Effects of climate and land use on landscape soil respiration in northern Wisconsin, USA: 1972 to 2001

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ABSTRACT: Changes in climate and land use affect soil respiration rates (SRR) significantly, but studies of such effects across entire landscapes are rare. We simulated responses of landscape mean SRR (LMSRR) to such changes from May to October over a 30-year period in a managed, predominantly forested landscape in northern Wisconsin, USA using a) six satellite–derived land cover maps (1972, 1978, 1982, 1987, 1992, and 2001); b) monthly air temperature data in the corresponding years of the cover maps; and c) SRR models driven by soil temperature (T_s) at 5-cm depth. LMSRR seemed to increase linearly by 77% from 0.625 in May to 1.104 g $CO_2.m^{-2}.hr^{-1}$ in July, and then decreased at an increasing rate to 0.411 g $CO_2.m^{-2}.hr^{-1}$ in October. LMSRR was more sensitive to an increase of minimum temperature than that of mean or maximum temperature, suggesting that SRR in high-latitude forests would be affected more by future climate change. LMSRR in September over the study period was similar to that of June but with 92% higher variation while both landscape mean air temperature and precipitation in September had lower variation than in June. This indicates that the top soil layer functions differently during soil warming and cooling phases. Changes in land-cover composition from 1972 to 2001 increased LMSRR by 2.8 to 3.1% while 2 °C differences in growing season mean air temperature increased the SRR by 6.7 to 7.0%. The combined effects of both variables on the SRR are more complex, varying from 3.8 to 10.0%.

KEY WORDS: Landscape soil respiration; temperature variation; landscape composition; model; carbon flux.

1. INTRODUCTION

Soil respiration (SR) is the release of CO_2 from soils due to the production of CO_2 by roots and soil organisms. Such belowground processes are controlled by both abiotic and biotic factors; and are therefore related to climate change and land use dynamics (Raich & Schlesinger 1992, Jackson et al. 2000, Ogle et al. 2003). SR is a necessary component in quantifying ecosystem carbon sources/sinks related to the global carbon budget (Tans et al. 1990, Field et al. 1992, Dixon et al. 1994, Ciais et al. 1995, Grace et al. 1995). Particular attention has been focused on high, northern latitude ecosystems as a consequence of their climatic sensitivity, expanse, high carbon density, and observations of disproportionate warming (Bonan et al. 1992, Chapman & Walsh 1993, Environment Canada 1995, Overpeck et al. 1997, IPCC 2000). Recent flux measurements at individual high-latitude sites suggest that, at least in the short term, any direct effect of warming on net primary production may be more than offset by an increase in soil respiration caused by global warming (Oechel et al. 1993, Schulze et al. 1999, Oechel et al. 2000).

The additional carbon resulted from human activity has raised levels of atmospheric CO_2 by 30% mainly through the respiration of vegetation and soils. (http://www.metoffice.gov.uk/research/hadleycentre/pubs/brochures/B2000/climate.html) Land clearing and combustion of fossil fuels are two major causes for elevating atmospheric CO_2 concentrations from 280 to > 360 ppm in the last 200 years (Keeling et al. 1995). Various models have predicted that the total amount of carbon released annually to the atmosphere increases with the global deforestation rate (Alcamo et al. 1996, Yamagata & Alexandrov 1999). Twenty percent of existing forests and woodlands have been logged and/or converted to other uses worldwide since the pre-industrial era (Richards 1991). Turner et al. (1993) calculated that 45% of the potential forest cover of the continental USA had been converted to other land-cover types. Although intensive and dramatic transformations of land are less prevalent in public-owned areas, a trend of increasing timber harvest and fragmentation in Chequamegon National Forest between 1972 and 2001 was detected (Bresee et al. 2004).

Despite the importance of SR in carbon balance at various spatial and temporal scales, as well as numerous ecosystem- and global-level studies on SR (Raich & Schlesinger 1992, Howard & Howard 1993, Lloyd & Taylor 1994, Raich & Potter 1995, Thierron & Laudelot 1996, Potter & Klooster 1998, Raich et al. 2002, Ma et al. 2003). there has been little effort in understanding how changes in temperature and land use could affect SR rates (SRR) across landscapes. Analyses of the interactions between changes in temperature and land-cover mosaic on landscape mean SRR (LMSRR) are even rarer. Such studies pertaining to differences in SRR among various patch types that comprise a managed landscape can provide information for land managers to understand how landscape SR is altered by human-induced disturbances such as timber harvest under climate change.

This study is designed to evaluate how growing season LMSRR respond to changes in monthly mean soil temperature and land-cover at an inter-annual scale in a managed forest landscape over three decades. Three specific questions this study addresses are (1) What are the relative effects of temperature and land-cover changes on SRR across the landscape, (2) How does the seasonal trend in LMSRR vary interannually as a function of soil temperature, and (3) What are the implications of the seasonal variation in soil temperature for regional and global SRR and carbon budgets?

2. METHODS

2.1. Study area

Our study area (about 39,000 ha) is located in the Washburn Ranger District of the Chequamegon National Forest (CNF) in northern Wisconsin, USA (46°30' - 46°45' N, 91°02' - 91°22' W), where extensive research on biodiversity, microclimate, carbon and water cycles, and edge effects has been conducted since 1994 (Gustafson & Crow 1996, Chen et al. 1999, Saunders et al. 1999, Zheng & Chen 2000, Brosofske et al. 2001, Euskirchen et al. 2001, Euskirchen et al. 2002, Watkins et al. 2003). The geology is characterized by Precambrian shield bedrock and a late Wisconsin-age glaciated landscape. The topography is flat to rolling with elevations ranging from 232-459 m. Terraces and pitted outwash landforms are composed of deep, coarse-textured soils. The climate is characterized by a short/hot summer with a growing season of 120-140 days and cold winters. Long-term monthly mean temperature from December to February in a

30-year period (1971-2000) is -10 °C in Ashland, WI (http://mcc.sws.uiuc.edu/Temp/WI/470349_tsum.html), about 20 km southeast of the geographic center of the CNF. Annual precipitation ranges from 660-700 mm (Albert 1995). Forests accounted for about 83% of the study area in 2001.

Six land-cover maps and climatic data sets in the corresponding years over a 30-year period, field data on soil temperature (T_s), SR, and other meteorological data (Noormets et al. 2004) in the landscape since 2001 were developed, constructed, or collected. These data allow us to quantify relationships between air temperature and T_s, and between T_s and SRR.

2.2. Land-cover maps

Multi-year land cover maps from 1972 to 2001 were generated from satellite data (Landsat MSS and TM) at approximate 5-year intervals except between 1992 and 2001 (1972, 1978, 1982, 1987, 1992, 2001), which identified six major cover types 1) hardwood (HW), mixed hardwood/conifer (MIX), regenerating forest/shrub (RFS, hereafter referred to as young growth (YG)), jack pine (JP), red pine (RP), and non-forested bare ground (NFBG, hereafter referred as NF) (Bresee et al. 2004). The overall accuracy for all images and cover types was about 80% (Bresee et al. 2004). We resampled all pixels to a standard 60-m resolution for landscape level analysis.

