Foliar respiration acclimation to temperature and temperature variable Q_{10} alter ecosystem carbon balance

K I R K R . W Y T H E R S *, P E T E R B . R E I C H *, M A R K G . T J O E L K E R † and P A U L B . B O L S T A D *
*Department of Forest Resources, University of Minnesota, 115 Green Hall, 1530 Cleveland Ave N., Saint Paul, MN 55108, USA,
†Department of Forest Science, Texas A&M University, College Station, TX 77843-2135, USA

Abstract

The response of respiration to temperature in plants can be considered at both short- and long-term temporal scales. Short-term temperature responses are not well described by a constant Q_{10} of respiration, and longer-term responses often include acclimation. Despite this, many carbon balance models use a static Q_{10} of respiration to describe the short-term temperature response and ignore temperature acclimation.

We replaced static respiration parameters in the ecosystem model photosynthesis and evapo-transpiration (PnET) with a temperature-driven basal respiration algorithm (Rd_{acclim}) that accounts for temperature acclimation, and a temperature-variable Q_{10} algorithm (Q_{10var}). We ran PnET with the new algorithms individually and in combination for 5 years across a range of sites and vegetation types in order to examine the new algorithms' effects on modeled rates of mass- and area-based foliar dark respiration, above ground net primary production (ANPP), and foliar respiration–photosynthesis ratios.

The Rd_{acclim} algorithm adjusted dark respiration downwards at temperatures above 18 °C, and adjusted rates up at temperatures below 5 °C. The Q_{10var} algorithm adjusted dark respiration down at temperatures below 15 °C. Using both algorithms simultaneously resulted in decreases in predicted annual foliar respiration that ranged from 31% at a tall-grass prairie site to 41% at a boreal coniferous site. The use of the Rd_{acclim} and Q_{10var} algorithms resulted in increases in predicted ANPP ranging from 18% at the tall-grass prairie site to 38% at a warm temperate hardwood forest site.

The new foliar respiration algorithms resulted in substantial and variable effects on PnETs predicted estimates of C exchange and production in plants and ecosystems. Current models that use static parameters may over-predict respiration and subsequently under-predict and/or inappropriately allocate productivity estimates. Incorporating acclimation of basal respiration and temperature-sensitive Q_{10} have the potential to enhance the application of ecosystem models across broad spatial scales, or in climate change scenarios, where large temperature ranges may cause static respiration parameters to yield misleading results.

Keywords: acclimation, ANPP ecosystem model, PnET, production, Rd:A, respiration, temperature

Received 29 September 2003; revised version received 16 September 2004; accepted 21 October 2004

Introduction

Concern about climate change (Houghton *et al.*, 1992; Vitousek, 1994) and associated long-term impacts on the planet (e.g. Lubchenco *et al.*, 1991; Woodwell & Mackenzie, 1995; Falkowski *et al.*, 2000) has intensified interest in the flux of carbon (C) between the terrestrial

Correspondence: Kirk R. Wythers, fax + 612 625 5212,
e-mail: kwythers@umn.edu

biosphere and the atmosphere. Carbon dioxide (CO_2) flux is of particular concern because it is a greenhouse gas and is the form in which most C moves between the biosphere and the atmosphere. Over the last 200 years, atmospheric CO_2 concentration has increased by 30% (Keeling *et al.*, 1996). A likely outcome of this change is an alteration in global temperature patterns. Estimated increases of + 1.4 to + 5.8 °C in mean global surface temperature have been predicted to occur from 1990 to 2100 (Houghton *et al.*, 2001; McCarthy *et al.*, 2001), and

these changes are likely to vary substantially among regions and exhibit seasonal and diurnal variation.

Regardless of scale, atmospheric C is fixed into plant biomass through photosynthesis and returned to the atmosphere via respiration. The difference between these fluxes determines C balance in ecosystems. While C is released back to the atmosphere through both autotrophic and heterotrophic pathways, autotrophic respiration accounts for roughly half of the total respiratory C flux (Farrar, 1985; Houghton *et al.*, 2001). Therefore, autotrophic respiration plays a substantial role in governing ecosystem C balance (Field *et al.*, 1992; Ryan *et al.*, 1995, 1996). Accurate modeling of the response of autotrophic respiration to changing climate will be essential in order to effectively predict the impact of climate change on the global C balance. Given the established links between plant respiration and temperature, it may be useful to re-examine the mechanisms and assumptions built into process oriented ecosystem models, common tools for evaluating the effects of climate on C balance patterns over a variety of temporal and spatial scales.

C balance models that operate at the tissue level of organization (i.e. leaf, stem, and root) are often used to examine feedbacks between environmental change and ecosystem productivity. Models that simulate system behavior in terms of a C balance typically do so with a collection of interactive algorithms that estimate C assimilation, respiration, and allocation. For a more complete review of process models see Ågren *et al.* (1991), Ryan *et al.* (1996), and Mäkelä (2000). While most process models incorporate temperature into their respiratory calculations, they do so at varying levels of complexity, using a range of assumptions and generalizations. The difficulty in capturing plant respiration's many sources of variation in a mathematical model owes to the debate in how to best represent (or to represent at all) these sources of variation. A better understanding of how plant respiration responds to temperature change can only aid in the construction of more flexible and generalizable algorithms.

Many biological processes, including respiration, are dependent upon temperature. Biological processes are often ascribed to Van't Hoff's reaction rate-temperature rule, and modeled as exponential functions. The respiration–temperature response function is such an exponential relationship. A form of the respiration response function which permits direct estimates of the Q_{10} parameter is often expressed as:

$$Rd = Rd_{ref}Q_{10}^{[(T-T_{ref})/10]}, \qquad (1)$$

where Rd is dark respiration, Rd_{ref} is the specific respiration at a reference temperature ($^{\circ}$C), and Q_{10} is

a ratio between a respiration rate at one temperature and the respiration rate at a temperature 10 $^{\circ}$C lower (Lavigne & Ryan, 1997; Bolstad *et al.*, 1999; Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003; Larcher, 2003).

Many carbon balance models use approaches that fix the Q_{10} at or near 2.0, and fix Rd_{ref} as a proportion of photosynthesis (e.g. Ryan, 1991; Aber & Federer, 1992; Melillo *et al.*, 1993; Aber *et al.*, 1995, 1996, 1997; Schimel *et al.*, 1997; Cramer *et al.*, 1999; Kimball *et al.*, 2000; Sands *et al.*, 2000; Stockfors, 2000; Clark *et al.*, 2001; Potter *et al.*, 2001a,b; Sampson *et al.*, 2001; Sitch *et al.*, 2003). However, respiration response to short- and long-term changes in temperature often do not follow a simple exponential Q_{10} (Gifford, 2003; Larcher, 2003). In particular, two issues which may be problematic under such approaches are: (1) the degree to which short term (seconds to minutes) dark respiration response to temperature departs from a simple exponential function (Wager 1941, Tjoelker *et al.*, 2001) and (2) the fact that acclimation to temperature may shift the entire temperature response function (regardless of its shape) (Atkin & Tjoelker, 2003).

Although respiration responds to temperature on both short- and long-term time scales, the Q_{10} of respiration describes the short-term sensitivity of respiration to temperature (i.e. seconds to hours). The near-instantaneous exponential respiration function described by Q_{10} has been shown to inadequately fit empirical observations in plants (Belehrádek, 1930; Wager, 1941) (reviews by James, 1953; Forward, 1960; Berry & Raison, 1981) and soils (Lloyd & Taylor, 1994). Nevertheless, no general alternative had been proposed. Recently, however, Tjoelker *et al.* (2001) showed that the observed responses could be better fit with a quasi-exponential function whose exponent varied with temperature. Tjoelker *et al.* (2001) synthesized the results of published foliar Q_{10} of respiration values across a range of plant taxa (grasses, forbs, and woody plants) and across a range of biomes (tropical, temperate, boreal, and arctic), and concluded that the respiratory Q_{10} declined linearly with increasing measurement temperatures in a consistent manner among a range of taxa and climactic conditions. In essence, dark respiration exhibits decreasing Q_{10} values (measured over 5–10 $^{\circ}$C intervals) with increasing measurement temperature and the response appears consistent among species, and across diverse biomes (Tjoelker *et al.*, 2001). This evidence suggests that the use of a static Q_{10} of 2.0 is inappropriate for large temperature ranges.

In addition to near-instantaneous temperature response, rates of respiration are known to acclimate to thermal environment over longer time periods (days to months) through adjustments in the overall elevation of

the temperature response function. Respiratory C exchange rates are known to acclimate with time to prevailing temperatures in plant leaves (Larigauderie & Körner, 1995; Tjoelker et al., 1999a, b; Atkin et al., 2000a), roots (Gunn & Farrar, 1999; Tjoelker et al., 1999a), soils (Luo et al., 2001), and ecosystems (Enquist et al., 2003). Such acclimation can be substantial (Gunderson et al., 2000) and rapid (Atkin et al., 2000a, b; Bolstad et al., 2003), and therefore have significant effect on C balance. Acclimation to temperature may result from a change in Q_{10}, a shift in the elevation (intercept) of the temperature response function, or a combination of both (Tjoelker et al., 1999b; Atkin et al., 2000a, b; Atkin & Tjoelker, 2003).

