

# Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones

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## Abstract

The ongoing changes in the global climate expose the world's ecosystems not only to increasing CO<sub>2</sub> concentrations and temperatures but also to altered precipitation (*P*) regimes. Using four well-established process-based ecosystem models (LPJ, DayCent, ORCHIDEE, TECO), we explored effects of potential *P* changes on water limitation and net primary production (NPP) in seven terrestrial ecosystems with distinctive vegetation types in different hydroclimatic zones. We found that NPP responses to *P* changes differed not only among sites but also within a year at a given site. The magnitudes of NPP change were basically determined by the degree of ecosystem water limitation, which was quantified here using the ratio between atmospheric transpirational demand and soil water supply. Humid sites and/or periods were least responsive to any change in *P* as compared with moderately humid or dry sites/periods. We also found that NPP responded more strongly to doubling or halving of *P* amount and a seasonal shift in *P* occurrence than that to altered *P* frequency and intensity at constant annual amounts. The findings were highly robust across the four models especially in terms of the direction of changes and largely consistent with earlier *P* manipulation experiments and modelling results. Overall, this study underscores the widespread importance of *P* as a driver of change in ecosystems, although the ultimate response of a particular site will depend on the detailed nature and seasonal timing of *P* change.

*Keywords:* climate change, DGVM, drought, ecosystem modelling, NPP, precipitation, soil respiration, water limitation, water stress

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## Introduction

By the end of this century, global air temperature (*T*) is likely to rise by several degrees, along with substantial changes in the spatial pattern and amount of precipitation (*P*) (IPCC, 2007). There are, however, substantial differences among climate models as to the magnitude

and even the direction of  $P$  change in many regions (e.g. Giorgi & Bi, 2005). Also, the climate models often deliver inaccurate estimates of the intensity and frequency of rainfall events in their control simulations (Sun *et al.*, 2006). The consequences of changes in rainfall patterns for ecosystems thus remain poorly understood for many regions of the world. A common projection across climate models, however, is a tendency towards intensification of the hydrological cycle, with wetter conditions in the tropics and at high latitudes and further drying in subtropical regions (IPCC, 2007).

While there is much (experimental) evidence as to the responses of the world's ecosystems to direct effects of increased  $T$  (e.g. Parmesan & Yohe, 2003; Badeck *et al.*, 2004; Luo, 2007) or increased atmospheric  $\text{CO}_2$  content (e.g. Körner *et al.*, 2005; Luo *et al.*, 2006), less is known about effects of changes in  $P$  amount, frequency and intensity, or combinations thereof. However, altered  $P$  patterns will have ramifications for the structure and functioning of most inland ecosystems, because water is an elemental driver of virtually all chemical and biological processes including photosynthesis, plant growth and survival, microbial activity, net primary production (NPP), soil respiration and biodiversity (e.g. Lieth, 1975; Mielnick & Dugas, 2000; Weltzin *et al.*, 2003).

The degree to which ecosystems are currently water limited thus indicates how responsive they will be to future changes in  $P$ . For example, the water limitation of photosynthesis and, thus, NPP is determined by the balance between (a) atmospheric transpirational demand as controlled by atmospheric  $\text{CO}_2$  concentration and meteorological conditions (temperature, wind speed, radiation) and (b) soil water supply as controlled basically by soil moisture (see e.g. Federer, 1982). If the latter equals or exceeds the former, the conductance of water and carbon through the plant's stomata will occur at its potential, water unlimited rate; if, however, the supply falls below the demand, stomatal conductance – and consequently NPP – will be water limited. The degree of water limitation of NPP is, therefore, to be expressed optimally as the ratio between the actual, water-limited stomatal conductance and the potential conductance (Wainwright *et al.*, 1999; Gerten *et al.*, 2007).

It is to be expected that changes in  $P$  will have a small effect upon NPP under cold conditions (such as in the winter season in temperate and boreal ecosystems, when limitation by low temperature and radiation prevails) and under wet conditions (such as in humid tropical ecosystems) (Nemani *et al.*, 2002; Lee & Veizer, 2003; Gerten *et al.*, 2005). In contrast, severely water-limited dry land ecosystems, or ecosystems growing in summer-dry climates, are expected to respond to increased  $P$  with large NPP increases, while reduced rainfall should have little effect (as found by Knapp & Smith, 2001).

