Optimum soil water for soil respiration before and after amendment with glucose in humid tropical acrisols and a boreal mor layer

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Accepted 22 March 2000

Abstract

The measurements of water content most often used by soil microbiologists are gravimetric water content \( W_g \), volumetric water content \( W_v \), percentage of water holding capacity (\%WHC), percentage of water filled porosity (\%WFP), and water potential \( W_p \). This study investigated the relationship of these water measurements to soil respiration, before and after substrate addition (glucose, nitrogen and phosphorus), focusing on the water contents at which the exponential respiration rates after amendments \( \mu \) were at their maximum. Three tropical Haplic Acrisols and one boreal mor layer were used. One Acrisol had high loss of ignition (LOI 17.4% w/w) and high clay content. The second Acrisol had high clay content and low LOI (3.9%), and the third had low clay content and low LOI (5.7%). The mor layer had a LOI of 95.6%. The maximum \( \mu \) was found at \(-15\) kPa, (50% WHC), irrespectively of the soil type. The decrease in \( \mu \) above \(-15\) kPa was not as pronounced for the Swedish mor layer as for the Acrisols. At water potentials above \(-2\) kPa the respiration rate was no longer exponential for the Acrisols, making it impossible to define \( \mu \). For \( W_g \), WFP, and \( W_v \) the maximum differed greatly between the soils. The maximum for basal respiration was found to be at higher water content than the maximum for \( \mu \). However, the water contents used were not high enough to specify optimum water content for basal respiration except for the humus rich Acrisol which was at 66% of the WHC or about \(-5\) kPa. It is suggested that respiration measurements of the Acrisols, after substrate addition, should not be made using water contents exceeding \(-15\) kPa or 50% WHC. Because of the dependency of method, WHC must be defined and complemented by water potential. The use of WFP, \( W_v \), and \( W_g \) is not recommended for adjusting the water contents of these soils.

Keywords: Microbial activity; Water potential; Water holding capacity; Water filled porespace; Gravimetric water content; Soil

1. Introduction

The microbial activity, measured as \( \text{CO}_2 \) evolution rate, is commonly used when evaluating the effects of different land use (e.g., Rout and Gupta, 1989; Luizao et al., 1992; Basu and Behera, 1993; Ruess and Seagle, 1994). Exponential \( \text{CO}_2 \) evolution rate after addition of easily available substrate (e.g. glucose) has been used to investigate anthropogenic induced changes in the soil (Johansson et al., 1998) and differences between litter fractions (Marstorp, 1996).

It is widely recognized that any study on microbial activity needs to consider the water relation of the soil microorganisms (e.g. Harris, 1981). Usually, the response has been to adjust the water content to a specific value, and measure the microbial activity at that water content (e.g., Luizao et al., 1992; Feigel et al., 1995; Johnson et al., 1996). However, there has been no agreement on methods for water measurement, and consequently, even though quite a number

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PH: S0038-0717(00)00073-0
of reports from soils around the world have been published, little consensus has followed.

The problem is further complicated by the suspicion that the activity and water relation might differ for different microbial indices. Most studies have assumed that the water relation to soil respiration before and after substrate addition would be the same. It is possible that the addition of substrate itself has an effect on the water content at maximum microbial activity. Reasons for this may be that the osmotic potential of the soil solution is changed, or that the kinetics of substrate diffusion is different if new easily available substrate is added.

The measurements of water content most often used by soil microbiologists have been gravimetric water content ($W_g$), volumetric water content ($W_v$), percentage of water holding capacity (%WHC), percentage of filled porosity (%WFP), and water potential ($W_p$). Gravimetric water content ($W_g$) is expressed as the mass of water per mass of dry soil. It is calculated as the mass difference before and after heating a subsample of the soil to a defined temperature during a specified time (often 12 h at 105°C). The disadvantage is that the bulk density of the sample is not taken into account. Because the microbially important variables, porosity and organic content of the soil varies with the bulk density, it is very complicated to generalize results from samples of different bulk densities (Linn and Doran, 1984; Neilson and Pepper, 1990) and it can only be used for very similarly structured soil.

