

The observed responses of forest carbon dioxide exchange to climate variations from daily to annual time scale

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Abstract: The climate factors controlling forest carbon dioxide exchange may vary as a function of time scales. This hypothesis is examined using direct measurements of net ecosystem exchange (*NEE*) of CO₂ and meteorological data obtained over multiple years from four forest sites in North America. We find that: (1) the relationship between nighttime *NEE* (respiration) and temperature is strong on daily, monthly and seasonal time scales, but breaks down on an annual time scale. Autumn respiration rates are 1 to 3 times higher than spring respiration rates and the temperature sensitivity of soil respiration is lower in summer than in spring and autumn. (2) Unlike temperature, precipitation is poorly correlated with *NEE* on daily, monthly, and seasonal time scales but is well correlated on an annual time scale. Forest *NEE* is influenced by annual variability in precipitation because soil moisture during the growing season, which is often associated with forest growth and CO₂ uptake, is controlled in part by cold season precipitation. (3) Net radiation is a comprehensive climate variable that is related to temperature, light, water vapor, cloud cover, and albedo; and it is correlated with *NEE* on all time scales. (4) Although *NEE* is correlated to photosynthetically active radiation on daily, monthly and seasonal time scales, the relationship breaks down on an annual time scale because the respiration component of *NEE* is not coupled to light. (5) We observe that drought stress has a very strong effect on forest uptake of CO₂. The radiative index

of dryness, defined as a ratio of annual net radiation and precipitation, is proposed as a governing parameter for the interannual variability of *NEE* of CO₂.

1. Introduction

Characterizing the relationship between the interannual variability of climate and net ecosystem-atmosphere exchange (*NEE*) of carbon dioxide is necessary for understanding interannual variability in the global CO₂ budget. The generally held principle in plant ecology and agriculture is that plant and soil respiration rates will increase with higher mean temperature [Grace and Rayment, 2000; Piovesan and Adams, 2000]. Consequently, that approach has been widely used to simulate the response of terrestrial ecosystems to global warming [Braswell *et al.*, 1997; Jenkinson *et al.*, 1991; Cao and Woodward, 1998; Trumbore *et al.*, 1996]. However, recent evidence indicates that the dependence of terrestrial ecosystem respiration on the mean annual temperature is in question [Valentini *et al.*, 2000; Giardina and Ryan, 2000; Janssens *et al.*, 2001; Sanderman *et al.*, 2002]. Based on spectral analysis, Baldocchi *et al.* [2001a] found that there are phase lags between CO₂ flux and climate factors. Thus, the impacts of climate factors on *NEE* of CO₂ may vary as a function of time scale.

This hypothesis can be tested using eddy-covariance measurements [Baldocchi *et al.*, 1988; 2001b; Wofsy *et al.*, 1993]. The eddy covariance method provides direct measurements of net carbon dioxide fluxes between forest and atmosphere with minimal disturbance to the underlying vegetation, and data can be collected continuously. CO₂ flux data for many sites around the global are archived within the FLUXNET database [Falge *et al.*, 2001].

2. Method

We examined data from four flux tower sites in North America: Harvard Forest in Massachusetts (HV), Walker Branch in Tennessee (WB), WLEF in Wisconsin (WL) and North BOREAS in Canada (NB) (Table 1). The HV forest is 50-70 years old, dominated by red oak and red maple, with scattered stands of hemlock, and white and red pine [Goulden *et al.*, 1996a]. The WB forest stand consists of oak, hickory, maple, tulip poplar and loblolly pine, and has been undisturbed since agricultural abandonment in 1940 [Baldocchi, 1997]. The region immediately surrounding the WL tower is a mixture of upland and wetland forest including maple, aspen, fir, red pine and alder [Mackay *et al.*, 2002]. The NB site is typical of the North American boreal forest [Goulden *et al.*, 1998]. The forest immediately around the NB tower is a mosaic of upland stands and bog, comprised of stunted black spruce on the uplands and sphagnum moss in the poorly drained low-lying areas [Goulden *et al.*, 1996b].

We test the relationships found for those four sites with data from other sites, including LO (Loobos, Netherlands), TH (Tharandt, Germany), HE (Hesse, France), HL (Howland, USA), HY (Hyytiala, Finland), LW (Little Washita, USA), NO (Norunda, Sweden), VI (Vielsalm, Belgium), and WE (Weiden Brunnen, Germany). The site information for the flux towers involved in this study is summarized in Table 1.

Eddy covariance/surface layer budget methods were used at the towers to quantify *NEE*. Methodological details can be found in publications (see reference in Table 1) for each site.

To examine the interannual variability of *NEE*, complete data sets are needed. The FLUXNET database provides data sets in which gaps are filled using standardized methods [Falge *et al.*, 2001]. The data are stored in a unified format and available in daily, weekly, monthly, and annual time resolutions. The data we used are filled by a consistent nonlinear regression method with a low u^* (friction velocity) correction, filtering out flux data below a site-specific u^* threshold. The gap-filled fraction is shown in Table 1, which includes both the missing and u^* filtered *NEE* data. The relationship between nighttime *NEE* (respiration) and temperature is used to fill missing or u^* screened data. These functionally filled data might have an influence on our analysis in the relationship between nighttime *NEE* and temperature. We excluded any filled data in the nighttime *NEE*- temperature analysis. We have also examined the difference in the nighttime *NEE*-temperature analysis between gap-filled and non gap-filled data sets. No significant difference between these two methods is found. Therefore, using gap filled data may not result in a significant change in either the relationships between *NEE* and climate factors or the consistency of these relationships across time scales.

Systematic measurement errors may exist in FLUXNET data among sites [Moncrieff *et al.*, 1996; Goulden *et al.*, 1996b]. These errors are due to a lack of intersite calibration. Therefore, analysis in this paper is mainly limited to temporal dynamics and variability (daily, monthly, seasonal and annual) for each site and we do not examine the spatial dynamics across sites. Consistency among the relationships between *NEE* and climate factors across time scales is compared among sites. These comparisons should not be affected by systematic offsets.

3. Results and Discussion

3.1 Respiration and Temperature

The response of forest respiration to temperature on different time scales is shown in Figure 1. The nighttime *NEE* in Figure 1 is the sum of autotrophic and heterotrophic respiration. A sharp increase in respiration with temperature is observed on daily, monthly and seasonal time scales. However, this relationship breaks down on an annual time scale. This finding is consistent among the four forest sites. Analysis of data from EuroFlux sites has also shown that annual forest respiration is not sensitive to mean annual temperature [Valentini *et al.*, 2000; Janssens *et al.*, 2001]. Therefore, a conclusion can be drawn that the short-term relationship between forest ecosystem respiration and temperature is not valid on an annual time scale. What is responsible for this independence of annual respiration and mean annual temperature?

Belowground CO_2 efflux generally dominates whole-system respiration in forested ecosystems, and may hold the answer to this question. Soil organic carbon and root biomass can be assumed to be at a quasi-steady state in mature forests, allowing litterfall to provide an estimate of heterotrophic respiration. Both litterfall and autotrophic root

respiration are related to forest growth, as demonstrated by linear correlation between observed annual soil respiration and annual net primary productivity (*NPP*) at other sites [Janssens *et al.*, 2001; Raich and Schlesinger, 1992]. Annual *NPP* depends not only on temperature but also on light, precipitation, net radiation, soil fertility and other factors. A weak correlation between *NPP* and temperature was observed by Janssens *et al.*, [2001]. Figure 1 also shows that mean autumn respiration rates are much larger than spring respiration rates; mean autumn respiration is 1.1 times mean spring respiration for WB, 1.3 times for HV, 1.8 times for WL, and 2.3 times for NB. This difference may not be caused by temperature for the deciduous forests because large amounts of readily decomposable litter become available in autumn. We hypothesize that the abundant litter is responsible for this difference for sites WB, HV and WL. For site NB, temperature is a key factor for this difference. Litter availability changes little from spring to autumn because coniferous forests lose their old needles continuously. However, soil is largely frozen in spring and thawed in autumn, so there is more organic matter available for decomposition in autumn.

Another explanation for the breakdown of the respiration-temperature relationship is that the temperature sensitivity of soil respiration decreases with increasing temperature [Luo *et al.*, 2001; Oechel *et al.*, 2000]. The relationship between soil respiration R_e and temperature T is usually expressed as a simple exponential function, $R_e = Ae^{BT}$. And the temperature sensitivity of soil respiration is defined as

$$\frac{1}{R_e} \frac{dR_e}{dT} = \frac{1}{R_e} BAe^{BT} = B. \quad (1)$$

The temperature sensitivity parameter B is not a constant throughout the year, and is likely to reflect substrate availability and quality for heterotrophs [Zogg *et al.*, 1997], and forest phenology and growth stage. We used the multi-year daily data of mean nighttime *NEE* and air temperature (no filled data) to fit a simple exponential function $R_e = Ae^{BT}$ season by season for each site. The seasonal values of the temperature sensitive parameter B and mean seasonal temperature T are listed in Table 2. For sites HV, WB, LO and TH, the sensitivity of forest respiration to temperature in summer is the lowest, and there is no correlation between respiration and temperature. For site WL, the sensitivity of forest respiration to temperature for spring and autumn is greater than for summer and winter. The highest values of B occurred in spring for all sites except for NB. Spring may be the season during which forest respiration is most sensitive to temperature, because (1) the litter has been physically degraded during the winter and is more labile to degradation by forest microbes; (2) heterotrophic populations of decomposers increase rapidly during this period; and (3) respiration associated with new leaf, shoot, and root growth by forest vegetation is highest during this season. Autumn respiration may be less sensitive than spring, because autumn respiration may be limited by reduced plant activity and decomposable litter input as discussed above. Respiration in summer is less sensitive to temperature than in spring or fall because the quantity and quality of fresh organic substrates are less available and harder to decompose. In winter there is almost no correlation between respiration and temperature for colder winter sites WL, HV, NB and TH. Winter temperatures for these four sites are in the lower range of

soil microbial activity. NB is different from the others because soil thaw proceeds slowly and is not complete until late summer [Goulden *et al.*, 1998]; here the highest values of temperature sensitivity B appear in summer and autumn, not in spring when soils are still frozen. If, therefore, ecosystem respiration is insensitive to summer and winter temperatures, and annual mean temperature is controlled by summer and winter extremes, then mean annual respiration and mean annual temperature may be poorly correlated.