2.3. Climate data

We examined the LMSRR from May to October (hereafter referred as the growing season), although this is slightly longer than actual growing days in the study area (Albert 1995). We chose this time period for three reasons: (1) air temperatures were available at a monthly time step, (2) SRR-T_s relationships were established based on the data collected during this period, and (3) summer SR constitutes the majority of annual SR. A study at similar latitude indicated that soil respiration under a mixed forest during the period accounted for about 75% of annual SR (Janssens et al. 2000). Kurganova et al. (2003) reported that forest soil CO_2 fluxes during the growing season comprised approximately 76-78% of annual SR from taiga soils in southern Russia.

Monthly minimum and maximum air temperature (T_{min} and T_{max}, °C) during the growing seasons of the 6 years corresponding to the land-cover maps (1972, 1978, 1982, 1987, 1992, and 2001) were obtained from the National Oceanic and Atmospheric Administration web site (ftp://ftp.ncdc.noaa.gov/pub/data/prism100). Monthly mean temperatures were derived from averaging T_{min} and $T_{max.}$ We used 1987 and 1992 climatic data to detect how climate change could affect LMSRR for two reasons 1) they showed the maximum difference (15.4 °C in 1987 vs. 13.4 °C in 1992) in landscape growing season mean temperatures among the 6 years over the 30-year study period; 2) The 2 °C difference was approximately in the middle range of the 0.8 – 3.5 °C global mean temperature increase by A.D. 2100 predicted by general circulation models (GCD) developed independently in many countries (Stocks et al. 2000). The growing season means of these 2 years were symmetrically distributed from the 14.4 °C, a 30-year mean growing season air temperature (1971-2000) in the landscape. The original temperature data with 4-km spatial resolution were resampled to 60-m resolution to match the resolution of land-cover maps for the simulations.

2.4. Soil temperature estimation and validation

Air temperatures ($T_{a,}$ °C) at 1.5 m and soil temperatures at 10-cm depth ($T_{s10,}$ °C) were simultaneously collected during the 2002-growing season from meteorological stations in hardwood, red pine, and young forest stands. The T_a was measured with HMP45AC probes (Vaisala, Finland) and T_{s10} were recorded using soil CS107 temperature probes (Campbell Scientific (CSI), Logan, UT, USA). Both variables were sampled every 20 seconds and the half hour averages were stored in CR10 data loggers (CSI). Daily mean T_a and T_{s10} were then calculated for establishing regression models between the two variables. Previous studies at regional and continental scales suggested that daily soil temperatures at top layers are correlated linearly with air temperatures in the previous day with some degree of time lag (Zheng et al. 1993, Brown et al. 2000). We used soil and air temperature observations on the same day to establish the linear models to convert air temperatures to soil temperatures. This may not provide the best fit, but it is practical and necessary for this study because the actual air temperature inputs for the entire landscape that were available to us are monthly daily means.

Soil temperatures at 5- and 10-cm depths (T_{s5} and $T_{s10,}$ respectively) were simultaneously measured using HOBO H8 (Onset Computer Corp, Pocasset, Mass.) data logger at 14 hardwood, pine, and regenerating forests. We recorded half-hourly soil temperature from three TMC6-HA or TMC6-HB temperature sensors. Each data logger had two sensors installed at 5 cm and 10 cm depths of soils. Measurements were recorded from 20 May to 31 October 2003. T_{s5} and T_{s10} were smoothed with a three-day moving average for establishing regression models for three generalized cover types during soil warming (May-July) and cooling (August-October) periods, respectively (Table 2).

We conducted a two-step procedure to predict T_{s5}, the driving variable used in our SRR models (Euskirchen et al. 2003), from T_a. This procedure was necessary because there were no simultaneous measurements of T_a and T_{s5} available to establish direct relationships between the two variables. First, monthly mean air temperatures were converted to monthly mean soil temperatures at 10-cm depth based on regressions developed from field measurements for major cover types (e.g., hardwood, pine, and regenerating forest/shrub, Table 1) in 2002. Second, we adjusted monthly mean soil temperatures at 10-cm depth to soil temperature at 5-cm depth based on field measurements in 2003. The relationships were grouped to two periods: soil warming (May to July) and soil cooling (August to October) for three cover types (Table 2). The models developed for hardwood, pine, and young growth were used for hardwood and mix forests, red pine and jack pine, and young growth and NF, respectively.

We also used other independent field soil temperature measurements at 5-cm depth obtained from 17 sites throughout the growing seasons of 1999 and 2000 in the landscape to verify coarse-resolution air temperature data and our methodology in both temporal (grouped by month) and spatial (grouped by sites) dimensions.

2.5. Estimating soil respiration rates (SRR) across entire landscape

Although both soil temperature (T_s) and soil moisture (M_s) control SR, T_s shows greater impacts on soil respiration in non-arid areas (Edwards 1975, Houghton et al. 1983, Parker et al. 1984, Zheng et al. 1993, Lloyd & Taylor 1994, Davidson et al. 1998, Janssens et al. 2000, Raich et al. 2002, Euskirchen et al. 2003, Jones et al. 2003). We used SRR-T_s models for the major cover types (Table 3) developed from previous study in the area (Euskirchen et al. 2003) to estimate LMSRR. We did not use models that include an M_s term for a primary reason that there was no soil moisture available and no suitable surrogate across the landscape during our study period. In addition, soil temperature and soil water content tend to be negatively correlated through the growing season (Davidson et al. 1998) and T_s has had the most explanatory power in the study area, explaining 45 to 73% of the variability in SRR (Euskirchen, 2003). The inclusion of 'an M_s term' and a T_s x M_s interaction term into our SR model increased the r^2 values only by 0.04 to 0.12 for 3 cover types (Euskirchen, 2003). These 3 types combined accounted for 21 to 31% of the total area during the 30-year study period. Furthermore, while monthly precipitation amounts are available, these cannot be readily translated into M_s because the intensity and frequency of precipitation, soil properties, and rates of evapotranspiration all effect how monthly precipitation translates into M_s. To calculate SRR for mixed forests, we used both hardwood and softwood equations weighted by their field observed proportions ($SRR_{mix} = SRR_{hw} * 0.6 + SRR_{jp} * 0.2 + SRR_{rp} * 0.2$).

2.6. Effects of temperature and land cover on SRR

We maximized the detectable influence of temperature and land cover by selecting two extremes of each variable among the 6 years. The two land-cover maps were for the years of 1972 and 2001, between which decreased forestlands and increased non-forest and young growth areas were the greatest (Fig. 1a). Climatic data sets were for 1987 and 1992, which showed the greatest difference in growing season mean temperatures (15.4 °C and 13.4 °C, respectively, Fig. 1b) among the 6 years. We simulated the LMSRR at a monthly step using 4 different combinations 1) 1972 land-cover map and 1992 temperature data (used as base run for comparisons with other combinations), 2) 1972 land-cover map and 1987 temperature data, 3) 2001 land-cover map and 1992 temperature data, and 4) 2001 land-cover map and 1987 temperature data. Growing season LMSRR were then calculated. We further completed the analyses of growing season LMSRR among the four testing scenarios by comparing 1 and 2 to determine the sole effects of temperature, comparing 1 and 3 to illustrate the sole effects of land-use change, and comparing 1 and 4 to examine the effects of the changes in temperature and land use combined.

To compare seasonal variations between LMSRR and air temperature from May to October among the six simulated years, we calculated the coefficient of variation (CV, %) for both variables in each given month because the units for the 2 variables were not in the same magnitude. To examine the inter-annual relationship between LMSRR and air temperature among the 6 years, we calculated the relative changes for both variables by dividing the values in each given year by their means of the 6 years.