Volumetric water content ($W_v$) and Water filled porosity (WFP) allows soils of different densities to be compared because they are expressed relative to volume instead of mass. $W_v$ is expressed relative to the total volume and WFP to the total pore volume of the sample. For example, West et al. (1992), concluded that respiration had a linear relation to $W_v$ independently of the rate at which four soils of differing texture were dried. WFP is, according to Grundmann et al. (1995), the water unit that is easiest to compare between soils, and also takes air filled pore space into account. Johnson et al. (1996) refers to unpublished data when stating that respiration rate reaches a plateau between 52 and 60% of WFP and then declines rapidly when exceeding 60%. In an often-cited report, Linn and Doran (1984) determined Water Filled Porosity (WFP) and CO₂ evolution in untilled and tilled soil. Their results indicated a maximum at 60%. In a later and less well-known report, Doran et al. (1990) extended this work to 18 soils of different textures. Medium to fine textured soils had optimum activity above 60% WFP, while coarse textured soils had their maximum below 60% WFP. A third group consisting of two highly weathered Hawaiian soils had their maximum above 70%. If WFP is used, one is limited to measurements on samples with known bulk density (undisturbed samples) or need to have a procedure for compacting the soil to a well-defined bulk density (Linn and Doran, 1984). Neilson and Pepper (1990) measured soil respiration after compacting soils to different bulk densities and pointed out the limitation of using water filled pore space as an index of soil aeration for soils of very different bulk densities. It can also be noted that all the 18 soils in the study of Doran et al. (1990) were agricultural soils and had bulk densities above 1 g cm⁻³.

Water holding capacity (WHC) is possibly the most used water measure in soil microbiology (Linn and Doran, 1984). Generally, a ratio of the WHC of 0.5–0.7 is said to be the water content for maximum respiration (Linn and Doran, 1984), but sometimes a value as low as 0.4 is stated (Killham, 1994). Linn and Doran (1984) criticised the use of WHC because they argued it depends on soil type, and that the methods for its determination are often poorly defined. Indeed, few reports, which adjusted the water content to a particular ratio of WHC, mention the procedure for obtaining the value. Since, for example, Carter (1993) describes three methods for WHC determination of peat soils only, and Lowery et al. (1996) describes one method for “Field Water Holding Capacity”, it is not clear which method was used if no references are given.

Water potential and its equivalent, water activity, is often promoted as a measure of water available to microbes as it relates to processes with the same consequences for microorganisms independently of soil type (e.g., Reid, 1980; Killham, 1994). The microbial cells need to equilibrate their internal water potential to the surrounding soil, which could limit microbial growth and activity (Harris, 1981). Another limiting factor might be substrate diffusion, which is related to water potential because the thickness of the water film on the soil particles decreases with decreasing water potential (Papendick and Campbell, 1981). Sparling et al. (1989) demonstrated that the substrate induced respiration (SIR) responded very similarly to osmotic potential over a wide range of soils (including soils from dry, intermediate and wet moisture regimes). SIR decreased log-linearly from −400 to −8000 kPa. Orchard et al. (1992) also found a log-linear relationship between water potential and respiration. The slope was similar for two different soils and for different drying treatments. The same result was achieved with soils dried and rewetted four times (Orchard and Cook, 1983). The problem with the water potential measurement is that the optimum activity is expected in the range of −100 to 0 kPa, where measurements tend to be difficult, and small changes in water potential might represent large differences in relative water content. Therefore, most studies have measured water potentials well below the optimum for microbial activity and
growth, and have tended to emphasize the driest conditions for growth and activity (Skopp et al., 1990). Often volumetric water content is suggested to better reflect the limited aeration in soils (e.g., Papendick and Campbell, 1981; Skopp et al., 1990; Tate, 1995). According to Skopp et al. (1990): “the prediction of microbial growth and activity (non-equilibrium processes) from physical principles does not appear possible using only the water activity (an equilibrium property)”.