3.2 *NEE* and Precipitation

Precipitation is another key factor controlling forest carbon dioxide exchange. The relationship between *NEE* and precipitation from monthly to annual time scales for the four sites is shown in Figure 2. For daily to seasonal time scales, there is no significant correlation between *NEE* and precipitation for deciduous forest sites HV and WB and poor correlation for the coniferous forest site, NB, and mixed forest, WL. However, annual *NEE* is significantly correlated with the annual precipitation at NB, WB and HV, but not at WL.

This slow time response is almost certainly due to the depth of the forest root zone and the soil water holding capacity. Some root systems are deep enough to make use of ground water in addition to current precipitation. Soil moisture depletion periods and recharge periods are usually much longer than a season, and soil moisture recharge typically occurs in winter months [Lee, 1980]. The soil moisture in warm months (the depletion period) is partly related to the cumulative water excess in the recharge period in cold months.

The annual net uptake of CO₂ is negatively correlated with the annual precipitation at NB (Figure 2a). The NB site, unlike the others in this study, is characterized by discontinuous permafrost [Goulden *et al.*, 1998]. The deep soil layers do not thaw until mid to late summer. During the preceding soil thaw period, the soil is moist or saturated because the frozen soil layer at the bottom prevents snowmelt water and precipitation from percolating to deeper soil layers. It is also during this soil thawing period that the apparent net uptake of CO₂ occurs; soil moisture and nutrients are available for photosynthesis. After the soil thawing period, respiration rates increase, matching or exceeding photosynthesis rates until early October. The near zero net uptake of CO₂ at the site in the fully thawed period results from the increase of respiration in the growing volume of unfrozen soil [Goulden *et al.*, 1998]. The net uptake of CO₂ in the fully thawed period is not very sensitive to precipitation. However, precipitation does play an important role in *NEE* during the soil thawing period. The daily *NEE* and precipitation data show that if daily precipitation is larger than 20 mm in the soil thawing period, a large spike in net uptake of CO₂ follows (not shown). This net uptake following large rainfall events is caused not by the positive effect of precipitation on photosynthesis, but by the inhibition by precipitation of soil respiration when the active soil layer becomes saturated due to poor drainage. 1998 was the warmest and driest year in the measurement period at NB; winter temperature was 6 °C above the average, and the evapotranspiration was also significantly larger than in other years in spring and summer. Three large rainfall events occurred during the soil thawing period in 1998: 25 mm in day 124, 42

mm in day 193 and 44 mm in days 168-171. Sharp dips in *NEE* (net uptake) follow each of these three rainfall events. This enhancement of carbon uptake during the period of soil thaw made this driest year have the maximum annual uptake (Figure 2a). Another large rainfall event, 35 mm in day 220 of 1998, occurred just after the soil thaw. Its effect on the inhibition of soil respiration was relatively small. Annual precipitation was larger in both 1995 and 1997, but large rainfall events ($>20 \text{ mm d}^{-1}$) occurred in the fully thawed period. Thus, the soil respiration was not appreciably inhibited by the precipitation. NB was a weak carbon source in 1995 and 1997 (Figure 2a). 1996 was the coldest year in the study; the soil was frozen more deeply and the growing season was shorter. Two large rainfall events in the soil thawing period (34 mm in days 139-141 and 28 mm in day 172) were followed by two large net uptake dips. The two large rainfall events during soil thaw and the shorter fully thawed period were the main reasons that NB acted as a weak carbon sink in 1996.

The annual *NEE* at WL is not correlated with annual precipitation (Figure 2b). The WL site is in a region of cold temperate mixed forest with abundant wetlands. The topography is slightly rolling with an elevation difference of roughly 45 m between the highest and lowest elevations. The elevation changes create a heterogeneous landscape of saturated (wetland) and unsaturated (upland) soils. The upland comprises about 63% of the area, and wetland about 37% of the area [Ahl *et al.*, 2003]. The complex forest landscape at WL is a net source for CO_2 to the atmosphere each year (Figure 2b). As shown in Figure 1, ecosystem respiration rates at WL are relatively higher than the other sites. Wetlands and wetland margin ecosystems may play an important role in the persistent release of CO_2 from the forest landscape at WL to atmosphere. Water table shift may have resulted in net carbon loss at wetland margins through drying [Weltzin *et al.*, 2001] or rewetting effects [Borken *et al.*, 1999]. Therefore, we postulate that the impact of annual precipitation on upland ecosystem *NEE* is opposite that on wetlands and wetland margin ecosystem *NEE*. It should be noted that net carbon loss at WL in 2001 is larger than that in the other years (Figure 2b), caused by a widespread forest tent caterpillar infestation, which reduced daytime *NEE* (net uptake of CO_2) from the onset of leaf defoliation in May until the leaves re-flushed in August.

The annual net uptake of CO_2 at HV tends to be higher in years with lower precipitation except for 1998 (Figure 2c). Our hypothesis is that in the summer of a dry year (1997, for example), the soil respiration is reduced because of lack of moisture in the surface soil. However, the overstory trees have deep enough roots to tap into the groundwater table and do not show any sign of drought stress in the summer of 1997. This may be a function of the regional climate; only 1998, the second of three dry years in the measurement period, shows the effects of a long drought in the form of dramatically reduced CO_2 uptake. HV is in a local topographic minimum, which means that the groundwater table is closer to surface and the soil moisture depletion period will be longer than at a higher relative elevation. One reason that uptake is reduced in 1998 may be that the successive dry years caused the groundwater table to fall deeply enough to affect the photosynthesis of trees. However, the unusual value of *NEE* in 1998 at HV could not have been due only to drought, because similar precipitation is observed in 1999 (the third of three dry years), but *NEE* in this year is normal (Figure 2c). Therefore,

the much less annual net uptake of CO₂ in 1998 may be caused by non-climate perturbations.

The annual net uptake of CO₂ at WB is positively correlated with annual precipitation (Figure 2d). Despite the fact that the precipitation in 1998 is close to the precipitation in 1996, there is more CO₂ uptake in 1998 because spring precipitation in 1998 is much more abundant than in 1996.

3.3 *NEE* with Net Radiation and *PAR*

Figure 3 shows the correlation between *NEE* and net radiation (R_n) on monthly, seasonal and annual time scales for the four sites. Good correlation exists on short time scales and also on an annual time scale because net radiation is a comprehensive function of multiple variables. Short-wave radiation is closely related to the albedos of clouds and the underlying surface, and long-wave radiation depends on air temperature, humidity, cloudiness, and the vertical gradients of temperature and moisture in the atmosphere [Budyko, 1974]. Net radiation is also closely related to the photosynthetically active radiation (*PAR*), one of the main factors controlling photosynthesis. It is likely that cloud cover is the dominant cause of interannual variability in net radiation and *PAR* observed at these sites.

We expect strong negative monthly and seasonal correlations between *NEE* and R_n because within an annual cycle, R_n is strongly correlated with temperature and time of year. R_n is highest in the summer when CO₂ uptake is the highest and lowest in the winter when CO₂ uptake is lowest. A strong negative correlation is observed at each of the four sites in figure 3. Because interannual variability in R_n is caused largely by cloud cover, we may expect light-limited sites to have opposite correlations of annual *NEE* to R_n than water-limited sites. The slope of the annual regression for WB is opposite to that from the other sites in Figure 3 because WB is more sensitive to drought than the other sites (see next section). The minimum annual net uptake of CO₂ in 1995 is due to large R_n (Figure 3d), implying stronger potential evapotranspiration (see next section), and minimum precipitation (Figure 2d). 1998, the year with the largest uptake, has the minimum R_n (Figure 3d) and the maximum precipitation (Figure 2d).

The relationship between *NEE* and *PAR* (Figure 4) is similar to that between *NEE* and R_n (Figure 3) on daily, monthly and seasonal time scales. On an annual time scale, however, *NEE* is not correlated with *PAR* as it is with R_n . *PAR* is a key factor for photosynthesis [Ruimy *et al.*, 1995] but has no direct effect on respiration. For instance, nighttime *NEE* (respiration) is related to temperature, while nighttime *PAR* is always zero. However, nocturnal surface temperature is linked to R_n , because the long wave emissions from a surface are a primary component of R_n at night. Therefore, nighttime and cold season *NEE* are independent of *PAR* but related to R_n to some extent through the effect of temperature on respiration.

3.4 *NEE* and Dryness Index

The net radiation is the energy available at the earth's surface for generating sensible and latent turbulent heat fluxes and heat inflow into the soil and vegetation. Potential evapotranspiration R_n/L , where L is the enthalpy of vaporization, is a measure of the maximum possible evapotranspiration using all available net radiation. *Budyko* [1974] defined the ratio of the potential evapotranspiration to precipitation (P) as a radiative index of dryness, I

$$I = \frac{R_n}{LP}, \quad (2)$$

and used it successfully to classify geobotanic zones. In natural processes, energy and mass budgets are interdependent. The radiative index of dryness combines both energy and mass conservation laws. In this section, we explore the relationship between I and NEE of CO_2 .