3. RESULTS

Changes in LMSRR from May to October generally followed the patterns of monthly mean air temperature, but had more moderate rates of change (Fig. 2a). LMSRR values were the highest in July (1.03 to 1.15 g $CO_2.m^{-2}.hr^{-1}$) and averaged 1.10 g $CO_2.m^{-2}.hr^{-1}$ among the 6 years. The lowest LMSRR occurred in October and was 63% less than that of July on average. The values varied from 0.38 to 0.44 g $CO_2.m^{-2}.hr^{-1}$, with an average of 0.41 g $CO_2.m^{-2}.hr^{-1}$ (Fig. 2a). September had the greatest inter-annual variation in LMSRR and May had the smallest with standard deviations (STD) of 0.055 $CO_2.m^{-2}.hr^{-1}$ and 0.016 g $CO_2.m^{-2}.hr^{-1}$, respectively. Comparison of CVs between LMSRR and air temperature from May to October demonstrated that: (1) LMSRR showed smaller variation than that of air temperature in all months except in May; (2) variations of LMSRR in soil cooling months (August to October) varied more than in the warming months (May to July) while air temperature varied less in the cooling months than in the temporally symmetric warming months (e.g., August vs. July and September vs. June).

Temporal dynamics of monthly LMSRR before and after their peak value in July differed (Fig. 2a). The LMSRR increased linearly to a peak and then seemed to decrease at an accelerating rate. LMSRR values in May, June, August, September, and October averaged about 57, 78, 94, 73, and 37% of their July's SRR, respectively. LMSRR decreased by 49% from September to October. While the CV value (7.5%) of LMSRR in September was much higher than that in June (3.9%), the CV value of mean landscape air temperature was lower than that in June (Fig. 2b). A similar pattern was also observed in precipitation that CV value (27%) in September was smaller than that in June (30%) among the 6 years (data not shown).

Changes in inter-annual growing season LMSRR followed the same trend of growing season mean air temperature variations except in 1982 (Fig. 3a). The inconsistent pattern in 1982 and a mismatched magnitude of changes in 1987 clearly indicated that other factors such as land-use pattern and distribution of temperature within the growing season would also affected LMSRR variation. Of the cover types, changes in the area of young growth influenced the inter-annual growing season LMSRR variation most (data not shown).

Variation of growing season LMSRR among the 6 years correlated well with temperature fluctuation. Minimum temperature (T_{min}) had a stronger relationship with LMSRR than mean or maximum temperature (slope = 0.034, r^2 = 0.91, Fig. 4a).

Validation between the measured and estimated soil temperatures at 5-cm depth using regression models (Table 2) suggested that the monthly air temperature data from the NOAA web site (ftp://ftp.ncdc.noaa.gov/pub/data/prism100) and our presented methodology to convert air temperature to soil temperature are valid for landscape level analyses. Our field measurements were widely distributed across the landscape (Fig. 5a). While the estimated soil temperatures matched well temporally ($R^2 = 0.95$, N = 6, $p = 0.001$, Fig. 5b), they did not do so spatially ($R^2 = 0.25$, N = 17, $p = 0.05$, Fig. 5c).

Our results indicated that increasing growing season mean air temperature by 2 degrees in the CNF could raise LMSRR by 6.7% based on landscape mosaic in 1972 and 7% on landscape mosaic in 2001 (Fig. 6). When air temperatures were kept constant, changes in land-cover composition from 1972 to 2001 increased LMSRR by 2.8% in a cooler year (1992) and 3.1% in a warmer year (1987). The combined effects of changes in air temperatures and land-cover composition on SRR were more complicated, varying from 3.8 % to 10.0%, depending on how land cover interacted with climate.

4. DISCUSSION

We examined the effects of changes in temperature and land use on LMSRR over a 30-year period in a managed forest landscape. The range of variation in each of the driving variables was close to magnitudes previously reported. For example, from 1972 to 2001, the inter-mediate and mature forest cover types declined about 12% while the non-forested and young growth cover types increased from 22% to 34% in the CNF (Fig. 1a).

The annual mean loss rate of forest cover (0.4%) in the CNF was similar to that reported in the Appalachian highlands, NC and the Olympic peninsula, WA, USA, where the annual mean loss rate of forest cover on public land was about 0.3% during a 16-year period from 1975 to 1991 (Turner et al. 1996). Differences in monthly mean temperatures from June to September between 1987 and 1992 used in this study ranged from 2 to 5 °C (Fig. 1b). The range corresponds to the 2 to 6 C° projected increases in summer averages in northern latitudes (http://earthobservatory.nasa.gov/Study/DirtCarbon).

The LMSRR values of June and September among the 6 years were of similar magnitude (Fig. 2), however, a t-test indicated that mean air temperature in June (16.3 °C) was significantly higher than that in September (13.7 °C, $p = 0.02$). While the CV (7.5%) of LMSRR in September among the 6 years was 92% higher than that in June (3.9%), both CV values for air temperature and total precipitation (9.5% and 27%, respectively) in September were lower than those in June (10.5% and 30%). Such disagreement strongly suggested that depths of litter layer associated with cover types across the landscape could be an important factor determining spatial variation of soil temperature in its cooling process, thus, contributing to the larger variation in LMSRR.

The litter layer probably has less effect than the forest canopy on reducing maximum topsoil temperatures, but a much greater effect than the canopy in raising the minimum topsoil temperature during soil cooling (Li 1926, Armson 1977, Pritchett & Fisher 1987). During soil warming, solar radiation is the principal source of heat and topsoil temperature varies more or less with the temperature of the air immediately above it (Pritchett & Fisher 1987). Consequently, soil temperature increases linearly from May to July following the general pattern of seasonal trend in air temperature. During soil cooling (August to October), however, the source of heat is from deeper soil and the decreases in soil temperature lag behind those of air temperature. The magnitude of which could be affected by the thickness of litter layer (Pritchett & Fisher 1987, Johnson-Maynard et al. 2004). Spatially and inter-annually heterogeneous litter layers may also explain the larger variation in September LMSRR we demonstrated. During the cooling process, the litter layer could play an important role in slowing the rate of soil cooling by preventing long-wave radiation from escaping from the soil. Once heat gained during the warming period is depleted below certain threshold value, sharp decreases in topsoil temperature were expected.

Inter-annual variation of LMSRR did not always vary accordingly with that of mean air temperature, indicating that other factors such as land-cover composition and temporal pattern of temperature distribution across growing season may also determine the general direction and degree of changes in LMSRR, compared to those changes in air temperature. For example, growing season mean air temperature of 1982 was 1.2% below the average air temperature of the six years while the LMSRR increased (0.6%, Fig. 3a) because the air temperature in July was 0.9 °C higher than the 6-year average. Growing season mean temperature increased substantially in 1987 (6.4%), compared to that of mean value, while SRR only increased little (0.2%). The minor increase in SRR can be attribute to a 37% reduction (from1982) in the area of young forest, which has the highest SRR among all land covers (Figs. 3a & 3b).

