusetts (Davidson et al., 1998). The peak soil temperatures and CO₂ fluxes usually occur in the mid to late afternoon. If measurements are

Table 2

Number of flux measurements required for various degrees of precision (within ±10 to ±50% of the full population mean) and at various confidence levels (80–99%) based on a population of 36 measurements at the Harvard Forest in July 2001, where the mean was 147 mg C m⁻² h⁻¹ and the standard deviation was 46

Interval about the full population mean (%)	99% confidence (α = 0.01)	95% confidence (α = 0.05)	90% confidence (α = 0.10)	80% confidence (α = 0.20)
±10	75	41	29	17
±20	19	10	7	4
±30	8	5	3	2
±40	5	3	2	1
±50	3	2	1	1

consistently made at the warmest part of the day, this temporal sampling bias could cause a significant error in extrapolated daily rates. In addition to soil temperature, plant activity that is related to light could affect soil respiration. A sharp drop in soil respiration was observed after sunset in a cattle pasture that did not covary with more slowly decreasing soil temperature (Davidson et al., 2000). If a daily manual sampling regime spans several hours, then the order of measuring sites should be randomized, so that diel variation does not become confounded with differences among study sites measured repeatedly on different days.

Automated chambers offer a means of obtaining good temporal resolution of fluxes over diel cycles and around wetting events (Crill et al., 2000). However, the tradeoff is that the expense of deploying and maintaining automated chambers often limits their number to a few chambers. They are also more difficult to

move around. Hence the additional temporal resolution comes at the expense of poorer characterization of spatial heterogeneity. Where resources are best deployed depends upon the objectives of the study. Ideally, deployment of a few continuously operating automated chambers and several chambers that are manually sampled less frequently would provide good characterization of both spatial and temporal variation.

In two-part chamber designs where the chamber base is left in place in the field, the initial effects of severing roots and disturbing soil structure during chamber insertion becomes moot after a few days or weeks. In cases where chamber bases cannot be left in place, it is necessary to test how long after chamber insertion one must wait before measuring fluxes. In clayey soils of Amazonian cattle pastures, we found it sufficient to wait only 30 min after inserting chambers about 2 cm (Verchot et al., 1999), but we prefer to wait

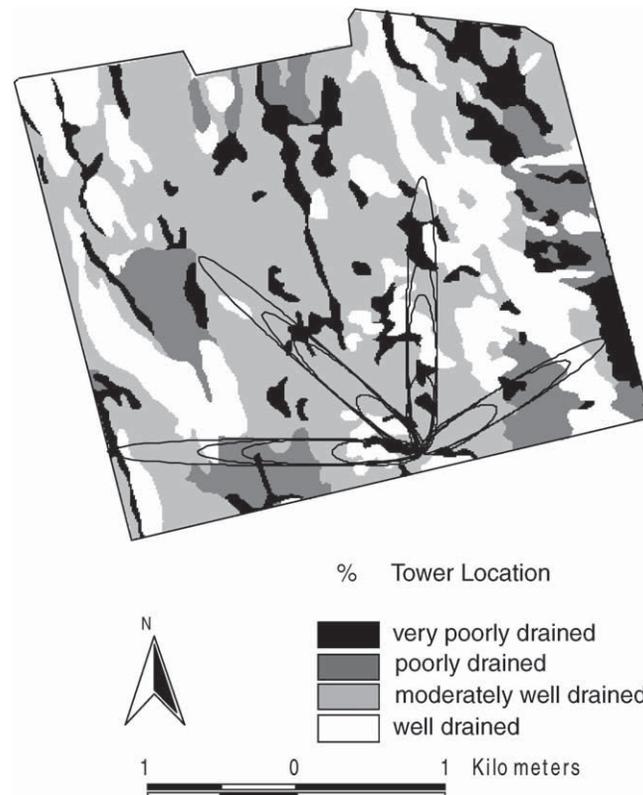


Fig. 6. Soil map of the Howland Experimental Forest area (from Levine et al., 1994), with ellipses overlaid as purported tower footprints of four lengths (600, 1200, 1500, and 2100 m) at four rotation angles from the tower site (270°W, 315°NW, 0°N, and 55°NE). The dominant wind direction is from the northwest.