To obtain further information about microbial activity in soil at various soil moisture contents, we examined the relationship between four different water measures ($W_g$, %WFP, %WHC and $W_p$) and basal respiration, and between these water measures and the exponential increase in respiration after amendments with glucose ($\mu$). We focused on the water contents where $\mu$ was at its maximum. Three tropical Acrisols and one boreal mor layer were studied.

2. Materials and methods

2.1. Research area

Three of the soils were sampled in the Mendolong research area, situated at an altitude of 650–750 m at the foothills of Mt. Lumako 35 km southeast of the coastal city Sipitang (115.5° E, 5.0° N) Sabah, Malaysia. The vegetation consisted of lowland hill dipterocarp forest (Whitmore, 1984) which was lightly selectively logged in 1981. The mean annual precipitation was 3350 mm and the mean yearly runoff was 1995 mm (August 1985–July 1990, Malmer, 1992). A fourth soil was sampled from the mor layer of a boreal haplic Podsol outside the Swedish University of Agricultural Sciences, Umeå (14° E, 64° N). The mean annual precipitation for that area was 630 mm, and the mean annual temperature 2.8°C. The vegetation was a mixed coniferous forest (Pinus sylvestris and Pinus sylvestris) with a field layer dominated by Vaccinium myrtillus.

Haplic Acrisols developed on sandstones and shales predominate large parts of S.E. Asia. Topsoil textures in Acrisols of this area range from sandy loam to clay loam. Porosity in undisturbed forest soil is high, ranging from 59 to 70% (Malmer and Grip, 1990), and bulk densities are as low as 0.64 g cm$^{-2}$ in the uppermost 5 cm of the soil (Malmer et al., 1998). The loss of ignition (LOI, %w/w) in the topsoil is in the range 2.5–20% (Malmer et al., 1998). Three different Acrisol profiles were sampled (Table 1) by bulking four soil sampling rings (diameter = 72 mm, height = 50 mm) for each profile to three composite samples. The profiles were chosen to cover the most common range of organic and clay content in the area. One profile had high organic content (LOI 17.4%) and high clay content, one profile had high clay content and low LOI (3.9%) and one profile had low clay content and low LOI (5.7%). The Swedish sample was collected from the organic mor layer (LOI 95.6%) of a Podsol having negligible clay content.

The Malaysian samples were frozen prior to transport by air to Sweden and then kept in a freezer. A few days before measurements, the samples were transferred to room temperature. The Swedish soil was kept at 5°C before being equilibrated to room temperature.

2.2. Water measurements

All soils were first tested for WHC and $W_g$. Percentage WFP was calculated as shown in Eq. (2). $W_p$ was measured independently for all replicates of the adjusted soils.

In the first study set, the Acrisols were adjusted to a %WFP of 40, 50, 60, 70 or 80. Four replicates of each soil were moistened with deionized water to achieve each water content used for microbial measurement. Because the samples at the two highest %WFP did not show log-linear growth, a new set of samples of the Ac and As soil were adjusted to 36, 42, 48, 54 or 60% WHC. The basal respiration for the As and Ac soils of the first study was not satisfactory due to unexpected temperature fluctuations in the laboratory. Therefore, only basal respiration measurements from the second set was used for these soils.

It was shown by Nordgren et al. (1988) that a water content of 250% (w/w) of the organic content was giving the maximum $\mu$ for three mor layers. Therefore, the Swedish mor layer in the present study was adjusted to 150, 200, 250, 300, 350 or 400% of the organic content with three replicates for each water content. However, because no decrease was seen above 250%, a new set of samples was adjusted to 200, 250, 300, 550 or 700% of the organic content.