We have confirmed that LMSRR is more sensitive to increases of minimum soil temperatures than to that of maximum temperatures (Fig. 4a). Our findings agreed with other reported results that the temperature sensitivity of soil CO_2 efflux decreases with increasing soil temperature (Howard & Howard 1993, Lloyd & Taylor 1994). For example, in the absence of moisture limitations, an increase from 0 to 1 deg C would result in a 22% increase in respiration, while an increase from 25 to 26 deg C leads to a 5% increase (Lloyd & Taylor 1994). The findings could have direct and significant impact on carbon cycles in high-latitude ecosystems related to future regional and global carbon budget studies, especially in North America and Eurasia. While the Intergovernmental Panel on Climate Change stated that the observed increase in global mean temperature over the last century was 0.3 – 0.6 °C (Watson et al. 1995), major winter and spring warming (2 – 3 °C) has occurred in the past three decades in west-central and northwestern Canada and Alaska and virtually all of Siberia (Environment Canada 1995, Hansen et al. 1996). A similar warming trend was apparent in our study area with a 1.9 °C increase in annual mean air temperature during a 30-year period (Fig. 4b). Therefore, understanding patterns of seasonal change in soil temperature caused by climate change is critical for reassessing annual soil respiration and ecosystem carbon budgets in northern latitudes because high-latitude forests may undergo the greatest climatically induced changes in the 21st century, among all biomes (Bonan et al. 1992, Myneni et al. 1997). The effect of increased temperatures on net carbon exchange will vary depending on its timing. If the warming mainly occurs in winter months then it may have little impact on SR or photosynthetic (PSN) processes. In fall or spring months, it may enhance SR efflux more than PSN, and in summer months, the influence may enhance PSN more than SR. Consequently, effects of climate change on ecosystem net carbon exchange may be negligible in the winter, while it may enhance the source strength in the fall or spring. In the summer, the sink strength of these forests may increase. A temporal understanding of warming could improve our ability to estimate net carbon exchange between terrestrial ecosystems and the atmosphere.

Field measurements of T_{s5} suggested that the monthly mean air temperature data from NOAA and our methodology to convert the air temperature to soil temperature are valid for LMSRR studies. Although spatial correlation between the observed and estimated soil temperatures showed a lower level of significance ($p = 0.05$, $R^2 = 0.25$), compared to the level of significance for temporal correlation ($p = 0.001$, $R^2 = 0.95$) (Figs. 5b & 5c), this conformation revealed that the estimated soil temperatures corresponded to their spatial variations in reality at some degree. It should be noted that less significant correlation between the observed and estimated soil temperatures on spatial than on temporal dimension is expected because of a mismatch in spatial resolutions. While the estimated soil temperatures were based on air temperature data at 4-km pixel resolution, observed soil temperatures were collected at much finer spatial resolution (10s meters) at which many local factors such as soil physical properties, soil water content, and slope and aspect of the terrain can affect the measurements. Kang et al. (2004) reported that the topographic effects strongly affected on solar radiation and temperature at scales from 30 to 2160 m.

This study demonstrated that the combined effects of changes in air temperatures and land-cover composition on SRR were more complicated than the effects from a single variable: larger variation resulted from combined effects (Fig. 6). The variation can be caused by the direction of change in land-cover types when each type exhibits different SRR. The observed variation can also be affected by how the land-cover change and climate change interacted. For example, if a landscape potentially experiences high SRR through the creation of young forest but undergoes a cooler-than-average year, then the effects on SRR are contradictory, and the two factors may moderate one another. If the landscape dominated by younger forests interacts with a warmer-than-average year, then the effects on SRR complement each other and enhance landscape SRR. We have demonstrated that the cumulative effect, however, doest not necessarily equal to the sum of effects from the two individual factors (e.g., 10% > 6.7% + 2.8%, Fig. 6)

There were several possible error sources associated with our LMSRR estimates. First, there are inconsistencies in the temporal scales on which the SRR and temperature regressions were built, or on which the air temperature and cover type composition acted because of lack of historical data. Second, our estimated LMSRR might be higher than actual values because the SRR-Ts models were developed using field data collected between 7 am to 7 pm. A lack of nighttime SRR, however, should have minimal effect on our analyses since the study was focused on relative changes of LMSRR during the growing season among the years. Third, our SRR models could be better if they included soil moisture component (Kang et al. 2004), however, the lack of adequate data necessitates use of less than ideal models. While inter-annual variability in SR has been previously correlated with inter-annual differences in precipitation for dry biomes such as savannas, bushlands, and deserts (Raich et al. 2002), it may not be as critical in our relatively moist study area. Fourth, when working from land cover maps, their accuracy must be considered during interpretation of results. We used a model for young forests (Table 3) to estimate SRR for the RFS cover type because it was the closest one by definition. The disparate compositions of vegetation included in this cover type may differ in their SRR. Similarly, the composition of the cover type may have changed with management intent across the interval of our study. And finally, SRR-T_s models for different cover types may also introduce uncertainty in evaluating effects of land-cover changes on LMSRR. For example, statistically, only the young growth model significantly differs from the models for other types ($p = 0.05$). Despite these weaknesses, this study elucidated the interaction between changes in temperature and land-cover composition on SRR across an entire landscape, provided useful characterization of seasonal changes in LMSRR among the years, and established a framework for future, regional soil carbon efflux studies related to changes in climate and land use.

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Figure Captions

Figure 1. (a) Changes in land-cover composition in Chequamegon National Forest (CNF) between 1972 and 2001, and (b) differences in monthly mean air temperature between 1987 and 1992.

Figure 2. (a) Seasonal changes of landscape mean soil respiration rates (LMSRR) from May to October among the six simulated years and the mean monthly air temperature (°C) of the 6 years, and (b) comparison of coefficient of variations (CV, %) between LMSRR and air temperature, from May to October among the six simulated years in Chequamegon National Forest (CNF).

Figure 3. (a) Comparison of temporal variation (1972 – 2001) between growing season landscape mean soil respiration rates (LMSRR, g $CO_2.m^{-2}.hr^{-1}$) and mean air temperatures (°C) calculated as relative changes to their means of the 6 years, and (b) changes in cover type composition among the 6 years: HW = hardwood, MIX = mixed hardwood/conifer, JP = jack pine, RP = red pine, NF = non-forested, and YG = young growth.

Figure 4. (a) Relationships between landscape mean soil respiration rates (LMSRR) and landscape minimum air temperature (LMSRR = 0.034 * T_{min} + 0.43, r^2 = 0.91), maximum air temperature (LMSRR = 0.020 * T_{max} + 0.38, r^2 = 0.39), and mean air temperatures (°C) (LMSRR = 0.030 * T_{mean} + 0.38, r^2 = 0.68) from May to October. Each point represents growing season LMSRR and air temperatures for

one of the 6 years (1972 – 2001), and (b) A warming trend in the study area based on the observations from 1964 to 1993 (after 3-year running average) at the Farm Experimental Station, Ashland, WI (data since 1994 were missing).

Figure 5. (a) Spatial distribution of the 17 plots whose soil temperatures at 5-cm depth were used for soil temperature regressions, and (b) temporal validation of regressions, points represent monthly mean temperature (N = 6, from May to October), and (c), spatial validation of soil temperature regressions, points represent the growing season mean soil temperature for a given plot (N = 17).

Figure 6. Changes in landscape mean soil respiration rates (LMSRR) between 1972 and 2001 caused by climate change and land-use change were quantified under four scenarios: 1) 1972 land-cover map (72lc) and 1992 growing season monthly air temperature data (92t, the coldest growing season among the 6 years); 2) 72lc and 1987 growing season monthly air temperature data (87t, the hottest growing season among the 6 years); 3) 2001 land-cover map (01lc) and 92t; and 4) 01lc and 87t. SRR calculated from the scenario one was used as base value for comparison with other simulated SRR values. Bar represents one standard deviation and values in % at the top show the relative changes in SRR compared to the base value. Values between the arrow sign are relative changes (always using the larger number as numerator) between the two indicated scenarios.