The relationship between NEE and I for the six sites that had more than three years of data is shown in Figure 5. The slopes of regression curves are different among the sites. We hypothesize that moist, warm deciduous sites such as WB are the most drought sensitive, while coniferous forest sites are radiation limited (NB, LO and TH). WL and HV show an intermediate response. NB site is located in a geographic zone of discontinuous permafrost. The most important environmental constraint on NEE at NB is not precipitation (although precipitation does play a role in inhibiting soil respiration after large daily rainfall events during the soil thawing period as discussed in section 3.2), but the timing and depth of soil thaw [Goulden *et al.*, 1998] which depends on the amount of available energy R_n . The poor correlation of annual NEE and I at WL is likely due to differing responses of uplands and wetlands to I . The relationship between NEE and I at HV site is more complicated probably because a large part of its footprint is poorly drained. The interannual variability of NEE at WB is dominated by dryness (Figure 5d). At WB the net uptake of CO_2 is greatly restricted by drought stress. Statistical analysis indicates that the correlation ($R^2=0.89$, not shown) between gross ecosystem photosynthesis and I is much higher than correlation ($R^2=0.30$, not shown) between ecosystem respiration rates and dryness. This implies that the stomatal opening mechanisms of trees are more sensitive to drought stress than are soil microbes. The average annual precipitation during the measuring periods at the two temperate coniferous forest sites LO and TH are 1011 (mm) and 1117 (mm), respectively. We postulate that net radiation is more critical than precipitation to the net uptake of CO_2 at these two sites.

Figure 6 shows the relationship between site-average annual NEE (filled circle) and site average dryness across FLUXNET sites that have two or more years data (Table 1). The site NB with dryness that is off the scale and an agricultural site under human control are not included in Figure 6. The site-average annual $NEEs$ represent the strength of carbon sinks/sources for the landscapes around the flux towers, which differs from the relationship between interannual variability of NEE and dryness as shown in Figure 5. Unlike interannual variability in NEE , the site-to-site variability in NEE must be governed by factors such as forest stand age that are not accounted for by the dryness parameter or other climate variables. Site-to-site comparisons are also vulnerable to site-

specific systematic errors. Despite these caveats, we find that the site annual *NEEs* are fairly well correlated with dryness. WE, a mountainous site (elevation is 780 m) where runoff may be a significant percentage of the annual precipitation in (2), and actual dryness should be higher than that shown in Figure 6, and NB (values noted in the figure caption) are notable exceptions. The forest at WE also has poor nutrient availability, diseased living trees and excessive decomposing dead wood.

The trend (solid line) in Figure 6 suggests that moist sites are currently carbon sinks, and that the magnitude of the sink increases as dryness decreases. It may be that potential carbon sinks and sources are weaker under dryer climate conditions, and that due to similar disturbance histories many of the temperate forest sites represented here are carbon sinks. There is a large variability of site-average *NEE* in Figure 6 for a given average *I*. This variability may be caused by vegetation type, stand age, nutrition supply, landscape, topographical position, and other non-dryness factors. The interannual variability in *NEE* at single sites do not always have the same slope as the intersite comparison shown in Figure 6. Additional study is warranted.

3. Conclusions

Multi-year micrometeorological flux data from four long-running forest flux tower sites in North America show that the climate factors that control *NEE* are not the same across time scales. Some relationships between *NEE* and climate factors on short-term time scales are not valid on an annual time scale, and vice versa. The relationship between soil respiration and temperature is robust on daily, monthly and seasonal time scales but breaks down on an annual time scale. Two reasons are suggested for this break down: (1) Annual soil respiration is proportional to annual litter production, which is a weak function of mean annual temperature. Data show that, in spite of similar spring and autumn seasonal temperatures, autumn soil respiration is greater than spring soil respiration for the deciduous forests due to the dependence of soil respiration on litter production. Evidently, a large portion of the litterfall is decomposed in the autumn of a year. (2) The temperature sensitivity of ecosystem respiration decreases with increasing temperature. Data show that the temperature sensitivity of summer respiration is lowest for most sites. There is no correlation between respiration and temperature when the temperature is below freezing.

NEE is poorly correlated to precipitation on daily, monthly and seasonal time scales but is strongly correlated with precipitation on an annual time scale. Precipitation is expected to have an impact on forests over an annual period or even longer because the soil moisture during the depletion season (warm months) is partly related to the cumulative water excess in the recharge season (cold months).

Net radiation is a comprehensive climate variable that is related to temperature, light, water vapor, cloud cover, and albedo; therefore, it is expected to be well correlated with *NEE* on all time scales. Tower data support this hypothesis. Although the response relationship of *NEE* to *PAR* is good on daily, monthly and seasonal time scales, it breaks down on an annual time scale because the respiration component of *NEE* is not coupled to light.

The radiative index of dryness, a measure of water and energy balance, is suggested as a comprehensive climate variable, suitable for describing interannual variability in *NEE*. Four of six sites (WB, NB, TH and LO) show a strong correlation between dryness and annual *NEE*, while two sites (WL and HV) show more ambiguous results. Further work is needed to expand the number of sites and site-years available for analysis, and to elucidate the mechanisms responsible for the correlation between *NEE* and climate. This study suggests a relatively simple climate index such as dryness may successfully describe a large fraction of interannual variability in *NEE* within, and perhaps across, terrestrial ecosystems.

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References

- Ahl, D.E., S.T. Gower, D.S. Mackay, S.N. Burrows, J.M. Norman, and G. Diak, Light use efficiency of a heterogeneous forest in northern Wisconsin: Implications for remote sensing and modeling net primary production, *Remote Sensing of Environment*. (In press)
- Aubinet, M., B. Heinesch, B. Longdoz, Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability, *Global Change Biology*, 8, 1053-1071, 2002.
- Aubinet, M., B. Chermanne, M. Vandenhaute, B. Longdoz, M. Yernaux, E. Laitat, Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes, *Agricultural and Forest Meteorology*, 108, 293-315, 2001.
- Bakwin, P. S., P.P. Tans, D.F. Hurst, and C. Zhao, Measurements of carbon dioxide on very tall towers: Results of the NOAA/CMDL program, *Tellus*, 50b, 401-415, 1998.
- Baldocchi, D.D., B.B. Hicks, and T.P. Meyers, Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods, *Ecology*, 69, 1331-1340, 1988.
- Baldocchi, D.D., Measuring and modeling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought, *Plant, Cell and Environment*, 20, 1108-1122, 1997.

- Baldocchi, D.D., J. Finnigan, K. Wilson, K.T. Paw U, and E. Falge, On measuring net ecosystem carbon exchange over tall vegetation on complex terrain, *Boundary-Layer Meteorology*, 96, 257-291, 2000.
- Baldocchi, D.D., E. Falge and K. Wilson, A spectral analysis of biosphere-atmosphere trace gas flux densities and meteorological variables across hour to year time scales, *Agricultural and Forest Meteorology*, 107, 1-27, 2001a.
- Baldocchi, D. D., coauthors, Fluxnet: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bulletin of the American Meteorological Society*, 82, 2415-2434, 2001b.
- Berger, B.W., K.J. Davis, C. Yi, P. S. Bakwin, and C. Zhao, Long-term carbon dioxide fluxes from a very tall tower in a northern forest: Flux measurement methodology, *J. Oceanic and Atmos. Tech.*, 18, 529-542, 2001.
- Borken, W., Y.-J. Xu, R. Brumme, and N. Lamersdorf, A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects, *Soil Sci. Soc. Am. J.*, 63, 1848-1855, 1999.
- Braswell, B. H., D. S. Schimel, E. Linder, and B. Moore III, The response of global terrestrial ecosystems to interannual temperature variability, *Science*, 278, 870-872, 1997.
- Budyko, M. I., *Climate and Life*, 508 pp., Academic Press, New York, 1974.
- Cao, M., and F. I. Woodward, Dynamic responses of terrestrial ecosystem carbon cycling to global climate change, *Nature*, 393, 249-252. 1998.
- Davis, K. J., P. S. Bakwin, C. Yi, B. W. Berger, C. Zhao, R. Teclaw, and J. G. Isebrands, The annual cycles of CO₂ and H₂O exchange over a northern mixed forest as observed from a very tall tower, *Global Change Biology*, 9, 1278-1293, 2003.
- Falge E., Baldocchi, D.D., Olson, R.J., P. Anthoni, M. Aubinet, Ch Bernhofer, G Burba, R Ceulemans, R Clement, H Dolman, A Granier, P Gross, Th Grünwald, D Hollinger, N-O Jensen, G Katul, P Keronen, A Kowalski, Chun Ta Lai, B E. Law, T Meyers, J Moncrieff, E Moors, J. W Munger, K Pilegaard, Ü Rannik, C Rebmann, A Suyker, J Tenhunen, K Tu, S Verma, T Vesala, K Wilson, Steve Wofsy, Gap filling strategies for long term energy flux data sets, a short communication, *Agricultural and Forest Meteorology*, 107, 71-77, 2001.
- Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, Ch., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A, Granier, A, Guðmundsson, J., Hollinger, D., Kowalski, A, Katul,G., Law,B, Malhi,Y., Meyers,T., Monson,R., Munger,JW, Oechel,W., Paw U,KT., Pilegaard,K, Rannik,U, Rebmann, C, Suyker,A, Valentini, R., Wilson,K, and Wofsy, S, Seasonality of