In most ecosystems, the extent of water limitation varies seasonally, often reaching a minimum in winter (when transpirational demand is low) and a maximum in summer, that is, during the warm growing period (when demand is high and soil moisture often relatively low). Hence, not only dry land ecosystems but also temperate and boreal ecosystems that are water limited during part of the year can be affected by  $P$  decreases, in that extended droughts have the potential to aggravate the existing seasonal water limitation and thereby to significantly reduce NPP (Huxman *et al.*, 2004; Ciais *et al.*, 2005). In addition, ecosystems do respond not only to changes in  $P$  amount but also to changes in  $P$  intensity and frequency, with grassland (dry land) ecosystems being particularly sensitive to short- and long-term rainfall variability (e.g. Knapp *et al.*, 2002; Williams & Albertson, 2006).

Overall, ecosystems located in different climatic zones are likely to respond differently to changes in  $P$ , as determined primarily by their seasonally varying disposition to change controlled by the degree of water limitation. Because our knowledge about impacts of changes in  $P$  amount and variability is mostly drawn from single ecosystem studies and, therefore, limited (Weltzin *et al.*, 2003; Porporato *et al.*, 2004), there is a clear need for experimental and model-based comparative studies across biomes.

In the present modelling study, we investigated year-around effects of changes in  $P$  mean annual amount, seasonal timing, frequency and intensity on NPP for a suite of ecosystem types located in different climatic zones. Four ecosystem models were employed to account for differences in the projections that might occur due to different process representations. Analysis was guided by the following questions: (1) Do ecosystems that differ (seasonally) with respect to water limitation respond differently to  $P$  changes? (2) How important is the seasonal timing of  $P$  change in the different ecosystems? (3) How pronounced are changes in frequency and intensity of  $P$  as compared with an evenly distributed change in  $P$  amount?

## Material and methods

### Sites and data

All precipitation scenarios specified later in the text were run for the following sites: the Flakaliden conifer forest in Sweden (Bergh *et al.*, 1999), a seminatural heathland at Mols Bjerge in Denmark (Beier *et al.*, 2004), a heathland hilltop within Clocaenog forest in Wales/UK (Emmett *et al.*, 2004), an oak-dominated forest in the Walker Branch watershed in Tennessee/US (Hanson *et al.*, 2005), the (regularly burned) Konza tallgrass prairie LTER site in Kansas/US (Knapp *et al.*, 1998), an annual-dominated grassland in the Jasper Ridge Biological Reserve in California/US (Dukes

*et al.*, 2005) and the tropical Tapajós National Forest in Brazil (Nepstad *et al.*, 2002). These locations represent different ecosystems (forests vs. grasslands), climatic regimes and consequent water limitation states (for details see Table 1 and Fig. 1). All of them are characterized by a dry and a wet season, but they differ in terms of the degree of water limitation particularly in the dry season and in terms of precipitation amounts and temperature levels within the seasons. Thus, they are expected to respond differently to changes in *P*.

### The models

Four process-based ecosystem models (LPJ, DayCent, ORCHIDEE, TECO) developed for regional and global applications, including future scenarios, were applied for the earlier listed sites and their results compared.

The LPJ Dynamic Global Vegetation Model is a biogeography–biogeochemistry model of intermediate complexity that computes key ecosystem processes such as establishment, growth and mortality, and competition between nine plant functional types (PFTs), as well as the related above- and belowground carbon and water dynamics (Sitch *et al.*, 2003; Gerten *et al.*, 2004). LPJ has a demonstrated capability to reproduce observed vegetation structure and dynamics, carbon and water fluxes at various scales (e.g. Sitch *et al.*, 2003; Gerten *et al.*, 2004; Hickler *et al.*, 2004).

The DayCent model is the daily version of the CENTURY ecosystem model that was designed to simulate carbon, nitrogen and phosphorus cycling and plant production of ecosystems at a monthly time step (Parton *et al.*, 1993). DayCent additionally incorporates more detailed submodels for simulating soil moisture, soil *T*, soil nitrogen, trace gas flux and soil organic matter on a daily time step while plant growth is updated weekly (Parton *et al.*, 1998; Del Grosso *et al.*, 2001). DayCent has been used previously for simulating long-term responses of grassland production and soil carbon and nitrogen to land use change, climate change and elevated CO<sub>2</sub> (e.g. Del Grosso *et al.*, 2001).