Gravimetric water content was measured as:

$$W_g = (W_{fw} - W_{dw})/W_{dw}$$

(1)

$W_{fw}$ was the mass of the moist soil and $W_{dw}$ was the mass of the soil dried at 105°C for 12 h.
Water filled porosity was calculated as:

\[
\text{WFP} = \frac{(W_{tw} - W_{dw})/\rho_w}{V_p}
\]  

(2)

\(W_{dw}\) was as above and \(V_p = W_{tw}/\rho_b - W_{dw}/(\text{LOI} \times 1.3 + (1 - \text{LOI}) \times 2.65)\). The density of the mineral solids was assumed to be 2.65 g cm\(^{-3}\), and the density of organic solids 1.3 g cm\(^{-3}\) (represented by LOI, i.e. the ratio lost after 4 h in 500°C to the dry weight before ignition). \(W_{tw}\) was, in this case, the mass of the soil in question after loose packing in the container. \(\rho_b\) was the bulk density (g cm\(^{-3}\)) of the sample and \(\rho_w\) the density of water (g cm\(^{-3}\)).

Water holding capacity (WHC) was measured by soaking the soil for 12 h in a plastic cylinder (diameter = 35 mm, height = 40 mm) with a 0.3 mm nylon mesh in the bottom. After the soil was drained for 1 h, the soil was emptied into a container and the WHC was determined as for gravimetric water content.

Water potential was measured by the filter paper method (Deka et al., 1995). In each of the containers used for incubating the soil samples, a Whatman No. 42 filter paper was placed in good contact with the soil. This means that the effective potential measured was the matrix potential (Al Khafaf and Hanks, 1974). After equilibration for 6 days the filter paper was weighed, dried at 105°C, and reweighed. Deka et al. (1995) made a regression of matric potential measured by the filter paper technique against measurements made using tensiometers and a psychrometer over potentials ranging between \(-1\) kPa and \(-10\) MPa and obtained an \(R^2\) value of 0.995 indicating a good agreement between the methods.

2.3. Microbial measurements

The respiration was measured every hour at 20°C (±0.1°C) in a respirometer (Respicond III and IV, Nordgren Innovations, Djäkneboda 99, SE-918 93 Bygdeå, Sweden). The respirometer uses KOH to capture CO\(_2\) respired from the samples. Platinum electrodes measure changes in conductivity in the KOH solution. From the decrease in conductivity the amount of CO\(_2\) respired was calculated (Nordgren, 1988, 1992). For the mineral Acrisols 20 g soil on a dry weight basis was used for each incubation. For the Swedish mor layer, 1 g on a dry weight basis was used. Basal respiration rate (\(BRESP\)) was calculated as the average respiration rate of 40 hourly measurements after the respiration had stabilized. The time needed for stabilization was about 120 h (Fig. 1). The exponential increase in respiration (\(\mu\)) was determined after addition of a powder containing 0.2 g glucose, 5 mg KH\(_2\)PO\(_4\) and 32.5 mg NH\(_4\)SO\(_4\). It was calculated as the best fit of the linear phase after logarithmic transformation to the base 10 (Nordgren et al., 1988). The exponential phase ranged between 12 and 26 h (Fig. 1).

3. Results

3.1. The exponential respiration increase (\(\mu\))

All soils showed similar response when water potential decreased below \(-10\) kPa (Fig. 2). The relation could be described by the log-linear regression (Eq. (3)) In this equation, \(W_p\) should be expressed in kPa:

\[
\mu = 5.03 \times 10^{-2} - 3.5 \times 10^{-3} \ln(-W_p)
\]  

(3)

\(R^2 = 0.709\)

At water potentials higher than \(-10\) kPa the \(\mu\) for microorganisms in the Ph soil did not decrease as in the Acrisols (Fig. 2) and has therefore not been
included in the log-linear regression (Eq. (4)) of the data between −2 and −10 kPa:

\[ \mu = 1.05 \times 10^{-2} + 1.11 \times 10^{-2} \ln(-W_p) \]

\[ R^2 = 0.527 \]