- ecosystem respiration and gross primary production as derived from FLUXNET measurements, *Agricultural and Forest Meteorology*, 113, 53-74, 2002.
- Giardina, C. P. and M G. Ryan, Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature, *Nature*, 404, 858-861, 2000 .
- Goulden, M.L., J.W. Munger, S.M. Fan, B.C. Daube, and S.C. Wofsy, Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability, *Science*, 271, 1576-1578, 1996a.
- Goulden, M.L., J.W. Munger, S.M. Fan, B.C. Daube, and S.C. Wofsy, Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy, *Global Change Biology*, 2, 1996b.
- Goulden, M.L., B.C. Daube, S.M. Fan, D. J. Sutton, A. Bazzaz, J.W. Munger, and S.C. Wofsy, Physiological responses of a black spruce forest to weather, *J. Geophys. Res.*, 102, 28987-28996, 1997.
- Goulden, M.L., S.C. Wofsy, J. W. Harden, S. E. Trumbore, P. W. Crill, S. T. Gower, T. Fries, B.C. Daube, S.M. Fan, D. J. Sutton, A. Bazzaz and J.W. Munger, Sensitivity of boreal forest carbon balance to soil thaw, *Science*, 279, 214-217, 1998.
- Grace, J. and M. Rayment, Respiration in the balance, *Nature*, 404, 819-820, 2000.
- Granier, A., E. Ceschia, C. Damesin, E. Dufrêne, D. Epron, P. Gross, S. Lebaube, V. Le Dantec, N. Le Goff, D. Lemoine, E. Lucot, J.M. Ottorini, J.Y. Pontailler, and B. Saugier, The carbon balance of a young beech forest, *Functional Ecology*, 14, 312-325, 2000.
- Grunwald, Th, and Ch. Bernhofer, Data gap filling with regression modelling, *Forest Ecosystem Modeling, Upscaling and Remote Sensing* (eds R.J.M. Ceulemans, V. Veroustrate, J.B.H.F. Van Rensbergen), SPB Academic Publishing bv, The Hague, The Netherlands, pp. 61-67, 1998.
- Hollinger D.Y., F.M. Kelliher, E.-D. Schulze, G. Bauer, A. Arneth, J.N. Byers, J.E. Hunt, T.M. McSeveny, K.I. Kobak, A. Sogachov, F. Tatarinov, A. Varlagin, W. Ziegler, N.N. Vygodskaya, Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agricultural and Forest Meteorology*, 90, 291-306, 1998.
- Hollinger, D. Y., S. M. Goltz, E. A. Davidson, J. T. Lee, K. Tu, and H. T. Valentine, Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest, *Global Change Biology*, 5, 891-902, 1999.
- Janssens, I. A., H. Lankreijer, G. Matteucci, A.S. Kowalski, N. Buchmann, D. Epron, K. Pilegaard, W. Kutsch, B. Longdoz, T. Grünwald, L. Montagnani, S. Dore, C. Rebmann, E.J. Moors, A. Grelle, Ü Rannik, K. Morgenstern, S. Oltchev, R. Clement, J.

- Gudmundsson, S. Minerbi, P. Berbigier, A. Ibrom, J. Moncrieff, M. Aubinet, C. Bernhofer, N.O. Jensen, T. Vesala, A. Granier, E.D. Schulze, A. Lindroth, A.J. Dolman, P.G. Jarvis, R. Ceulemans, R.Valentini, Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Global Change Biology*, 7, 269-278, 2001.
- Jenkinson, D. S., D. E. Adams, and A. Wild, Model estimates of CO₂ emissions from soil in response to global warming, *Nature*, 351, 304-306, 1991.
- Lee, R., *Forest Hydrology*, 349 pp., Columbia University Press, New York, 1980.
- Lindroth, A., A. Grelle, and A.-S. Morén, Long-term measurements of boreal forest carbon balance reveals large temperature sensitivity, *Global Change Biology*, 4, 443-450, 1998.
- Luo, Y., S. Wan, D. Hui, and L. L. Wallace, Acclimatization of soil respiration to warming in a tall grass prairie, *Nature*, 413, 622-625, 2001.
- Mackay, D.S., D.E. Ahl, B.E. Ewers, S.T. Gower, S.N. Burrows, S. Samanta, and K.J. Davis, Effects of aggregated classifications of forest composition on estimates of evapotranspiration in a northern Wisconsin forest, *Global Change Biology*, 8, 1-13, 2002.
- Markkanen, T., Ü. Rannik, P. Keronen, T. Suni and T. Vesala, Eddy covariance fluxes over a boreal Scots pine forest, *Boreal Environment Research*, 6, 65-78, 2001.
- Meyers, T. P., A comparison of summertime water and CO₂ fluxes over rangeland for well watered and drought conditions, *Agricultural and Forest Meteorology*, 106, 205-214, 2001.
- Moncrieff, J. B., Y. Malhi and R. Leuning, The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water, *Global Change Biology*, 2, 231-240, 1996.
- Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane, Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming, *Nature*, 406, 978-981, 2000.
- Piovesan, G. and J. M. Adams, Carbon balance gradient in European forests: Interpreting EUROFLUX, *J. Veg. Sci.*, 11, 923-926, 2000.
- Raich, J. W. and W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus*, 44B, 81-99, 1992.
- Ruimy, A., P.G. Jarvis, D.D. Baldocchi and B.Saugier, CO₂ fluxes over plant canopies: a literature review, *Advances in Ecological Research*, 26, 1-68, 1995.

- Sanderman, J., R. Amundson and D. D. Baldocchi, The effect of temperature on the residence time of soil organic carbon: A comparative analysis, *Global Biogeochemical Cycles*, doi:10.1029/2001GB001833, 2003.
- Trumbore, S. E., O. A. Chadwick, and R. Amundson, Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change, *Science*, 272, 393-396, 1996.
- Valentini, R., G. Matteucci, A.J. Dolman, E.-D. Schulze, C. Rebmann, E.J. Moors, A. Granier, P. Gross, N.O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grünwald, M. Aubinet, R. Ceulemanns, A.S. Kowalski, T. Vesala, Ü. Rannik, P. Berbigier, D. Loustau, J. Mundson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncreiff, L. Montagnani, S. Minerbi, and P.G. Jarvis, Respiration as the main determinant of carbon balance in European forests, *Nature*, 404, 861-865, 2000.
- Vesala, T, J. Haataja, P. Aalto, N. Altimir, G. Buzorius, E. Garam, K. Hämeri, H. Ilvesniemi, V. Jokinen, P. Keronen, T. Lahti, T. Markkanen, J.M, Mäkelä, E, Nikinmaa, S. Palmroth, L. Palva, T. Pohja, J. Pumpanen, Ü. Rannik, E. Siivola, H. Ylitalo, P. Hari, and M. Kulmala, Long-term field measurements of atmosphere-surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry, *Trends in Heat, Mass & Momentum Transfer*, 4, 17-35, 1998.
- Vesala, T., T. Markkanen, L. Palva, E. Siivola, S. Palmroth, and P. Hari, The effect of spatial and temporal variations of photosynthetically active radiation on CO₂ exchange estimates of a Scots pine canopy, *Agricultural and Forest Meteorology*, 100, 337-347. 2000.
- Welzin, J. F., C. Harth, S. D. Bridgman et al., Production and microtopography of bog bryophytes: response to warming and water-table manipulations, *Oecologia*, 128, 557-565, 2001.
- Wilson, K.B., and D.D. Baldocchi, Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America, *Agric. For. Meteorol.*, 100, 1-18, 2000.
- Wofsy, S.C., M.L. Goulden, J.W. Munger, S.M. Fan, P.S. Bakwin, B.C. Daube, S.L. Bassow, and F.A. Bazzaz, Net exchange of CO₂ in a mid-latitude forest, *Science*, 260, 1314-1317, 1993.
- Yi, C., K. J. Davis, P. S. Bakwin, B. W. Berger, and L. Marr, The influence of advection on measurements of the net ecosystem-atmosphere exchange of CO₂ from a very tall tower, *Journal of Geophysical Research*, 105, 9991-9999, 2000.
- Zogg, G. P., D. R. Zak, D. B. Ringelberg, N. W. MacDonald, K. S. Pregitzer, and D. C. White, Compositional and functional shifts in microbial communities due to soil warming, *Soil Sci. Am. Soc. Am. J.*, 61, 475-481, 1997.

List of Illustrations

Figure 1. Relationship between the nighttime *NEE* (respiration) and air temperature (*T*) on daily, monthly, seasonal and annual time scales shown by the multi-year data sets measured at the forest tower sites: (a) NB (1995-1998); (b) WL (1997-2001); (c) HV (1992-1999); (d) WB (1995-1998). The detail for the site information can be found from Table 1. The solid lines are the best fit for each site. In the seasonal panel, winter is December-January-February, spring is March-April-May, summer is June-July-August, autumn is September-October-November. The gap filled data from the FLUXNET data were excluded. A data point in the daily panel represents mean nighttime *NEE* for a night if data points are more than four, that is a good approximation because nighttime *NEE* is more steady than daytime *NEE* [Yi *et al.*, 2000; Davis *et al.*, 2003]. The monthly, seasonal and annual data points were obtained from the daily data. Very similar results (not shown) were also obtained from the gap filled data, indicating no significant difference in this analysis when using no filled data versus with the gap filled data.

Figure 2. Relationship between *NEE* and precipitation on monthly, seasonal and annual time scale for each site: (a) NB (1995-1998); (b) WL (1997-2001); (c) HV (1992-1999); (d) WB (1995-1998). The solid lines are the best fit for each site. The numbers on the data points denote years. A large caterpillar infestation occurred at WL in 2001.

Figure 3. Relationship between *NEE* and net radiation on monthly, seasonal and annual time scales for the sites: (a) NB (1995-1998); (b) WL (1997-2001); (c) HV (1992-1999); (d) WB (1995-1998). The solid lines are regression lines indicating trends. The numbers on the data points are years. A large caterpillar infestation occurred at WL in 2001.