Typically, temperature acclimation to a warmer environment results in a downward shift of the short-term temperature response function. This shift is reflected in decreased respiration at a standard temperature in warm acclimated plants compared with cold acclimated plants. Consequently, the response of respiration to variation in thermal environment (over days to seasonal) will differ from predictions based on short-term temperature response functions.

In spite of the evidence that short-term temperature responses in plants often do not fit the simple static Q_{10} exponential relationship, and although many modelers recognize the imperfections of the Q_{10} relationship, it is still in wide use because until now there has not been a clear and generalizable alternative. All but three of the 19 published models that we reviewed used either a static Q_{10}, parameter, a static Rd parameter, or both (Table 1). Moreover, despite evidence of thermal acclimation of Rd_{ref}, none of these models include acclimation. In attempts to circumvent some of these problems, models have been developed that do not calculate respiration at all, but assume net primary production (NPP) is a fixed proportion of gross primary production (GPP) (Coops et al., 1998; Waring et al., 1998; Waring & McDowell, 2002). This approach has been used to estimate leaf area and GPP at the stand scale (Waring & McDowell, 2002), estimate volume growth at the landscape scale (Coops & Waring, 2001), estimate global GPP (Gifford, 2003), and suggests that warming of the biosphere has had little effect, thus far on autotrophic C emissions (Gifford, 2003). However, the approach may fail to account for site-level climatic and plant functional variation. In addition, C balance details that are important at local scales and exist with the range of observed R : P ratios may be lost in global averages. Another alternative to a fixed Q_{10} has been to describe more than one Q_{10}–temperature relationship. For example, the TEM model (Raich et al., 1991) uses one relationship between 0 and 5 °C, the constant 2.0 between the temperatures 5 and 20 °C, and a second

Table 1 Process-based ecosystem models and their primary literature sources

Model	Principal literature
3-PG[‡]	Landsberg & Waring (1997)
BEPS[†]	Liu et al. (1997)
BIOMASS[†]	McMurtrie et al. (1990)
BGC family[†]	Running & Coughlan (1988)
CENTURY[†]	Parton et al. (1987)
COCA/FEF[†]	Hari et al. (1999)
COMMIX	Bartelink (2000)
FINNFOR[†]	Këllomaki & Väisänen (1997)
FORDYN[†]	Luan et al. (1996)
FORGRO[†]	Mohren & Kramer (1997)
GOTILWA[†]	Gracia et al. (1999)
LPJ[†]	Sitch et al. (2003)
NASA-CASA	Potter et al. (2001a, b)
PnET family[†]	Aber et al. (1996)
PROMOD[†]	Sands et al. (2000)
SECRETS[†]	Sampson et al. (2001)
SPAM[†]	Frolking et al. (1996)
SPAM2[†]	Clark et al. (2001)
TEM	Raich et al. (1991)

[†]Models that use a static Q_{10} or Rd parameters.
[‡]Models that use a static $Rd : A$.
PnET, photosynthesis and evapo-transpiration.

relationship between the temperatures 20 and 40 °C. The TEM approach, however, does not capture the whole response of the general relationship described by Tjoelker et al. (2001).

The purpose of this study was to test the degree to which variation in short-term temperature–respiration functions and acclimation to temperature in these functions influence total foliar respiratory flux from a broad range of terrestrial ecosystems. To do so, we simulated C balances for a range of vegetation types and across a climate gradient using photosynthesis and evapo-transpiration (PnET), a physiologically based, process-oriented ecosystem model (Aber et al., 1995, 1996). We selected four ecosystems representing diverse climate and vegetation types. We examined the consequences of alternative temperature response and respiration acclimation algorithms on modeled C budgets under both historic climate and climate warming scenarios. Given the inherent logic in most of the reviewed models, our results should be qualitatively general and applicable.

Methods

We compared simple static respiration parameters and alternative respiration algorithms within model simulations across a range of vegetation types and sites. We chose sites that represented a 20° latitudinal range, with

concomitant changes in vegetation and climate. We modified PnET parameters (from Aber *et al.*, 1995) for: (1) Northern Boreas (NOBS), a coniferous boreal forest (55°N, 98°W, near Thompson, MB, Canada) dominated by a *Picea mariana* overstory with some occasional *Larix laricina*, and a sparse occurrence of *Pinus banksiana* and *Populus balsamifera*, (2) Harvard Forest (HARV), a cold temperate hardwood forest (42°N, 72°W, near Petersham, MA, USA) dominated by *Acer saccharum* mixed with *Quercus rubra*, *Fraxinus* spp., *Tilia* spp., and *Fagus* spp., and an understory comprised of saplings of shade-tolerant species and *Vaccinium* spp., (3) Konza Prairie (KONZ), a tall-grass prairie (39°N, 96°W, near Manhattan, KS, USA) dominated by a mixture of *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and assorted forbs, and (4) Coweeta Hydrologic Laboratory (COWET), a cool temperate hardwood forest (35°N, 83°W, near Otto, NC, USA) representing a low elevation site comprised of *Quercus prinus*, *Acer rubrum*, *Liriodendron tulipifera*, *Carya* spp., and other *Quercus* spp. We used 5 years of local climate data from each site (1994–1998) (see Table 2 for parameter values). Daytime and night-time interannual growing season temperatures were reasonably consistent for all 5 years at each site (Table 3). Across sites, daytime and night-time temperatures were lowest at NOBS and increased for HARV, KONZ, and COWET, respectively.

The canopy subroutines of PnET are constructed around a group of algorithms that apply physiological relationships between foliar nitrogen, photosynthetic capacity, vertical scaling of leaf mass area, and leaf life-span (Reich *et al.*, 1992, 1994; Gower *et al.*, 1993; Ellsworth & Reich, 1993; Aber *et al.*, 1995, 1996). Phenology is controlled by a cumulative heat sum algorithm (Aber *et al.*, 1996). The model adds foliage mass when growing degree day conditions are met. Leaf off follows Aber *et al.* (1996), dropping leaves based on each canopy layer's C balance and a limit which prevents senescence from occurring before a particular day. We ran the model for 100 years with randomized and repeated climate data from local meteorological stations for each site in order to stabilize C pools before we output data used for these comparisons.

In its original form, PnET uses a Rd parameter fixed at 10% of leaf net photosynthetic capacity (A_{max}) at 20 °C and a Q_{10} of respiration fixed at 2.0 (Aber *et al.*, 1996). To test the effects of temperature acclimation on dark respiration and the effects of a temperature-variable Q_{10}, we substituted new algorithms for basal respiration and Q_{10} of respiration individually and in combination. In order to simulate the effects of temperature acclimation of respiration at the leaf level, we introduce a simple linear temperature dependence

Table 2 Site-specific PnET parameters for a black spruce site at Northern BOREAS (NOBS), an eastern hardwoods site at Harvard Forest (HARV), a tall-grass prairie site Konza Prairie (KONZ), and a broad leaved deciduous site at Coweeta Hydrologic Laboratory (COWET)

Parameter	NOBS	HARV	KONZ	COWET
Site variable				
Lat (°)	55	42	39	35
Whc	12	12	20	18
Canopy variables				
K	0.5	0.58	0.68	0.58
folNCon (%)	0.8	1.9	1.6	2.0
SlwMax	200	100	100	100
SlwDel	0	0.2	0.2	0.2
folReten (years)	6	1	1	1
GddFolStart	300	100	550	600
GddFolEnd	1200	900	1800	900
GddWoodStart	300	100	0	1000
GddWoodEnd	1200	900	0	1500
Photosynthesis variables				
AmaxA	5.3	−46	−75	−46
AmaxB	21.5	71.9	190	71.9
BaseFolRespFrac[†]	0.1	0.1	0.1	0.1
HalfSat	250	200	300	300
AmaxFrac	0.76	0.75	0.8	0.75
PsnTOpt	20	24	28	24
PsnTMin	0	2	4	2
respQ_{10}[‡]	2	2	2	2
Water balance variables				
dvpd1	0.05	0.05	0.05	0.05
dvpd2	2	2	2	2
PrecIntFrac	0.15	0.11	0.06	0.11
WueConst	10.9	10.9	46.5	10.9
FastFlowFrac	0.09	0.1	0.1	0.1
F	0.04	0.04	0.04	0.04
Allocation variables				
cFracBiomass	0.45	0.45	0.45	0.45
RootAllocA	0	0	0	0
RootAllocB	2	2	2	2
GRespFrac	0.25	0.25	0.25	0.25
RootMRespFrac	1	1	2	1
WoodMRespFrac	0.04	0.07	0.07	0.07
PlantCReserveFrac	0.75	0.75	0.75	0.75