Most water potentials higher than −2 kPa were excluded because above −2 kPa the growth rates were not exponential, and therefore \( \mu \) could not be determined. The two relationships cross at −15 kPa. The Ph soil had the same relationship as the Acrisols until the maximum at about −15 kPa. However, the plateau of the maximum extended to higher water potentials for the Ph soil compared to the Acrisols (about −2 kPa). Therefore, an alternative quadratic regression (Eq. (5)) using data up to −2 kPa was calculated for the Ph soil:

\[ \mu = 6.20 \times 10^{-9} (-W_p)^2 - 2.00 \times 10^{-5} (-W_p) \]

\[ + 4.09 \times 10^{-2} \]

\[ R^2 = 0.713 \]

Also for WHC (Fig. 3a), the optimum for the different soils were close (43–48%). The more organic-rich soils however had less steep optima. The optima for WFP (Fig. 3b) had a larger range (30–45%), where the soils with higher organic content had the higher values. The optimum growth rate for \( W_g \) differed largely ranging from below 0.4 to 4.0 g g\(^{-1}\) (Fig. 3c).

### 3.2. Basal respiration

In all soils the basal respiration had its maximum at higher water contents than the maximum for \( \mu \) (Fig. 4). Using a quadratic relationship, the maximum basal respiration for the Ah soil was at 67% of the WHC (corresponding to about −5 kPa);

![Fig. 2. The relationship between water potential (\( W_p \)) and specific growth rate (\( \mu \)) in the four studied soils. For most water potentials above −2 kPa, growth rate was not exponential, and therefore \( \mu \) could not be determined.](image)

![Fig. 3. The relationship between water content and specific growth rate (\( \mu \)) in the four studied soils. (a) Moisture expressed as %WHC; (b) moisture expressed as %WFP; (c) moisture expressed as \( W_g \). For most water contents corresponding to water potentials above −2 kPa, growth rate was not exponential, and therefore \( \mu \) could not be determined.](image)
For the other soils the respiration was not measured at water contents high enough for the maximum to be achieved. At the measured water contents the $R^2$ for a linear relationship to %WHC were as low as 0.28 for the As soil and 0.16 for the Ac soil. The Ph soil, however, had a strong linear relationship (Eq. (7)):

\[
\text{BRESP} = 3.70 \times 10^{-5} (\%\text{WHC}) + 1.50 \times 10^{-3}
\]

\[
R^2 = 0.951
\]

4. Discussion

Many studies have found a log-linear relation between water potential and microbial activity (e.g., Orchard and Cook, 1983; Cook et al., 1985; Orchard et al., 1992). Few, however, have used water potential at such high water contents that they have been able to define a maximum for microbial activity. Ross (1989) used WHC and obtained maximum microbial C with soils wetted to 50% or more of the WHC. This maximum corresponded to a water potential of about $-10$ kPa or higher. This result was in close accordance with the maximum for $\mu$ obtained for all the soils in this study. Also, Rixon and Bridge (1968) reported limited aeration in the range of $-1$ to $-10$ kPa when using the respiratory quotient to indicate full aeration, and Miller and Jonson (1964) noted maximum soil respiration at $-50$ kPa in one soil whereas it was $-15$ kPa in four other soils. Myers et al. (1982) studied net nitrogen mineralisation in five cultivated Australian soils, and 32 cultivated and forested western Canadian soils and found the optimum mineralisation at water potentials between $-30$ and $-10$ kPa.

The rate of decrease in $\mu$, when exceeding $-15$ kPa (Fig. 1), was large for the Acrisols, and when water potential was above $-2$ kPa, no stable exponential growth rate could be defined. For most of the soils the growth rate above $-2$ kPa was irregular with several short exponential phases and commonly also linear and curved relationships. It is therefore important to take care not to exceed $-2$ kPa when measuring $\mu$ after substrate addition. For the Swedish mor layer there were no such drastic decrease in growth rate between $-15$ and $-2$ kPa. The relationship up to $-15$ kPa, however, was very similar to the Acrisols. The ratio of glucose/organic matter (w/w) was 0.57 for the Ah soil, 1.75 for the As soil, 2.56 for the Ac soil and 2.09 for the Ph soil. It therefore seems unlikely that the different response of $\mu$ in the Ph soil, at water potentials above $-2$ kPa, was related to the rate of substrate addition. In the range $-10$ to $-90$ kPa it was not possible to detect any change in $W_p$ for any of the soils. Due to the variation in the measurements it was

![Figure 4](https://example.com/figure4.png)

Fig. 4. The relationship between water content and soil basal respiration per gram of dry soil, where (a) is showing water content is expressed as water potential (a) and as %WHC (b).
not possible to know if this plateau was real or apparent.