ORCHIDEE (Krinner *et al.*, 2005) is a process-oriented integrated global land-surface model consisting of three submodules: a global land surface scheme (Ducoudré *et al.*, 1993), a global continental carbon cycle model and a dynamic model of long-term vegetation dynamics including competition and disturbances based on LPJ (the latter module being switched off in the present study). The model simulates the turbulent fluxes of CO<sub>2</sub>, water and energy at a half-hourly time step, while the ecosystem carbon and water dynamics (allocation, plant respiration, growth, mortality, soil organic matter decomposition, water infiltration and runoff) are calculated at a daily time step. ORCHIDEE accounts for

14 PFTs that share the same equations, but use a different set of parameter values. The only exception is phenology, for which a PFT-specific parameterization exists (Botta *et al.*, 2000).

TECO is a terrestrial ecosystem model and evolved from a carbon sequestration (TCS) model (Luo & Reynolds, 1999). The model was designed to examine ecosystem responses to perturbations in global change factors and has been extensively applied in modelling studies at the Duke Forest CO<sub>2</sub> enrichment experiment (Luo *et al.*, 2001, 2003; Xu *et al.*, 2006).

The model-specific approaches to calculate NPP, atmospheric demand for transpiration, soil moisture, soil water supply, stomatal conductance and water limitation of NPP are summarized in Table 2.

### Calculation of water limitation

For each site, NPP – defined here as the sum of above- and belowground NPP – and its water limitation were simulated by each model following the parameterizations outlined in Table 2 and analysed on a monthly basis. We took the ratio between actual (water limited) and potential canopy conductance as a measure of NPP water limitation (see ‘Introduction’), referred herein as  $L_{\text{NPP}}$  (from DayCent another value was used, see later).  $L_{\text{NPP}}$  is scaled between 0 (indicating maximum water limitation, when there is no water in the soil that can be taken up by plants) and 1 (indicating absence of water limitation, when soil water supply is equal to or higher than atmospheric demand). The four models differ with respect to the computation of stomatal conductance and transpiration, which affects the values of  $L_{\text{NPP}}$  and thereby NPP. For example, LPJ calculates atmospheric transpirational demand by considering the mesoscale accommodation between transpiring vegetation and convective boundary layer, while water supply is constrained by plant hydraulic traits (allowing a maximum transpiration of 5 mm day<sup>-1</sup>) and actual soil moisture (Huntingford & Monteith, 1998; Sitch *et al.*, 2003; Prentice *et al.*, 2004). In DayCent, by contrast, potential plant production is reduced linearly if the ratio between available soil water and potential evapotranspiration falls below an upper threshold; when a lower threshold of that ratio is reached, production ceases (Parton *et al.*, 1998; see Stehfest *et al.*, 2007). Note, in the case of DayCent, the ratio between available water and potential evapotranspiration was used here as a proxy for  $L_{\text{NPP}}$  which is not directly computed by this model.

