Géographie physique et Quaternaire

Temperature and the boreal-subarctic maximum in soil organic carbon
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Temperatur und maximale Akkumulation organischen Materials in den borealen und arktischen Gebieten

David K. Swanson, Barbara Lacelle et Charles Tarnocai

Volume 54, numéro 2, 2000

URI : https://id.erudit.org/iderudit/004874ar
DOI : https://doi.org/10.7202/004874ar

Éditeur(s)

Les Presses de l'Université de Montréal

ISSN

0705-7199 (imprimé)
1492-143X (numérique)

Citer cet article

Swanson, D. K., Lacelle, B. & Tarnocai, C. (2000). Temperature and the boreal-subarctic maximum in soil organic carbon. *Géographie physique et Quaternaire*, *54*(2), 157–167. https://doi.org/10.7202/004874ar

Résumé de l'article

Dans les plaines du centre de l'Amérique du Nord et de la Sibérie occidentale, l'accumulation du carbone organique dans le sol et l'étendue des sols tourbeux sont maximales là où les températures annuelles moyennes du sol sont près de 0° C et diminuent généralement vers le nord et le sud. La présence de ce grand bassin de carbone dans les régions boréale et subarctique est probablement le résultat d'une faible provision de chaleur dans le sol comparativement à celle de l'air. Cela procure à l'air un « avantage thermique » qui permet le métabolisme des plantes vertes, contrairement à la très faible capacité de décomposition des microorganismes présents dans le sol, ce qui favorise l'accumulation du carbone. Cet « avantage thermique » de l'air est maximal là où les températures moyennes annuelles du sol sont près ou à quelques degrés sous la limite inférieure de l'activité biologique des organismes adaptés au froid et des plantes, soit près de 0° C.

Géographie physique et Quaternaire, 2000, vol. 54, n° 2, p. 157-167, 7 fig., 1 tabl.

TEMPERATURE AND THE BOREAL-SUBARCTIC MAXIMUM IN SOIL ORGANIC CARBON

David K SWANSON*, Barbara LACELLE and Charles TARNOCAI, first author: Department of Plant, Animal, and Soil Sciences, University of Alaska, Fairbanks, Alaska, 99775-7140, U.S.A.; second and third authors: Agriculture and Agri-Food Canada, K.W Neatby Building, room 1135, Ottawa, Ontario K1A 0C6.

ABSTRACT On the plains of central North America and western Siberia, soil carbon storage and cover by organic soils are highest in the region with mean annual soil temperatures near 0 °C, and generally decrease to the north and south. The location of this large soil carbon sink in the boreal and subarctic is probably due in part to the low heat availability in the soil as compared to the air in these regions. The thermal advantage of the air environment gives green plants a metabolic advantage over decomposers in the soil, which favors soil carbon accumulation. The thermal advantage of the air environment relative to the soil is greatest where mean annual soil temperatures are near or a few degrees below the lower limit of biological activity for cold-adapted soil organisms and plants, *i.e.* near 0 °C.

RÉSUMÉ *La température et l'acccumulation maximale de matière organique dans les régions boréales et subarctiques du sol.* Dans les plaines du centre de l'Amérique du Nord et de la Sibérie occidentale, l'accumulation du carbone organique dans le sol et l'étendue des sols tourbeux sont maximales là où les températures annuelles moyennes du sol sont près de 0 °C et diminuent généralement vers le nord et le sud. La présence de ce grand bassin de carbone dans les régions boréale et subarctique est probablement le résultat d'une faible provision de chaleur dans le sol comparativement à celle de l'air. Cela procure à l'air un « avantage thermique » qui permet le métabolisme des plantes vertes, contrairement à la très faible capacité de décomposition des microorganismes présents dans le sol, ce qui favorise l'accumulation du carbone. Cet « avantage thermique » de l'air est maximal là où les températures moyennes annuelles du sol sont près ou à quelques degrés sous la limite inférieure de l'activité biologique des organismes adaptés au froid et des plantes, soit près de 0 °C.

ZUSAMMENFASSUNG *Temperatur und maximale Akkumulation organischen Materials in den borealen und arktischen Gebieten.* In den Ebenen von Zentral-Nordamerika und West-Sibirien wird eine maximale Akkumulation und Ausdehnung von organischem Kohlenstoff im Boden da erreicht, wo die durchschnittlichen jährlichen Bodentemperaturen um die 0 °C sind, und sie nimmt im Allgemeinen nach Norden und Süden ab. Das Vorhandensein dieses breiten Kohlenstoff-Beckens in dem borealen und subarktischen Gebiet ist wahrscheinlich auf das geringe Wärme-Vorkommen im Boden im Vergleich zu der Luft zurückzuführen. Der « thermische Vorteil » der Luftumgebung begünstigt den Stoffwechsel der grünen Pflanzen gegenüber den Zersetzungsprozessen in der Erde, was die Kohlenstoffakkumulation im Boden begünstigt. Der « thermische Vorteil » der Luftumgebung im Verhältnis zum Boden ist da am größten, wo durchschnittliche jährliche Bodentemperaturen nahe bei oder einige Grad unter der unteren Grenze der biologischen Aktivität von an Kälte angepassten Boden-Organismen und Pflanzen sind, d.h. nahe bei 0 °C.

Manuscrit reçu le 23 février 1999 ; manuscrit révisé accepté le 13 juin 2000

* Present address: USDA-NRCS, 590 University Ave. Suite B, Fairbanks, Alaska 99709-3641, U.S.A; ffdks@aurora.alaska.edu

INTRODUCTION

Soils of the boreal and subarctic regions are a major carbon sink. In Canada, the soils of these zones contain on the average about 50 kg m^{-2} organic carbon, distinctly more than the soils of zones further north or south (Tarnocai, 1998). A similar pattern is observed in Russia (Orlov and Biryukova, 1995). Combining estimates of the soil organic carbon from these two sources yields about 340 Gt organic carbon in the soils of boreal and subarctic Canada, European Russia, and western Siberia, probably about a quarter of the world's soil organic carbon (Post *et al.*, 1982). In addition, the wetlands that contain much of this organic carbon are a major source of atmospheric methane (Matthews and Fung, 1987; Aselmann and Crutzen, 1989). Hence the factors responsible for the existence of the boreal-subarctic soil organic carbon sink are of interest with respect to the global carbon balance, greenhouse gas fluxes, and climate change.

