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Carbon exchange of deciduous broadleaved forests in temperate and Mediterranean regions

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Symbols

N_p, for NPP
N_{ec}, Net ecosystem carbon exchange, as measured by micrometeorologists
N_B, Net biome productivity
G_p, Gross primary productivity
J_{pmax}, maximum flux density of canopy photosynthesis
R_{eco}, ecosystem respiration
R_{plant}, plant respiration
R_{auto}, soil autotrophic respiration
R_{hetero}, soil heterotrophic respiration
R_{soil}, total soil respiration
E_a,actual evaporation
E_p, potential evaporation
V_{cmax}, maximum carboxylation velocity (measured as maximum assimilation rate under saturating light and saturating CO_2)
C_i, internal CO_2 concentration
R_d, leaf dark respiration
?, ribulose 1,5-bisphosphate carboxylase oxygenase (RUBISCO) specificity factor
A, CO_2 assimilation rate
K_c, Michaelis–Menten constant for CO_2
K_o, Michaelis–Menten constant for O_2
J_{max}, maximum electron transport rate
A_{max}, maximum assimilation rate (at saturating light and ambient CO_2)

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m, proportionality coefficient
rh relative humidity
g_s, stomatal conductance
C_s,CO_2 concentration
T_{soil}, soil temperature
?, volumetric soil moisture
f, scaling factor
α, quantum yield
Q, Photon flux density
Q_p, Saturating photon flux density
Q_a, available light intensity
L, leaf area index
ΔL, fraction of NPP in live biomass
ΔD, fraction of NPP in detritus
ΔH, fraction of NPP lost to herbivory
Q_{10}
N, natural frequency of eddy covariance fluxes

'*Form follows function*', Louis Henri Sullivan (1856–1924), architect

'Form follows function – that has been misunderstood. Form and function should be one, joined in a spiritual union', *Frank Lloyd Wright (1869–1959), protégé of Louis Henri Sullivan and architect*

1. Introduction

Over the course of history, temperate and Mediterranean forests have been intertwined with mankind. First, they coexist with a large fraction of humanity. Second, they are a major resource for fuel, timber, and derived wood products. And, third, they are a part of our psyche, as they have been the locale of many legends and much history. When walking through the woods, many key questions come to the mind of a forest ecologist, including what climate and soil factors influence the form of the forest? How does that forest form interact with climate to affect functioning? How will the form and function of forests change in the future as the environment changes?

One way to address these questions is through integrated field and modeling studies of carbon exchange (Running *et al.* 1999; Canadell *et al.*, 2000) and ecosystem dynamics (Foley *et al.*, 1998; Bugmann, 2001). The tools of this trade include long-term eddy covariance measurements of CO_2 exchange between the forest and the atmosphere, field campaigns on the physiological capacity and water relations of the leaves and trees, studies on soil respiration, and periodic inventories of plant biomass and soil carbon (Reich and Bolstad, 2001; Gower, 2003).

The objective of this chapter is to synthesize carbon flux field data that can be used to parameterize and validate models that couple biophysics, ecophysiology, biogeochemistry, and ecosystem dynamics; the intent of these models is to understand how the carbon balances of forests ecosystems respond to their environment and disturbances on multiple time-scales. Specifically, our goal is to describe the carbon balance

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of deciduous broadleaved forests in temperate zones and in the adjacent Mediterranean zones of the world. To accomplish this goal we adopt a biophysical and ecophysiological perspective. First, we survey information on the assimilation and respiration of leaves of trees in temperate forests and respiration from the underlying soil. Then we examine the processes controlling net and gross carbon exchange information at the scale of the canopy. Throughout the paper we attempt to examine and discuss the dynamics of carbon exchange components of temperate forests on hourly, daily, and annual time-scales.

2. Fundamental concepts

The net amount of carbon that a forest ecosystem is able to acquire over the course of a year is called net ecosystem productivity (N_e; g (C) m^{-2} per year). It is defined as the difference between gross primary productivity (G_p) and ecosystem respiration (R_{eco}):

$$N_e = G_p - R_{eco} \quad (1)$$

Over the course of a year N_e is positive if the ecosystem is a sink for carbon. Alternatively, micrometeorologists assess net ecosystem carbon exchange, which is a metric opposite in sign from $N_e - N_e = -N_{ec}$.[Q2] Variations in G_p will occur temporally, on hourly, daily, and seasonal time-scales, as sunlight, temperature, and soil moisture, among other variables, alter photosynthesis. Spatial variation in G_p will arise because of differences in available nitrogen, soil type, climate/exposure, leaf area index, stand age, and species mix. Alternatively, one can define G_p as the sum of net primary productivity, N_p, and autotrophic respiration, R_{auto}. As a rule of thumb, autotrophic respiration constitutes about half of G_p (Gifford, 1994).[Q24]

Ecosystem respiration, R_{eco}, consists of autotrophic respiration by the leaves, plant stems, and roots (R_{auto}) and heterotrophic respiration by the microbes and soil fauna (R_{hetero}):

$$R_{eco} = R_{plant} + R_{soil} = R_{auto} + R_{hetero} \quad (2)$$

If one studies an ecosystem for many years, then one must consider net biome productivity (N_B), which includes carbon losses due to disturbances such as fire, insect infestations, and pathogen damage (Schulze *et al.*, 2000).[Q25]

3. Geographic distribution

The geographic distribution of deciduous broadleaved forests is wide. Temperate, deciduous broadleaved forests, also known as hardwoods, range between the 30 and 50 degrees latitude bands of North America, Europe, and Asia (Barnes, 1991). In the Mediterranean climates of Europe, California, Chile, South Africa, and Australia one finds a mix of deciduous and evergreen broadleaved tree species. On an area basis, temperate broadleaved forests occupy about 1 420 million ha (1 hectare (ha) = 10^4 m^2), a value that represents about 10% of the terrestrial biosphere (Melillo *et al.*, 1993).

The climate space inhabited by temperate deciduous broadleaved forests, by definition, is not exceedingly wet or dry, nor exceedingly cold or hot (*Table 1*). In

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general, temperate deciduous forests reside in climates where annual precipitation ranges between 800 and 1400 mm and annual precipitation exceeds its annual potential evaporation (Holdridge, 1947). Mean minimum winter temperatures in this habitat range between 0 and –20 °C, with bud hardiness being a more important thermal factor for determining survival limits than is stem hardiness (Woodward, 1986;[Q25] Barnes, 1991); hardening lowers the freezing point of the protoplasm by accumulating sugars and other osmotic reducing substances (Larcher, 1975).

By contrast, Mediterranean broadleaved forests (which are either deciduous or evergreen) experience warm and wet winters and hot and dry summers. Minimum winter temperatures for Mediterranean oak and walnut, for example, are above 5 °C, while mean maximum summer temperatures are greater than 33 °C (*Table 1*). With

Table 1. *Data on the relation between mean climate conditions and genera of hardwood trees growing in North America. Where denoted, the data are separated for the western and eastern portions of the continent. The data are derived from Thompson et al. (1999) (http://pubs.usgs.gov/pp/1999/p1650-a/datatables/hgtable.xls). Columns are included for the mean temperature (degrees Celsius) of the coldest month, the mean annual temperature, the mean maximum temperature during July, growing degree days above 5 °C, annual precipitation (millimeters), and the moisture index, which is defined as actual evaporation (*$\mathbf{E}_a$*) divided by potential evaporation (*$\mathbf{E}_p$*).*

Taxon	Coldest month mean temperature (°C)[Q5]	Annual mean temperature (°C)	July mean maximum temperature (°C)	Above 5 °C growing degree days	Annual precipitation (mm)	Moisture index, E_a/E_p
Acer	–6.6	7.1	29.8	2 000	885	0.94
Acer Eastern NA	–5.2	9.2	28.8	2 500	1 010	0.97
Acer Western NA	–6.9	4.2	29.2	1 100	750	0.75
Alnus	–16.4	0.8	29.1	1 100	735	0.93
Alnus Eastern NA	–18.1	0.6	29.1	1 100	770	0.96
Alnus Western NA	–15.1	0.3	28.3	9 00	510	0.72
Betula	–19.8	–1.0	30.8	900	605	0.87
Carya	1.0	13.6	30.1	3 400	1 070	0.96
Castanea	3.5	14.9	28.6	3 700	1 200	0.97
Fraxinus	–4.8	9.5	33.1	2 500	875	0.94
Fraxinums Eastern NA	–6.1	8.6	29.5	2 400	910	0.95
Fraxinus Western NA	9.0	17.2	33.1	4 500	485	0.49
Juglans	0.1	12.9	31.3	3 300	995	0.95
Juglans Eastern NA	–1.0	12.4	29.4	3 100	1 030	0.96
Juglans Western NA	8.7	16.3	31.3	4 300	625	0.69
Ostrya/Carpinus	–2.1	11.4	29.7	2 900	1 045	0.96
Quercus	–0.9	11.7	33.8	2 900	905	0.94
Quercus Eastern NA	–2.8	11.2	31.8	2 900	960	0.95
Quercus Western NA	6.5	14.6	33.8	3 600	540	0.63
Tilia	–5.7	8.8	27.4	2 400	940	0.97
Ulmus	–4.9	9.7	31.9	2 600	920	0.96