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Figure 5 Annual *NEE* (circles) versus the radiative index of dryness for the sites: (a) NB (1995-1998); (b) WL (1997-2001); (c) HV (1992-1999); (d) WB (1995-1998), (e) LO (1997-2000); (f) TH (1997-2000). The radiative index of dryness is defined in the text. The solid lines are the best fit, the numbers indicate years. A large caterpillar infestation occurred at WL in 2001.

Figure 6 Site-average annual *NEE* (filled circles) versus the radiative index of dryness for the sites: WL (1997-2000); HV (1992-1999); WB (1995-1998); LO (1997-2000); TH (1997-2000); HE (1997-1998); HL (1996-1997); HY (1999-2000); LW (1997-1998); NO (1996-1997); VI (1997-1998); and WE (1998-1999). The solid lines are the best fit. The caterpillar year 2001 is not included in the WL site-average. The site-average *NEE* ($-3 \text{ gC m}^{-2} \text{ yr}^{-1}$) and site-average dryness (2.92) for NB (1995-1998) are not shown. The year-site data points are indicated by plus.

Table 1. Site information for flux tower sites.

Site	State/Country	Abbr.	Coordinates	Period	Gap fraction filled for period (%) ^a	Vegetation type/dominant species ^b	Reference
North Boreas ^c	Manitoba/Canada	NB	55° 54' N 98° 30' W	1995-1998	38.5	Evergreen coniferous forests, black spruce trees	<i>Goulden et al.</i> [1998]
Park Falls WLEF ^c	Wisconsin/USA	WL	45° 57' N 90° 16' W	1997-2001	31.1	Mixed evergreen and deciduous forests, Wetland and upland, aspen, maple, fir, Red pine, alder	<i>Bakwin et al.</i> , [1998]; <i>Yi et al.</i> , [2000]; <i>Berger et al.</i> , [2001]; <i>Davis et al.</i> , [2003]
Harvard ^c	Massachusetts/USA	HV	42° 32' N 72° 11' W	1992-1999	44.4	Deciduous broadleaf forest, hardwood, white pine, hemlock, spruce swamp, conifer plantation, oak/maple	<i>Wofsy et al.</i> , [1993]; <i>Goulden et al.</i> [1996a; 1996b]
WalkerBranch ^c	Tennessee/USA	WB	35° 58' N 84° 17' W	1995-1998	37.0	Broad-leaved forest, deciduous forest, oak/hickory	<i>Baldocchi</i> , [1997]; <i>Baldocchi et al.</i> , [2000]; <i>Wilson and Baldocchi</i> , [2000]
Hesse ^d	Sarrebouurg/France	HE	48°40' N 07° 04' E	1997-1998	8.0	Deciduous broadleaf forest, Fagus sylvatica, quercus, tilia cordata, betula alba	<i>Valentini et al.</i> [2000]; <i>Granier et al.</i> [2000]
Howland ^c	Maine/USA	HL	45° 12' N 68° 44' W	1996-1997	44.2	Deciduous evergreen needle forest, Red spruce, eastern hemlock, other conifers such as balsam fir, white pine, northern white cedar, and hardwoods	<i>Hollinger et al.</i> [1998; 1999]
Hyytiälä ^d	Finland	HY	61° 51' N 24° 17' E	1999-2000	39.5	Evergreen coniferous forests, pinus sylvestris, calluna, vaccinium myrtillus	<i>Vesala et al.</i> [1998, 1999] <i>Markkanen et al.</i> [2001]
Loobos ^d	Netherlands	LO	52° 10' N 5° 45' E	1997-2000	44.8	Evergreen coniferous forests, pinus sylvestris	<i>Valentini et al.</i> [2000]
Little Washita ^c	Oklahoma/USA	LW	34° 58' N 97° 59' W	1997-1998	39.2	Grasslands, rangeland	<i>Meyers</i> [2001]
Norunda ^d	Sweden	NO	60° 05' N 17° 28' E	1996-1997	36.1	Evergreen coniferous forests, pinus sylvestris, picea abies, vaccinium	<i>Lindroth et al.</i> [1998]
Tharandt ^d	Germany	TH	50° 58' N 13° 34' E	1997-2000	44.2	Evergreen coniferous forests, picea abies, deschampsia flexuosa	<i>Grunwald and Bernhofer</i> [1998] <i>Valentini et al.</i> [2000]
Vielsalm ^d	Belgium	VI	50° 19' N 06° E	1997-1998	40.5	Deciduous broadleaf forests, mixed forest, fagus sylvatica, pseudotsuga menziesii, picea abies, mosses	<i>Aubinet et al.</i> , [2001; 2002] <i>Valentini et al.</i> [2000]
WeidenBrunnen ^d	Germany	WE	50° 10' N 11° 53' E	1998-1999	51.3	Evergreen coniferous forest, picea abies, Deschampsia flexuosa	<i>Valentini et al.</i> [2000]

^a The gap filled includes both missing *NEE* data and filtering out *NEE* data below a site-specific *u** threshold.

^b For more information on vegetation type classification of these sites see Fagle et al. [2002].

^c AmeriFlux project.

^d EUROFLUX project.

Table 2. Seasonal distribution of the temperature sensitivity of forest respiration. The daily data of mean nighttime NEE and mean temperature as shown in Figure 1 without any filled data were used to fit a simple exponential function $R_e = Ae^{BT}$ season by season for each site. The values of temperature sensitivity parameter B ($^{\circ}C^{-1}$) and mean seasonal temperature T ($^{\circ}C$) are listed with R^2 and mean seasonal temperature T ($^{\circ}C$).

Season	NB		WL		HV		WB		LO		TH							
	B	R^2	T	B	R^2	T	B	R^2	T	B	R^2	T						
Spring	0.0554	0.51	-5.4	0.0971	0.58	4.7	0.0708	0.45	5.6	0.0685	0.43	13.3	0.0753	0.32	9.4	0.0893	0.58	7.4
Summer	0.0632	0.47	13.2	0.0460	0.18	16.9	0.0187	0.03	17.1	0.0139	0.01	22.4	0.0126	0.01	14.9	0.0290	0.09	14.3
Autumn	0.0839	0.77	-0.7	0.0901	0.52	7.4	0.0339	0.17	8.3	0.0617	0.43	13.9	0.0743	0.48	9.9	0.0700	0.45	7.8
Winter	0.0080	0.01	-19.8	0.0286	0.04	-5.9	0.0456	0.11	-3.6	0.0361	0.51	4.4	0.0800	0.47	4.2	0.0411	0.16	1.5