The most important factor that controls the distribution of organic soils and other soils high in organic carbon on most landscapes is soil wetness: organic matter tends to accumulate where saturation of soils with water inhibits exchange of oxygen and hence hinders decomposition (Moore and Bellamy, 1974; Clymo, 1983). However, the soil temperature regime also affects the accumulation of soil organic carbon. For example, wetlands in the tropics are primarily marshes and swamps lacking peat, while those in boreal and tundra regions are mostly peatlands (Aselmann and Crutzen, 1989). A second example is the surprisingly thick accumulation, up to 0.4 m, of organic soil material on steep, north-facing slopes in subarctic central Alaska, despite a rather dry climate with mean annual precipitation of only 30 cm (Krause *et al.*, 1959). Low soil temperatures inhibit organic-matter decomposition in colder climates (Kirschbaum, 1995), favoring accumulation of soil organic carbon. Carbon fixation in the boreal forest is most rapid when air temperatures are high and soil temperatures are low (Goulden *et al.*, 1998). The purpose of this paper is to present a simple model for the effect of continental-scale variations in temperature on accumulation of soil organic carbon, and thereby attempt to explain the occurrence of the large store of soil organic carbon in boreal and subarctic regions.

"THERMAL ADVANTAGE" OF THE AIR ENVIRONMENT RELATIVE TO THE SOIL

Soils in cold climates furnish little heat for the soil-dwelling organisms that break down organic matter. For example, a soil in a black spruce forest near Ft. Norman, Northwest Territories, Canada shows an average annual sum of 1027 degree-days above 0 °C at 5 cm depth, decreasing sharply to just 58 degree-days above 0 °C at 50 cm and none below (Fig. 1A). These values are considerably less than the average annual sum of 1756 degree-days above 0 °C for the air at the same site, in spite of the fact that the mean annual air temperature is about 3 °C lower than the mean annual soil temperature. Degree-days above 5 °C show a similar trend, decreasing from 998 in the air to 402 at 5 cm in the soil to 0 °C below 20 cm depth (Fig. 1A).

If the sum of degree-days above either 0 or 5 °C is a reasonable index of the heat available for biological activity by cold-adapted organisms (Young, 1971; Heal and French, 1974; Edey, 1977; Rannie, 1986; George *et al.*, 1988; Honeycutt *et al.*, 1988), then clearly detritus-feeding organisms and microbial decomposers, which live almost entirely in the soil, are at a metabolic disadvantage relative to terrestrial plants, major parts of which are located in the air. Hence the producers should tend to outpace decomposers. It is no surprise then that the site portrayed by Figure 1A has accumulated a 33 cm thick surface organic layer and peat deposits are widespread in the surrounding region. More generally, if all else is equal (notably wetness), soil organic matter should accumulate most where the air has the greatest "thermal advantage" relative to the soil.

In an analogous soil (loamy and nearly level) from a much warmer climate in the southern U.S. (southeastern Texas), sums of degree-days greater than 0 or 5 °C suggest that the air environment has no thermal advantage at any depth relative to the soil; in fact, the air appears to have a slight thermal disadvantage relative to the soil (Fig. 1B).

The thermal advantage of air over soils in cold climates is a result of the much greater thermal "inertia" of soils than air. Summer air temperatures can be high almost regardless of the coldness of the preceding winter. Soils, on the other hand, retain a "memory" of the winter's cold; strong chilling of soil in the winter can reduce the sum of biologically active temperatures in the soil in the subsequent summer. This effect is absent in warm climates (Fig. 2).

A SIMPLE MODEL OF THE LATITUDINAL TREND IN AIR AND SOIL HEAT SUPPLY

To model the latitudinal trend in sum of air degree-days, we assumed that the monthly mean air temperature curve is a sine wave with amplitude of 15 °C (*i.e.* range of 30 °C). This range is a typical value for moderately continental temperate, boreal, and arctic climates. The annual sum of degree-days above 0 °C and 5 °C in the air was calculated for the series of mean annual air temperatures from -15 °C to +20 °C, which covers the span of climates from high arctic (warmest monthly mean air temperature of 0 °C) to subtropical (coldest monthly mean of +5 °C).

A similarly simple index of heat availability for soils is more difficult to find, because heat availability in soils varies vary greatly both down-profile (*e.g.*, Fig. 1A) and spatially on a local scale (Brown, 1973). To compute the degree-day sums for the model soils, we assumed that the annual wave in monthly mean soil temperatures is like the air's wave, but with amplitude damped to 0.75, 0.5, or 0.25 that of the air. Damping to half the air's annual amplitude typically occurs within the upper 20 cm of soils in the boreal and subarctic (Tarnocai *et al.*, 1995; Adams and Viereck, 1997; Goulden *et al.*, 1998), and hence this degree of damping is a reasonable approximation of the soil environment for organic-matter decomposition in this region.

To account for the possible difference between mean annual air temperature (MAAT) and mean annual soil temperature

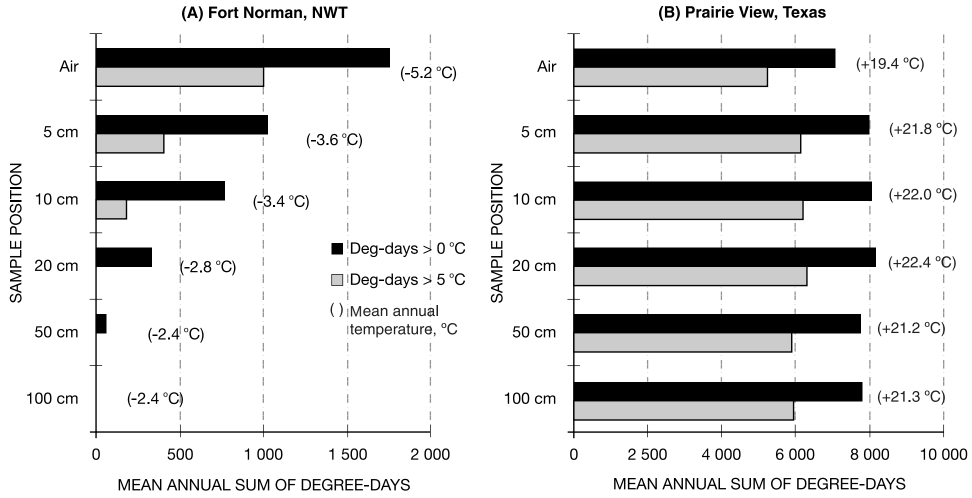


FIGURE 1. Mean annual sum of degree-days above 0 °C and 5 °C, for (A) the air and an Orthic Turbic Cryosol (Typic Histoturbel) under black spruce (*Picea mariana*) forest near Fort Norman, Northwest Territories, Canada and (B) a fine-loamy, siliceous, thermic Plinthaquic Paleudalf under grass near Houston, Texas. The mean annual temperatures of the air and the soil at various depths are given to the right of the graph bars. Norman Wells Pipeline Environmental Research and Monitoring Program (Tarnocai *et al.*, 1995), site 3A-1, 64° 55' N, 125° 35' W; and US Department of Agriculture, Natural Resources Conservation Service data, Prairie View, Texas soil monitoring site, 30° 05' N, 95° 59' W.