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regards to annual precipitation, trees in Mediterranean climates have adapted to survive on less precipitation (500–1000 mm per year) and endure extended periods when potential evaporation exceeds precipitation. Mediterranean trees are able to survive on a limited supply of water by regulating their stomata and limiting transpiration during the dry season when potential evaporation is high (Joffre *et al.* 1999; Eamus and Prior, 2001; Xu and Baldocchi, 2003).

4. Composition, form, and function

To many lay people, a general impression of the structure and beauty of temperate broadleaved forests come from films such as 'The Adventures of Robin Hood', with widely spaced trees depicted in 'Sherwood Forest'. This idealized version is unrepresentative of temperate deciduous forests that are distributed across the globe. In the next section we discuss many structural and functional attributes of temperate broadleaved forests.

4.1 *Composition and form*

Great diversity exists in composition, form, and function of temperate broadleaved forests (Hicks and Chabot, 1985; Barnes, 1991, Parker, 1995; Reich and Bolstad, 2001). Most significantly, temperate broadleaved forests come in two forms: deciduous and evergreen. The main genera of deciduous trees include the oak (*Quercus)*, beech (*Fagus)*, popular/aspen (*Populus)*, maple (*Acer*), basswood (*Tilia*), hickory (*Carya*), and birch (*Betula*). The main genera for evergreen broadleaved forests include *Nothofagus*, *Eucalptus*, and *Quercus*.

Structural diversity comes in the guise of differences in basal area, height, and the leaf area index. One cause of structural diversity can be attributed to how climate and soil factors interact to affect the functioning of the forest. In principle, the function of an assemblage of trees in a forest is to intercept and absorb light and to use this light energy to assimilate carbon. The goal of this activity is to provide the substrate for structural components of the trees and energy to build wood, leaves, and roots and to maintain their metabolism. Of course there are costs towards achieving these goals. The opening of stomata to capture CO_2, for instance, allows water vapor to escape. Consequently, the trees need to grow where more water is available, through precipitation, than is lost through evaporation and transpiration. Second, the respiratory costs of supporting the light-harvesting superstructure must be less than the ability of the system to harvest light energy, in the form of carbon. Over geological/evolutionary time-scales, inter- and intra-plant competition for light, water and nutrients, and reproductive success have conspired to affect the structure of trees in a forest (Bugmann, 2001).

Land-use history is another important factor for understanding the structure and function of contemporary temperate forests. Because temperate forests exist in highly populated regions, they have been greatly disturbed over the past few centuries. Consequently, few old-growth temperate broadleaved forests, like the archetypal Sherwood Forest, exist. Today, most temperate forests are aggrading (Nabuurs, 2003). This is because a large-scale change in land use occurred at the transition between the 19th and 20th centuries. As significant fractions of rural populations moved to urban settings they abandoned farmlands and their changed cooking and

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heating sources from wood to fossil fuels. The current age distribution of temperate forests has an important ramification on the net amount of carbon that these forests acquire over a year because the carbon balance of these stands is far from equilibrium (Friend *et al.*, 1997; Bugmann *et al.*, 2001).

Temperate broadleaved forests generally form closed canopies, which intercept over 95% of incoming sunlight (Jarvis and Leverenz, 1986;[Q26] Baldocchi and Collineau, 1994) and possess leaf area indices that typically range between 4 and 7 (Hutchison *et al.*, 1986; Parker *et al.*, 1989); a recent literature survey of leaf area index of temperate forests reports a centroid value of 5.1 ± 1.8 for temperate deciduous broadleaved forests (Asner *et al.*, 2003). The height of many mature deciduous forests stands range between 20 and 30 m, but the vertical profile of leaf area depends on stand age (Aber, 1979; [Q27]Harding *et al.*, 2001). The vertical distribution of leaf area in young stands (less than 20 years) is relatively even, as shade and sun tolerant trees compete against one another for light. As the stand closes at intermediate ages (about 40 years), a disproportionate amount of leaf area is positioned in the upper third of the canopy and the stem space is relatively open because efficient light capture by the canopy crown suppresses understorey plants (Hutchison *et al.*, 1986; Parker, 1995; Harding *et al.*, 2001). At maturity (older than 80 years), mortality starts to cause gaps, allowing understorey plants to flourish. This causes an appreciable amount of leaf area to be distributed throughout the forest. Finally, at old-age the profile of leaf area is bimodal, with a peak of leaf area density in the understorey and crown.

Mediterranean broadleaved forests, in contrast, form sparse, open canopies, with isolated trees in many circumstances. These forests cover between 20 and 80% of the land and are 5–10 m tall. Consequently, the leaf area is much lower than temperate forests; the centroid leaf area index for Mediterranean forests is 1.71 ± 0.76 (Asner *et al.*, 2003).

4.2 *Function*

Leaf photosynthesis and respiration are two measures of physiological functioning. In the next section we survey measures of photosynthetic capacity and respiration, and examine their temporal dynamics and sources of spatial variation.

4.2.1 Leaf photosynthesis

Over the past decade, the process-based biochemical model of Farquhar *et al.* (1980) has emerged as the dominant paradigm for computing leaf photosynthesis (A). When light is ample and RUBP[Q3] is saturated, photosynthesis can be quantified as:

$$A = \left(1 - \frac{0.5O}{\tau C_i}\right) \frac{V_{c\,max}\, C_i}{C_i + K_c\,(1 + O/K_O)} - R_d \qquad (3)$$

where O and C_i are the concentrations of oxygen and CO_2 in the intercellular air space, τ is the RUBISCO-specific factor, and K_c and K_o are the Michaelis–Menten constants for CO_2 and O_2, respectively. R_d, represents CO_2 evolution from mitochondria in the light, rather than that associated with photorespiratory carbon oxidation (Farquhar *et al.* 1980). The maximum velocity of carboxylation, V_{cmax}, is one of the key model parameters and is derived from the initial slope of A–C_i curves at saturating light levels. The model parameter V_{cmax} is evaluated from the lower region of A/C_i curve, when C_i was less than 150 μmol mol^{-1}:

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Wullschleger (1993)[Q28] has shown that other model parameters of the Farquhar model (dark respiration, R_d, and the maximum rate of electron transport, J_{max}) scale with V_{cmax}, and other researchers show that photosynthetic capacity (A_{max}) scales with leaf nitrogen (Reich *et al.*, 1998). So if one has one piece of information on photosynthesis, one can conceivable have all the model parameters needed to implement a leaf photosynthesis model. A caveat to this supposition is that most published values of V_{cmax} assume that mesophyll conductance is infinite. Their value will be error prone when mesophyll conductance is finite and the CO_2 concentration at the chloroplast does not equals that in the substomatal cavity (Ethier and Livingston, 2004).
In *Table 2* we present data from our survey of V_{cmax} measurements on temperate deciduous trees. A representative value for V_{cmax} of deciduous trees centers at about 50 μmol m^{-2} s^{-1}, but much lower and higher values are observed.

In an attempt to distill these data, we plotted the relationship between A_{max} and V_{cmax} from hundreds of leaf measurements of broadleaved deciduous trees in contrasting environments in *Figure 1*. V_{cmax} is clearly a function of A_{max}, but the relationship is not universal.