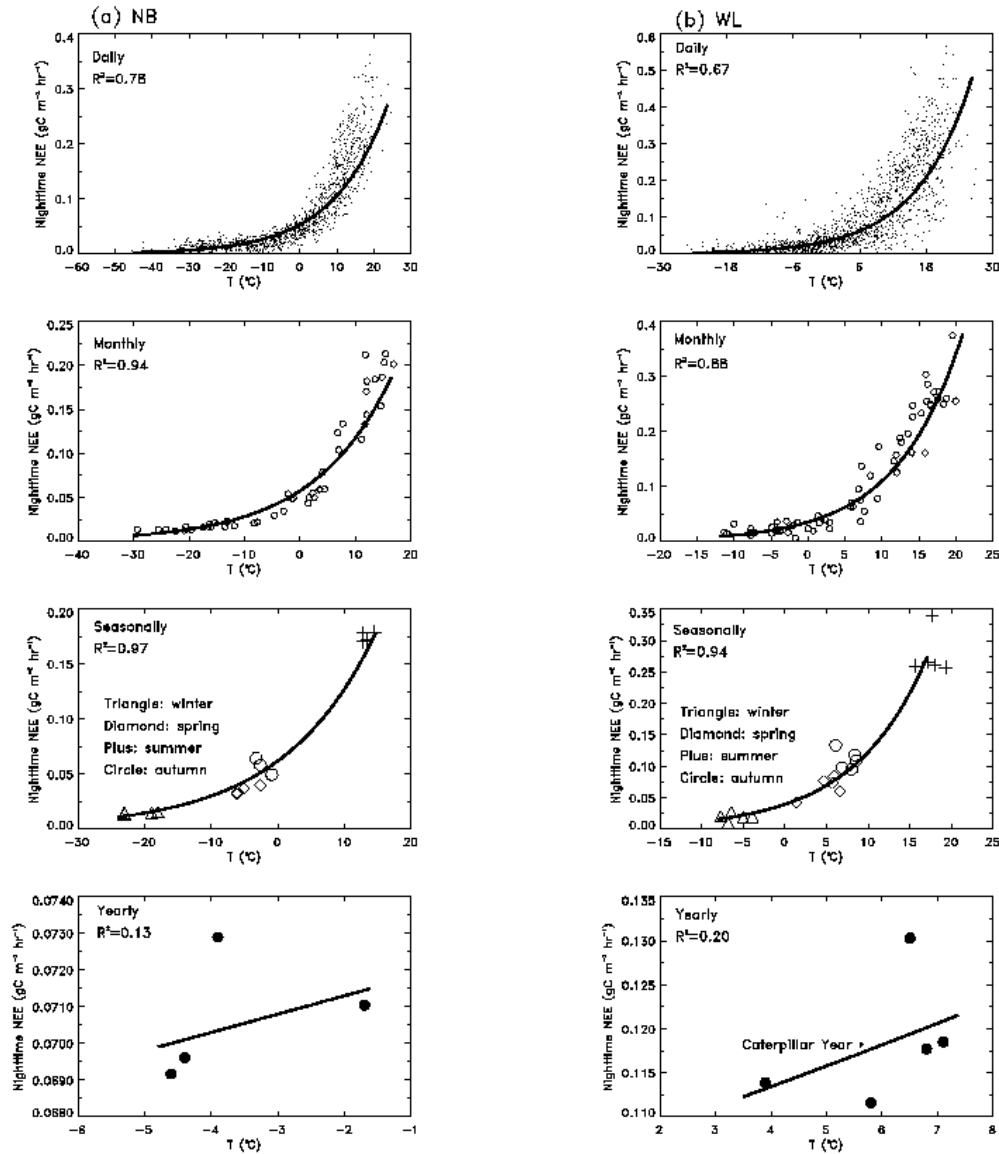


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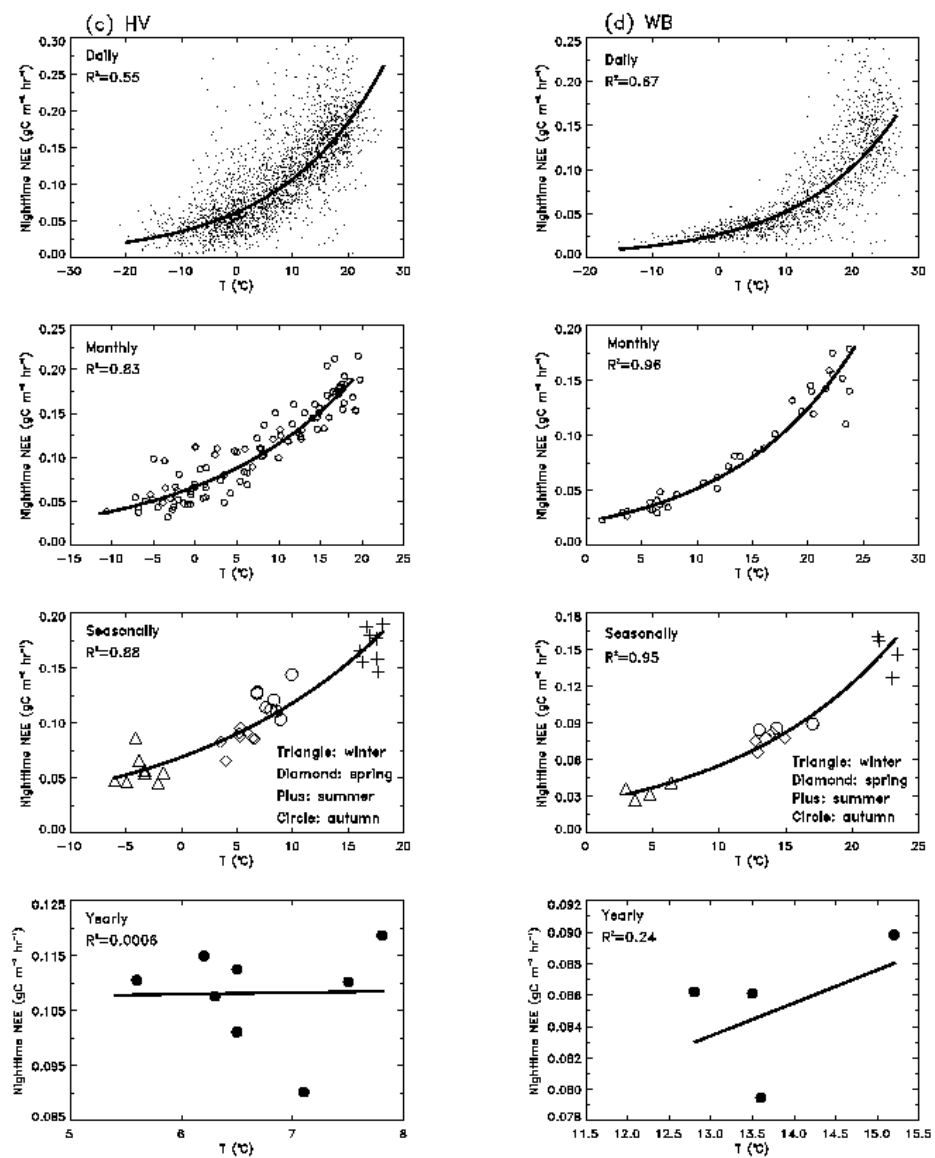


Figure 1. (continued)

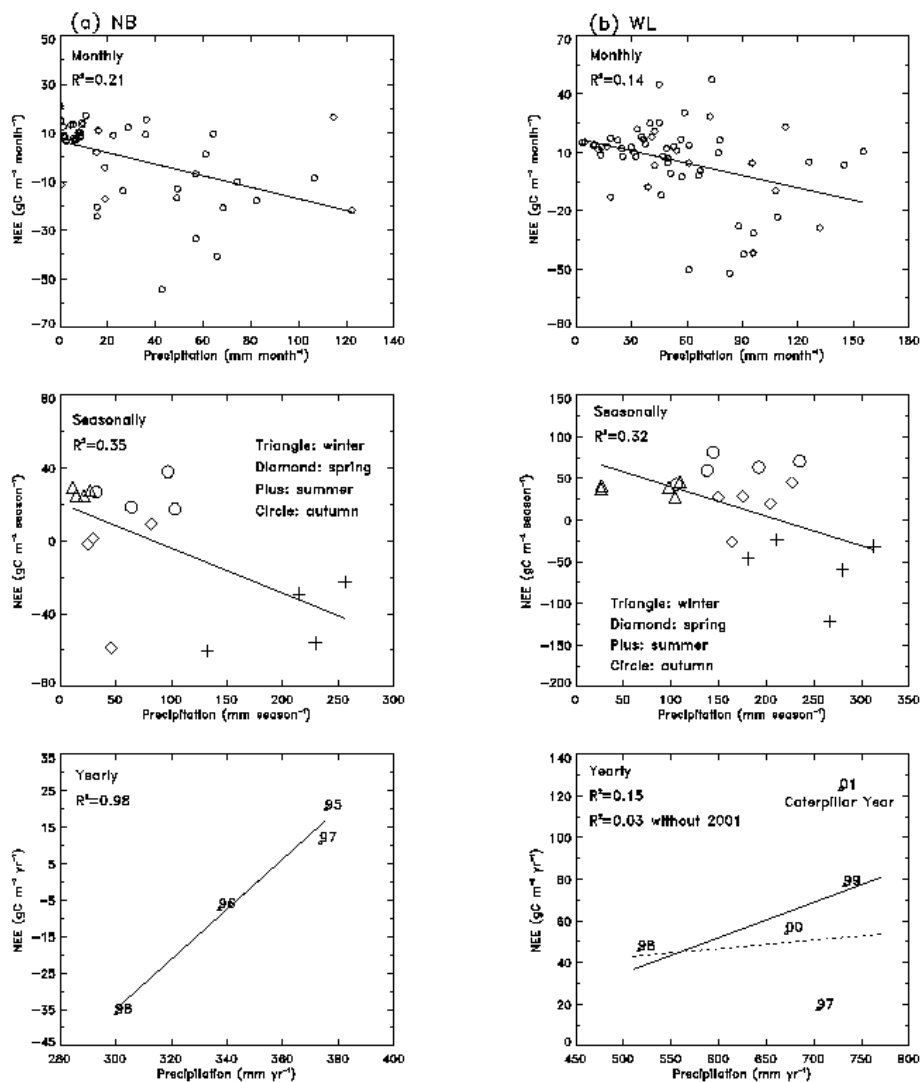


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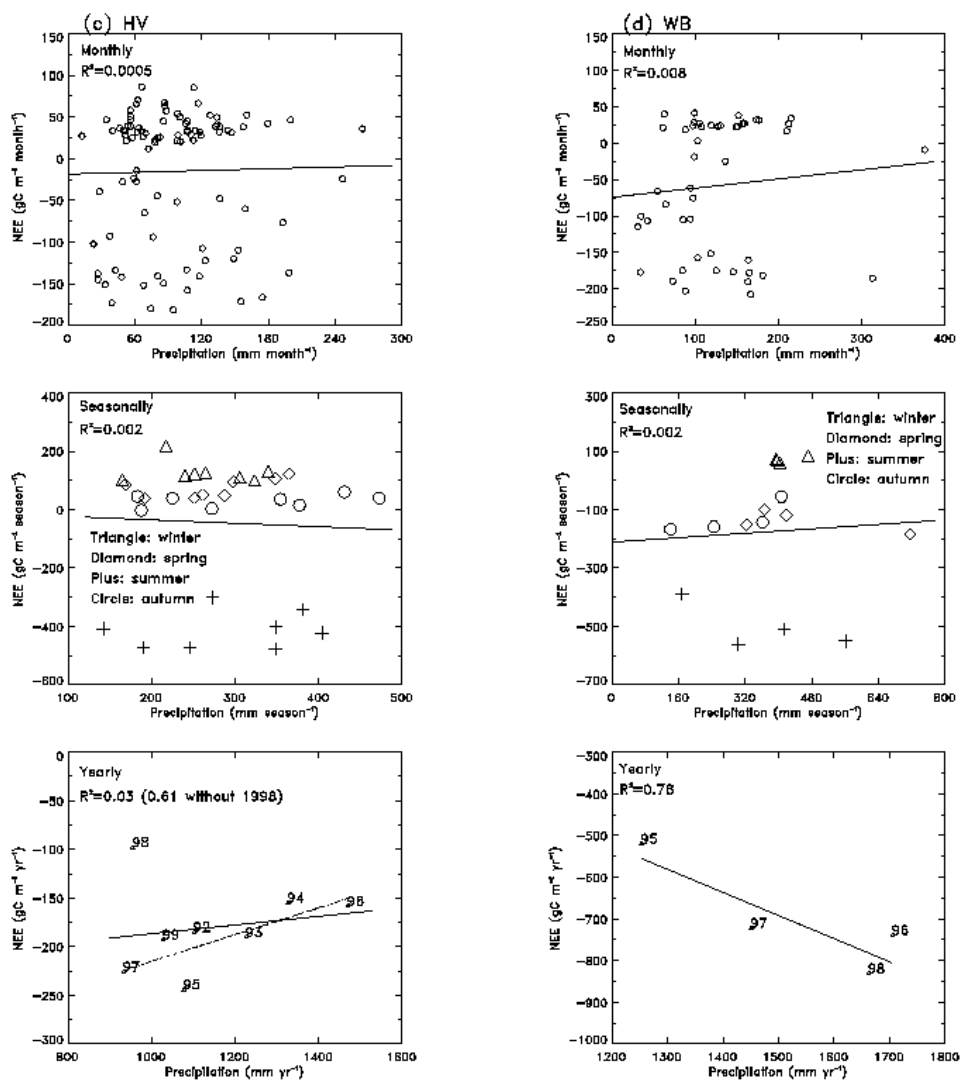