*Le total de degrés-jours au-dessus de 0 °C et 5 °C de (A) l'air et d'un cryosol turbique orthique (Typic Histoturbel) sous forêt de sapin (*Picea mariana*) près de Fort Norman, dans les Territoires du Nord-Ouest et (B) d'un Plinthaquique Paleudalf sous herbacées, près de Houston, au Texas. Les températures annuelles moyennes de l'air et du sol à différentes profondeurs sont données à droite du graphique. Norman Wells Pipeline Environmental Research and Monitoring Program (Tarnocai* et al.*, 1995), site 3A-1, 64° 55' N, 125° 35' O ; et US Department of Agriculture, Natural Resources Conservation Service, site d'observation à Prairie View, au Texas, 30° 05' N, 95° 59' O.*

(MAST), the sum of soil degree-days was calculated by assuming MAST 0, 2, or 4 °C higher than the MAAT. In temperate, boreal, and arctic regions the MAST under natural vegetation is typically a few degrees greater than MAAT, and the exact difference is controlled mainly by soil surface properties, snow depth, soil wetness, and plant cover (Brown, 1970; Goodrich, 1978; Rieger, 1983).

MODEL RESULTS AND DISCUSSION

For our hypothetical latitudinal series of climates, the sum of air degree-days above 0 °C exceeds zero as soon as the mean air temperature of the warmest month exceeds 0 °C (which corresponds to MAAT of -15 °C) and increases steadily thereafter with increasing MAAT (Fig. 3). The trend in degree-days above 0 °C in the model soil with temperature amplitude half of the air's, in contrast, remains at 0 degree-days until soil temperatures in the warmest month exceed 0 °C (this varies depending on the assumed difference bewteen MAST and MAAT), after which it increases steeply and eventually intersects the air degree-days curve.

The difference between the annual sum of degree-days for the air and for the model soils (Fig. 4) is an indicator of the thermal advantage of the air relative to the soil. The position of the maximum air thermal advantage over the soil varies less between the three assumed differences MAST – MAAT if the air's advantage is plotted *vs.* MAST (Fig. 4) than vs. MAAT as in Fig. 3. At low MAST, the air's advantage is small because the sum of degree-days in the air is low. If the temperature wave in the soil is damped to half the air's amplitude (Fig. 4B), the peak air advantage occurs at MAST = 0 to 4 °C, depending on the assumed difference MAST – MAAT. For greater damping (to 0.25 times the air's amplitude, Fig. 4C) all three peaks occur near 0 °C, while for high values of MAST – MAAT and little damping (Fig. 4A), the air advantage is eliminated. As MAST increases beyond the optimum near 0 °C, the air thermal advantage decreases to zero if MAST = MAAT and subzero (*i.e.* thermal disadvantage for the air) if MAST > MAAT. The curves level off at a minimum value beyond the point where MAAT = 15, *i.e.* where the air temperature mean of the coldest month is 0 °C (the base temperature) or higher.

Trends are the same if the degree-day base temperature is set at 5 °C rather than 0 °C, except the curves are all shifted 5 °C to the right, so that the maximum difference between the air and soil occurs at or a few degrees below 5 °C MAST.

In general then, the maximum difference between air and soil degree-days occurs where the MAST is equal to or a few degrees lower than whatever degree-day base temperature is used. In other words, the maximum thermal advantage for the air environment relative to the soil occurs where the MAST is near the lower limit of biologically active temperatures. In reality, this lower limit is indistinct. Respiration of cold-adapted soil microbes has been measured down to -7 °C but rates are low below 0 °C and increase rapidly between 0° and 5 °C (Flanagan and Veum, 1974; Schlentner and Van Cleve,

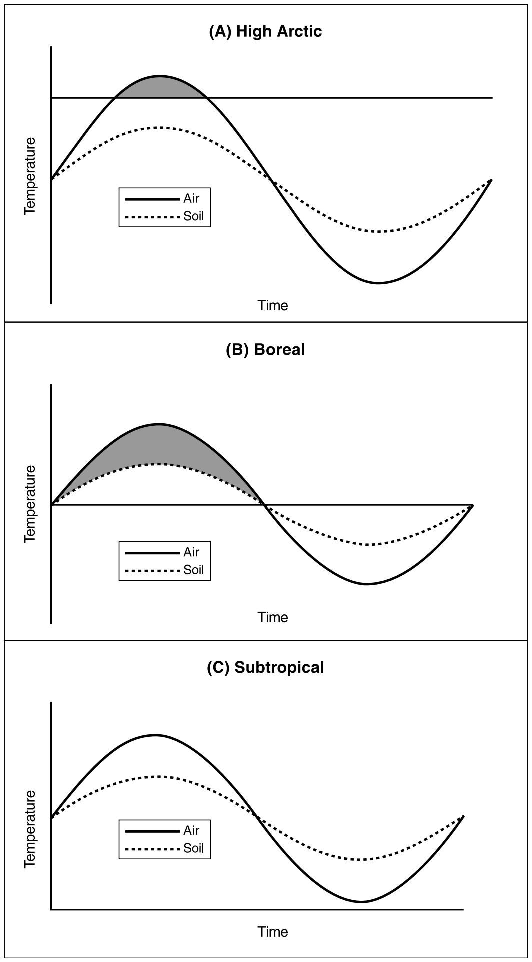


FIGURE 2. Source of the air's thermal advantage relative to the soil. The diagrams portray the mean temperature of the air and the soil relative to a chosen degree-day base temperature (*e.g.*, 0 or 5 °C) through the year. For simplicity the lag in the soil's wave relative to the air is not depicted. In the high arctic situation (A), mean annual soil and air temperatures are well below the degree-day base temperature. The sum of degree-days in the air, represented by the shaded area, is small and the sum for the soil is zero, resulting in little degree-day advantage for the air environment. In the boreal situation (B), mean annual air and soil temperatures are near the degree-day base temperature. The degree-day sum for the air substantially exceeds the sum for the soil, by the amount represented by the shaded area. In the subtropical situation (C), mean monthly air and soil temperatures stay above the base temperature all year long, and the degree-day sums for the air and soil, represented by the entire areas under the respective curves, are similar.

L'origine de l'« avantage » thermique de l'air sur le sol. Les graphiques montrent la température moyenne de l'air et du sol relativement à une température de base choisie pour les degrés-jours (par exemple, 0 °C ou 5 °C) pour toute l'année. Pour simplifier, le décalage entre les courbes du sol et de l'air n'est pas montré. Dans l'arctique (A), les températures annuelles moyennes du sol et de l'air sont bien en dessous de la température de base choisie. Le total des degrés-jours de l'air est faible (en grisé) et dans le cas des sols, il est de zéro ; l'« avantage » en degrés-jours de l'air est donc minime. En région boréale (B), les températures annuelles moyennes de l'air et du sol sont près de la température de base choisie. Le total des degrés-jours de l'air excède considérablement ceux du sol, par la quantité en grisé. En région subtropicale (C), les températures mensuelles moyennes de l'air et du sol restent au-dessus de la température de base toute l'année, et les totaux de degrés-jours de l'air et du sol sont similaires.