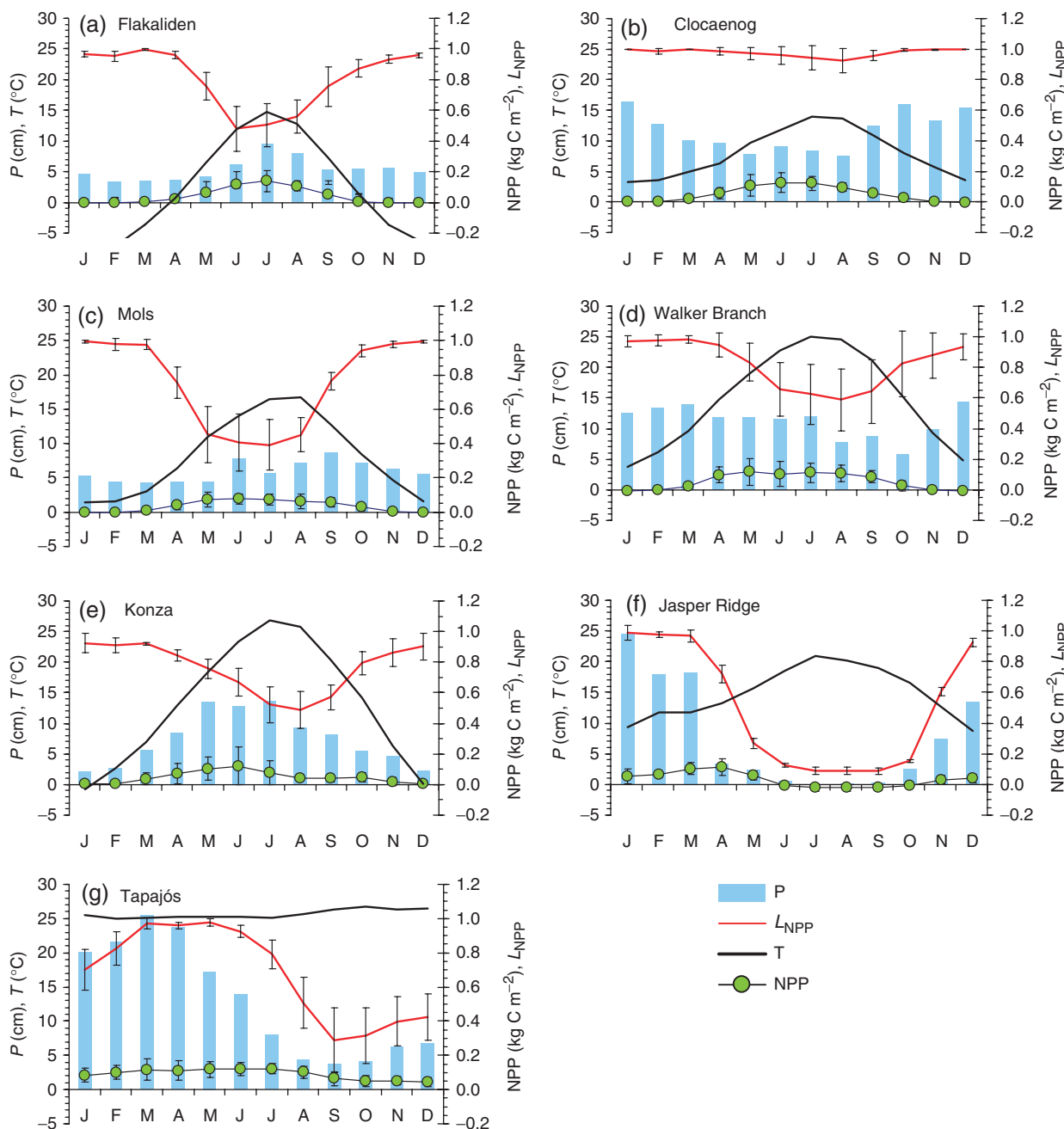
### The scenarios

All scenarios are based on a common time period, 1990–2003, for which daily climate data were available for all

**Table 1** Study site characteristics. *T*, *P* and water limitation of NPP ( $L_{NPP}$ ; model average) are given for the relatively water-limited season (Tapajós, August–January; other sites, May–October) and the nonwater-limited season (Tapajós, February–July; other sites, November–April)