[†]Indicates a parameter for which Eqn. (1) was substituted in acclimation simulations, and [‡]Indicates a parameter for which Eqn. (2) was substituted in acclimation simulations. See Aber *et al.* (1995, 1996) for parameter definitions.

of basal respiration as a proportion of leaf A_{max} as follows

$$Rd_{acclim} = A_{max}[0.14 - 0.002\,T], \quad (2)$$

where Rd_{acclim} is dark respiration, A_{max} is photosynthetic capacity, and T is temperature (°C). Consequently, Rd_{acclim} as a proportion of A_{max} declines with

Table 3 Mean daytime and night-time growing season temperatures ($^{\circ}$C) for four sites (growing season as defined by days for which the mean temperature is greater than 0 $^{\circ}$C)

Year	NOBS		HARV		KONZ		COWET	
	Night	Day	Night	Day	Night	Day	Night	Day
1994	3.8	16.2	12.8	22.5	15.9	26.9	16.3	28.8
1995	3.5	18.0	11.5	19.9	15.8	27.8	15.5	26.7
1996	4.3	18.1	12.4	21.3	16.1	27.3	16.1	27.6
1997	4.2	18.4	13.2	20.8	16.0	27.6	15.3	27.7
1998	5.0	19.0	13.5	22.0	15.3	27.7	17.7	29.2
$\bar{x}$	4.0	17.9	12.7	21.3	15.8	27.5	16.2	28.0

See Table 2 for site acronyms.

increasing temperature. Assuming no appreciable acclimation in leaf A_{max} to ambient temperature (or minimal in comparison with acclimation in respiration), acclimation in leaf respiration rate alone would result in a declining proportion of leaf respiration to A_{max} with increasing environmental temperature for leaves measured at the same temperature. The relationship was derived from field-based measures of needle dark respiration in numerous *Pinus banksiana* populations at three sites (MI, USA, MN, USA, and Ontario, Canada) across seasons (M. Tjoelker, J. Oleksyn, P. Reich, unpublished data). In that dataset, specific respiration rates at a standard temperature ranged from 20% higher to 20% lower than the seasonal mean ($= 4.0 \, \text{nmol g}^{-1} \text{s}^{-1}$, $s = 0.6$) across the range of mean daily air temperatures of 9–21 $^{\circ}$C. Although there is evidence that species differ in temperature acclimation to dark respiration, the magnitude (proportional change) of temperature acclimation of respiration observed for jack pine and used in this study is generally comparable with findings in studies of oak, pine, and other temperate and boreal species (Tjoelker *et al.*, 1999a; Atkin *et al.*, 2000b; Bolstad *et al.*, 2003). Few studies have examined leaf level $Rd : A$ ratios in relation to variation in growth or ambient temperatures, although it is thought that $Rd : A$ may vary within a limited range (Reich *et al.*, 1998a, b; Cannell & Thornley, 2000). Our purpose here is to test the consequences of assumed temperature acclimation effects on leaf level $Rd : A$ for ecosystem scale carbon balance. The dependence of Q_{10var} on measurement temperature is from Tjoelker *et al.* (2001):

$$Q_{10var} = 3.22 - 0.46T, \quad (3)$$

where Q_{10var} is the Q_{10} of foliar respiration and T is temperature ($^{\circ}$C). From here on, we will refer to these new relationships as Rd_{acclim} and Q_{10var} algorithms, respectively. Collectively, the new algorithms make a net contribution of two additional parameters to the PnET model.

We modified PnET-II to operate on a daily time-step in order to redefine the response each successive night using Q_{10var} and Rd_{acclim}. Source code is available on request. There is evidence that the shift of the acclimation curve can occur over a period as short as one to several days (Atkin *et al.*, 2000a, b; Bolstad *et al.*, 2003). Thus, the elevation of the curve (i.e. Rd_{acclim}) and the mean temperature ($^{\circ}$C) each night is used to set Q_{10var}. Together, these drive the complete dark respiration adjustment.

We output 5 years (1994–1998) of predicted daily night-time respiration from foliage, annual total mass- and area-based foliar respiration, foliar respiration to photosynthesis ratios ($Rd : A$), and annual above ground NPP (ANPP). To develop the necessary comparisons, we ran the model with the original static respiration parameters for each of the above scenarios, then reran the model after substituting the Rd_{acclim} algorithm only, then again with the Q_{10var} algorithm only, and finally with both new algorithms simultaneously. In order to examine the effects of the Rd_{acclim} and Q_{10var} algorithms on temperature warming scenarios, we ran the model in both static-and modified respiration-parameter modes with historic climate and under a simple $+2 \, ^{\circ}$C (daytime and night-time) temperature warming scenario.

Results

Temperature response

Predicted respiration rates using alternative respiration algorithms differed from respiration estimates based on static parameters and there was variation in magnitude and shape of the respiration temperature response among sites (Fig. 1). The decreases in predicted respiration, averaged across seasons and substituting both alternative respiration algorithms, ranged from 30% for a temperate hardwood forest at COWET to 60% for a tall-grass prairie at KONZ (Tables 3 and 4). Although temperature acclimation should conserve
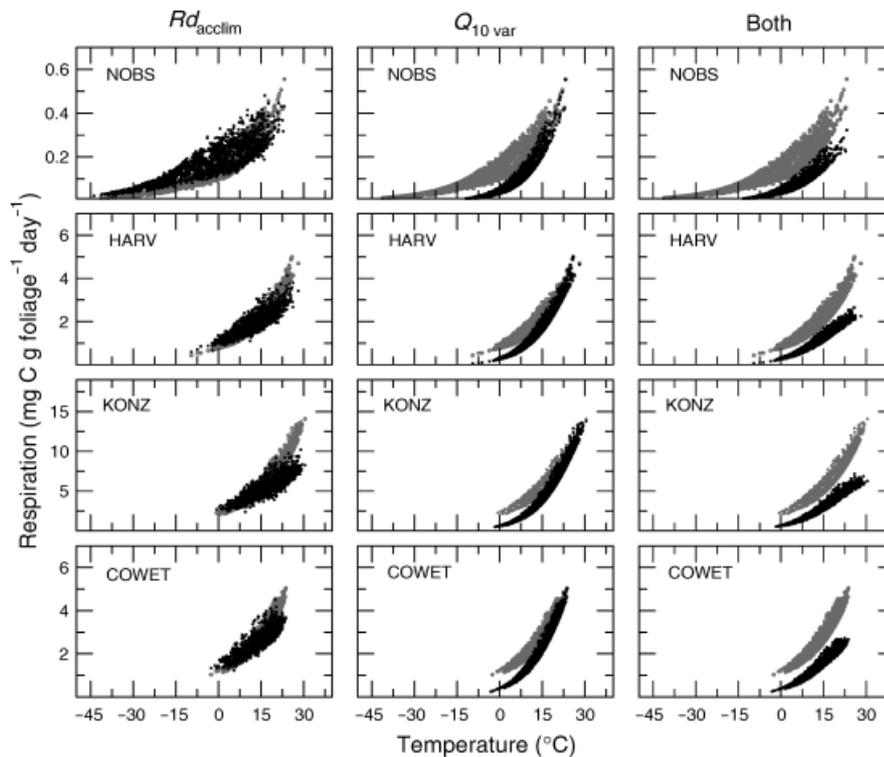
Fig. 1 Canopy dark respiration response to night-time temperature. Gray circles represent 5-year model runs of photosynthesis and evapo-transpiration (PnETs) static Rd and static Q_{10} parameters. Black x's represent modeled temperature response data after substituting Rd_{acclim} and Q_{10var} individually and in combination. See Table 2 for site acronyms.

foliar respiratory C during warm periods and release C during cool periods, the net effect was to conserve C across the entire temperature trajectory.

Predicted respiration rates after substituting Rd_{acclim} alone were lower at high temperatures, and higher at low temperatures, relative to estimates based on static parameters (Fig. 1). While NOBS showed small differences in predicted respiration rates based on Rd_{acclim} relative to estimates based on static parameters, respiration differences were larger under warmer conditions at the warmer sites. Predicted respiration rates calculated after substituting Rd_{acclim} diverged from those calculated with static parameters above 18 °C and below 5 °C. At temperatures greater than 18 °C, respiration rates estimated with the Rd_{acclim} algorithm resulted in differences that ranged from 0.5 mg C g foliage^{-1} day^{-1} lower at NOBS, to 4.0 mg C g foliage^{-1} day^{-1} lower at KONZ. Below 5 °C, respiration differences estimated with Rd_{acclim} were slightly higher at all sites.