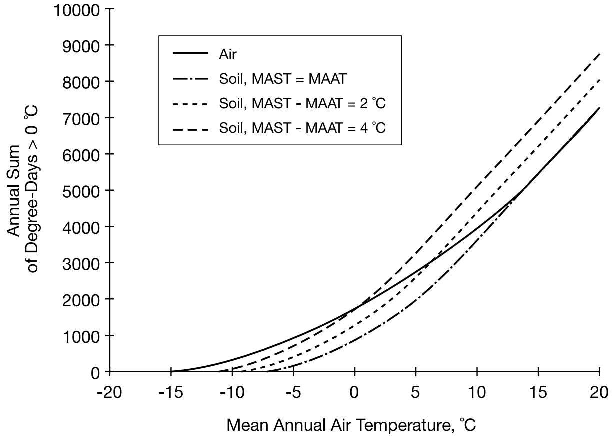


FIGURE 3. Model annual sum of degree-days above 0 °C in the air and soil for a hypothetical series of mean annual air temperatures from -15 °C to +20 °C. Mean monthly air temperatures are assumed to follow a sine wave of amplitude 15 °C (range 30 °C). The soil curves are similar but with temperature variation damped to half that of the air. The three different soil curves represent mean annual soil temperature (MAST) equal to mean annual air temperature (MAAT), MAST 2 °C higher than MAAT, and MAST 4 °C higher than MAAT.

Courbes modèles de totaux annuels de degrés-jours supérieurs à 0 °C dans l'air et le sol pour une série hypothétique de températures annuelles moyennes de l'air de - 15 °C à + 20 °C. On suppose que les températures mensuelles moyennes de l'air suivent une courbe sinusoïdale de 15 °C d'amplitude (étendue de 30 °C). Les courbes du sol ressemblent à celles de l'air, mais la variation de la température représente la moitié de celle de l'air. Les trois courbes du sol représentent : la température annuelle moyenne du sol (TAMS) équivalent à la température annuelle moyenne de l'atmosphère (TAMA) ; la TAMS plus élevé de 2 °C que la TAMA ; et la TAMS plus élevée de 4 °C que la TAMA.

1985). Heal and French (1974) and Honeycutt *et al.* (1988) found a good correspondence between organic-matter decomposition and degree-days above 0 °C. Kirschbaum's (1995) compiled results from many published respiration studies confirm that decomposition rates increase rapidly in the 0 to 5 °C range. Likewise, cold-adapted plants can photosynthesize when ambient air temperatures are a few degrees below 0 °C, but productivity then is low and increases rapidly above 0 °C (Billings and Mooney, 1968). If the effective lower limit of organic-matter decomposition and green plant production is in the 0 to 5 °C range, the model suggests that the maximum thermal advantage for the organisms in the air environment relative to the soil should be in soils with MAST near 0 °C.

The model also suggests that the thermal advantage of the air is roughly proportional to the annual range in monthly mean air temperatures. Figure 5 depicts the change in the thermal advantage of the air environment relative to the soil from maritime (10 °C annual range) to highly continental (50 °C range) climates. The air's thermal advantage for a model soil near the optimum MAST (MAST = 2 °C) roughly doubles as the air temperature range increases from 10 to 50 °C. The reason is that a large annual range in temperatures allows both for a warm, productive summer and strong chilling of the soil in the winter.

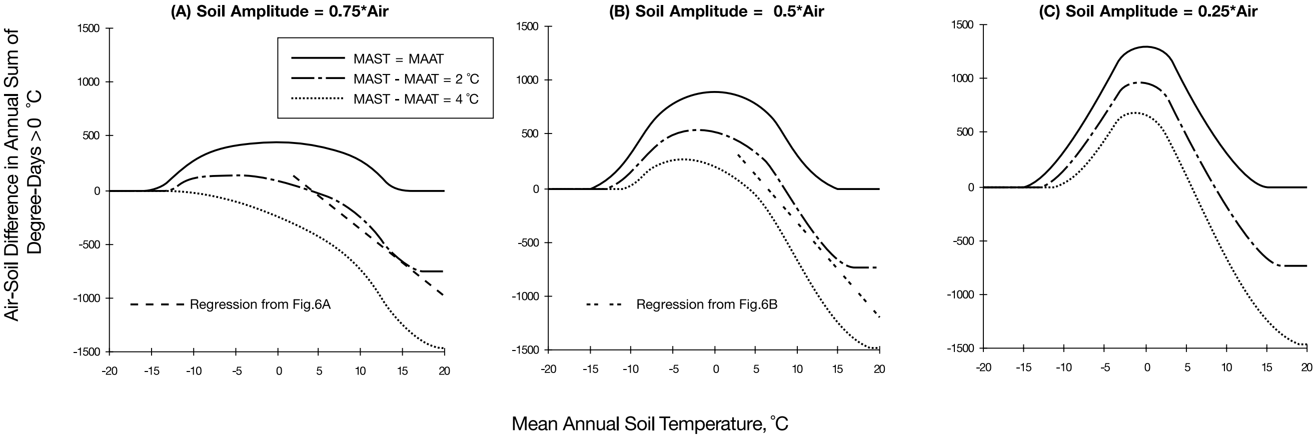


FIGURE 4. Difference between the annual sum of degree-days above 0 °C in the soil and air *vs.* mean annual soil temperature for the three differences MAST – MAAT described in Figure 3, assuming the annual wave in monthly mean soil temperatures is damped to (A) 0.75, (B) 0.50, and (C) 0.25 that of the air. The regression line from field data in Figure 6A is plotted in (4A) and the trend line from Figure 6B is plotted in (4B).

Différence entre le total annuel de degrés-jours supérieur à 0 °C dans le sol et dans l'air sur la température annuelle moyenne du sol pour les trois cas présentés à la figure 3, en supposant que la variation annuelle des températures mensuelles moyennes du sol est à (A) 0,75, (B) 0,50 et (C) 0,25 de celles de l'air. La régression linéaire calculée à partir des données de la figure 6A est donnée en (4A), et celle de la figure 6B, en (4B).