Site	Location	Water-limited season		Water-unlimited season		NPP ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )			Reference		
		<i>T</i> (°C)	<i>P</i> (mm month <sup>-1</sup> )	$L_{NPP}$ (–)	<i>T</i> (°C)	<i>P</i> (mm month <sup>-1</sup> )	$L_{NPP}$ (–)	Observed		Simulated	Dominant vegetation
Flakaliden	64°07'N 19°27'E	9.1	64	0.65	–4.6	43	0.96	428	492 (± 149)	Norway spruce ( <i>Picea abies</i> )	Bergh <i>et al.</i> (1999)
Cloacaenog	53°23'N 3°28'W	11.3	102	0.96	4.6	130	0.99	200	531 (± 280)	Shrubs ( <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Empetrum nigrum</i> )	Beier <i>et al.</i> (2004), Emmett <i>et al.</i> (2004)
Mols	56°23'N 10°57'E	13.2	69	0.57	3.1	51	0.95	–	356 (± 158)	Shrubs and grasses ( <i>C. vulgaris</i> , <i>Deschampsia flexuosa</i> )	Beier <i>et al.</i> (2004)
Walker Branch	35°58'N 84°17'W	21.3	97	0.69	8.1	127	0.95	730 (± 69)	718 (± 294)	Oak-dominated hardwoods ( <i>Quercus</i> , <i>Acer</i> , <i>Nyssa</i> , <i>Oxydendron</i> , <i>Liriodendron</i> )	Hanson <i>et al.</i> (2005)
Konza	39°12'N 96°35'W	21.5	105	0.63	4.7	43	0.89	348	610 (± 270)	Perennial C <sub>4</sub> tallgrass (predominantly <i>Andropogon gerardii</i> )	Knapp <i>et al.</i> (1998)
Jasper Ridge	37°24'N 122°13'W	18.5	10	0.14	11.3	142	0.86	332 (± 68)	345 (± 124)	Annual grasses ( <i>Avena barbata</i> , <i>A. fatua</i> ) and forbs ( <i>Geranium dissectum</i> )	Dukes <i>et al.</i> (2005)
Tapajós	2°90'S 54°95'W	26.2	76	0.44	25.2	183	0.91	817 (± 67)	1255 (± 410)	Broadleaved evergreen forest ( <i>Coussarea racemosa</i> , <i>Erisma uncinatum</i> )	Nepstad <i>et al.</i> (2002)

*T* and *P* are for 1990–2003 (Jasper Ridge, 1990–2004 except 2003; Tapajós, 1989–2003 except 1995), measured directly at the sites, except for: Cloacaenog up to 1999, homogenized data from Alwen/Alwen Dam; Jasper Ridge up to 1993, regression-scaled observations from Napa State Hospital; Konza, data from Manhattan; Mols, data from Tirstrup, Danish Meteorological Institute; Tapajós, data from Belterra, missing values filled in by scaled values from Santarém. Observed NPP values are multiannual averages (± range across years) from the sources and for the years indicated in Fig. 2 (Konza, 1984–1999); additional estimates for Flakaliden (average 2001–2002) are from A. Lindroth (personal communication) and for Cloacaenog (average 1998–2003) from B. Emmett (personal communication). The error bars for modelled NPP indicate the range across the four models.



**Fig. 1** 14-year average seasonal course of observed  $T$  ( $^{\circ}\text{C}$ ; black line) and  $P$  (cm; blue bars) plotted on the left axis, as well as simulated NPP ( $\text{kg C m}^{-2} \text{ month}^{-1}$ ; line with green dots) and its water limitation  $L_{\text{NPP}}$  (red line) plotted on the right axis, for each of the seven study sites. NPP and  $L_{\text{NPP}}$  are averages across the four models; error bars indicate  $\pm 1$  standard deviation.

sites (with the exceptions noted in Table 1). Specifically, we used daily  $T$  and  $P$  monitored on-site or at the nearest meteorological station (single missing values were interpolated or computed by linear regression with data from another representative station; see notes of Table 1). LPJ and ORCHIDEE also used radiation data; in the case that these were not available, radiation

was scaled from monthly cloud cover data (CRU global climate dataset, Mitchell & Jones, 2005) and disaggregated linearly to quasidaily values. ORCHIDEE also used values for vapour pressure deficit from the same dataset. Additionally, annual values of atmospheric  $\text{CO}_2$  concentration (from Keeling & Whorf, 2004) and site-specific information (dominant vegetation type cf.