From this growing body of photosynthesis data some general themes are emerging between photosynthesis and leaf structural and functional properties (Reich *et al.*, 1997; Reich and Bolstad, 2001; Niinemets, 2001). First, leaf photosynthesis on an area basis increases linearly with leaf nitrogen on a unit area basis (*Figure 2*). Second, leaf mass per unit area increases linearly with leaf nitrogen per unit area (*Figure 3*). Consequently, leaf photosynthesis per unit area increases linearly with leaf mass per unit area. The mechanism for this correlation stems from the high nitrogen content of RUBISCO, the photosynthesis enzyme.

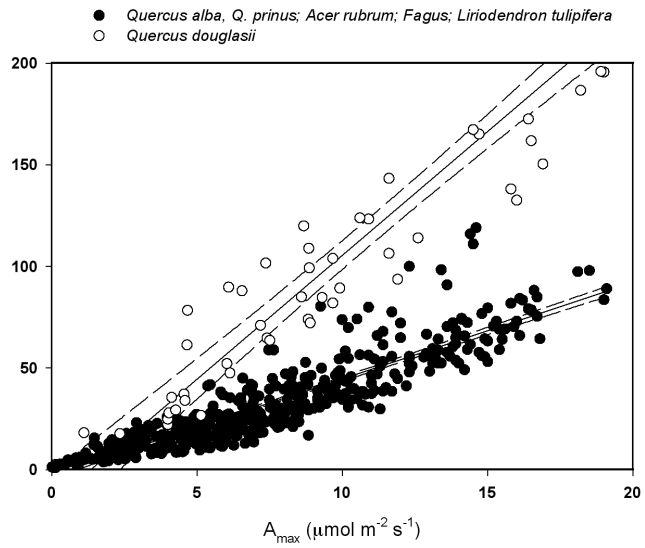

Figure 1. *Relationship between maximum photosynthesis rates at light saturation (Q_p = 1500 μmol m^{-2} s^{-1}) and ambient CO_2 (350 parts per million (p.p.m.)) and V_{cmax}. Data of Xu and Baldocchi (2003) are for a xeric oak in a Mediterranean climate (Quercus douglasii) and data of Wilson et al. (2000)[Q29] are for a mixture of deciduous tree species in an eastern deciduous forest biome.*

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Table 2. *Survey of photosynthetic capacity (V_{cmax}) at 25 °C for tree species growing in the temperature deciduous forest zone*

Species	Site	V_{cmax} (μmol m^{-2} s^{-1})	Reference[Q45]	Comment
Deciduous trees		47 ± 33	Wullschleger, 1993[Q28]	16 species
Acer pseudoplantus	Nancy, France	77.8	Dreyer *et al.*, 2001	seedlings
Betula pendula	Nancy, France	70.5	Dreyer *et al.*, 2001	
Fagus sylvatica	Nancy, France	66.3	Dreyer *et al.*, 2001	
Fagus excelsior	Nancy, France	84.6	Dreyer *et al.*, 2001	
Juglans regia	Nancy, France	63.6	Dreyer *et al.*, 2001	
Quercus petraea	Nancy, France	87.7	Dreyer *et al.*, 2001	
Quercus robur	Nancy, France	90.5	Dreyer *et al.*, 2001	
Quercus coccifera	Portugal	58.2	Tenhunen *et al.*, 1990	
Arbutus unedo	Portugal	46.6	Harley *et al.*, 1986	
Quercus alba	Oak Ridge, TN	73	Harley and Baldocchi, 1995	Sun leaves
Quercus alba	Oak Ridge, TN	52	Harley and Baldocchi, 1995	Shade leaves
Quercus alba	Oak Ridge, TN	28.9	Wilson *et al.*, 2001	spring D100–150
Acer rubrum	Oak Ridge, TN	30–50	Wilson *et al.*, 2001	spring D100–150
Quercus alba	Oak Ridge, TN	48.2	Wilson *et al.*, 2001	summer D150–250
Acer rubrum	Oak Ridge, TN	20–50	Wilson *et al.*, 2001	summer D150–250
Quercus alba	Oak Ridge, TN	25.7	Wilson *et al.*, 2001	Late summer, D250–325
Acer rubrum	Oak Ridge, TN	~15	Wilson *et al.*, 2001	Late summer
Quercus douglasii	Ione, CA	62.90	Xu and Baldocchi, 2003	April
Quercus douglasii	Ione, CA	103.06	Xu and Baldocchi, 2003	May
Quercus douglasii	Ione, CA	68.91	Xu and Baldocchi, 2003	June
Quercus douglasii	Ione, CA	57.88	Xu and Baldocchi, 2003	July
Quercus douglasii	Ione, CA	46.42	Xu and Baldocchi, 2003	August
Quercus douglasii	Ione, CA	33.64	Xu and Baldocchi, 2003	September
Quercus rubra	Blackrock, New York	55.5	Turnbull *et al.*, 2002	Upper canopy
Quercus rubra	Blackrock, New York	57.6	Turnbull *et al.*, 2002	Middle canopy
Quercus rubra	Blackrock, New York	48.9	Turnbull *et al.*, 2002	Lower canopy
Quercus prinus	New York	49.3	Turnbull *et al.*, 2002	Upper canopy
Quercus prinus	New York	57.3	Turnbull *et al.*, 2002	Middle canopy
Quercus prinus	New York	44.4	Turnbull *et al.*, 2002	Lower canopy
Acer rubrum	New York	53	Turnbull *et al.*, 2002	Upper canopy
Acer rubrum	New York	43	Turnbull *et al.*, 2002	Middle canopy
Acer rubrum	New York	32.4	Turnbull *et al.*, 2002	Lower canopy
Plantanus orientalis	Kyoto, Japan	29.9	Kosugi *et al*[Q6]	expansion
Plantanus orientalis	Kyoto, Japan	47.8	Kosugi *et al*	mid-summer
Plantanus orientalis	Kyoto, Japan	23.6	Kosugi *et al*	fall
Plantanus orientalis	Kyoto, Japan	45	Kosugi *et al*	June
Liriodendron tulipifera	Kyoto, Japan	34.9	Kosugi *et al*	June
Prunus	Kyoto, Japan	51.9	Kosugi *et al*	June
Cercidiphyllum	Kyoto, Japan	27.8	Kosugi *et al*	June

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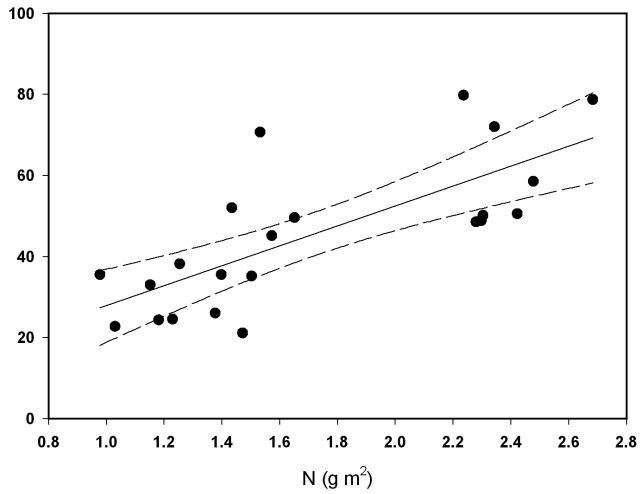

Figure 2. *Relationship between V_{cmax} and leaf nitrogen content on an area basis. Data of D. Baldocchi and G. Geidt for Oak Ridge, Tennessee, USA, during summer 1996. Measurements were made on leaves of Quercus alba.*

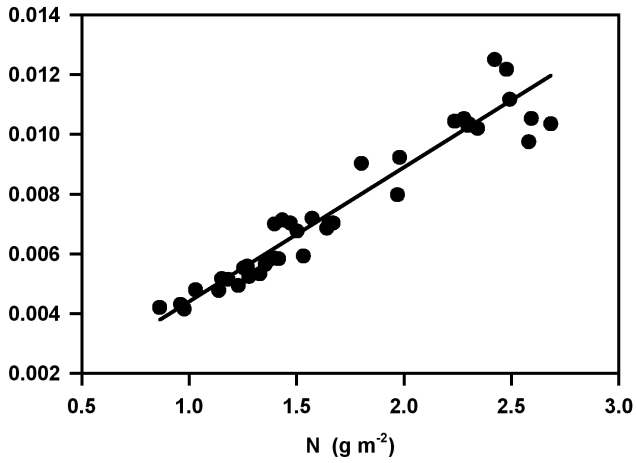

Figure 3. *Relationship between specific leaf weight and nitrogen content on an area basis for* Quercus alba *(data of D. Baldocchi and G. Geidt, Oak Ridge, Tennessee, USA, summer 1996).*

What are the consequences of these trends? Within a forest, upper sunlit leaves are thicker than those in the shaded understorey, thereby explaining the vertical canopy gradients leaf nitrogen and photosynthetic capacity that also exists (Chen *et al.*, 1993). Another implication of these results is that canopies with low leaf area indices have more sunlit leaves (Niinemets, 2001; Reich and Bolstad, 2001), so the leaves of these canopies are thicker and have greater photosynthetic capacity (Xu and Baldocchi, 2003).