The model presented above has several limitations that should be kept in mind. First, there are some problems with the use of degree-days as indicators of biological rates (Clymo, 1983). Rates of biological processes are not strictly proportional to temperature, rates are affected by temperature variability in addition to means, and different degree-day base temperatures should be used for different organisms and different regions. Second, the "cold" and "warm" sides of the curves depicted in Figure 4 are not strictly comparable, because the difference MAST – MAAT varies with latitude (it is greater in regions with significant snow cover), because the damping of soil temperatures due to absorption and release of latent heat of freezing occurs only in cold soils, because permafrost impedes soil drainage only on the "cold" side of the diagram, and because permafrost aggradation interferes with peat accumulation (Robinson and Moore, 2000) only on the "cold" side also. Third, the annual wave in monthly mean soil temperatures is not a perfect sine wave as assumed here, especially in soils with significant freeze and thaw of soil water.

In spite of these shortcomings, the trends depicted in Figure 4 generally agree with trends in measured air and soil degree-day sums and the distribution of soil organic carbon.

COMPARISON OF THE MODEL WITH MEASURED SOIL AND AIR HEAT SUPPLY

To test whether soil and air heat supply show the latitudinal trends predicted by our simple model, we compared degree-day sums for the air with the soil at 10 cm and 50 cm depths for soil temperature monitoring sites in midcontinental North America (Fig. 6). Trends in the measured thermal advantage of the air relative to the soil generally follow those of the model. The various data sets in Figure 6 are discussed separately below.

THE ARCTIC NORTH OF 70° N

Soil temperature data for far northern localities are very sparse, but they confirm that the air has no significant thermal advantage over the soil in these climates. Data from Barrow, Alaska (71.4° N, MAST = -9.3 °C) and Resolute, Nunavut (74.7° N, MAST = -10.5°) show little difference in degree-days sums between the air and soil (Fig. 6). Air temperature data alone for high arctic stations indicate less air thermal advantage over the soil in the arctic than in the boreal/subarctic. The Canadian arctic islands have annual sum of air degree-days above 0 °C of less than 400 (Edlund and Alt, 1989), and thus on the basis of air temperatures alone the air-soil difference must be lower than the near-optimum values of 400 to 2000 degree-days in the boreal/subarctic described below.

THE MACKENZIE VALLEY TRANSECT: BOREAL, SUBARCTIC, AND LOW ARCTIC

This transect includes 21 stations on a wide variety of soils with natural vegetation from 69.6° N near the Arctic Ocean in the Mackenzie River Delta to 60.6° in northern Alberta (Fig. 6). The two most northerly of these stations are in the tundra, while the remainder are south of treeline. Soils are nearly level and span the range of wetness conditions from well-drained sandy soils to water-saturated peatlands. Most of these stations show significant thermal advantage of air over the soil, generally 400 to 1000 degree-days when the air is compared to the soil at 10 cm depth and 900 to 1800 degree-days when the air is compared to 50 cm depth in the soil. The air thermal advantages are greater when the air is compared to 50 cm depth in the soil due to greater damping at 50 cm than 10 cm. The thermal advantage appears to peak in this data set in the vicinity of MAST = 0 °C and decrease for cold soils (MAST below 6 °C) and perhaps also for warm soils (MAST above 3 °C).

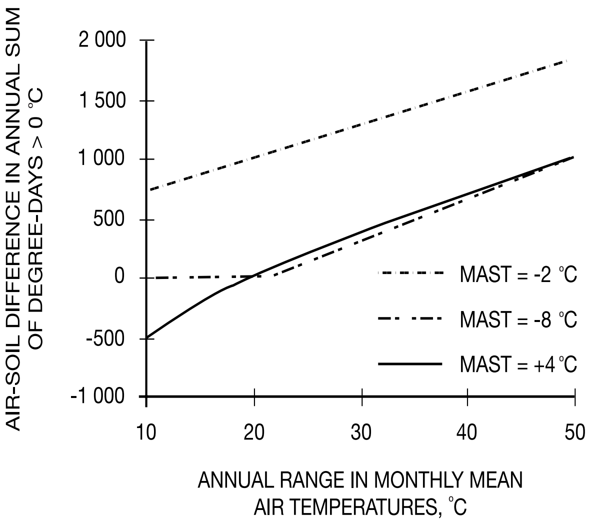


FIGURE 5. Difference between the annual sum of degree-days above 0 °C in the soil and air *vs.* annual range in monthly mean air temperatures. The model soil is assumed to have a MAST 2 °C higher than MAAT, and the annual wave in monthly mean soil temperatures is damped to 0.50 that of the air.

Différence entre le total annuel de degrés-jours supérieur à 0 °C dans le sol et dans l'air sur l'amplitude annuelle des températures mensuelles moyennes. On suppose que la TAMS du sol modèle est de plus de 2 °C que la TAMA, et la variation annuelle des températures mensuelles moyennes est à 0,50 de celle de l'air.

The air thermal advantage for the peatland soils (stations with Organic soils or Organic Cryosols) in this data set is similar to that of the non-peatland soils (Table I). The 10 cm depth is a minor exception: temperatures at this depth in peatlands were somewhat warmer than in non-peatlands (probably due to lack of overstory shading combined with low soil thermal conductivity), resulting in air thermal disadvantage with respect to this depth that is somewhat less than non-peatlands, yet still substantial. Analyses of variance comparing air thermal advantage of imperfectly and poorly drained soils (n = 12) with well-drained soils (n = 9) revealed no significant differences at any depth. Thus high values for air thermal advantage across this wide variety of soils indicates that it is a regional soil property determined by the macroclimate.

MANITOBA ORGANIC SOILS

Organic soils under native forest vegetation in central (54.5° N, MAST 0 to 2 °C) and southern Manitoba (49° to 50° N, MAST 3° to 4 °C) show large air thermal advantages (Fig. 6B; data are available for the 50 cm depth only). The stations with MAST near 0 °C had air thermal advantages of over 2000 degree-days, the highest we observed anywhere. The air thermal advantage is lower in the warmer (3° to 4 °C) Manitoba organic soils but is still quite high, 1000 to 1200 degree-days. The latter are near the southern limit of the boreal zone.