**Table 2** Formulation of key processes to calculate NPP and its water limitation in the four models used

Model	Photosynthesis/NPP	Evaporative demand	Soil moisture	Stomatal conductance and $L_{NPP}$
LPJ	Farquhar scheme generalized by Collatz <i>et al.</i> (1992); NPP is derived after subtracting costs for maintenance and growth respiration from gross primary production (Sitch <i>et al.</i> , 2003).	Derived from Priestley–Taylor (Haxeltine & Prentice, 1996).	Infiltration after subtraction of interception loss; percolation through two layers (50 and 100 cm); (sub)surface runoff above field capacity; evaporation from upper 20 cm (Gerten <i>et al.</i> , 2004).	Reduced hyperbolically if soil water supply < atmospheric demand (Federer, 1982; Huntingford & Monteith, 1998; Gerten <i>et al.</i> , 2004).
DayCent	Radiation-use efficiency based on radiation, soil water stress and $T$ (Parton <i>et al.</i> , 2001).	Derived from Penman–Monteith (Parton <i>et al.</i> , 1998).	Infiltration/percolation through several layers after subtraction of interception loss; bare soil evaporation; runoff is the sum of infiltration excess and saturation excess; (Parton <i>et al.</i> , 1998; Del Grosso <i>et al.</i> , 2001).	Function of leaf area, potential evapotranspiration and moisture of wettest soil layer in rooting profile (Parton <i>et al.</i> , 1998; Stehfest <i>et al.</i> , 2007).
TECO	Leaf-level photosynthesis model by Farquhar <i>et al.</i> (1980), multiple levels of canopy with light transmission by Beer's law.	Constant relative humidity at 70%.	Runoff occurring when $P >$ field capacity; evapotranspiration as in Sellers <i>et al.</i> (1996).	Stomatal conductance after Ball <i>et al.</i> (1987), regulated by canopy conductance and soil water supply; growth regulated by soil moisture scalar (Weng & Luo, 2008).
ORCHIDEE	Half-hourly photosynthesis from Farquhar <i>et al.</i> (1980), Collatz <i>et al.</i> (1992); stomatal conductance by Ball <i>et al.</i> (1987).	Derived from Penman–Monteith.	Infiltration after subtraction of interception loss; two soil layers; runoff above field capacity (Ducoudré <i>et al.</i> , 1993).	Stomatal response to relative humidity. Conductance reduced via slope of the Ball <i>et al.</i> (1987) relationship, as a function of soil moisture and root profile (threshold from McMurtrie <i>et al.</i> , 1990).

Table 1; water holding capacity) were used as model forcing. For ORCHIDEE, a simple weather generator was used to produce the required 30 min data from the daily data.

For the control run (Ctrl), all models were driven by the measured meteorological data. In order to represent a range of possible changes in  $P$  amount, frequency and seasonality, we defined five scenarios (see Table 3), which were constructed by manipulating the observed daily  $P$  values as follows. For the doubled (DP) and the halved precipitation (HP) scenarios, every day  $P$  received 200% and 50%, respectively, of the observed amount. For the Df scenario,  $P$  frequency was doubled [i.e.  $P$  amount was halved for every rain day and the remainder assigned to the next dry day(s)]. In the case of a sequence of several rain days, the 'saved' water was assigned proportionally to the same number of dry days. For the Hf scenario,  $P$  frequency was halved (i.e. two consecutive  $P$  events were combined to one). In the

**Table 3** Overview of the simulations performed for each site and with each model

Scenario	Notation
Control	Ctrl
Doubled precipitation amount	DP
Halved precipitation amount	HP
Doubled precipitation frequency at constant annual amounts	Df
Halved precipitation frequency at constant annual amounts	Hf
Seasonal drought ( $P$ from July/August added to $P$ of January/February)	SP

SP scenario, we emulated the occurrence of a seasonal drought without changing annual  $P$  amount, in that the daily values from two summer months (July, August) were moved to winter (January, February).

Following  $P$  manipulation experiments (e.g. Knapp *et al.*, 2002), these scenarios are stylized in that they reflect the changes projected by climate models in a very general way, instead of using actual projections for each site. This is justified because of the nontrivial differences among the climate scenarios in terms of projected magnitude and sign of change in  $P$  amount and variability (see 'Introduction'), rendering it necessary to display effects of diverse assumptions about climate ( $P$ ) change. Moreover, an across-system comparison of impacts of particular aspects of change is facilitated if the same scenarios are applied to each site. We note that the scenario definitions represent rather extreme assumptions about the  $P$  changes that may occur in the future. Yet, although the assumption that  $P$  will double or halve throughout a year is probably unrealistic, it is quite possible that this will be the case for parts of a year. Also, the Hf and Df scenarios lie well within the range of documented rainfall regimes of at least some of the sites under study (see e.g. Knapp *et al.*, 2002 for Konza), and the assumption on which the SP scenario is based (i.e.  $P$  increase in winter and decrease in summer) agrees with climate projections at least for large parts of Europe.