Table 1. Regression equations used for converting monthly air temperatures (T_a, °C) to soil temperatures at 10-cm depths (T_{s10}, °C) based on field observations from May to October for three cover types in Chequamegon National Forest: HW = hardwood, P = pine, YG = young growth, and ** for hardwood but generated from observations under young growth and matured pine combined in October due to missing data.

CoverType	Month	Equation	r^2	N	*P*
HW	May	$T_{s10} = 0.40T_a + 3.3$	0.77	31	0.001
HW	June	$T_{s10} = 0.46T_a + 5.9$	0.79	30	0.001
HW	July	$T_{s10} = 0.24T_a + 13.0$	0.25	29	0.01
HW	August	$T_{s10} = 0.36T_a + 10.4$	0.58	31	0.001
HW	September	$T_{s10} = 0.51T_a + 7.3$	0.91	26	0.001
HW	October**	$T_{s10} = 0.39T_a + 3.5$	0.49	49	0.001
P	May	$T_{s10} = 0.42T_a + 3.0$	0.80	27	0.001
P	June	$T_{s10} = 0.46T_a + 6.0$	0.75	30	0.001
P	July	$T_{s10} = 0.28T_a + 12.5$	0.55	31	0.001
P	August	$T_{s10} = 0.31T_a + 11.6$	0.54	31	0.001
P	September	$T_{s10} = 0.53T_a + 7.1$	0.83	30	0.001
P	October	$T_{s10} = 0.34T_a + 3.2$	0.52	21	0.001
YG	May	$T_{s10} = 0.52T_a + 5.6$	0.75	26	0.001
YG	June	$T_{s10} = 0.42T_a + 10.3$	0.83	30	0.001
YG	July	$T_{s10} = 0.36T_a + 12.9$	0.75	31	0.001
YG	August	$T_{s10} = 0.39T_a + 11.6$	0.73	31	0.001
YG	September	$T_{s10} = 0.60T_a + 6.8$	0.85	30	0.001
YG	October	$T_{s10} = 0.46T_a + 3.8$	0.60	28	0.001

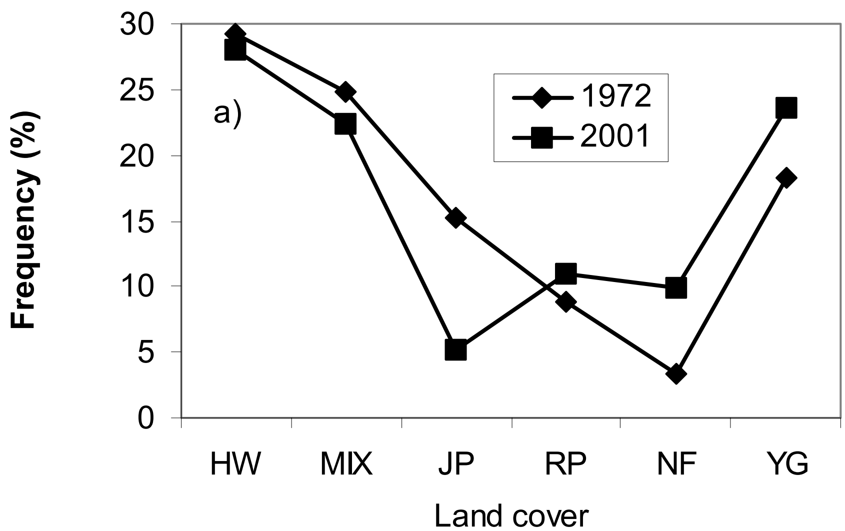
Table 2. Regression equations used for converting soil temperatures at 10-cm depth (T_{s10}, °C) to soil temperatures at 5-cm depth (T_{s5}, °C) based on field observations for soil warming period (May to July) and soil cooling period (August to October) for three cover types: HW = hardwood, P = pine, YG = young growth.

CoverType	Month	Equation	r^2	N	*P*
HW	May-July	$T_{s5} = 1.08T_{s10} - 0.7$	0.95	68	0.001
HW	August-October	$T_{s5} = 1.37T_{s10} - 4.0$	0.93	92	0.001
P	May-July	$T_{s5} = 1.03T_{s10} + 2.4$	0.80	71	0.001
P	August-October	$T_{s5} = 1.22T_{s10} - 2.0$	0.96	91	0.001
YG	May-July	$T_{s5} = 1.05T_{s10} + 3.0$	0.96	68	0.001
YG	August-October	$T_{s5} = 1.20T_{s10} - 1.5$	0.96	92	0.001

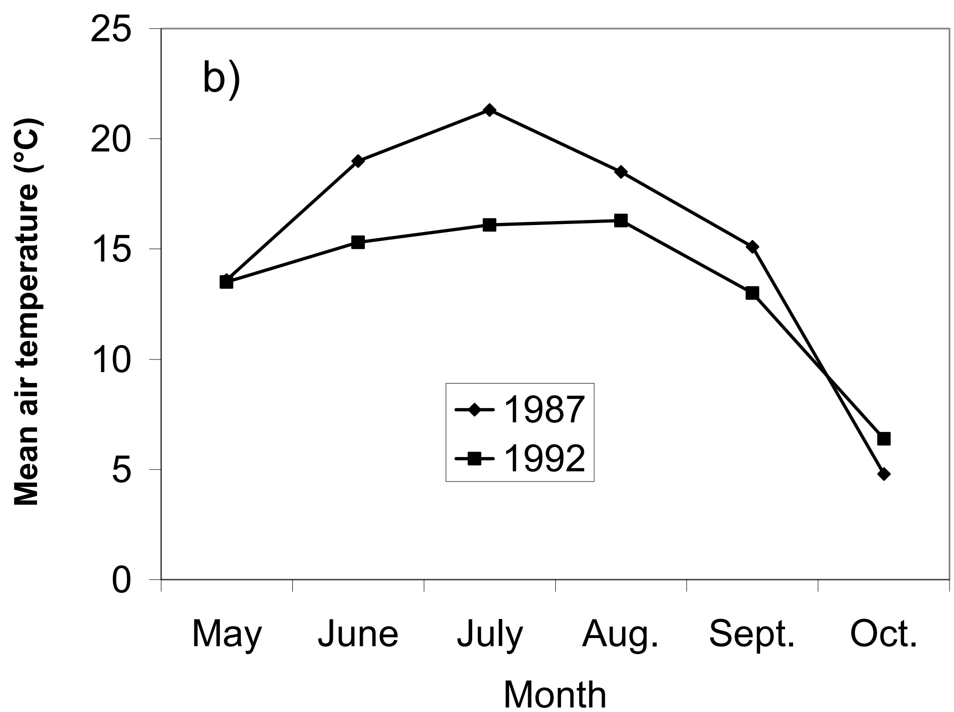
Table 3. Soil respiration rates (SRR, g $CO_2.m^{-2}.hr^{-1}$) for major cover types in the study area (HW=hardwood, NF=non-forested, YG=young growth, JP=jack pine, and RP=red pine). T_{s5} = soil temperature at 5-cm depth (°C) (Euskirchen et al. 2003).