MID-LATITUDE CANADIAN AES AND USDA-NRCS STATIONS

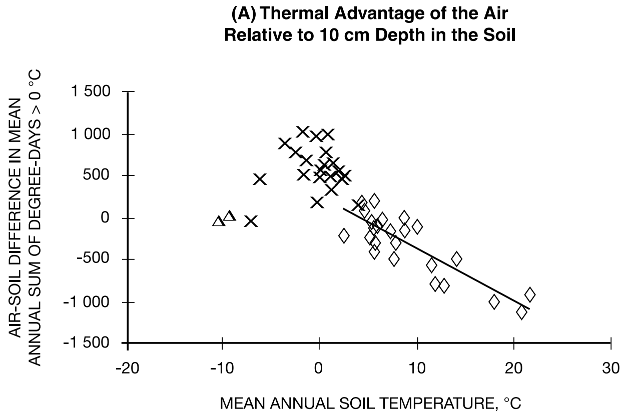
These 26 stations are on level sites with turfgrass vegetation on a variety of non-wetland soils between 58° and 30° N latitude in midcontinental North America. The air thermal advantage decreases significantly as mean annual soil temperatures increase from 3° to 22 °C in this dataset (Fig. 6). The highly significant regressions of air thermal advantage *vs.* MAST agree well with the model runs made using conditions similar to the mean conditions for the data sets (Fig. 4; the regressions from Fig. 6 are plotted on the model curves with damping similar to the means for the data: the 10 cm depths had mean damping of 0.73, so the corresponding regression was placed on Fig. 4A, while the 50 cm depths had mean damping of 0.57, and the corresponding regression was placed on Fig. 4B). Trends in air thermal advantage are similar with somewhat weaker correlation if the thermal advantage is plotted against latitude (r^2 = 0.56 and 0.58 for 10 cm and 50 cm depth, respectively) or MAAT (r^2 = 0.58 and 0.57 for 10 cm and 50 cm depth) rather than MAST; these regressions are still highly significant (all F-test $P < 0.0001$). The fact that air thermal advantages relative to both 10 cm and 50 cm depths in the soils have a similar trend shows that organic matter at essentially any depth in the soil would be subject to this thermal effect.

Analysis of this midcontinental North American soil temperature data revealed an additional reason why the air in warm climates tends to have no thermal advantage over the soil: damping of the annual air temperature wave by the soil is less effective in warm soils. Both snow cover, and absorption and release of latent heat by freezing and thawing of soil water damp temperature variations in cold soils relative to the air; this damping is over and above the damping due simply to the specific heat of soil materials. As a result, in warm soils the annual wave of monthly mean temperatures in the upper soil horizons where organic matter decomposition occurs is damped less relative to the air than in cold-soils. Thus the decomposition environment in warm soils resembles the situation depicted in Figure 4A, ensuring that the air experiences no thermal advantage.

The data set from Canadian AES and USDA monitoring sites is useful because it is collected in a standardized fashion, publicly available, multi-year, and spans a wide range of latitudes. Its drawback for our study is that it excludes the wetland soils where much soil organic carbon accumulates. However, available evidence suggests that wet soils also display a major southward decrease in air thermal advantage. For the air thermal advantage to decrease from 1000-2000 °C degree-days in the cold-climate wet soils shown in Figure 6B (the Manitoba peat soils with MAST of 0 to 4 °C) down to no air thermal advantage in warm wet soils (the southern US wetland soils with MAST of 18 °C, see below) requires a slope similar to the regression line for the AES/NRCS data in Figure 6B. While showing a similar north-south trend, the air thermal advantage of forest soils is higher than that of the disturbed AES/NRCS soils, due to greater difference between MAST and MAAT and less thermal damping in disturbed soils (Ping, 1987; Hayhoe and Tarnocai, 1993).

SOUTHEASTERN US WETLAND SOILS

The temperature regime of 33 forested soils in the lowlands of Louisiana, Mississippi, and South Carolina is described by Megonigal *et al.* (1996). Most of these soils are



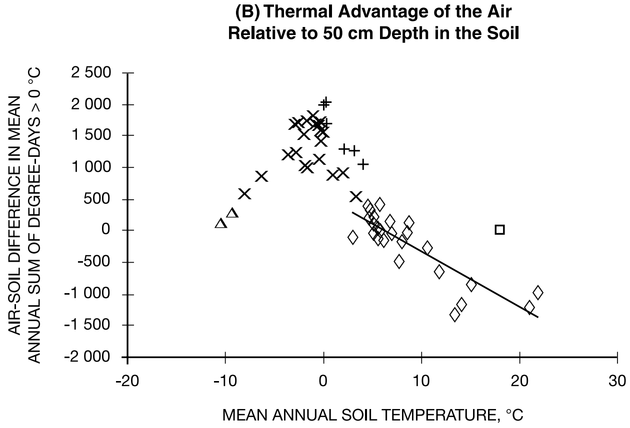


FIGURE 6. Air thermal advantage, the difference between sum of air and soil degree-days at 10 cm depth (A) and 50 cm depth (B), in midcontinental US and Canada. The points (Δ) are from Barrow, Alaska (71.3° N) and Resolute, Nunavut (74.7° N). The points (x) are 21 stations along a transect from the Mackenzie River Delta near the Arctic Ocean (69.6° N) to northern Alberta (60.6° N; Norman Wells Pipeline Environmental Research and Monitoring Program; Tarnocai *et al.*, 1995). The points (+) are from 7 organic soils with native forest vegetation in Manitoba , ranging from 54.5° to 49° N (Mills *et al.*, 1977). The points (◊) represent all stations from the Canadian Atmospheric Environment Service (Environment Canada, 1994) and US Department of Agriculture, Natural Resources Conservation Service databases located between the Appalachian Mountains and Rocky Mountains, excluding those in dry climates in the western Great Plains. Stations range from 58.4° N in the northern prairie provinces to 30.1° N near the Gulf of Mexico. Vegetation is turfgrass. Linear regression of air thermal advantage (*y*) *vs.* MAST (*x*) yields y = 229.02 - 60.20x, $r^2 = 0.72$, $P < 0.0001$ for plot (A), and 561.01-88.30x, $r^2 = 0.73$, $P < 0.0001$ for plot (B). The point (❑) represents the mean air thermal advantage for 33 forested, mostly wetland soils in southeastern USA (Megonigal *et al.*, 1996).

L'« avantage thermique » de l'air, la différence entre les totaux de degrés-jours dans l'air et dans le sol à (A) 10 cm et (B) 50 cm de profondeur, à quelques sites des États-Unis et du Canada. Les symboles (Δ) sont de Barrow, en Alaska (71,3° N) et Resolute, au Nunavut (74,7° N). Les symboles (x) représentent 21 stations le long d'un transect à partir du delta du Mackenzie (69,6° N) jusqu'au nord de l'Alberta (60,6° N)(Norman Wells Pipeline Environmental Research and Monitoring Program ; Tarnocai et al.*, 1995). Les symboles (+) représentent 7 sols organiques sous forêt d'origine, au Manitoba, du 54,5° au 49° N (Mills* et al.*, 1977). Les symboles (◊) représentent toutes les stations comprises dans les bases de données du Service de l'environnement atmosphérique (Environment Canada, 1994) et du Natural Resources Conservation Service (US Department of Agriculture), situées entre les Appalaches et les Rocheuses, sauf les stations en climat aride des Plaines de l'Ouest. Ces stations s'étendent de 58,4° N dans le nord des Prairies à 30,1° N près du golfe de Mexique. La végétation est de la pelouse en plaque. La régression linéaire de l'« avantage thermique » de l'air (y) sur TAMS (x) donne y = 229,02 – 60,20x, $r^2 = 0,72$, $P < 0,0001$ en (A) et 561,01 – 88,30x, $r^2= 0,73$, $P < 0,0001$ en (B). Le symbole (❑) représente l'« avantage thermique » moyenne de l'air pour 33 sols forestiers, la plupart mouillés, au sud-est des États-Unis (Megonigal* et al.*, 1996).*