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From our survey and our own data, we also conclude that the gradients of V_{cmax} and leaf nitrogen within a stand can be as great as the gradient of V_{cmax} and leaf nitrogen across the deciduous forest biome of sunlit leaves. Hence, one needs to consider sampling position when extracting such information from the literature and using it in a model.

Information is needed on the seasonality of V_{cmax} to apply photosynthesis models over the course of the growing season (Baldocchi and Wilson, 2001). Unfortunately, such data remain relatively rare. However, interesting patterns are emerging based on the limited data we have on-hand (*Figure 4*; Wilson *et al.*, 2000; Kosugi *et al.*, 2002;[Q29] Xu and Baldocchi, 2003). For temperate forest trees in mesic climates, V_{cmax} experiences modest seasonality (Wilson *et al.* 2000; Kosugi *et al.*, 2002).[Q29] It attains a maximum value of about 50 μmol m^{-2} s^{-1} around midsummer and declines at time approaches fall and eventual leaf senescence. In contrast, trees growing in a Mediterranean ecosystem achieve extremely high values of V_{cmax} (≈110 μmol m^{-2} s^{-1}) during their short growing season, when moisture is ample (Xu and Baldocchi, 2003); these V_{cmax} values are comparable to values of fertilized crops (Wullschleger, 1993).[Q28] Then V_{cmax} and leaf nitrogen drops dramatically as soil moisture is depleted. It is interesting to note that the areas under the V_{cmax} time curves, in *Figure 4*, are similar for the mesic and xeric trees. This result suggests that certain optimization strategies may be at play between the magnitude and the time course of V_i in xeric environments. If leaves on trees with short growing seasons are to acquire enough carbon to offset respiratory costs, they must develop light harvesting systems that have very high photosynthetic capacities during the short period water is available. To achieve high rates of photosynthesis they need the mechanics to do so, which comes at the expense of developing thick leaves. We find this line of logic interesting, as it is consistent with the findings of Niinemets (2001). There also has to be an additional constraint on the total leaf area that the ecosystem can support, as in dry environments a closed canopy with high leaf areas cannot be sustained because this behavior would engender high evaporative costs, too.

4.2.2 Leaf respiration

The growing body of data on leaf respiration is delineating important relational patterns that can be exploited to parameterize models, too. First, a body of data is showing that R_d scales with leaf nitrogen, so consequently R_d scales V_{cmax} (Reich *et al.*, 1998; Turnbull *et al.*, 2003). There are times when these relations break, however. During the early stages of leaf development, respiration rates can exceed mid-summer basal rates by a factor of five, as construction costs of the growing leaf are inordinately high (Xu and Baldocchi, 2003). Furthermore, dark respiration rates in sunlight are much reduced compared to nocturnal rates, owing to the 'Kok' effect (Turnbull *et al*, 2002; Xu and Baldocchi, 2003).

4.2.3 Stomatal conductance

Over the past decade the Ball–Berry–Collatz model (Collatz *et al.*, 1992)[Q30] has emerged as a popular algorithm for computing stomatal conductance. Its strength rests on its coupling (though empirical) of stomatal conductance (g_s) to photosynthesis (A), relative humidity (rh), and leaf surface CO_2 concentration (C_s)

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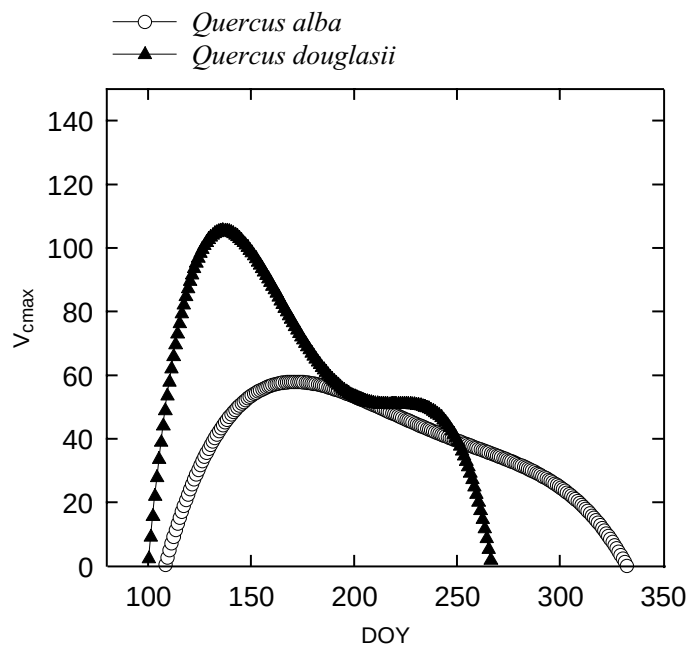

Figure 4. *Seasonal variation in* V_{cmax} *for a xeric (*Q. douglasii*) and mesic (*Q. alba*) oak species. Data are from Xu and Baldocchi (2003) and Wilson et al. (2001)[Q*

$$g_s \propto m \frac{A \cdot rh}{C_s} \tag{4}$$

Drawing on a growing body of data in *Table 3* we conclude that the coefficient of proportionality (m) is fairly constant, with a mean value of 10.4 ± 0.56.

There is some controversy as to the behavior of the coefficient, m, when trees are subject to drought. Sala and Tenhunen (1996)[Q31] report that the m coefficient decreases as soil dries. Modelers using the simple biosphere model, SiB, assume that m is constant, and instead decrease V_{cmax} with drought (Coello *et al.*, 1998);[Q32] members of this team were co-developers of equation (4). Most recently, Xu and Baldocchi (2003) conducted a seasonal study of V_{cmax} and m on a Mediterranean oak species and found that m remained relatively constant (8.8) as predawn water potential varied from –0.01 MPa to –4.0 MPa. Instead, leaf nitrogen content and, consequently, $V_{cmax,}$ decreased dramatically with progressive summer drought.

5. Stand-level carbon fluxes

As we write this report, the FLUXNET community has over forty site-years of carbon flux data from more than ten deciduous broadleaved forest sites. In *Table 4* we survey published values of net ecosystem CO_2 exchange (N_{ec}) that have been reported over the past decade from long term measurement studies over temperate forests. Values of N_{ec} range between –200 and –600 g (C) m^{-2} per year, and center at –315 ± 200 g (C) m^{-2} per year. Some high values are due to systematic bias errors at night, when respiration is underestimated (Baldocchi *et al.*, 2000). However, in general, high rates

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Table 3. *Literature survey of coefficients, m, of the Ball–Berry–Collatz stomatal conductance equation*

m	Taxon	Reference[Q46]
8.1	Populus tremuloides	Berry, 1995
9.5	*Quercus alba*	Harley and Baldocchi, 1995
9.5	*Acer rubrum*	Harley and Baldocchi, 1995
7.2–11.1	*Eucalyptus grandis*	Leuning, 1990
13.5	*Populus tremuloides*	Nikolov *et al.*, 1995
16.0	*Quercus ilex* (well watered)	Sala and Tenhunen, 1996
5.4	*Quercus ilex* (drought)	Sala and Tenhunen, 1996
9.3–18.0	*Eucalyptus grandis*	Leuning, 1995
8.9	*Quercus douglasii*	Xu and Baldocchi, 2003
10.0	*Acer saccharum*	Ellsworth *et al.*, 1994
13.4	*Acer saccharum*	Ellsworth and Reich, 1993
12.0	*Acer saccharum*	Tjoelker *et al.*, 1995
8.7	*Pinus flexilis*	Nikolov *et al.*, 1995
10.0	*Arbutus unedo*	Harley and Tenhunen, 1991
12.7	*Fagus sylvatica*	Medlyn *et al.*, 2001
10.1	Phillyea augustifolia	Medlyn *et al.*, 2001
8.2	*Pistacia lentiscus*	Medlyn *et al.*, 2001
6.2	*Quercus ilex*	Medlyn *et al.*, 2001
9.4	*Betula*	Medlyn *et al.*, 2001
2.9–6.4	*Picea abies*	Medlyn *et al.*, 2001
9.8	*Plantanus orientalis*	Kosugi *et al.*, 2003
9.3	*Liriodendron tulipifera*	Kosugi *et al.*, 2003
5.8	*Cercidiphyllum japonicum*	Kosugi *et al.*, 2003

reflect the demographics of temperate forests worldwide, which tend to be relatively young (Nabuurs, 2003) and their rates of net carbon exchange have not reached equilibrium—a balance between ecosystem photosynthesis and respiration (see, for example, Friend *et al.*, 1997).