Considering the range of organic content and texture of the soils in this study it should be safe to use a water potential of $-10$ to $-50$ kPa for comparing Acrisols. It is interesting that the completely different Swedish mor sample was showing such similar response to water potential. When also considering the four studies mentioned above (all finding the optimum between $-10$ and $-50$ kPa) it seems that, despite the often opposite notion (e.g., Skopp et al., 1990), there might be a direct physical relation between microbial activity and water, which is very well described by the water potential.

The exponential CO$_2$ evolution rate has often been interpreted by us and others as specific growth rate of the microbial biomass (e.g., Nordgren et al., 1988; Marstorp and Witter, 1999). The microbial growth and activity have commonly been said to be limited by either substrate or oxygen diffusion in the soil. However, when the microbes are growing exponentially the oxygen and substrate consumption should also rise exponentially. If the growth rate was limited by diffusion through the soil medium, how then can the same exponential growth rate be sustained for 12–26 h without an increase in the diffusion rate that corresponds to the increase in the rate of consumption (more than four times)? We suggest that the exponential growth is situated in such large pores that growth is not limited by the diffusion through the soil, but instead by diffusion through the water film surrounding the individual microorganism. The capillary force of water shapes this film as a meniscus formed between the organism and the surface on which the organism is attached, and a thin layer covering the part of the organism that is away from that surface (Fig. 5). The thin layer is not more than a few molecules thick at $-1000$ kPa and less than 0.003 $\mu$m at $-100$ kPa (Killham, 1994). The radius of curvature of the menisci formed by water can be estimated by the capillary rise equation:

\[ r(\mu m) = 150/W_p, (-kPa) \]

The full capillary rise equation also includes the surface tension and density of the liquid, the contact angle between the meniscus and wall, and the gravitational constant. The value 150 is obtained by assuming a contact angle of 0° for water in mineral soil. From this it follows that the approximate radius of the water meniscus at $-1000$ kPa is 0.15 $\mu$m, at $-100$ kPa is 1.5 $\mu$m, at $-50$ kPa is 3 $\mu$m, at $-15$ kPa is 10 $\mu$m and at $-2$ kPa is 75 $\mu$m. We suggest that $\mu$ can be related to the area and thickness of the thin water layer covering the microorganisms, and to the radius of the thicker water meniscus. The larger the meniscus surrounding the microorganism, the more available is the substrate. The growth rate increases with water potential in this way until growth is limited by the availability of oxygen because the area of thin water film is too small, or the water film is too thick. In Fig. 5 we have outlined how the water menisci formed at $-3$, $-15$, $-30$, and $-100$ kPa relate to an organism with a diameter of 5 $\mu$m. These values were chosen because $-3$ kPa was the limit for exponential growth, $-15$ kPa was at the optimum growth rate, and $-30$ to $-100$ kPa was the range where the growth rate started to decrease on the dry side of the optimum. The diameter of 5 $\mu$m was chosen because microbes of approximately this size seem to dominate the biovolume of most soils (Jenkinson et al., 1976).

Other processes that could be responsible for $W_p$ effects are the effects on internal metabolic processes and turgor pressure. However, these effects should be expected at lower $W_p$ than seen for optimum growth rate in this study (Harris, 1981).