Finally, the models forced by each scenario calculate a modified NPP value in equilibrium with a different  $P$  regime, but the impacts on this equilibrium NPP (e.g. through mortality, changes in PFT composition) of the *transient rate* at which  $P$  changes between Ctrl and scenario are not assessed in our modelling framework.

Percentage or absolute changes from the Ctrl scenario are denoted as  $\Delta\text{NPP}_{\text{HP}}$ ,  $\Delta\text{NPP}_{\text{DP}}$ , etc.

#### *Model initialization and validation*

The models were initialized with a 980-year spin-up by repeating the observation time series 70 times, so as to bring the long-term carbon stores into equilibrium; the transient control and scenario runs (using the observed and manipulated time series) were computed starting from this equilibrium state. Only the vegetation types that represent those presently dominant at the study sites (see Table 1) were allowed to grow in the models. These types were kept fixed in all simulations (i.e. no dynamic changes were allowed neither in the spin-up nor in the transient simulation periods). This was necessary to avoid establishment of potential natural vegetation, which at some of the study sites is different from the vegetation that actually grows there under human management. Also, occurrence of natural fires was suppressed in the models.

Unfortunately, long-term measurements of NPP were not available for each site, but from the existing data we could deduce that the model ensemble largely repro-

duced the observed interannual variability of NPP (Fig. 2) [i.e. the models captured well the different ecosystems' responses to climate variability (see also Table 1)]. Given that the four models had not been calibrated against the measurements, we consider these differences to be small enough for performing a valuable scenario analysis.

## **Results**

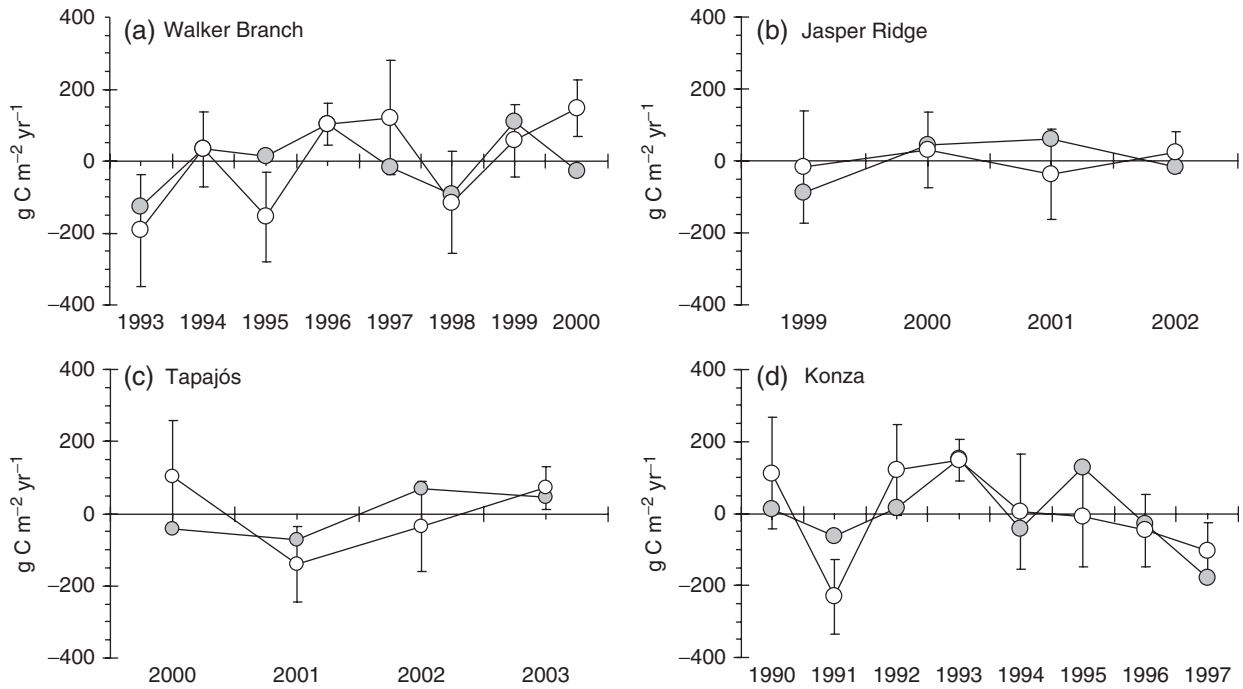
### *Relationships between current climate and water limitation of NPP*