To arrive at these annual sums, a forest experiences gains and losses of carbon over the course of a day and season, as light, temperature, leaf area and soil moisture change. In the following sections we discuss the temporal dynamics of ecosystem carbon exchange of temperate and Mediterranean deciduous forests.

6. Temporal dynamics of net ecosystem CO_2 exchange

6.1 *Temperate deciduous forests*

The annual sums reflected in *Table 4* are the consequence of seasonal changes in the activities and magnitudes of photosynthesis and respiration. Deciduous broadleaved forests are dormant and respiring during the winter and assimilate carbon and grow during the spring and summer (*Figure 5*). During the winter, respiration is a strong function of soil temperature, as adequate soil moisture is generally available (Greco and Baldocchi, 1996; Granier *et al.*, 2000; Schmid *et al.*, 2000; Pilegaard *et al.*, 2001).

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Table 4. *Literature survey of published values of N_{ec}, G_p and R_{eco} (grams of carbon per square meter per year) using the eddy covariance method over broadleaved deciduous forests*

Site	g (C) m^{-2} per year N_{ec}	Year	g(C) m^{-2} per year G_p	g(C) m^{-2} per year R_{eco}	Reference[Q47]
Prince Albert, Saskatchwan, Canada	–160	1994			Black *et al.*, 1996
Prince Albert, Saskatchwan, Canada	–144	1994			Black *et al.*, 2000
Prince Albert, Saskatchwan, Canada	–80	1996			Black *et al.*, 2000
Prince Albert, Saskatchwan, Canada	–116	1997			Black *et al.*, 2000
Prince Albert, Saskatchwan, Canada	–290	1998			Black *et al.*, 2000
Prince Albert, Saskatchwan, Canada	–70	1996	1 120	1 050	Barr *et al.*, 2002
Prince Albert, Saskatchwan, Canada	–120	1997	1 170	1 050	Barr *et al.*, 2002
Prince Albert, Saskatchwan, Canada	–270	1998	1 350	1 090	Barr *et al.*, 2002
Harvard Forest, Petersham, MA	–220	1991			Wofsy *et al.*, 1993
Harvard Forest, Petersham, MA	–280	1991			Goulden, 1996
Harvard Forest, Petersham, MA	–220	1992			Goulden, 1996
Harvard Forest, Petersham, MA	–140	1993			Goulden, 1996
Harvard Forest, Petersham, MA	–210	1994			Goulden, 1996
Harvard Forest, Petersham, MA	–270	1995			Goulden, 1996
Harvard Forest, Petersham, MA	–200	1992			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–190	1993			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–200	1994			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–250	1995			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–200	1996			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–210	1997			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–120	1998			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–230	1999			Barford *et al.*, 2001
Harvard Forest, Petersham, MA	–210	2000			Barford *et al.*, 2001
Borden, Ontario	–130	1996			Lee *et al.*, 1999
Borden, Ontario	–160	1997			Lee *et al.*, 1999
Borden, Ontario	–310	1998			Lee *et al.*, 1999
Borden, Ontario	–60	1996	1 200	1 140	Barr *et al.*, 2002
Borden, Ontario	–240	1997	1 330	1 100	Barr *et al.*, 2002
Borden, Ontario	–170	1998	1 410	1 240	Barr *et al.*, 2002
Takayama, Japan	–120	1994			Yamamoto, 1999
Takayama, Japan	–214	1999	1 146	984	Saigusa, 2002
Italy	–470	1994			Valentini *et al.*, 1996
Italy	–660	1997	1 302	636	Valentini *et al.*, 2000
Hesse, France	–218	1996	1 011	793	Granier *et al.*, 2000
Hesse, France	–257	1997	1 245	988	Granier *et al.*, 2000
Hesse, France	–257	1997	1 245	988	Granier *et al.*, 2002
Hesse, France	–68	1998	1 314	1 235	Granier *et al.*, 2002
Hesse, France	–296	1999	1 335	1 036	Granier *et al.*, 2002
Belgium	–157	1997			Valentini *et al.*, 2000
Belgium	–430	1997			Valentini *et al.*, 2000
Belgium	–600	1996–1997			Aubinet *et al.*, 2001
Belgium	–519	1998	1 386	867	Granier *et al.*, 2003

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Table 4. *continued*

Site	g (C) m^{-2} per year N_{ec}	Year	g(C) m^{-2} per year G_p	g(C) m^{-2} per year R_{eco}	Reference[Q47]
Morgan-Monroe Indiana	–240	2000			Schmid *et al.*, 2000
Morgan-Monroe Indiana	–237	1998			Ehman *et al.*, 2002
Morgan-Monroe Indiana	–287	1999			Ehman *et al.*, 2002
Oak Ridge, TN	–525	1994			Greco and Baldocchi 1996
Oak Ridge, TN	–660	1997			Baldocchi *et al.*, 2000
Oak Ridge, TN	–470	1995			Wilson and Baldocchi, 2001
Oak Ridge, TN	–576	1996			Wilson and Baldocchi, 2001
Oak Ridge, TN	–618	1997			Wilson and Baldocchi, 2001
Oak Ridge, TN	–592	1998			Wilson and Baldocchi, 2001
Oak Ridge, TN	–629	1999			Wilson and Baldocchi, 2001
Denmark, Soroe	–169	1997	1 271	1 048	Pilegaard *et al.*, 2001
Denmark, Soroe	–124	1998	1 335	1 191	Pilegaard *et al.*, 2001
Denmark, Soroe	–122	1997	1 025	875	Granier *et al.*, 2002
Denmark, Soroe	–71	1998	1 255	1 249	Granier *et al.*, 2002
Denmark, Soroe	–227	1999	1 355	1 245	Granier *et al.*, 2002
Germany, Hainich	–494	2000	1 580	1 086	Knohl *et al.*, 2003
Germany, Hainich	–490	2001	1 540	1 050	Knohl *et al.*, 2003
Michigan, Douglas Lake	–210	1999	1 350	1 140	Schmid *et al.*, 2003
Michigan, Douglas Lake	–210	2000			Schmid *et al.*, 2003
Michigan, Douglas Lake	–170	2001			Schmid *et al.*, 2003

The presence or absence of snow has a major impact on soil temperatures and the soil respiration from these forests. Snow insulates the soil surface, so warmer soil temperatures will occur when snow is present), causing greater rates of respiration (Goulden *et al.*, 1996a).