Figure 2. (continued)

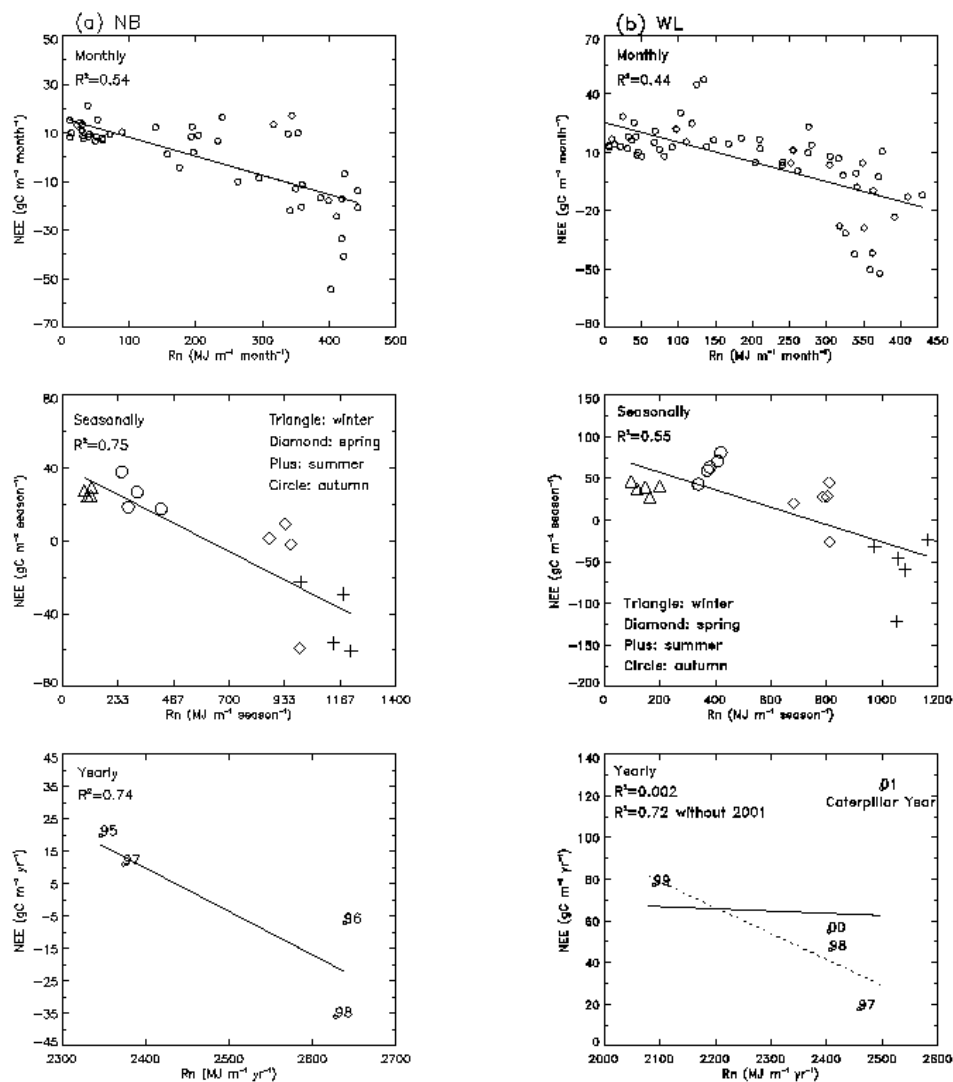


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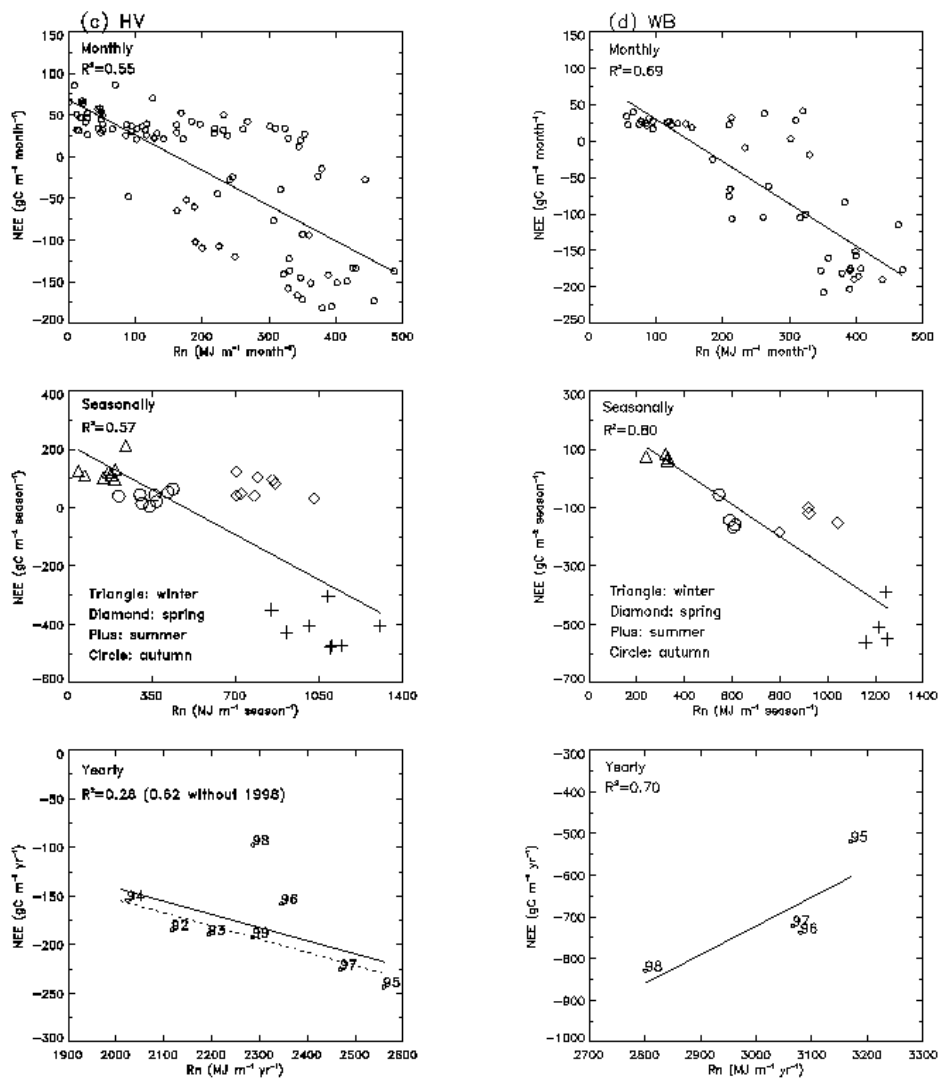


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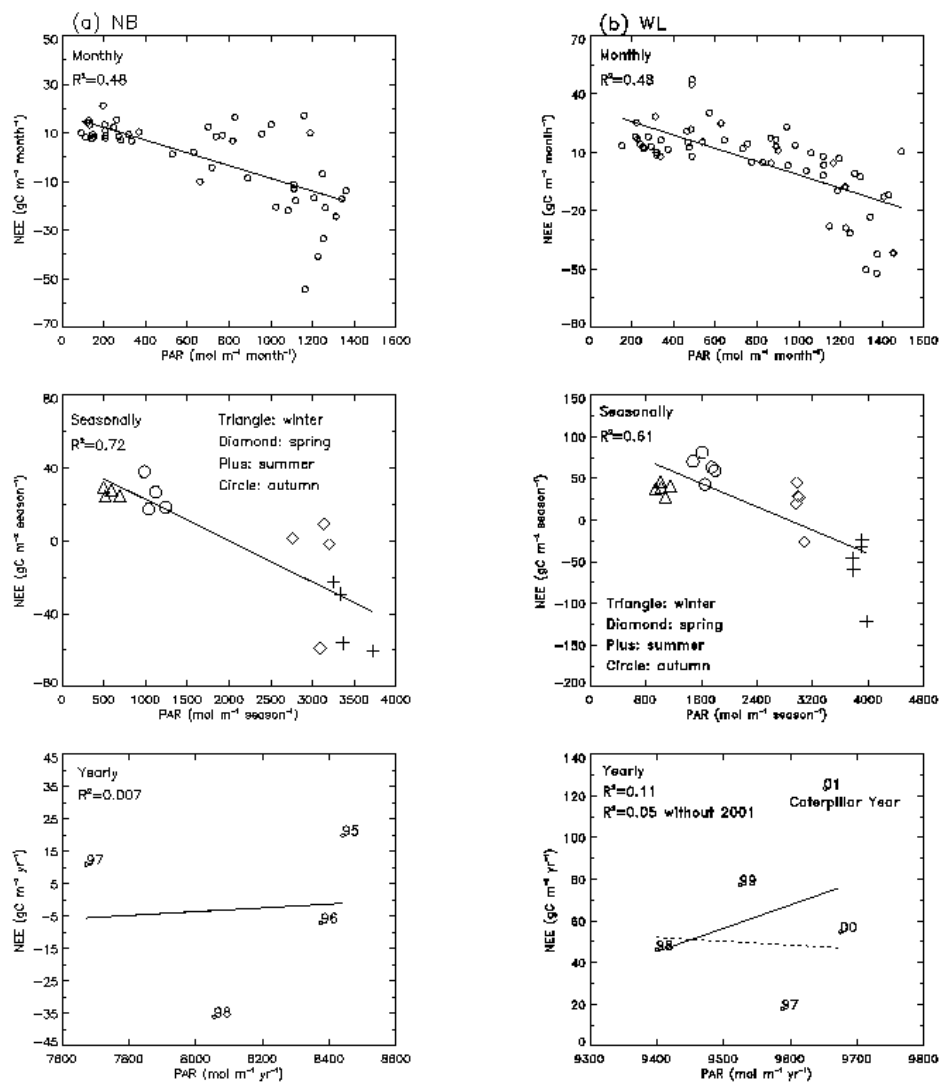