saturated within 30 cm of the surface for at least part of the year but have little surface organic soil material (20 cm or less). Mean monthly temperatures in the air and soil are above our chosen base temperature (0 °C) all year, and hence air thermal advantage can be calculated simply from the difference between MAAT and MAST times 365 days. We calculated an average MAAT of 17.9 °C for the five weather stations nearest their South Carolina study site for the months of their study, very close to their average MAST of 17.6 °C at 50 cm depth for 10 soils. Likewise, our average of 18.0 °C for the 11 weather stations nearest their Louisiana and Mississippi study sites is very close to their average MAST of 18.3 °C for 23 soils. Thus this large sample of southern wetland soils with MAST near 18 °C under natural vegetation shows little or no difference between air and soil degree-days at 50 cm. While these soils are cooler relative to the air than the non-wetland soils under turfgrass described above (probably due mainly to better shading by forest vegetation), their negligible air thermal advantages are significantly lower that our values of 1000 to 2000 degree-days for northern wetlands (Fig. 6B and Table I). Megonigal *et al.* (1996) also observed significant microbial respiration through the winter in southeastern wetland soils, when most green plants are dormant.

SOIL TEMPERATURE AND THE DISTRIBUTION OF SOIL ORGANIC CARBON

The implication of the model and the soil temperature data is that, all else being equal, soil organic carbon storage will be greatest in continental regions where the MAST is near 0 °C. Soil carbon stores should generally decrease northward from this region because of decreasing plant productivity, approaching zero in the high arctic where there is little or no growing season. And soil carbon should decrease southward from this region to a minimum in climates where air temperatures rarely fall below the lower limit of biological activity.

The effect of temperature on accumulation of soil organic carbon always interacts with and may be obscured by other factors such as soil age, texture, vegetation, and, most importantly, wetness (Birkeland, 1999). For example, organic soils are essentially absent in sufficiently cold but semiarid climates such as North Dakota, where they occur only on sites with consistent groundwater discharge (Mausbach and Richardson, 1994). Conversely, organic soils occur locally in the tropics under very wet conditions (Anderson, 1983). In general, however, a high thermal advantage of the air environment relative to the soil should allow more soil

TABLE I

Air Thermal Advantage[1] at Mackenzie Valley Soil Temperature Monitoring Stations

	Air Thermal Advantage Mean (±Std Dev), °C-days			
Difference computed between air degree-days and soil degrees-days at:	**Peatlands (*n* = 5)**	**Non-Peatlands (*n* = 16)**	**All Sites (*n* = 21)**	**AOV F-test Probability**
10 cm depth	362 ± 187	626 ± 271	564 ± 256	0.06
20 cm depth	898 ± 293	952 ± 338	929 ± 293	0.75
50 cm depth	1 306 ± 510	1 317 ± 386	1 314 ± 415	0.96

[1] Difference between annual sum of degree-days > 0 °C in the air *vs.* the soil at various depths. Data from the Norman Wells Pipeline Environmental Research and Monitoring Program; Tarnocai *et al.*, 1995.

organic matter to accumulate on a broader range of sites than in places where the air has no thermal advantage.

LOCATION OF THE ZONE WITH MAST NEAR 0 °C

Because soil temperatures show great local variability and data points are few, it is difficult to plot simple isotherms of soil temperature that could be compared to the soil organic carbon distribution. A useful proxy for the zone with MAST near 0 °C is the discontinuous permafrost zone, where soils with MAST above and below 0 °C coexist locally. Thus we would expect soil organic carbon to peak in the discontinuous permafrost zone. Given that the lowest soil temperatures in the boreal forest are often in wetlands (Brown, 1973), the widespread occurrence of organic soils just to the south of the southern limit of permafrost, where their MAST is only a few degrees above 0°, would also be expected. An added advantage of using the discontinuous permafrost zone to locate the region of MAST near 0 °C is that it, like organic soils but unlike recent climatic data, integrates climatic conditions over the long term (*i.e.* centuries).

SOIL ORGANIC CARBON DISTRIBUTION IN NORTH AMERICA AND NORTHWESTERN EURASIA

The extensive plains with humid climate in northern and eastern North America, northeastern Europe, and western Siberia are good places to examine the effect of temperature on the distribution of soil organic carbon. Maximum cover by organic soils and the associated maximum in soil organic carbon in North America occurs in central Canada, especially in a belt stretching from the western Northwest Territories, across northern Alberta to northern Ontario (Fig. 7; Canada Committee on Ecological (Biophysical) Land Classification, 1988). This belt is in fact mostly within or just south of the discontinuous permafrost zone as expected, and in a region with relatively large annual range in monthly mean temperatures, about 30 to 50 °C. North America's greatest peat concentration is in the Hudson Bay Lowlands (Sjors, 1963), where topography is flat, the climate is humid but continental, and permafrost discontinuous. Soil carbon generally decreases to the north of the optimum in the boreal/subarctic zone, reaching minimal levels in the high arctic. Soil organic carbon also generally decreases to the south, and even in the humid southeastern United States organic soils occur only on the very poorly drained coastal plains (Hofstetter, 1983).

The situation in northeastern Europe and on the West Siberian Plain is similar. The belt of maximum soil organic carbon in this region of Russia, which coincides with high cover by organic soils, lies within the discontinuous permafrost zone and up to about 400 km south of it (Walter, 1977; Fridland, 1988; Trofimov *et al.*, 1989; Orlov and Biryukova, 1995; Brown *et al.*, 1997). The Vasyugan peatland, probably the world's largest contiguous peatland at over 5 million ha (Liss and Berezina, 1981), is in the southern part of the West Siberian peat basin. Although the Vasyugan peatland lies about 300 km south of the limit of permafrost, the MAAT in its vicinity is near 0 °C, the range in monthly means is about 38 °C, and MAST is approximately +3 °C (Trofimov *et al.*, 1989; Pil'nikova, 1993); these values are near the optimum thermal advantage of air relative to the soil according to our theory and observations.

THE ROLE OF MOSSES

Non-vascular plants avoid the difficulty to vascular plants posed by a cold rooting zone during warm summers. Thus it is not surprising that non-vascular plants compete strongly with vascular plants in the boreal and subarctic, and mosses and fruticose lichens cover the ground in many places (Oechel and Van Ceve, 1986). We see three major implications for our hypothesis in this abundance of non-vascular plants. First, they help to maintain biomass productivity (Grigal, 1985) in spite of difficult soil thermal conditions. Second, mosses and lichens are fairly resistant to decomposition, which facilitates accumulation of organic matter in the soil (Heal and French, 1974; Moore, 1982; Clymo, 1983). Finally, mosses are effective at damping soil temperatures, which enhances the air thermal advantage (Viereck, 1970; Viereck *et al.*, 1983). Thus non-vascular plants, especially mosses, provide positive feedback to the thermal effect on accumulation of soil organic matter.