During spring a pronounced peak in respiration occurs due to stimulation of growth respiration as leaves emerge and the soil warms (Greco and Baldocchi, 1996; Granier *et al.*, 2000;[Q33] Schmid *et al.*, 2000; Pilegaard *et al.*, 2001). Daily respiration rates between 5 and 7 g (C) m^{-2} d^{-1} can occur during this period (Granier *et al.*, 2000),[Q33] thereby doubling or tripling respiration rates that occur earlier in the spring. As leaf-out occurs, the ecosystem experiences a pronounced switch between being a net source of carbon to being a net sink. This switch can represent a net change of carbon exchange on the order of 8 to 10 g (C) m^{-2} d^{-1}. Consequently, being able to predict or assess the date of leaf-out (by satellite observations or by phenological

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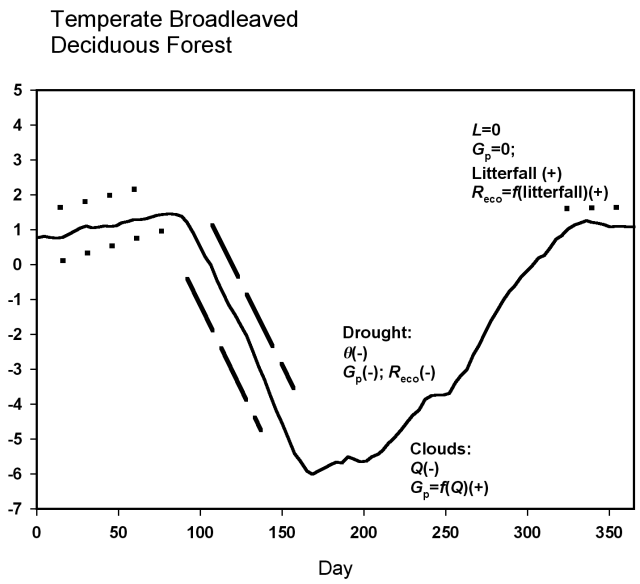

Figure 5. *Seasonal variation in daily sums of net CO_2 exchange of a temperate deciduous forest. Also shown are the environmental and biological factors that affect the seasonal dynamics of CO_2 exchange. These variables include volumetric soil moisture (θ), photosynthetic photon flux density (Q), soil temperature (T_{soil}) and leaf area index (L) (adapted from Baldocchi and Valentini, 2003). Data sources: Wofsy et al., 1993; Greco and Baldocchi, 1996; Valentini et al., 1996; Goulden et al., 1996a, b; Baldocchi et al., 2000; Granier et al, 2000; Schmid et al., 2000; Pilegaard et al., 2001; Granier et al., 2003; Knohl et al., 2003.[Q44]*

modeling) will have a major impact on assessing carbon exchange of this biome correctly (Baldocchi *et al.*, 2001).

Across the deciduous forest biome, the date of leaf out can vary by 30 days at a given site (Goulden *et al.*, 1996;[Q34] Wilson and Baldocchi, 2001) or by over 100 days across the deciduous forest biome (*Figure 6*). Using simple regression analysis we have found that length of growing season predicts over 78% of the variance associated with N_{ec} across a global network of deciduous forest carbon flux measurement sites.[Place Figure 6 about here]

Once a forest has attained full-canopy closure, available sunlight (the photosynthetic photon flux density, Q) explains most of the variability in hourly rates of carbon exchange, but in a non-linear and saturating fashion (Baldocchi and Harley, 1995; [Q35]Goulden *et al.* 1996;[Q34] Valentini *et al.* 1996; Granier *et al.* 2000,[Q33] 2003; Schmid *et al*, 2000; Pilegaard *et al.* 2001). The transparency of the atmosphere, however, complicates this relation. A growing body of field studies is showing that the initial slope of the light response curve (also known as light use efficiency increases as the fraction of diffuse radiation increases (Baldocchi, 1997; Gu *et al.*, 2001);[Q36] in general short-term N_{ec} is twice as sensitive to changes in diffuse light as to changes in direct light. The presence of clouds produces a decrease in the

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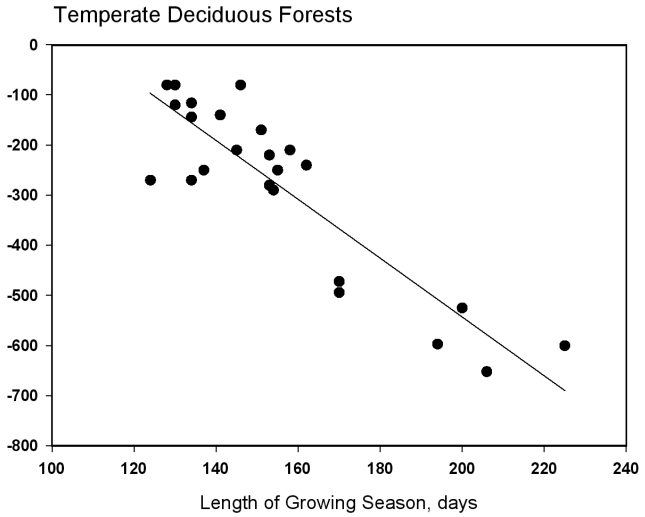

Figure 6. *Impact of length of growing season on net ecosystem carbon exchange, N_e, of temperate broadleaved forests. This plot updates the figure published by Baldocchi et al. (2001) by adding newer data from Schmid et al. (2003) and Knohl et al. (2003). The coefficient of determination is 0.78 and the regression slope is –5.87 g (C) m^{-2} d^{-1}.*

absolute amount of sunlight. But the greater fraction of diffuse sunlight causes a shift in the N_{ec}-light response curve, so the reduction in N_e is minimized. And in the presence of aerosols, an increase in the fraction of diffuse light can occur without decreasing Q, which will cause N_{ec} to increase.

Droughts tend to be episodic across the temperate deciduous forest biome. The occurrence of summer drought and high vapor pressure deficits will cause reductions in daytime photosynthesis (Goulden *et al.*, 1996;[Q34] Baldocchi, 1997; Granier *et al.*, 2003). Drying of the soil will also force reductions in soil respiration (Hanson *et al.*, 1989).[Q37] Together, these features reduce N_{ec} from values during normal summer conditions.

In the fall, leaves senesce, photosynthesis ceases and soil respiration experiences an enhancement due to the input of fresh litter that is readily decomposable. This leads to another respiratory pulse by the ecosystem as soils are still warm and fall rains stimulate respiration (Granier *et al.* 2000;[Q33] Goulden *et al.*, 1996).[Q34]

With over 8 000 hours of data available per year per site, alternative methods are can be used to digest this information and quantify the temporal dynamics of the fluxes. Fast Fourier transforms are one method. In *Figure 7* we compare power spectra of CO_2 fluxes measured at North American and European flux sites. Dominant power is associated with the seasonal and diurnal forcings due to the Earth's daily revolution on its axis and its annual revolution around the sun. Of secondary note are spectral peaks at weekly time-scales. The passage of weather fronts occurs on this time-scale and they cause photosynthesis and respiration to vary by altering direct and diffuse radiation, light use efficiency and vapor pressure deficits.

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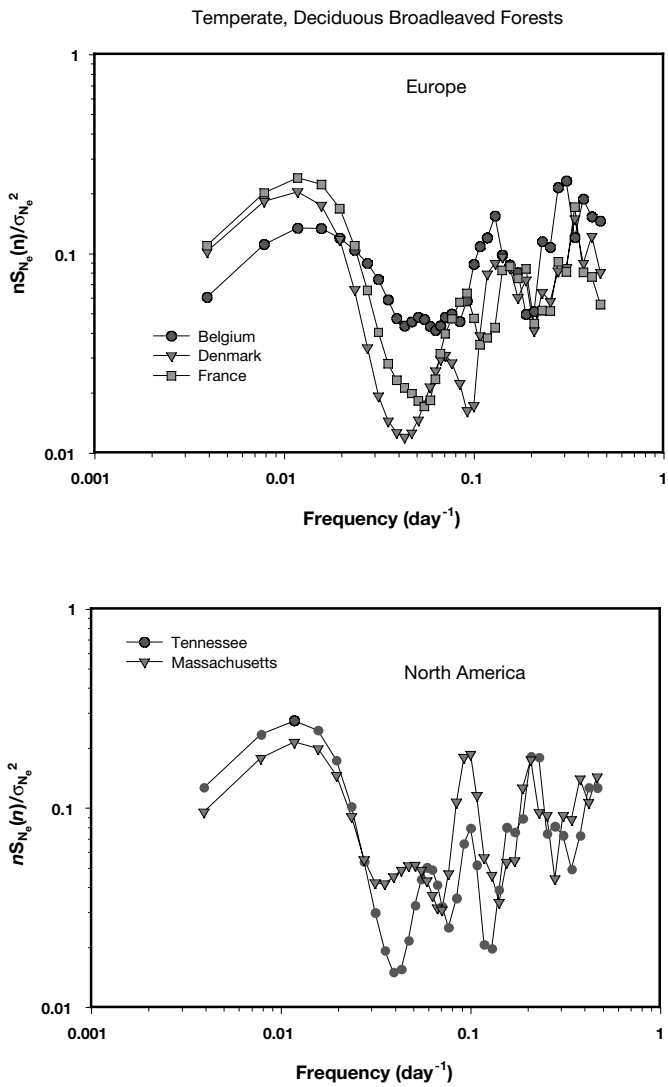

Figure 7. *Data are from the FLUXNET database (adapted from Baldocchi et al., 2001). The y-axis consists of the product of natural frequency (n) times the power spectra density for net ecosystem CO_2 exchange. This product is normalized by the variance (σ^2)of N_e.*

6.2 *Deciduous Mediterranean forests*

Many deciduous forests in Mediterranean regions consist of two distinct layers, an annual grass understorey, with multiple species and functional groups (grasses, forbs and nitrogen fixers), and tree overstorey. The grassland is green and physiologically functional during the late fall, winter and early spring. In contrast, the oak woodland is deciduous, dormant and respiring. During this period net rates of CO_2 uptake are symmetric about noon and the ecosystem is respiring at night (*Figure 8*). By spring,

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the tree leaves are expanding rapidly reaches full photosynthetic potential, causing a gradual increase in daytime CO_2 uptake rates. After the rains cease (around May), the grasses die and the trees gradually draw down the supply of moisture in the soil as they transpire. During the hot dry and rainless summer, their stomata carefully regulate water loss to avoid lethal cavitation (Griffin, 1973; Kiang, 2002)[Q38] while maintaining low rates of photosynthesis. As the intensity of the summer drought increases the time of peak CO_2 uptake shifts towards the morning and the magnitude of daytime photosynthesis decreases (*Figure 8*).