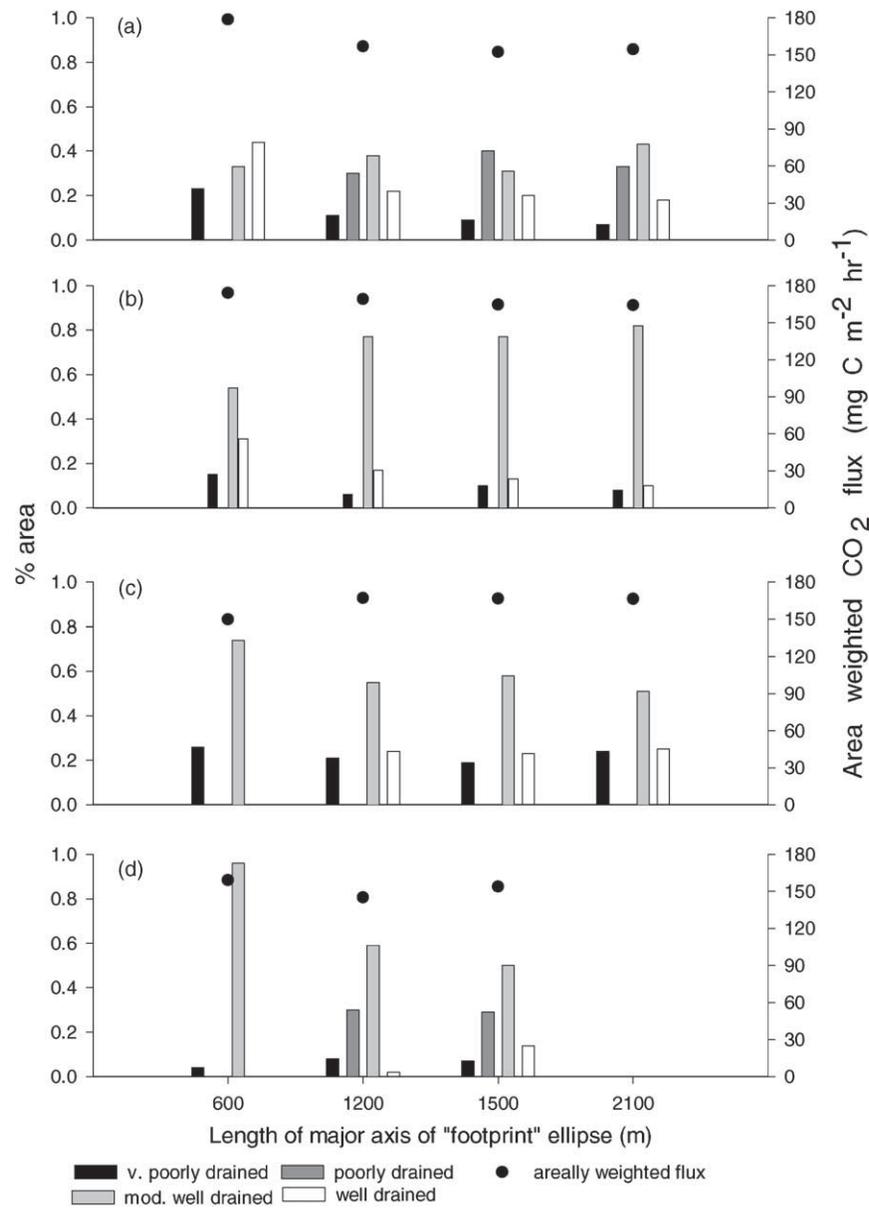


Fig. 7. The areas covered by each soil drainage class within each ellipse (bars and left Y-axis) and the area-weighted flux estimates (filled circles and right Y-axis) of each of the purported footprint ellipses shown in Fig. 6: (a) 270°W; (b) 315°NW; (c) 0°N; (d) 55°NE. Soil respiration measurements from 19 August 1997 (Savage and Davidson, 2001) were applied by drainage class, using the following mean estimates: 117 mg C m⁻² h⁻¹ in very poorly and poorly drained soils, 161 mg C m⁻² h⁻¹ in moderately well drained soils, and 224 mg C m⁻² h⁻¹ in well drained soils. The average hourly total ecosystem respiration estimated from a function of soil temperature based on nighttime eddy covariance on the tower was 205 mg C m⁻² h⁻¹.

a day whenever possible. There is no rule of thumb that can be reliably applied to all soil and vegetation types, and there is no substitute for pilot studies that measure the repeatability of flux estimates made following chamber insertion and throughout diel cycles.