In contrast to $\mu$, the basal respiration for the Acrisols had a weak relation to water content. The differences in basal respiration due to the different soil types were much larger than differences due to water content. The basal respiration for the Ph soil on the other hand increased from approximately 2 to 4 mg CO$_2$ h$^{-1}$ between $-2000$ kPa and $-2$ kPa (20–70% WHC). Most other studies have found a relation to water content corresponding to the stronger relation of the Ph soil (e.g., Orchard and Cook, 1983; Doran et al., 1990; Orchard et al., 1992; West et al., 1992). Nordgren et al. (1988), using the same apparatus as in this study, found less relation to water content in mor layers (similar to the Ph soil in this study) contaminated with high levels of heavy metals than in uncontaminated soils. Thus, the most likely conclusion is that this effect is a property of the soil. If the basal respiration was limited by substrate diffusion, the water relation should be more important than observed for the Acrisols in this experiment. Only for the organic-rich Acrisol, where additional measurements were made at higher water potentials, a maximum for basal respiration was seen. Therefore, the only general conclusion about water contents for optimum basal respiration that can be made is that it is situated at higher water...
contents than the optimum for $\mu$. The reason for this was probably that the growth of the microorganisms led to a higher oxygen consumption requiring a higher diffusion rate, and thus, a lower water content.

For WFP a common universal maximum for microbial activity is not possible. This is because any macro pores (large enough to be unable to hold water under freely draining conditions) would increase the volume of pores, and therefore decrease the %WFP, without affecting the conditions for respiration in the soil. The WFP of 60% that was found by Linn and Doran (1984) to be the water content giving maximum microbial activity must be a consequence of their soils not having large macro pores. This is indicated by the relatively high bulk densities of their soils (1.14 and 1.4 g cm$^{-3}$). Soils with widely differing macro porosity will be found in areas with many root channels and burrows of meso and macro fauna. In tropical forests with undisturbed top soils, bulk densities as low as 0.64 g cm$^{-3}$ have been reported (Malmer et al., 1998). Neilson (1990) pointed out the limitation of using water filled pore space as an index of soil aeration when interpreting soil respiration measured after compacting soils to different bulk densities.

For WHC the high ability to predict the optimum microbial activity is largely due to the effect of removing the volume of large pores unable of holding water, from the measurement. The problem with WHC is that it will be dependent on the method used. In particular, the degree of compaction and the height of the soil column will affect the water holding capacity. However, the result from this study indicates that as long as one procedure is strictly followed, the variance is low. Also, as long as compaction is restricted to large pores as would be expected by normal sample handling, or with slight shaking, WHC should not be affected. This was also confirmed by the low variation in our soils despite deliberate shaking of some samples. On the other hand, compaction by pressing strongly affected WHC in our soils (data not shown).

It is difficult to make general ecological conclusions from four soils, which include only two textural classes. However, when water content was measured as %WHC and gravimetric water content, the more organic-rich soils (the Ah and Ph soil) appeared to sustain a favorable $W_p$, allowing microbial growth over a wider range of water contents. This has the ecological implication that if soil moisture is fluctuating, microbial growth will be limited more often in the organic-poor soils than in the organic-rich soils (Figs. 2 and 3).

4.1. Conclusions

We recommend that for measurements of respiration in Acrisols the water content should not exceed 50% of WHC, or a maximum $W_p$ of $-15$ kPa, if substrate additions are made. Since the basal respiration has such low co-variation with water it is really no point exceeding this water content even if only basal respiration is measured. Also for the Swedish mor layer it is suitable to adjust the water content to a $W_p$ of $-15$ kPa or a WHC of 50%, if substrate additions are made. However, it is possible to use water contents as high as $-3$ kPa or 65% WHC without any substantial decrease in the growth rate. This might be more suitable if basal respiration is also studied.

If water holding capacity is used to express moisture content the procedure should be well defined and strictly followed. Because WHC measurements are dependent on the method, it is recommended that if WHC is used, it is complemented with the measurement of water potential. Neither, gravimetric ($W_g$) nor volumetric water contents ($W_v$ and WFP) are recommended when different tropical forest soils are compared.

Acknowledgements

This study was funded by equal parts of the Swedish Agency for Research Cooperation with Developing Countries (SAREC) and Sabah Forest Industries Sdn Bhd (SFI).

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