Episodic rain events during the summer period can cause huge pulses in soil respiration (Reichstein *et al.*, 2002;[Q39] Rey *et al*, 2002; Xu and Baldocchi, 2003). Two mechanisms are possible for producing enhanced respiration rates after summer rainfall events. One is a physical displacement of soil air and CO_2 by the downward moving front of water in the soil. But this effect is short-lived and the

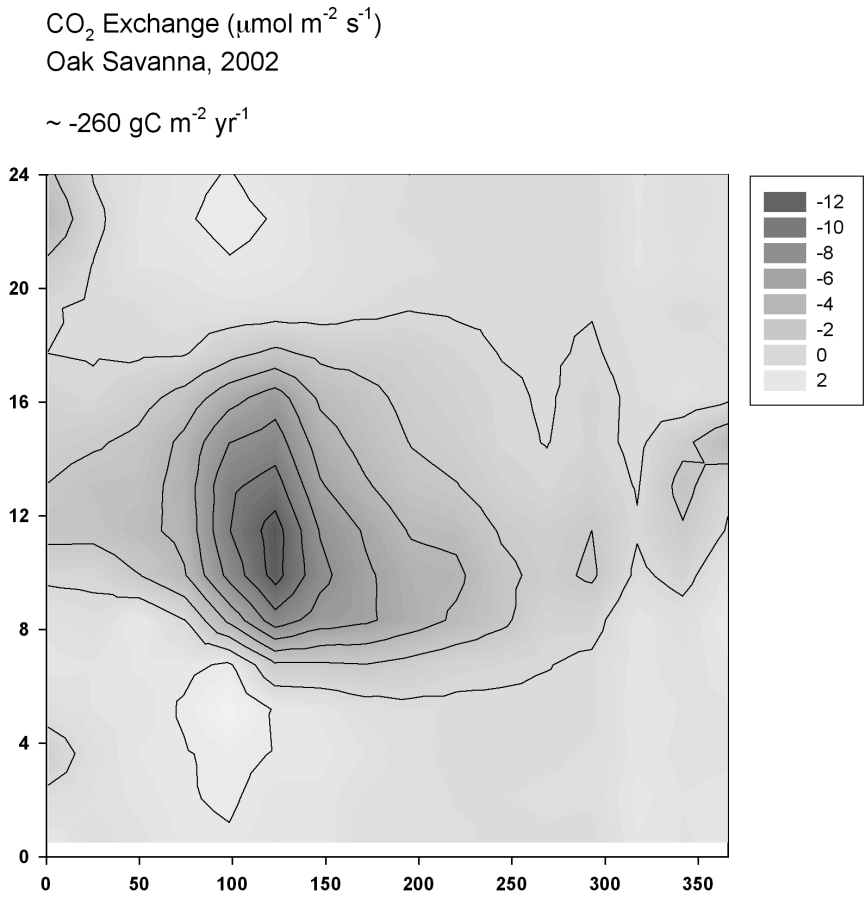

Figure 8. *Fingerprint plot of carbon exchange of an oak savannah growing in the Mediterranean climate of California during 2002. These data express how the diurnal curve of CO_2 exchange evolves over the course of a year (D. Baldocchi and L. Xu, unpublished data).*

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volume of air in the soil profile is relatively small. The other effect is attributed to a rapid activation of heterotrophic respiration; a set of classic papers by Birch (1958) and Orchard and Cook (1983)[Q40] show that dormant populations of microbes are able to start respiration, within hours, with the addition of water and microbial respiration rates ceases as soon as the soil layer dries. In ecosystems with low N_{ec}, such as savannah woodlands and Mediterranean ecosystems, a few large pulses of soil respiration have the potential to change the ecosystem from being a sink of carbon to a source.

6.3 *Canopy photosynthesis[Q1]*

Canopy photosynthesis of a temperate forest is a function of available sunlight, whether it is direct or diffuse, the leaf area index of the canopy, the photosynthetic capacity of leaves, air temperature and soil moisture (Ruimy *et al.*, 1995; Baldocchi and Amthor, 2001).[Q41] In most circumstances, variations in sunlight explain over 70% of the variance in canopy photosynthesis, so we focus on this variable in this chapter.

The response of canopy-scale CO_2 exchange rates to variations in sunlight are much different from that of leaves, which follow a Michaelis–Menten relationship and saturate at high light levels. The shape of the canopy light response curve depends on the time-scale of the integration. On an hourly basis, CO_2 exchange rates of temperate forests are a curvi-linear function of absorbed sunlight (Hollinger *et al*, 1994; Ruimy *et al.*, 1995; Baldocchi and Harley, 1995;[Q35] Granier *et al.*, 2002). Integrating carbon fluxes to a daily basis forces the functional relationship to become linear (Ruimy *et al.*, 1995), except when there is drought (Greco and Baldocchi, 1996).

The Michaelis–Menten function is a popular way of quantifying the response of hourly canopy photosynthesis measurements to changes in visible light (Falge *et al.*, 2002):[Q42]

$$J_p = \frac{\alpha \cdot Q_p \cdot J_{pmax}}{J_{pmax} + \alpha \cdot Q_p} \tag{5}$$

where α is quantum yield, Q is photon flux density of visible light and J_{pmax} is the maximum flux density of canopy photosynthesis. The quantum yield can be deduced by evaluating the derivative of this function with respect to Q when Q is zero.

In *Table 5* we present values of J_{pmax} and quantum yield that have been published for broadleaved forests. Maximum rates of canopy photosynthesis range between 20 and 30 μmol m^{-2} s^{-1} and quantum yields cluster around 0.04 mol CO_2 mol^{-1} photon for forests growing in North America and Europe. The lowest values of J_{pmax} and quantum yield are for the Mediterranean oak forest in Italy.

The reader, however, should be cognizant that the slope of the relationship between canopy CO_2 exchange rates and available sunlight (Q_a) is affected by whether the sky is clear or cloudy. For example, the initial slope of the canopy light response curve can double when sky conditions change from clear to cloudy (Hollinger *et al.*, 1994; Baldocchi, 1997; Gu *et al.*, 2002).