At all sites, respiration after substituting the Q_{10var} algorithm alone resulted in markedly reduced respiration rates at the low end of the temperature response curve compared with those that used the static Q_{10} parameters (Fig. 1). Both estimates converged at the upper end of the temperature range. Differences in dark respiration (because of altered Q_{10}) near 0 °C

ranged from less than 0.1 mg C g foliage^{-1} day^{-1} at NOBS, to 2.5 mg C g foliage^{-1} day^{-1} at KONZ. However, while respiration estimates were consistently high across sites at temperatures between 0 and 5 °C in simulations that used static parameters, the generally low respiration rates at these temperatures suggest that any differences in rates of respiratory C loss on the overall C balance might be a relatively small proportional change in terms of C on a per day basis.

Respiration estimates that used both the Rd_{acclim} and Q_{10var} algorithms in combination were consistently and substantially lower across the entire annual temperature range in simulations, relative to model runs using static parameters (Fig. 1). Between 5 and 20 °C, the respiration estimates based on the alternative respiration algorithms were roughly half as large as the static parameter estimates at all sites.

Foliage mass

Foliage mass predictions were similar for model runs using the alternative Rd_{acclim} and Q_{10var} algorithms and for those using static parameters for three of the four sites (Fig. 2), implying that alternative respiration algorithms had modest effect on canopy size. Foliage mass estimates were 8% higher at COWET using the
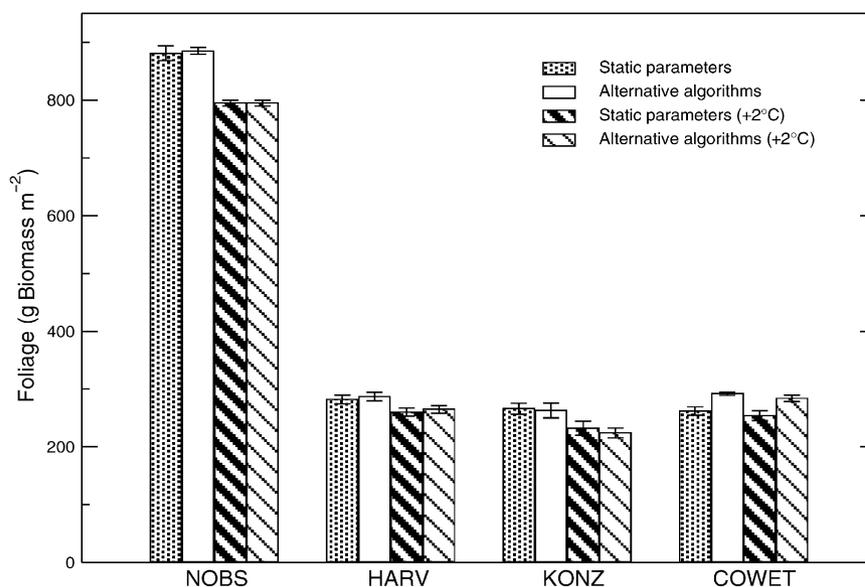
Fig. 2 Predicted foliage mass with and without alternative respiration algorithms for all sites using measured climate and temperature warming scenarios (+ 2 °C). Error bars represent 1 standard deviation. See Table 2 for site acronyms.

Table 4 Annual foliar respiration on a leaf mass basis (g C g leaf^{-1} yr^{-1}) predicted by PnET with static parameters (Static) and alternative (Altrn) respiration response algorithms

	NOBS				HARV				KONZ				COWET			
	Ambient		+ 2		Ambient		+ 2		Ambient		+ 2		Ambient		+ 2	
Year	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn
1994	0.19	0.11	0.22	0.13	1.25	0.75	1.46	0.89	3.95	2.47	4.67	2.86	1.81	1.24	2.17	1.44
1995	0.19	0.11	0.21	0.13	1.29	0.76	1.53	0.89	3.94	2.29	4.65	2.60	2.02	1.23	2.16	1.40
1996	0.19	0.11	0.22	0.13	1.22	0.75	1.44	0.86	3.78	2.25	4.47	2.66	1.89	1.16	2.41	1.41
1997	0.20	0.12	0.23	0.14	0.92	0.55	1.09	0.66	3.74	2.21	4.45	2.59	1.94	1.19	2.40	1.41
1998	0.21	0.12	0.24	0.14	1.05	0.67	1.26	0.80	4.32	2.51	5.15	2.98	2.16	1.40	2.30	1.60
$\bar{x}$ (V)	0.20(5)	0.11(5)	0.22(4)	0.13(4)	1.14(4)	0.70(13)	1.36(13)	0.82(12)	3.95(6)	2.35(6)	4.68(6)	2.74(6)	1.96(7)	1.24(7)	2.29(5)	1.45(6)

Measured climate is represented by Ambient. Two degree centigrade increase is represented by + 2. Means are represented by $\bar{x}$, coefficients of variation (as percent) are in parentheses. See Table 2 for site acronyms. PnET, photosynthesis and evapo-transpiration.

alternative algorithms relative to the static respiration parameters. Foliage mass (per unit ground area) decreased by approximately 10% for NOBS, HARV, and KONZ in elevated temperature scenario simulations, but there was no change in foliage mass at COWET with elevated temperature.

Annual foliar respiration

Alternative respiration algorithms reduced annual respiration compared with estimates based on static parameters. Annual foliar respiration estimates using both Rd_{acclim} and Q_{10var} algorithms in combination were lower in all years, at all sites, and for both ambient temperature and temperature warming scenarios when compared with simulations using static parameters

(Table 4). Results were consistent on both a mass basis and on a ground area basis (Table 5).

Modification of model respiration algorithms had a larger impact on estimated Rd than simulated warming. Five year mean respiration estimates, under a + 2 °C warming scenario, were roughly 5–15% higher for all sites when using either the static parameter model for both climate scenarios, or the alternative respiration algorithms for both scenarios. However, the respiration estimates using alternative respiration algorithms (i.e. Rd_{acclim} plus Q_{10var}) within the temperature warming (+ 2 °C) scenarios were substantially lower than the static parameter estimates from the ambient temperature simulations. These decreases suggest that model sensitivity to physiological algorithms is on a similar

Table 5 Annual foliar respiration on an area ground basis ($gC m^{-2}$ ground yr^{-1}) predicted by PnET with static parameters (Static) and alternative (Altrn) respiration response algorithms

	NOBS				HARV				KONZ				COWET			
	Ambient		+2		Ambient		+2		Ambient		+2		Ambient		+2	
Year	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn
1994	152	91	158	98	299	197	342	223	1241	859	1383	892	480	325	460	330
1995	148	87	156	94	299	199	347	220	1146	754	1240	773	449	322	531	352
1996	150	90	156	95	289	194	337	216	1143	748	1242	767	462	313	528	362
1997	158	94	163	99	191	140	236	165	1290	817	1405	823	458	319	556	372
1998	167	99	175	105	251	177	296	204	1368	857	1480	882	507	350	574	388
$\bar{x}$ (V)	155(5)	92(5)	162(5)	98(4)	266(17)	181(14)	312(15)	206(12)	1237(8)	807(7)	1350(8)	827(7)	471(5)	326(4)	530(8)	361(6)

Measured climate is represented by Ambient. Two degree centigrade increase is represented by +2. Means are represented by $\bar{x}$, coefficients of variation (as percent) are in parentheses. See Table 2 for site acronyms. PnET, photosynthesis and evapo-transpiration.
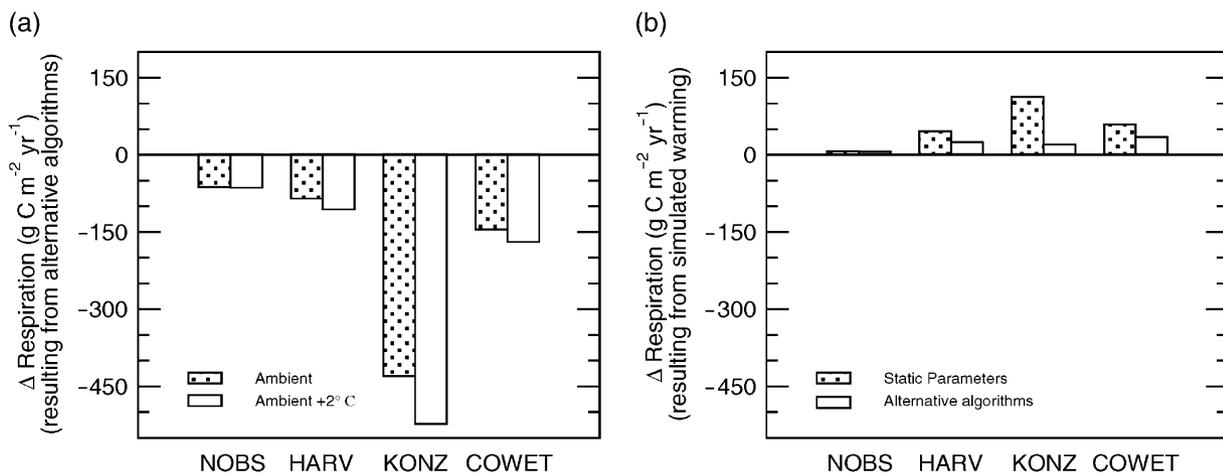
Fig. 3 Change in annual area based respiration illustrating (a) the decrease in respiration for ambient and elevated temperature simulations as a result of alternative respiration algorithms and (b) the increase in respiration for static parameter and alternative algorithm simulations as a result of elevated temperature. See Table 2 for site acronyms.

order or larger than effects of substantial climate warming.