4. Comparing chamber-based and tower-based respiration measurements

The footprint of a tower depends upon wind direction and speed and the heights of the tower and vegetation. A problem arises of how to compare total ecosystem respiration measured at the tower with soil respiration over a comparable area measured by chambers. How should the chambers be deployed to facilitate this comparison?

At the Howland Forest in central Maine, like the Harvard Forest in Massachusetts, we have determined that soil drainage class is an important controller of variation of soil CO₂ fluxes within the landscape (Savage and Davidson, 2001). Well drained soils usually have emissions two times larger than emissions from very poorly drained swampy areas. Taking advantage of a high-resolution soil drainage class map (Levine et al., 1994), we applied measured mean fluxes by drainage class to the soil map within a geographic information system (GIS). We overlaid ellipses of varying length to the dominant north-western and northern wind directions and calculated the average area-weighted flux for each ellipse (Fig. 6). Each ellipse was considered a possible tower footprint. Although there was significant variation in the proportional areas of well drained and very poorly drained soils among the ellipses, the effect of this spatial heterogeneity on area-weighted mean CO₂ fluxes was mostly fortuitously cancelled. The purported footprints that had larger areas of very poorly drained soils also happened to have larger areas of well drained soils and smaller areas of moderately well drained soils, resulting in area-weighted calculations of soil respiration that were at most only 15% different from other purported footprints (Fig. 7). A more sophisticated footprint analysis would give greater weighting to areas closer to the tower, but we found no consistent effect of ellipse size on the estimated area-weighted flux.

The mean total ecosystem respiration rate measured at the tower was 205 mg C m⁻² h⁻¹ and our estimates of area-weighted soil respiration were 150–180 mg C m⁻² h⁻¹, indicating that soil respiration was 73–88% of total ecosystem respiration. In this case, because the contributions from well drained soils (above average fluxes) and very poorly drained soils (below average fluxes) tended to cancel, we could have measured soil respiration only in the moderately well drained site at the base of the tower (161 mg C m⁻² h⁻¹) to obtain a reasonable estimate of average soil respiration being about 79% of total ecosystem respiration. However, this result could not have been predicted a priori and it is probably not a safe assumption to make for most tower-centric studies. Moreover, in addition to reporting that soil respiration was about 80% of total ecosystem respiration, we can now report that the uncertainty of this estimate due specifically to spatial heterogeneity at the landscape scale is about ±8%. This source of uncertainty may vary among landscapes and tower locations.

5. Conclusions

Chamber artifacts and biases can cause serious errors in soil respiration measurements, but these sources of error have been well described in the literature and can be minimized or avoided with proper chamber designs, data analyses, and spatial and temporal sampling regimes. The error caused by altering concentration gradients within the soil causes a bias towards underestimation of fluxes, but other common potential errors of chamber measurements are just as likely to cause underestimation as overestimation of fluxes. Therefore, it is curious that most disagreements between chamber-based and eddy covariance based estimates of soil respiration have consistently reported chamber-based measurements as larger (Goulden et al., 1996b; Hollinger et al., 1999; Janssens et al., 2000; Law et al., 1999; Norman et al., 1997). If the error was predominantly on the side of chamber measurements, the only mechanism that we could invoke that might explain overestimation of fluxes by chambers would be consistent underpressurization of chambers due to improper vents and flow restrictions on the upstream side of the chamber inlet. In our experience, however, only a modest and inconsistent error

was observed from slight underpressurization of the chamber, which can be minimized or avoided. Hence, disagreements between tower- and chamber-based estimates of respiration cannot currently be readily attributed to any of the known and well-characterized sources of error in chamber measurements.

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