THE IMPLICATIONS OF CLIMATE CHANGE

If temperature is largely responsible for the existence of the boreal-subarctic maximum in soil organic carbon, the main long-term effect of warming should be to move the carbon sink northward as suggested by Ovenden (1990) and not necessarily cause a net loss in soil organic carbon as predicted by Kirschbaum (1995). A net loss of soil carbon could occur as a result of warming if the parts of the latitudinal belt of optimum carbon accumulation were displaced

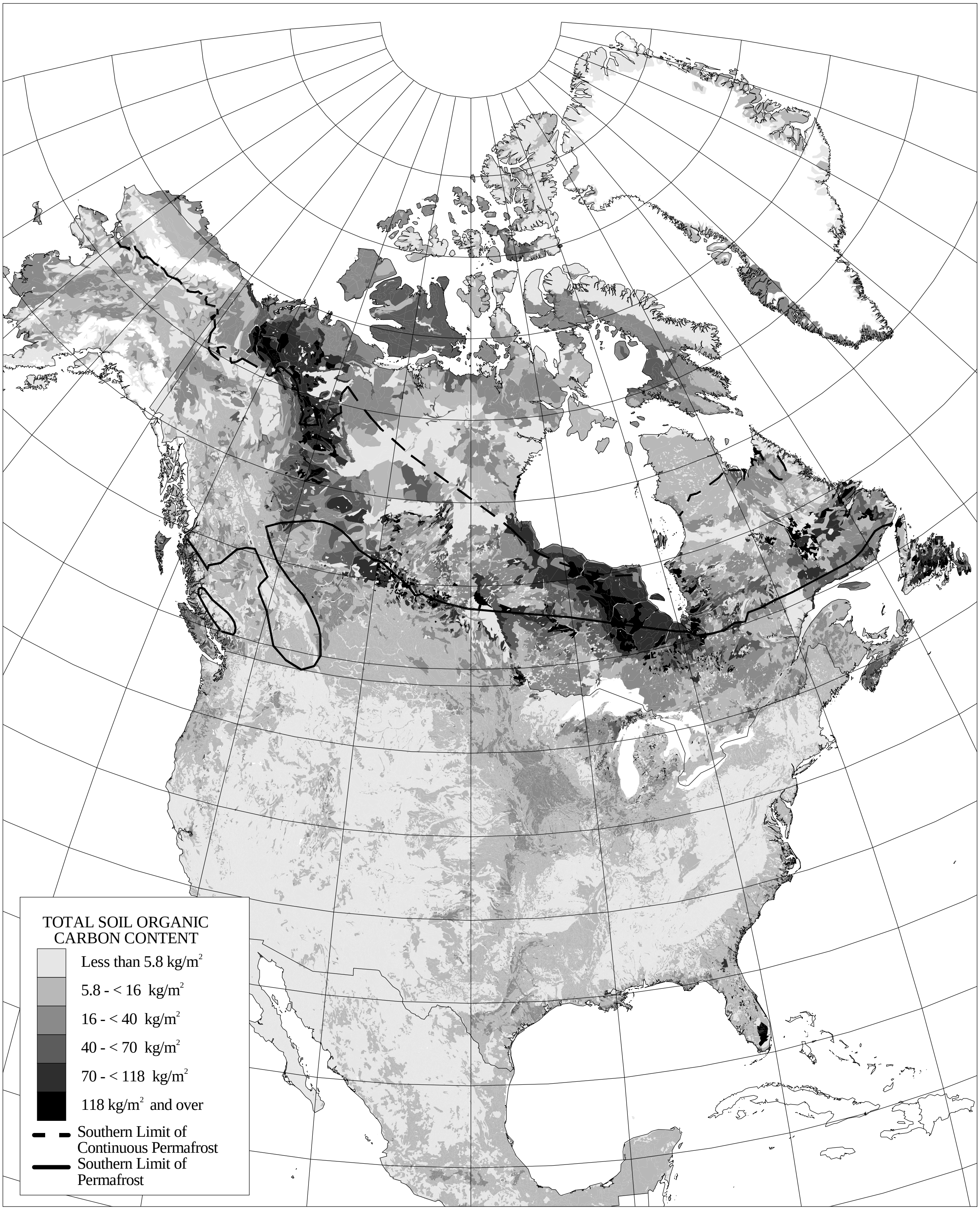


FIGURE 7. Soil organic carbon distribution of North America in relation to the discontinuous permafrost zone (modified from Lacelle *et al.*, 1997).

Répartition du carbone organique dans le sol en Amérique du Nord relativement à la zone de pergélisol discontinu (modifié de Lacelle et al., *1997).*

northward off the continents into the ocean. Zoltai's (1988) scenario for the northward shift of Canada's ecozones with doubled atmospheric CO_2 shows the boreal zone remaining on the continent and retaining its approximate current size, while part of the subarctic would be lost into Hudson Bay. Increased peat accumulation in the arctic would be expected to provide some compensation for loss of peat on the continent. Changes in rates of peat accumulation during the Holocene in the Canadian arctic calculated by Tarnocai and Zoltai (1988) are consistent with the idea that the arctic would become a better carbon sink with climatic warming.

If warming reduces the annual temperature range at high latitudes by warming of winter temperatures more than summer (Schlesinger and Mitchell, 1987; Chapman and Walsh, 1993), the air's thermal advantage over the soil would be reduced and with it the effectiveness of the high-latitude terrestrial carbon sink. Changes in the precipitation regime with warming and increasing plant productivity due to increased atmospheric CO_2 would undoubtedly modify these temperature-driven changes.

ACKNOWLEDGMENTS

This study was supported by the USDA Natural Resources Conservation Service global change program and Agriculture and Agri-Food Canada. Thanks to Barbara Miller and Henry Mount, USDA Natural Resources Conservation Service, and Andy Bootsma of Agriculture and Agri-Food Canada for help in obtaining soil temperature data. David Grigal, Stephen Robinson, Scott Smith, Lois Swanson, David Valentine, and an anonymous reviewer provided helpful comments. Temperature data collection at the Mackenzie Valley sites was funded by INAC. Temperature data collection at Canadian Atmospheric Environment Stations was funded by Environment Canada. Temperature data collection at most U.S. sites was funded by the US Department of Agriculture, Natural Resources Conservation Service. Data collection for Barrow, Alaska was funded by the NSF under the Geography and Regional Sciences and Arctic System Science programs and compiled by Kenneth M. Hinkel.

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