The effects of alternative respiration algorithms on annual respiration tended to be relatively greater at the warmer sites, especially at KONZ (Fig. 3). The effects of alternative respiration algorithms were slightly greater with climate warming relative to the ambient temperature simulations at three of the four sites. The effects of increased temperature on annual respiration tended to be greater at the warmer sites, and highest at KONZ, in simulations that used static parameters. However, the temperature enhancement in warming simulations that used alternative respiration algorithms was notably lower in three of the four sites. . These results suggest that incorporating realistic models of respiration is important, since response to climate warming, appears to vary with model characteristics.

Rd : A ratio

Rd : A ratios were consistently smaller ($\sim$ 40% less) in simulations that used Rd_{acclim} and Q_{10var} algorithms relative to estimates from static parameters (Fig. 4). In addition, $Rd : A$ ratios tended to be higher at sites with higher mean night- and daytime temperatures. $Rd : A$ ratios from simulations that used Rd_{acclim} and Q_{10var} algorithms tended to be less than $Rd : A$ ratios from simulations that used static respiration parameters. Predicted $Rd : A$ from simulations that used Rd_{acclim} and $Q_{10var}r$ algorithms ranged from 0.15 at NOBS to 0.27 at COWET. Predicted $Rd : A$ from static respiration parameters ranged from 0.25 at NOBS to 0.43 at COWET. Climate warming appeared to have no effect on $Rd : A$ estimates from simulations that used alternative respiration algorithms, while climate warm-
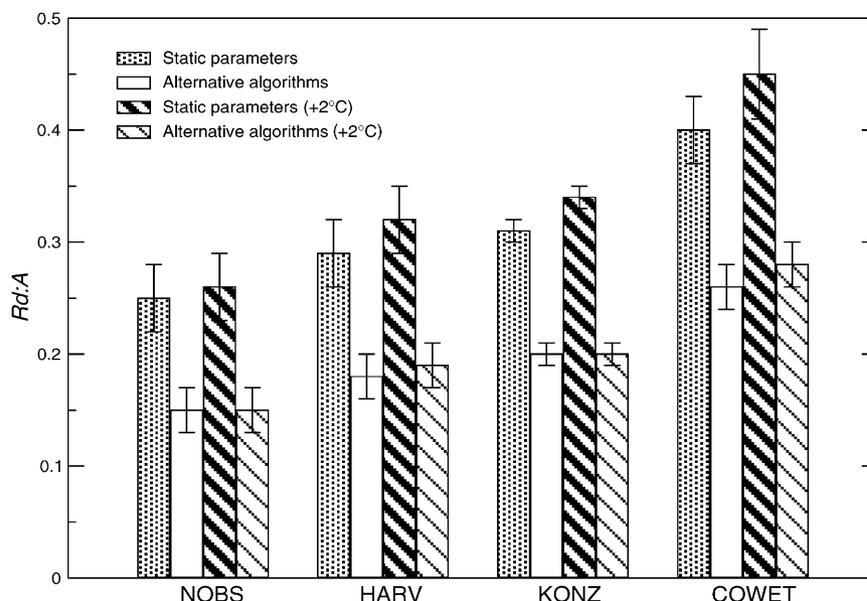
Fig. 4 $Rd:A$ ratios for 5 years, with and without alternative respiration algorithms, using measured climate and temperature warming scenarios ($+2\,°C$). Error bars represent 1 standard deviation among years. See Table 2 for site acronyms.

Table 6 ANPP (g biomass $m^{-2}\,yr^{-1}$) predicted by PnET with static parameters (Static) and alternative (Altrn) respiration response algorithms

	NOBS[†]				HARV				KONZ				COWET			
	Ambient		+2		Ambient		+2		Ambient		+2		Ambient		+2	
Year	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn	Static	Altrn
1994	358	478	394	512	677	843	722	945	431	526	383	464	704	1008	587	999
1995	348	468	390	508	679	852	726	956	416	502	361	453	660	999	636	1022
1996	363	484	388	507	673	851	697	941	401	486	348	451	677	995	620	1007
1997	340	459	370	487	624	802	645	891	409	497	354	439	680	994	652	1039
1998	344	464	384	503	640	789	682	889	430	530	346	450	746	1054	692	1099
$\bar{x}$ (V)	351(3)	471(2)	385(2)	503(2)	659(4)	827(4)	694(5)	924(3)	417(3)	508(4)	358(4)	451(2)	693(5)	1010(2)	637(6)	1033(4)

[†]Does not include bryophyte contribution.

Means are represented by $\bar{x}$ coefficients of variation (as percent) are in parentheses. See Table 2 for site acronyms. See Table 4 for descriptions of Ambient and $+2$. PnET, photosynthesis and evapo-transpiration; ANPP, above ground net primary production.

ing introduced larger $Rd:A$ estimates in simulations using static respiration parameters.

ANPP

Predicted ANPP from alternative respiration algorithms was higher in all years, under both climate scenarios, and at all sites relative to predictions from static parameters (Table 6). Response of ANPP to alternative respiration algorithms and to temperature were variable among ecosystems (Figure 5). ANPP response to alternative respiration algorithms (with both Rd_{acclim} and Q_{10var}) were larger at warmer sites than cooler sites, but smaller at the prairie site than all

forested sites. Moreover, it is notable that the two model types resulted in variable responses to climate warming at some sites. For example, annual ANPP at NOBS increased similarly (33 g biomass $m^{-2}\,yr^{-1}$) with warming in both fixed parameter simulations and in the alternative algorithm simulations (Rd_{acclim} and Q_{10var}), while annual ANPP at KONZ decreased in response to warming by approximately the same amount (58 g biomass $m^{-2}\,yr^{-1}$) in both the static parameter and the alternative algorithm simulations. At the two hardwood sites (HARV and COWET), response of simulated annual ANPP to climate warming was more positive using Rd_{acclim} and Q_{10var} algorithms compared with simulations that used the static respiration
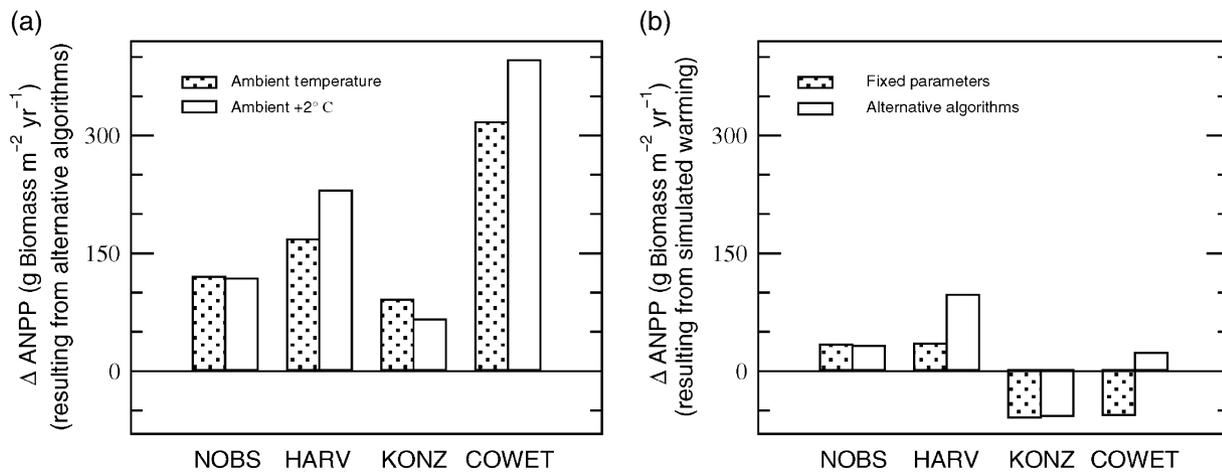
Fig. 5 Changes in above ground net primary production (ANPP) at (a) two different temperatures under the effects of alternative respiration algorithms, and (b) for alternative respiration algorithms and static parameters under the effects of elevated temperature. See Table 2 for site acronyms.

parameters. Annual ANPP at HARV increased with warming by 35 g biomass m^{-2} yr^{-1} in the original version, but increased by 97 g biomass m^{-2} yr^{-1} in the modified version. Annual ANPP at COWET decreased by 56 g biomass m^{-2} yr^{-1} with warming in the static respiration parameter version, but increased 23 g biomass m^{-2} yr^{-1} with warming in simulations that used the modified algorithms.