(HW)	$SRR = 0.2974 * e^{0.0635*Ts5}$, $r^2 = 0.73$
(NF)	$SRR = 0.2594 * e^{0.0513*Ts5}$, $r^2 = 0.67$
(YG)	$SRR = 0.3195 * e^{0.0715*Ts5}$, $r^2 = 0.65$
(JP)	$SRR = 0.3235 * e^{0.0514*Ts5}$, $r^2 = 0.45$
(RP)	$SRR = 0.3059 * e^{0.0611*Ts5}$, $r^2 = 0.55$

Fig. 1.



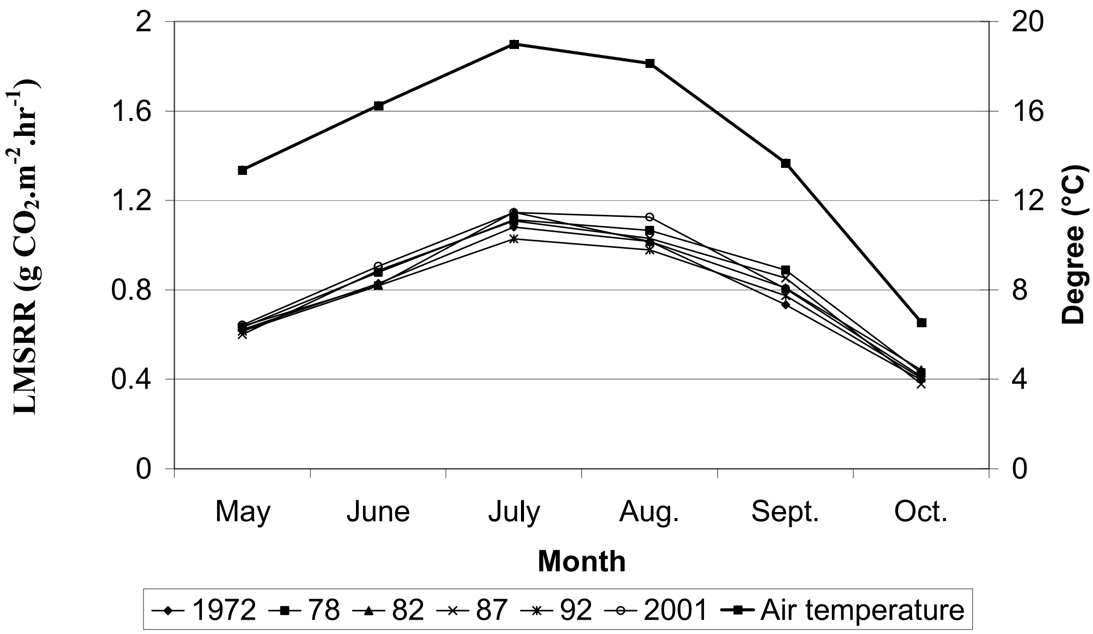
a)
1972
2001
Frequency (%)
30
25
20
15
10
5
0
HW
MIX
JP
RP
NF
YG
Land cover



b)
1987
1992
Mean air temperature (°C)
25
20
15
10
5
0
May
June
July
Aug.
Sept.
Oct.
Month

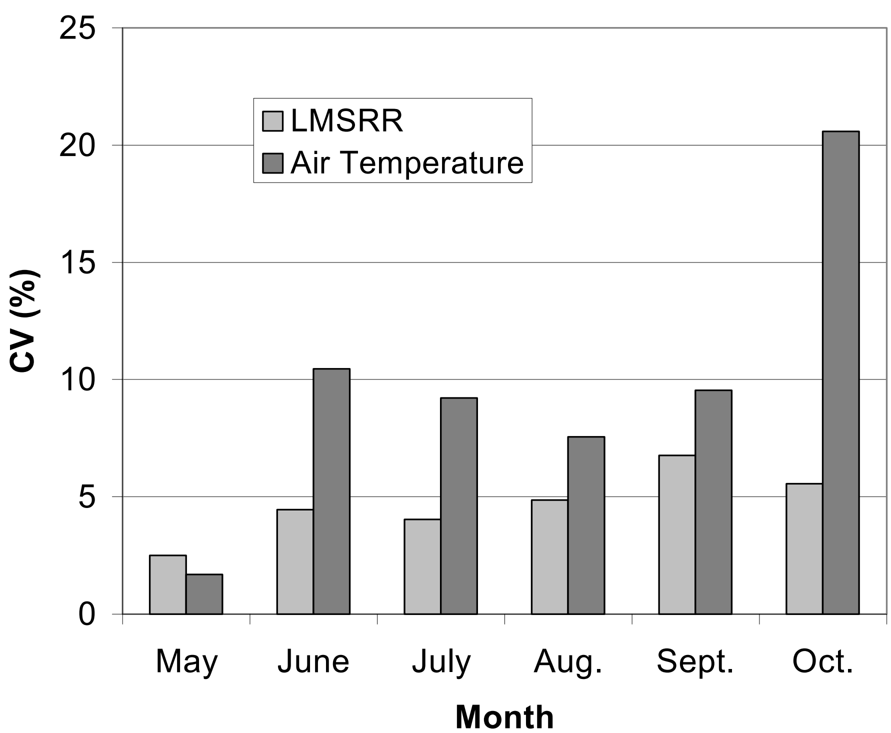
Fig. 2.

a)



2
1.6
1.2
0.8
0.4
0
20
16
12
8
4
0
LMSRR (g CO_2.m^{-2}.hr^{-1})
Degree (°C)
May
June
July
Aug.
Sept.
Oct.
Month
1972
78
82
87
92
2001
Air temperature

b)



25
20
15
10
5
0
CV (%)
LMSRR
Air Temperature
May
June
July
Aug.
Sept.
Oct.
Month

Fig. 3.