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Table 5. *Survey of model parameters for the relationship between canopy photosynthesis and photon flux density. The data are for deciduous forests and come from original sources and syntheses by Falge et al. (2002) and Ruimy et al. (1995).*

Forest	Location	Reference[Q48]	J_{pmax} (μmol m^{-2} s^{-1})	Quantum yield (mol CO_2 mol^{-1} photon)
Betula/Quercus	Takayama, Japan	Saigusa *et al.*, 2002	n.a.	0.042–0.070
Fagus	Hesse, France	Granier *et al.*, 2002	24.8	0.0446
Fagus	Soroe, Denmark	Granier *et al.*, 2002	25.3	0.0398
Quercus	Morgan Monroe, IN	Schmid *et al.*, 2000	24.9	0.0597
Quercus/Acer	Walker Branch, TN	Baldocchi and Harley, 1995	29.9	0.040
Populus/Acer	Douglas Lake, MI	Schmid *et al.*, 2003	28–37.1	0.055–0.0695
Nothofagus	Maruia, New Zealand	Hollinger *et al.*, 1994	17.0	0.043
Quercus ilex	Castelporziano, Italy	Valentini *et al.*, 1991	17.5	0.015
Broadleaved forests	Average across the biome	Ruimy *et al.*, 1995	24.6	0.037

6.4 *Ecosystem respiration[Q1]*

As noted in equation (1), ecosystem respiration consists of respiration by roots and soil heterotrophs. In general, soil respiration can be two-thirds to three-fourths of ecosystem respiration and one-third to one-half is root respiration (Hanson *et al* 2000; Raich and Tufekcioglu, 2000). On an annual time-scale, soil respiration correlates with litterfall (Raich and Tufekcioglu, 2000). In contrast, ecosystem respiration correlates strongly with soil temperature on hourly, daily, and monthly time-scales. However, recent studies show that ecosystem respiration is also a function of photosynthesis (Hogberg *et al.* 2001) and soil moisture (Reichstein *et al*, 2002).[Q39]

An example of the seasonal variation in soil respiration of a temperate forest is shown in *Figure 9*. Modulations in carbon effluxes are caused by seasonal changes in temperature, photosynthetic activity, rain events, drought and pulsed inputs of litter.

The Q_{10} function is a popular algorithm for expressing how ecosystem respiration varies as temperature (T) deviates from a base temperature, T_b:

$$R_{eco}(T) = R_{eco}(T_b)Q_{10}^{\frac{(T-T_b)}{10}} \quad (6)$$

The Q_{10} factor represents the proportionality factor by which ecosystem respiration increases with a 10 °C increase in temperature. On the basis of the temperature dependency of the kinetic rates of basic enzyme reactions one would expect a Q_{10} of 2. In *Table 6* we survey reference respiration rates and Q_{10} coefficients for temperate and Mediterranean broadleaved forests, and observe that Q_{10} values range between 1 and 5. In many circumstances, these anomalously high values are an artifact of how these quotients are assessed. First, respiration data is noisy and measurements may be biased low during cool periods with stable thermal stratification. Second, the range of temperature can be narrow during certain phenological periods. To circumvent this

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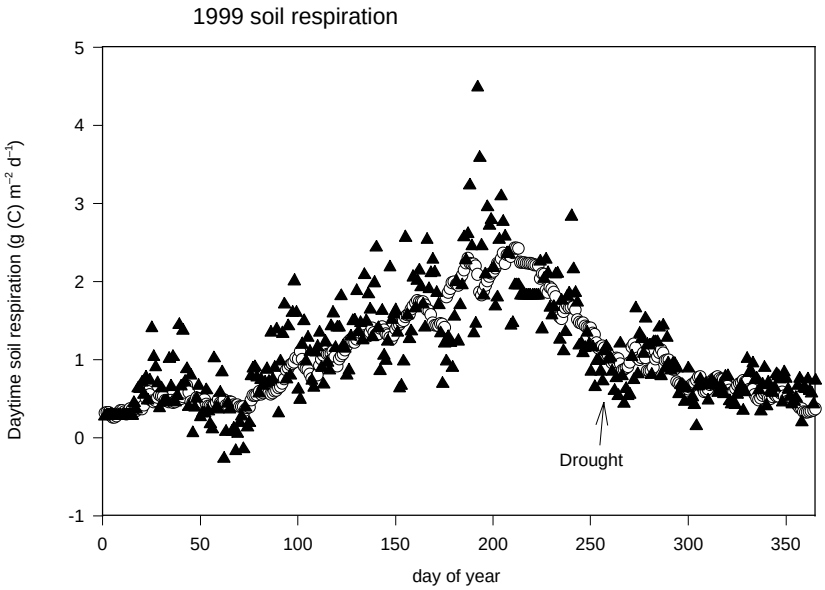

Figure 9. *Seasonal variation of CO_2 exchange measured with an understorey eddy covariance system and modeled. Data from Wilson and Baldocchi (2001).*

Table 6.**[Q51]** *Survey of the basal (b) or maximum (m) rates of ecosystem respiration and the Q_{10} respiration factor. Data are from original sources or the synthesis of Falge et al. (2002).*

Forest	Location	Reference[Q49]	R_{eco}	Q_{10}
Oak–maple	Oak Ridge, TN	Greco and Baldocchi, 1996	3.9, b	1.62 (a)[Q8]
Maple–tulip poplar	Morgan Monroe, IN	Schmid *et al.*,		
2000	1.08, b	1.89 (s)		
Oak maple	Petersham, MA	Goulden *et al.*, 1996	4.7, m	2.1 (s)
Beech	Central Italy	Valentini *et al.*, 1996	2.2 (a)	
Boreal aspen	Prince Albert, Sask	Black *et al.*, 1996	5.4 (s)	
Beech	Denmark	Granier *et al.*, 2002	6.8, m	2.53 (s)
Beech	Nancy, France	Granier *et al.*, 2002	7.4, m	3.53 (s)
Quercus ilex/pubescens	France	Reichstein *et al.*, 2002	3.91, b	2.10
Quercus ilex/suber	Italy	Reichstein *et al.*, [Q7]	4.54, b	1.65
Betula/Quercus	Japan	Saigusa *et al.* 2002	1.96, b	2.67
	Willow Creek, WI	5.7, m		
	Park Falls, WI	7.9, m		

problem, investigators often compute Q_{10} values by using data from across the growing season. This procedure, on the other hand, can force Q_{10} values to be artificially high. This is because they reflect the combine effects of growth, maintenance and reproductive respiration during the warmest months and only maintenance respiration during the coolest months.

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Based on equation (6), one could expect annual ecosystem respiration to increase as one moves south in the northern hemisphere, to warmer climates. But one has to be careful about drawing this conclusion, because as soils get warmer, they also get drier, which inhibits ecosystem respiration and forces Q_{10} to decrease, as found by Reichstein *et al.* (2002)[Q39] for an evergreen Mediterranean forest.

7. Ecosystem carbon balances

At annual and inter-annual time-scales ecologists study net primary productivity of temperate forests by measuring changes in the above and below-ground carbon pools. The classic definition of N_p, as assessed by biometry, is:

$$N_p = \Delta L + \Delta D + \Delta H \tag{7}$$

where ΔL is the live increment, ΔD is the increment in detritus, and ΔH increment lost to herbivory. In practice, equation (7) can be evaluated by examining the increments in wood, soil carbon, leaves, woody and fine roots (Curtis *et al.*, 2002; Gower, 2003). In Table 7 we report data from recent carbon balance studies at deciduous forest field sites.

We note that N_e produced by biometric measurements is smaller than values produced by eddy covariance measurements in many cases (Curtis *et al.*, 2002). These differences occur for a variety of reasons. For biomass measurements there are errors associated with the allometric scaling functions, the time duration between samples and biased sampling of below ground carbon pools. Eddy covariance measurements suffer from systematic bias errors that occur at night when the atmosphere is stable, causing this method to overestimate N_e in many circumstances.

8. Future issues

The study of temperate forest carbon balances remains an active and challenging problem. Five years ago the priorities for future work would have been along the lines of conducting eddy flux studies on annual time-scales. Viewed from today, we have crossed this barrier and we need to extend to the length of the flux time records to at least a decade to study the inter-annual scales of variance that occur in the temperate zone (Baldocchi and Wilson, 2001). Secondly, we need to assess the seasonally of photosynthesis and respiration model parameters, so we can apply biophysical models on these time-scales with confidence. This work will involve partitioning measurements of N_{ec} into its assimilatory and respiratory components. One approach to flux partitioning involves using a combination of soil respiration chambers, understorey eddy flux measurements and carbon isotopes (Baldochi and Vogel, 1996; Bowling *et al.*, 1999). New soil CO_2 sensors provide an alternative means of measuring soil respiration continuously and without artifacts by coupling them with flux-gradient theory (Tang *et al.*, 2003). Thirdly, we need to assess carbon fluxes in complex terrain with confidence and we need to under how to mechanistically correct fluxes at night when the atmosphere is stable and drainage flows transfer CO_2 at preferred locations. For up-scaling fluxes to the landscape and regional scales, we need to relate tower-based eddy fluxes with remote sensing signals and biomass contained within flux footprints.

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This work entails the need to partition fluxes into assimilatory and respiratory components and the production of better footprint models. Finally, we need to conduct biometric inventory studies over longer time-scales to understand lag effects and inter-annual variability on the production of biomass increments.

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