Discussion

Alternative algorithms: Rd_{acclim} and Q_{10var}

While substituting alternative respiration algorithms for static parameters reduced simulated plant respiration across a range of temperatures at all sites, this effect varied among sites (as seen in Fig. 1). The consequences of Rd_{acclim} and Q_{10var} together on modeled carbon budgets appears to be a consistent and substantial reduction in estimated respiratory carbon losses across the entire temperature range. Predicted respiration rates at very low temperatures should be low despite a high Q_{10} observed at low temperatures (Tjoelker *et al.*, 2001). This is because most models use respiration rates measured at relatively high temperatures (such as $20\,°C$) as their starting point. In order to have a higher Q_{10} at lower temperatures and converge on the same respiration rate at $20\,°C$, rates must be lower at very low temperatures than would be otherwise expected.

It is notable that the combined effects of the Rd_{acclim} and Q_{10var} algorithms appear greater than expected from a summing of their individual effects. This interaction is likely because at low temperatures in the combined model, the Q_{10var} algorithm causes large differences in predicted respiration rates compared with the static

model, despite similar basal rates. Conversely, at high temperatures in the combined model, lower basal rates because of acclimation result in lower respiration rates than the static model, despite similar Q_{10}'s. However, the magnitude of these effects appear to be dependent upon specific site environmental differences and may also reflect variation in concomitant plant physiology.

The changes in respiration because of model modifacation seen in Fig. 1 lead to associated changes in annual total respiration estimates. Total respiration on both a mass basis and a ground area basis were lower in simulations using the Rd_{acclim} and Q_{10var} algorithms compared with simulations using the static parameters. Decreases in annual respiration on a ground area basis that resulted from substituting Rd_{acclim} and Q_{10var} algorithms were 41%, 36%, 35%, and 31% for NOBS, HARV, KONZ, and COWET, respectively. These large differences in estimated carbon efflux between the original and alternative models support the conclusions of Gunderson *et al.* (2000) and Tjoelker *et al.* (2001) that ecosystem models should incorporate basal respiration acclimation and temperature-variable Q_{10} relationships, particularly if the model is to be applied across a large spatial extent where broad ranges in climate are to be expected.

While it should be noted that anytime model complexity is increased, an associated increase in uncertainty is risked. In this case we have increased the number of parameters in the PnET model (one additional parameter in the basal respiration calculation, and one additional parameter in the Q_{10} calculation). In justifying this change, we would argue that removing the parameters BFolResp and RespQ_{10} and replacing them with simple, generalizable, and biologically realistic algorithms that appear to hold up across biomes and across a broad range of taxa, is a

Table 7 Measured ANPP means from literature; using longest available records for sites as similar to and as close as possible to stands used in the modeling

Site	ANPP $(g\,m^{-2})$	Length of record	Source
NOBS	487*	3	Bond-Lamberty et al. (2001)
HARV	745	8	Knapp & Smith (2001)
KONZ	528†	21	Knapp et al. (1998)
COWET	1110‡	10	Bolstad et al. (2001)

*Well drained soils, stand age >20 years, does not include bryophyte contribution.
†Annually burned lowlands.
‡Calculated for 685 m elevation.
See Table 2 for site acronyms. ANPP, above ground net primary production.

complexity vs. generalizability trade-off that is worth making. In addition, we would argue that ecosystem models should be rooted in simple biological mechanisms wherever possible, and the new algorithms have a much stronger physiological basis than the earlier ones.

Finally, the reductions in foliar respiration that resulted from our new algorithms were of a magnitude that would explain the overestimated foliar respiration value relative to measured field data reported by Law et al. (2000) for PnET-II using static respiration parameters in a *Pinus ponderosa* system. Additionally, the nature of *Rd* acclimation and its importance as shown in models here in are consistent with work suggesting broad *Rd* acclimation across global climate gradients (Enquist et al., 2003).

Variation in reduced C loss to respiration on an annual basis among sites appears to be not only a function of the relative shape of the temperature response curve, but also the amount of time over the course of the season spent at any given end of the curve. In other words, the respiration–temperature response curve represents all thermal environments over the entire year. The amount of total C conserved on an annual basis will depend upon the relative proportion of the year spent at cold vs. warm ends of the temperature curve, and the relative shapes of the curves. For example, at sites with short growing seasons, such as NOBS, a large portion of the year will be spent at temperatures well below the physiological optimum for the species present, whereas sites with a longer growing season, such as COWET, a greater portion of the year will be spent at temperatures that favor physiologic activity.

Although field measurements of ANPP can include substantial uncertainties, they may be useful to compare with ANPP estimates from the static respiration vs. alternative respiration versions of PnET. Estimates of ANPP calculated from the combined alternative respiration algorithms were a closer match to published ANPP field data than ANPP based on static respiration parameters at three of the four sites (see Tables 6 and 7)

and of equally good fit at the other. At NOBS, KONZ, and COWET, estimated ANPP using the modified respiration algorithms were within 3%, 4%, and 9% of field observations, while estimates using the static respiration algorithms were within 28%, 21%, and 38% of field observations, respectively. At the fourth site, HARV, the two estimates were equally close (both were within about 11% of field observations). However, there is sufficient variability (and error) in measured ANPP across local gradients, among years, and among reports, that it is problematic to use reported field ANPP to assess the reliability of the static or alternative model output. Furthermore, given the fact that a simulation model can yield good agreement with measured field data through a collection of compensating errors, one must be careful to not take model agreement alone as the singular reason to modify (or to not modify) these kinds of process based ecosystem models. Given that the alternative respiration algorithms presented here incorporate well documented biological processes, which appear generalizable across biomes and a broad range of taxa, and appear to fit with published empirical data as well as or better than the static parameter output, these algorithms appear useful and should be pursued further.

The higher ANPP estimates for historic climate runs of 25%, 20%, 18%, and 31% at NOBS, HARV, KONZ, and COWET, respectively, from simulations using the Rd_{acclim} and Q_{10var} algorithms result from the representation of C conserved through respiration acclimation to temperature (Table 6). At the three forested sites, reduced respiratory efflux is almost directly translated into increased ANPP. However, at the prairie site, there is a greater amount of C conserved via the Rd_{acclim} and Q_{10var} algorithms than is represented in increased ANPP ($430\,g\,C\,m^{-2}\,yr^{-1}$ vs. $91\,g\,biomass\,m^{-2}\,yr^{-1}$, given a parameter of 0.45 to convert C to biomass, see Table 2). In the PnET model, the difference between conserved respiratory C and the additional C allocated to ANPP accumulates in the general plant C pool. There-

fore, once C is conserved through respiratory pathways, variation in allocation strategies among plant types (species) could affect how and where that C is partitioned. In addition, while Tjoelker *et al.* (2001) developed $Q_{10_{var}}$ from data that included grasses and forbs, Rd_{acclim} was based on data from trees only. For this reason Rd_{acclim} may not well represent dark respiration acclimation to temperature in the vegetation types prominent at KONZ.

Although $Rd:A$ ratios appear to scale to some degree, they are variable at the leaf level (Reich *et al.*, 1998a, b; Amthor, 2000), and at the whole plant level (Gifford, 2003), and published empirical data are not yet sufficient to comprehensively determine the degree to which $Rd:A$ ratios are constrained across species and environments. $Rd:A$ is of interest because $Rd:A$ ratios help place respiration in the context of an C balance, and aid in interpreting ANPP. Because implementing Rd_{acclim} and $Q_{10_{var}}$ algorithms in PnET-reduced respiration, and PnET does not include direct acclimation of photosynthesis to temperature, lower $Rd:A$ ratios are expected. Here an important question is whether photosynthesis acclimates or adjusts to increasing temperature and whether this is similar to Rd. However, given the distinctly different shapes of their temperature response curves, in the short term photosynthesis is relatively constant across a broad range of temperatures relative to Rd (Chabot and Lewis, 1976, Aubuchon *et al.*, 1978, Jurik, 1986, Jurik *et al.*, 1988; Gunderson *et al.*, 2000). Moreover, thermal acclimation for photosynthesis exhibits variable patterns among species (Slatyer & Morrow, 1977; Dougherty *et al.*, 1979; Jurik *et al.*, 1988; Ferrar *et al.*, 1989) and has not been well correlated with climate (Tranquillini *et al.*, 1986; Ferrar *et al.*, 1989). It is thus, still unclear how to best represent photosynthetic acclimation in an ecosystem model such as PnET.