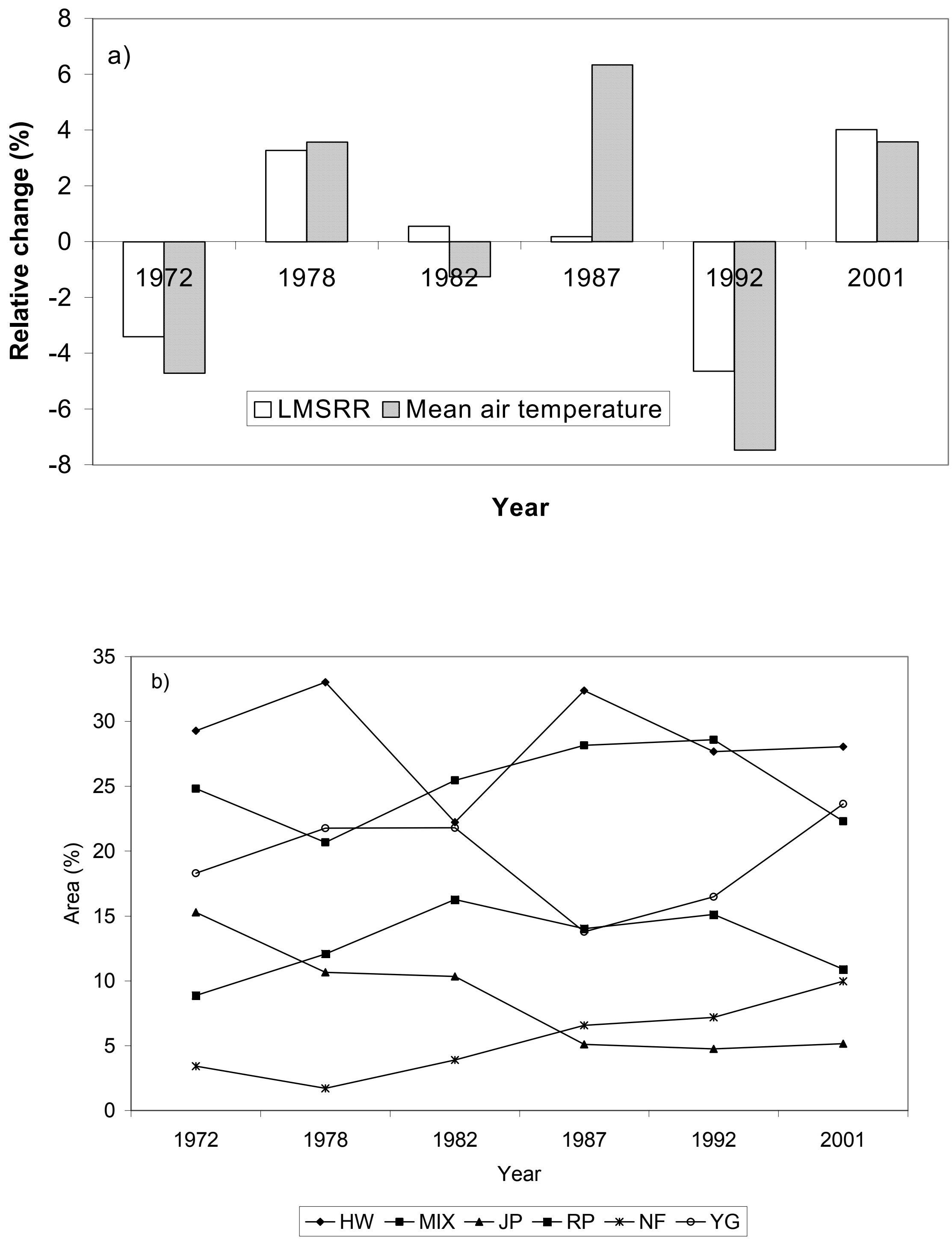
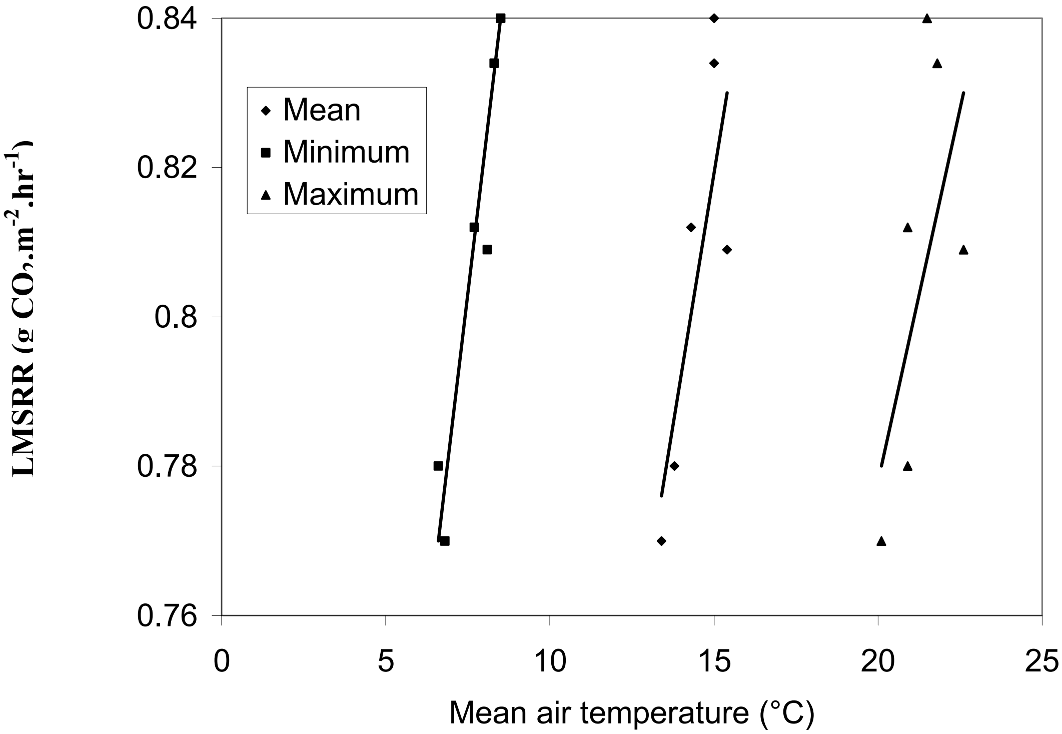

a)
8
6
4
2
0
-2
-4
-6
-8
Relative change (%)
1972
1978
1982
1987
1992
2001
LMSRR
Mean air temperature
Year
b)
35
30
25
20
15
10
5
0
Area (%)
1972
1978
1982
1987
1992
2001
Year
HW
MIX
JP
RP
NF
YG

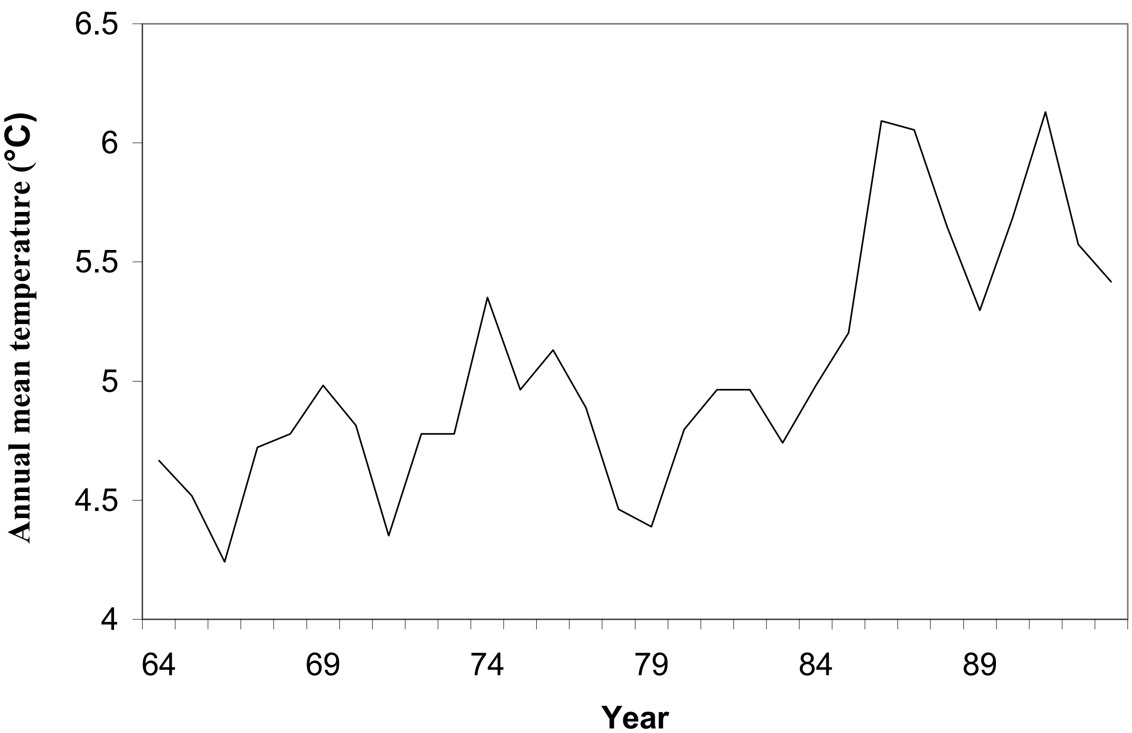
Fig. 4.

a)



0.84
0.82
0.8
0.78
0.76
LMSRR (g CO2.m-2.hr-1)
Mean
Minimum
Maximum
0
5
10
15
20
25
Mean air temperature (°C)

b)



6.5
6
5.5
5
4.5
4
Annual mean temperature (°C)
64
69
74
79
84
89
Year

Fig. 5.