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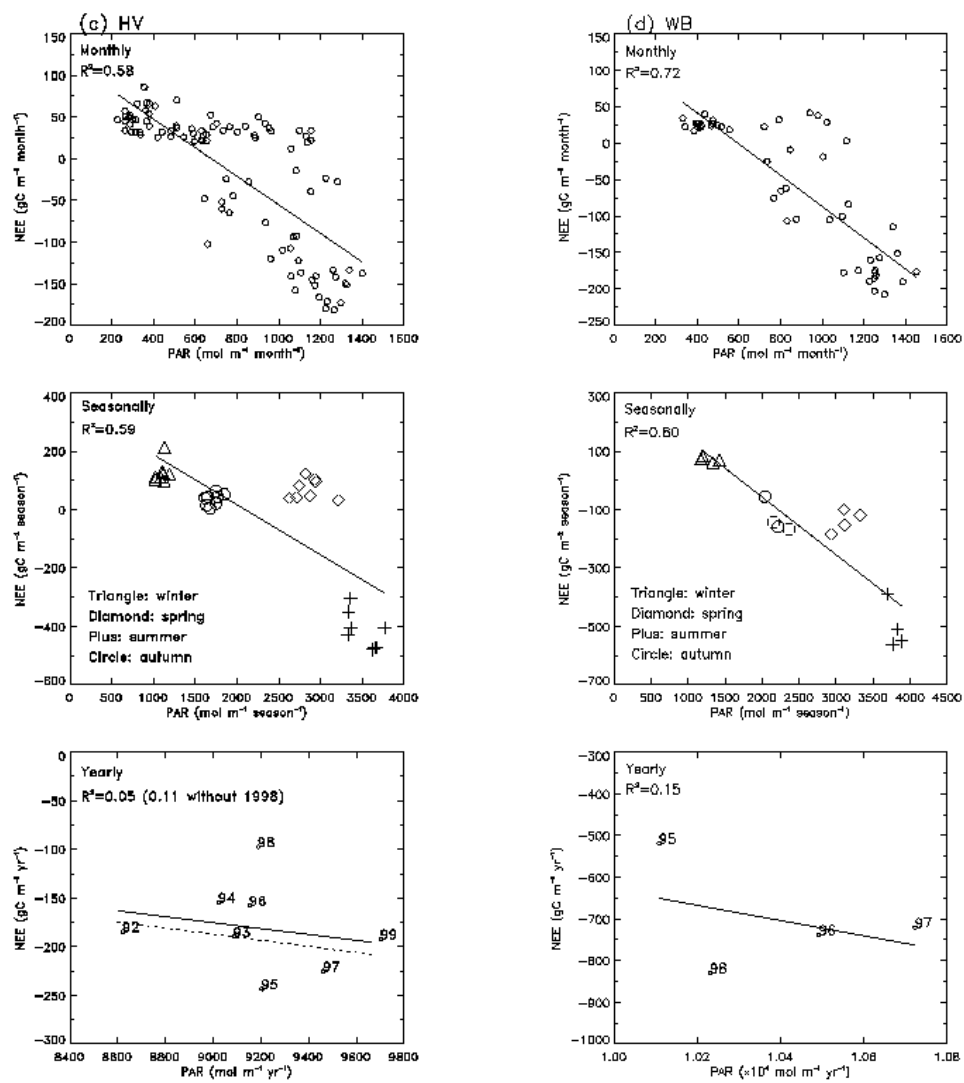


Figure 4. (continued)

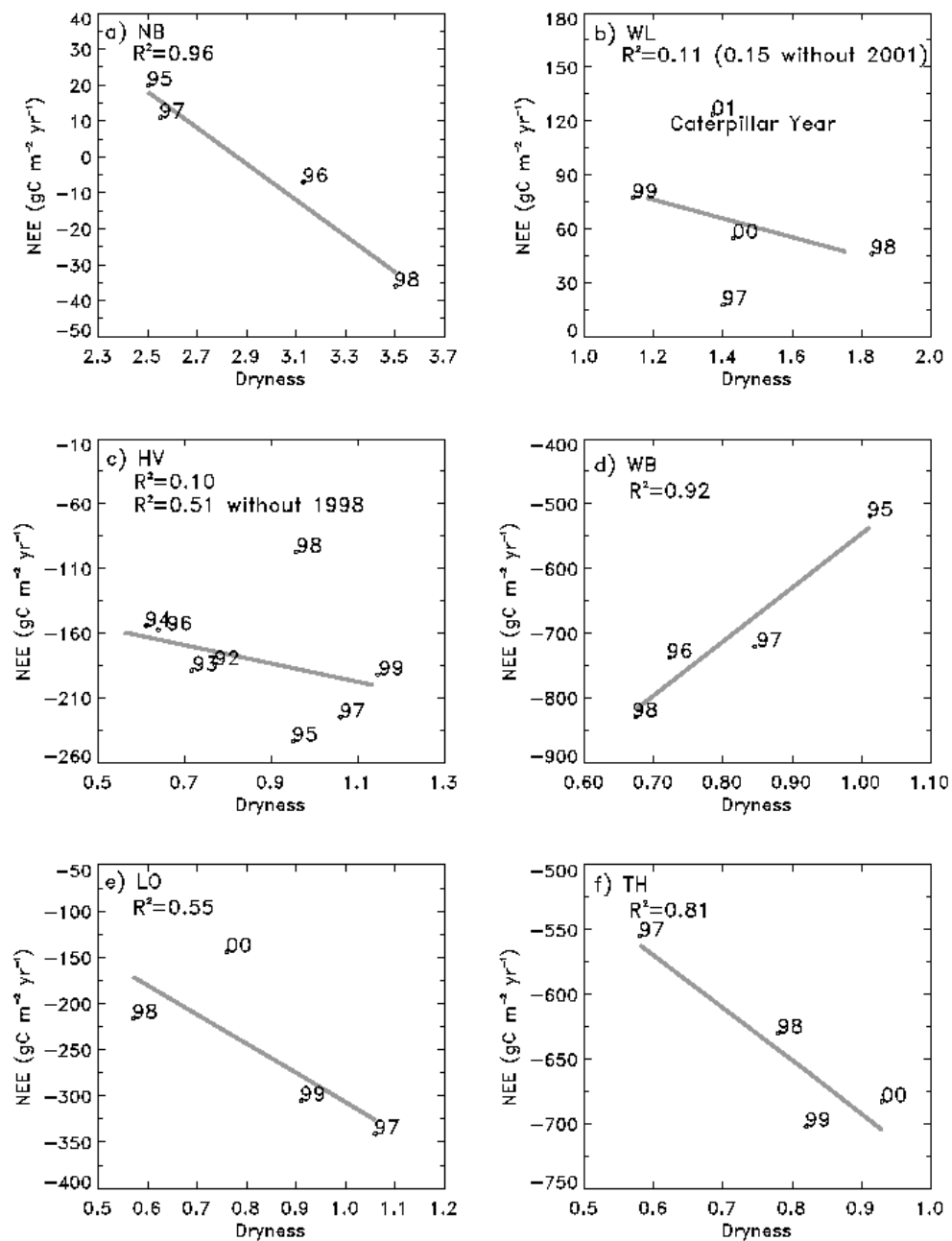


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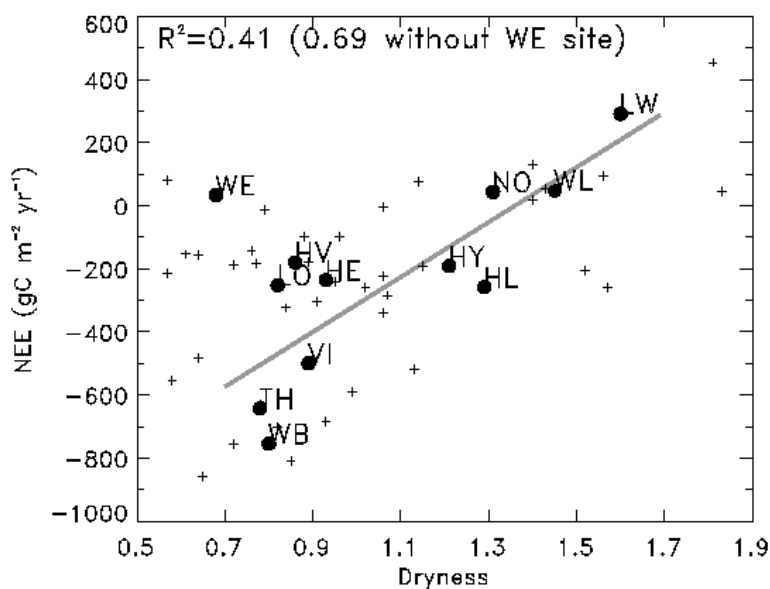


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