Although respiration in plants is known to acclimate (hours to days) to temperature (Tjoelker *et al.*, 1999a, b; Atkin *et al.*, 2000b, Bolstad *et al.*, 2003), and a general linear relationship describing the short-term temperature dependence of Q_{10} for foliar respiration appears to hold across biomes (Tjoelker *et al.*, 2001), the data on which Rd_{acclim} and $Q_{10_{var}}$ algorithms were based originated from broad thermal gradients. Tjoelker *et al.* (2001) reported mean Q_{10} values that ranged from 2.14 to 2.56 (tropical to arctic biomes, respectively). Tjoelker *et al.* (2001) suggested the need for more common temperature studies to isolate the effects of measurement temperature from acclimation. In addition, others have suggested that while some plant species exhibit a high degree of acclimation, some do not (e.g. Larigauderie & Körner, 1995). Nonetheless, our findings depart substantially from modeled ecosystem fluxes based on static respiration parameters and have substantial implications for the majority of commonly used ecosystem models.

Climate change

Given the importance of predicted climate change, the contrasts in respiration response to warming between the two model versions (alternative vs. static parameters) are of particular interest. Relative to historic climate, elevated temperature simulations increased annual respiration by between 1% and 12% at all four sites using both versions of the model, but the influence of model modification on these varied among sites. Predicted foliar respiration with static respiration parameters increased by 8% and 11% under the climate warming scenario at KONZ and COWET, respectively, but when modified respiration algorithms were incorporated into the model, warming increased predicted foliar respiration by only 2% and 1% at those same sites. In contrast, at NOBS and HARV (the cooler pair of our four sites) the predicted increases in respiration because of warming, were similar using both versions of the model. This suggests that models that incorporate respiration acclimation and temperature variable Q_{10} algorithms may yield different predictions of respiration response to climate warming than models using static respiration parameters, and that such differences may vary across systems. These particular observations could be in part because of down-regulation of respiration rates at higher temperatures, which are more common at the two warmer sites. This connection between thermal environment and respiration suggests that down-regulation of respiration could have a substantial impact on C balance and productivity, particularly at warm sites. The decrease in ANPP from the effects of elevated temperature at KONZ (Fig. 5b) may be in part because of KONZ being a more water-limited system than the three forest sites, or because of physiologic differences in vegetation, or because of PnETs allocation logic, or any combination of the above.

Our predictions of increasing $Rd:A$ ratios from colder to warmer climates, and from standard climate simulations to +2 simulations, support the experimental findings of Tjoelker *et al.* (1999a) that $Rd:A$ tended to increase with warming in boreal-tree seedlings. This may be because differences in the degree to which plant growth and size, growth respiration, and maintenance respiration respond to warming could affect $Rd:A$ ratios (Amthor, 2000), or be complicated by the effects of water stress (Cannell & Thornley, 2000).

Conclusions

Because the instantaneous temperature response function of plants is temperature dependent (Tjoelker *et al.*,

2001) and thermal acclimation of respiration appears to be common (Bolstad *et al.*, 2003; Tjoelker *et al.*, 1999a, b; Atkin *et al.*, 2000a,b; Luo *et al.*, 2001), our results suggest that: (1) Rd_{acclim} and $Q_{10_{var}}$ algorithms allow ecosystem models to account for respiration response to temperature in a more biologically realistic way than static parameter models can, (2) simple, generalized Rd_{acclim} and $Q_{10_{var}}$ algorithms alter modeled estimates of C exchange and production in plants and ecosystems and alter plant responses to warming scenarios, (3) incorporating Rd_{acclim} and $Q_{10_{var}}$ into process-based ecosystem models is important in that the effects of Rd_{acclim} and $Q_{10_{var}}$ appear to be as large or larger than the effects of major climate change and appears to be consistent with measured ANPP and eddy covariance estimates (Table 7, Law *et al* 2000, Enquist *et al*. 2003), (4) current models may over-predict respiration and result in either underestimated or inappropriately allocated productivity estimates, especially on warm sites or when running climate warming scenarios, and (5) algorithms that incorporate plant acclimation to temperature may enhance the use of ecosystem models across broad spatial scales or with simulated temperature change where large temperature ranges may cause erroneous results from models that use static respiration parameters. Finally, while these results represent incorporating Rd_{acclim} and $Q_{10_{var}}$ algorithms into the PnET model, it is likely that many other physiologically based ecosystem models that utilize static respiration parameters would yield similar results if similarly adjusted.

Acknowledgments

References

Aber JD, Federer CA (1992) A generalized, lumped parameter model of photosynthesis, evapotranspiration, and net primary production in temperate and boreal forest ecosystems. *Oecologia*, **92**, 463–474.

Aber JD, Ollinger SV, Driscoll CT (1997) Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling*, **101**, 61–78.

Aber JD, Ollinger SV, Federer CA *et al.* (1995) Predicting the effects of climate change on water yield and forest production in the northern United States. *Climate Research*, **5**, 207–222.

Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis validated by eddy correlation. *Oecologia*, **106**, 267–275.

Ågren GI, McMurtrie RE, Parton WJ *et al.* (1991) State-of-the-art models of production-decomposition linkages in conifer and grassland ecosystems. *Ecological Applications*, **1**, 118–138.

Amthor JS (2000) The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. *Annals of Botany*, **86**, 1–20.

Atkin OK, Edwards EJ, Loveys BR (2000a) Response of root respiration to changes in temperature and its relevance to global warming. *New Phytologist*, **147**, 141–154.

Atkin OK, Holly C, Ball MC (2000b) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant Cell and Environment*, **23**, 15–26.

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, **8**, 343–351.

Aubuchon RR, Thompson DR, Hinckley TM (1978) Environmental influences on photosynthesis within the crown of a while oak [*Quercus alba*]. *Oecologia*, **35**, 295–306.

Bartelink HH (2000) Effects of stand composition and thinning in mixed-species forests: a modeling approach applied to Douglas-fir and beach. *Tree Physiology*, **20**, 399–406.

Belehrádek J (1930) Temperature coefficients in biology. *Biological Reviews*, **5**, 30–58.

Berry JA, Raison JK (1981) Response of macrophytes to temperature. In: *Encyclopedia of Plant Physiology, New Series*, **Vol. 12A** (eds Lange OL), pp. 277–338. Springer, Berlin.

Bolstad PV, Mitchell K, Vose JM (1999) Foliar temperature-respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiology*, **19**, 871–878.

Bolstad PV, Vose JM, McNulty SG (2001) Forest productivity, leaf area and terrain in southern Appalachian deciduous forests. *Forest Science*, **47**, 1–9.

Bolstad PV, Reich PB, Lee T (2003) Rapid temperature acclimation of leaf respiration rates of *Quercus alba* (L.) and *Quercus rubra* (L.) and *Q. rubra*. *Tree Physiology*, **23**, 969–976.

Bond-Lamberty B, Wang C, Gower ST (2001) Net primary production and net ecosystem production in boreal black spruce wildfire chronosequence. *Global Change Biology*, **10**, 473–487.

Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. *Annals of Botany*, **85**, 45–54.

Chabot BF, Lewis AR (1976) Thermal acclimation of photosynthesis in northern red oak [*Quercus rubra borealis*]. *Photosynthetica*, **10**, 130–135.

Clark KL, Cropper WP, Gholz HL (2001) Evaluation of modeled carbon fluxes for a slash pine ecosystem: SPM2 simulations compared to eddy flux measurements. *Forest Science*, **47**, 52–59.

Coops NC, Waring RH, Landsberg JJ (1998) Assessing forest productivity in Australia and New Zealand using physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *Forest Ecology and Management*, **104**, 113–127.

Coops NC, Waring RH (2001) Estimating forest productivity in the eastern Siskiyou Mountains of southwestern Oregon using a satellite driven process model, 3-PGS. *Canadian Journal of Forest Research*, **31**, 143–154.

Cramer W, Kicklighter DW, Bondeau A *et al.* (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology*, **5**, 1–15 (s1).

Dougherty PM, Teskey RO, Phelps JE *et al.* (1979) Net photosynthesis and early growth trends of a dominate White Oak (*Quercus alba L.*). *Plant Physiology*, **64**, 930–935.

Ellsworth DS, Reich PB (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*, **96**, 169–178.

Enquist BJ, Economo EP, Huxman TE *et al.* (2003) Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–642.

Falkowski P, Scholes RJ, Boyle E *et al.* (2000) The Global Carbon Cycle: a test of our knowledge of earth as a system. *Science*, **290**, 291–296.

Farrar JF (1985) The respiratory sources of C0$_2$. *Plant Cell and Environment*, **8**, 427–438.

Ferrar JF, Slatyer RO, Vranjic JA (1989) Photosynthetic temperature acclimation in Eucalyptus species from diverse habitat, and a comparison with *Nerium oleander. Australian Journal of Plant Physiology*, **16**, 199–217.

Field CB, Chapin FS, Matson PA *et al.* (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics*, **23**, 201–235.

Forward DF (1960) Effect of temperature on respiration. In: *Handuch der Pflanzenphysiologie*, **Vol 12** (ed. Ruhland W), Part 2, pp. 234–258. Springer, Berlin.