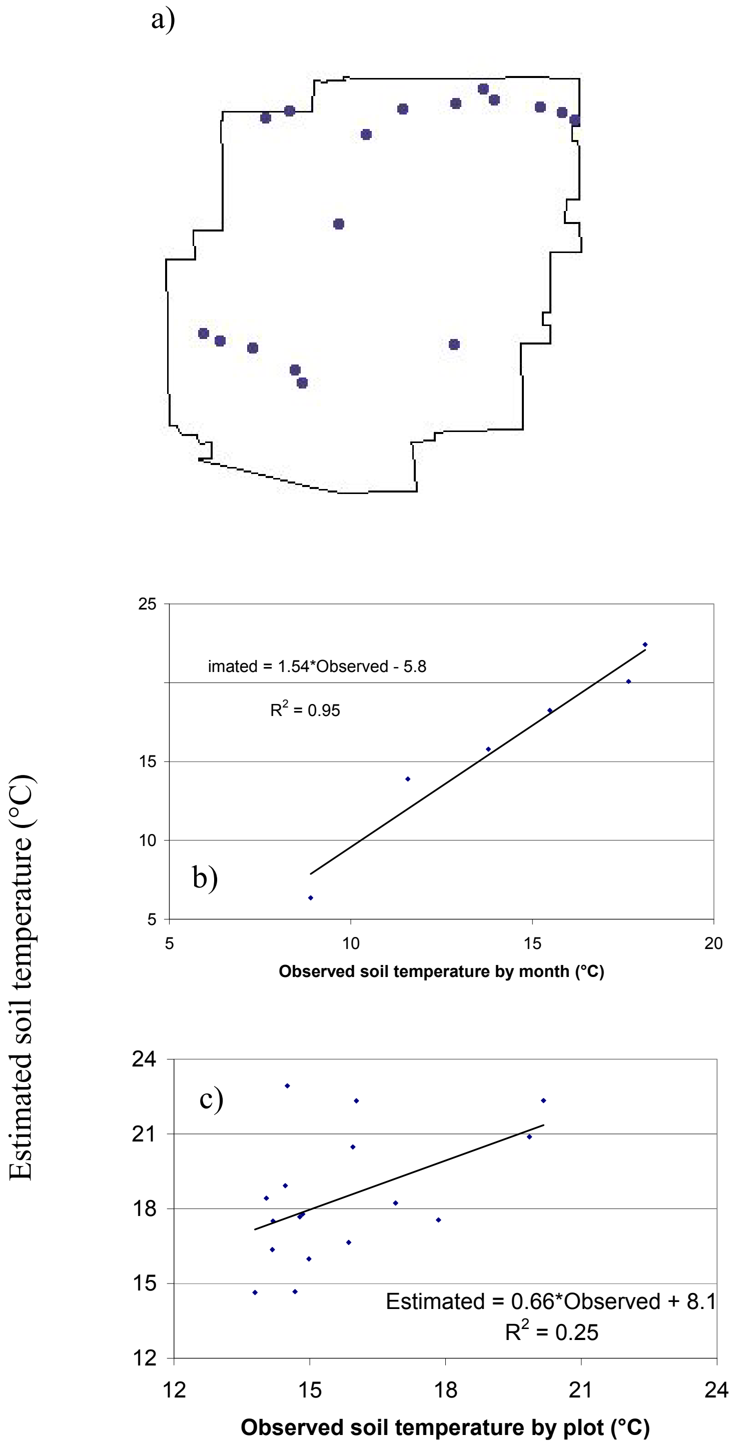
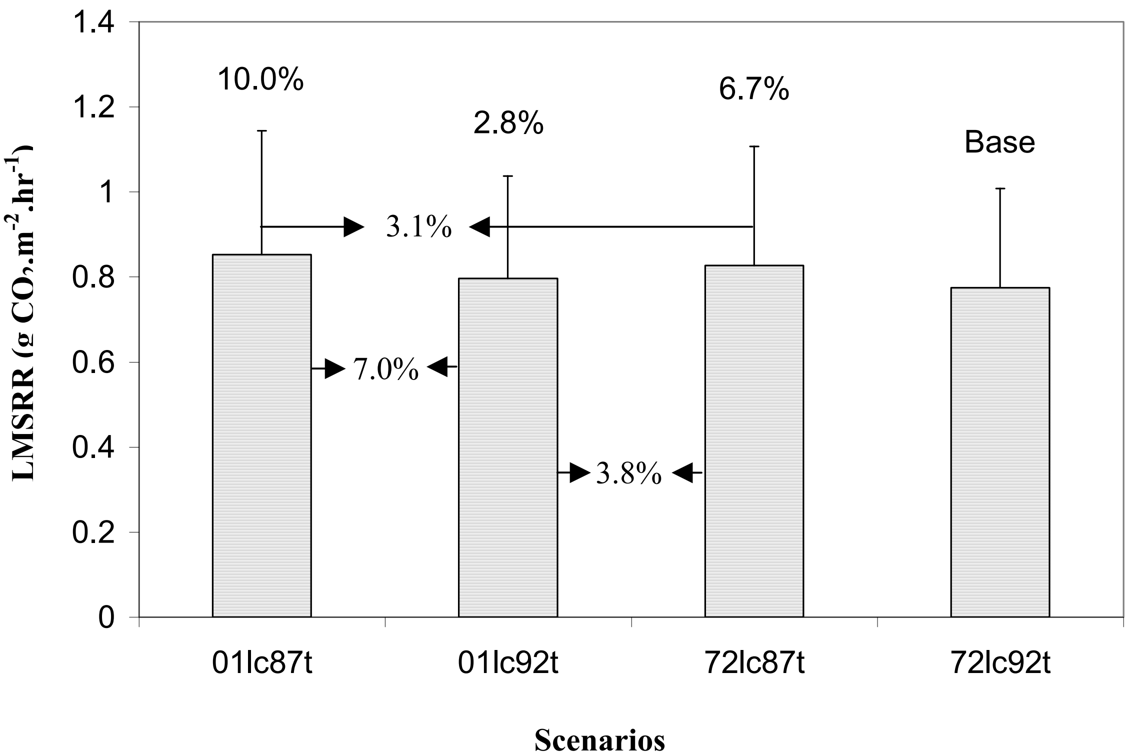

a)
b)
c)
Estimated soil temperature (°C)
imated = 1.54*Observed - 5.8
R2 = 0.95
25
15
10
5
5
10
15
20
Observed soil temperature by month (°C)
Estimated = 0.66*Observed + 8.1
R2 = 0.25
24
21
18
15
12
12
15
18
21
24
Observed soil temperature by plot (°C)

Fig. 6.



1.4
1.2
1
0.8
0.6
0.4
0.2
0
LMSRR (g CO_2.m^{-2}.hr^{-1})
10.0%
2.8%
6.7%
Base
3.1%
7.0%
3.8%
01lc87t
01lc92t
72lc87t
72lc92t
Scenarios