Frolking S, Goulden ML, Wofsy SC *et al.* (1996) Modelling temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biology*, **2**, 343–366.

Gifford RM (2003) Plant respiration in productivity models: conceptualization, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, **30**, 171–186.

Gower ST, Reich PB, Son Y (1993) Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiology*, **12**, 327–345.

Gracia CA, Tello E, Sabate S *et al.* (1999) GOTWILA: an integrated model of water dynamics and forest growth. In: *Ecology of Mediterranean Evergreen Oak Forests* (eds Rodé F, Retana J, Gracia CA, Bellot J), Springer-Verlag, Berlin.

Gunderson CA, Norby RJ, Wullschleger SD (2000) Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology*, **20**, 87–96.

Gunn S, Farrar JF (1999) Effects of a 4 °C increase in temperature on partitioning of leaf area and dry mass, root respiration and carbohydrates. *Functional Ecology*, **13**, 12–20.

Hari P, Mäkelä A, Berninger F *et al.* (1999) Field evidence for the optimality hypothesis of gas exchange in plants. *Australian Journal of Plant Physiology*, **26**, 239–244.

Houghton JT, Callander BA, Varney SK (1992) *Climate Change: The Supplementary Report to The IPCC Scientific Assessment.* Cambridge University Press, Cambridge. 200.

Houghton JT, Ding Y, Griggs DJ *et al.* (2001) *Climate Change 2001: The Scientific Basis.* Cambridge University Press, Cambridge. 881.

James WO (1953) *Plant Respiration.* Clarendon Press, Oxford. 282.

Jurik TW (1986) Seasonal patterns of leaf photosynthetic capacity in successional northern hardwood tree species. *American Journal of Botany*, **73**, 131–138.

Jurik TW, Briggs GM, Gates DM (1988) Springtime recovery of photosynthetic activity of white pine in Michigan. *Canadian Journal of Botany*, **66**, 138–141.

Keeling RF, Piper SC, Heimann M (1996) Global and hemispheric CO sinks deduced from changes in atmospheric O2 concentrations. *Nature*, **381**, 218–221.

Këllomaki , Väisänen H (1997) Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecological Modelling*, **97**, 121–140.

Kimball JS, Keyser AR, Running SW *et al.* (2000) Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps. *Tree Physiology*, **20**, 761–775.

Knapp AK, Briggs JM, Blair JM *et al.* (1998) Patterns and controls of above ground net primary production in tallgrass prairie. In: *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (eds Knapp AK, Briggs JM, Hartnett DC, Collins SL), pp. 193–221. Oxford University Press, Oxford.

Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of above ground primary production. *Science*, **291**, 481–484.

Landsberg JJ, Waring RH (1997) A generalized model of forest productivity using simplified concepts of radiation-use-efficiency, carbon balance, and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Larcher W (2003) *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups* (pp 120–126. Springer–Verlag, Berlin.

Larigauderie A, Körner C (1995) Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany*, **76**, 245–252.

Lavigne MB, Ryan MG (1997) Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiology*, **17**, 543–551.

Law BE, Waring RH, Anthoni PM *et al.* (2000) Measurements of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology*, **6**, 155–165.

Liu J, Chen JM, Cihlar J *et al.* (1997) A process-based boreal ecosystem productivity simulator using remote sensing inputs. *Remote Sensing of Environment*, **62**, 158–175.

Lloyd J, Taylor JA (1994) On temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Luan J, Muetzelfeldt RI, Grace J (1996) Hierarchical approach to forest ecosystem simulation. *Ecological Modeling*, **86**, 37–50.

Lubchenco J A, Olson AM, Brubaker LB *et al.* (1991) The sustainable biosphere initiative: An ecological research agenda. *Ecology*, **72**, 371–412.

Luo Y, Wan S, Hui D *et al.* (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature*, **413**, 624–625.

Mäkelä A, Landsberg J, Ek AR *et al.* (2000) Process-based models for forest ecosystem management: current state of the art and

challenges for practical implementation. *Tree Physiology*, **20**, 289–298.

McCarthy J, Osvaldo C, Leary N (2001) *Impacts, adaptation, and vulnerability. IPCC Working Group II Climate Change 2001, Third Assessment Report of the Intergovernmental Panel on Climate Change.* IPCC pp. 1000, http://www.grida.no/climate/ipcc_tar/wg2/index.htm.

McMurtrie RE, Rook DA, Kelliher FM (1990) Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen. *Forest Ecology and Management*, **30**, 381–413.

Melillo JM, McGuire AD, Kicklighter DW et al. (1993) Global climate change and terrestrial net primary production. *Nature*, **636**, 234–240.

Mohren GMJ, Kramer K (1997) Simulation of direct effects of CO_2 and temperature increase on forest growth: the LTEEF project. In: *Impacts of Global Change on Tree Physiology and Forest Ecosystems, Forest Sciences*, **52** (eds Mohren GMJ, Kramer K, Sabate S), pp 307–317. Kluwer Academic Publishers, Dordrecht.

Parton WJ, Schimel DS, Cole CV et al. (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Potter C, Bubier J, Crill P et al. (2001a) Ecosystem modeling of methane and carbon dioxide fluxes for boreal forest sites. *Canadian Journal of Forest Research*, **31**, 208–223.

Potter C, Davidson E, Nepstad D et al. (2001b) Ecosystem modeling and dynamic effects of deforestation on trace gas fluxes in Amazon tropical forests. *Forest Ecology and Management*, **152**, 97–117.

Raich JW, Rasetter EB, Melillo JM et al. (1991) Potential net primary productivity in South America: application of a global model. *Ecological Applications*, **1**, 399–429.

Reich PB, Koike T, Gower ST et al. (1994) Causes and consequences of variation in conifer leaf life-span. In: *Ecophysiology of Coniferous Forests* (eds Smith WK, Hinckley TM), pp. 225–254. Academic, San Diego.

Reich PB, Walters MB, Ellsworth DS (1992) Leaf lifespan in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.

Reich PB, Walters MB, Ellsworth DS et al. (1998a) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, **114**, 471–482.

Reichm PB, Walters MB, Tjoelker MG et al. (1998b) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology*, **12**, 395–405.

Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modeling*, **42**, 125–154.

Ryan MG (1991) A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiology*, **9**, 255–266.

Ryan MG, Gower ST, Hubbard RM et al. (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecoglia*, **101**, 133–140.

Ryan MG, Hubbard RM, Pongracic S et al. (1996) Foliage, fine-root, woody-tissue, and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology*, **16**, 333–344.

Sampson DA, Janssens IA, Ceulemans R (2001) Simulated soil CO efflux and net ecosystem exchange in a 70-year-old Belgian Scots pine stand using the process model SECRETS. *Annals of Forest Science*, **58**, 31–46.

Sands PJ, Battaglia M, Mummery D (2000) Application of process-based models to forest management: experience of PROMOD, a simple plantation productivity model. *Tree Physiology*, **20**, 383–392.

Schimel DSVEMAP Participants,Braswell BH (1997) Continental scale variability in ecosystem process models, data and role of disturbance. *Ecological Monographs*, **67**, 251–271.

Sitch S, Smith B, Prentice IC et al. (2003) Evaluation of ecosystem dynamics, plants geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Slatyer RO, Morrow PA (1977) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora Sieb. ex Spreng*. I Seasonal changes under field conditions in the Snowy Mountains area of southern Australia. *Australian Journal of Botany*, **25**, 1–20.

Stockfors J (2000) Temperature variations and distribution of living cells within tree stems: implications for stem respiration modeling ad scale-up. *Tree Physiology*, **20**, 1057–1062.

Tjoelker MG, Reich PB, Oleksyn J (1999b) Changes in leaf nitrogen and carbohydrates underlie temperature and CO acclimation of dark respiration in five boreal tree species. *Plant Cell and Environment*, **22**, 767–778.

Tjoelker MG, Oleksyn J, Reich PB (1999a) Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology*, **5**, 679–692.

Tjoelker MG, Oleksyn J, Reich PB (2001) Modeling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. *Global Change Biology*, **7**, 223–230.

Tranquillini W, Havranek WM, Ecker P (1986) Effects of atmospheric humidity and acclimation temperature on the temperature response of photosynthesis in your Larix dicidua Mill. *Tree Physiology*, **1**, 37–45.

Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.

Wager HG (1941) On the respiration and carbon assimilation rates of some arctic plants as related to temperature. *New Phytologist*, **40**, 1–19.

Waring RH, Landsberg JJ, Williams M (1998) Net production of forests: a constant fraction of gross primary production. *Tree Physiology*, **18**, 129–134.

Waring RH, McDowell N (2002) Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. *Tree Physiology*, **22**, 179–188.

Woodwell GM, Mackenzie FT (1995) *Biotic Feedbacks and the Global Climatic System: Will the Warming Feed the Warming?* Oxford University Press, New York. 416.