The present degree of water limitation differs considerably across the study sites and also varies within a year, as controlled by  $P$  and/or  $T$  (Figs 1 and 3). Monthly  $T$  and  $L_{\text{NPP}}$  were strongly negatively correlated for all sites with the exception of Jasper Ridge and Tapajós where  $P$  was the more dominant factor influencing  $L_{\text{NPP}}$  (Figs 3 and 4). This strong relationship suggests a higher water limitation in response to high evaporative demand in the warm season (which mostly corresponds to the growing period when NPP is highest, see Fig. 1). The relationship also suggests little water limitation ( $L_{\text{NPP}} > 0.8$ ) in winter when soil moisture reserves are replenished and when evaporative demand is minimal due to low temperature and radiation – specifically if  $T < 10^\circ\text{C}$ , a threshold that appears to be common to all the sites. Only for the tropical Tapajós site did we find periods with little water limitation under temperatures as high as  $25^\circ\text{C}$ , because  $P$  is sufficiently high in these warm periods (during the first half of a year) to compensate for temperature-driven water limitation. The absence of water limitation under cold conditions, irrespective of  $P$ , explains why water limitation is on an average unrelated to  $P$  in most of the ecosystems under study (Fig. 3).

In sum,  $L_{\text{NPP}}$  and, hence, NPP variations are largely decoupled from  $P$  variations in cold and/or very wet periods, but highly sensitive to  $P$  variations during the remainder of a year. It is, thus to be expected that effects of altered  $P$  on NPP will differ between dry, wet, cold and warm sites and also within a year at a particular site, as dependent on the seasonal course of  $L_{\text{NPP}}$ .

### *Effects of $P$ change under weak water limitation*

For the site that exhibited the lowest water limitation throughout a year, Clocaenog (cf. Figs 1b and 2b), simulated NPP in all models changed little – if at all – in the  $P$  scenarios applied here (Fig. 5 and Table 4). Only halving of  $P$  (HP scenario), or a severe drought in the middle of the growing season (SP scenario), appeared to decrease NPP at that site by ca. 10%. The HP scenario



**Fig. 2** Observed (grey) and simulated (white; mean  $\pm$  standard deviation across models) annual NPP ( $\text{g C m}^{-2} \text{yr}^{-1}$ ), presented as anomalies from the average over the respective observation time period. The observations are taken from the following sources: Walker Branch (1993–2000), Hanson *et al.*, 2003), generated with support from the US Department of Energy's Office of Science; Jasper Ridge (1999–2002), Dukes *et al.* (2005); Tapajós (2000–2003), P. Brando, personal communication, aboveground NPP scaled by a factor of 1.3 to obtain sum of above- and belowground NPP; Konza, LTER Net Primary Productivity database (<http://intranet.lternet.edu/cgi-bin/anpp.pl>, accessed in January 2007).

tended to produce the strongest responses at all the sites under conditions of weak water limitation, while doubling (Df scenario) and especially halving  $P$  frequency (Hf scenario) led to relatively weak changes in NPP (Table 4). Some sites responded as weakly in the water-unlimited season as did Clocaenog year-around (see Mols, Walker Branch and Tapajós in Fig. 5). However, at Flakaliden, Konza and Jasper Ridge, NPP was increased or decreased by up to about 30% during the water-unlimited season as well, because the initial levels of NPP were very low (mostly  $< 5 \text{ g C m}^{-2}$ ) or because, at Jasper Ridge, the sensitive spring period (April) was included in the water-unlimited season (Fig. 1). Also, the SP simulation generally produced no response at the latter site, because rainfall was close to zero in summer (see Fig. 1) such that a shift of  $P$  to winter was ineffective.

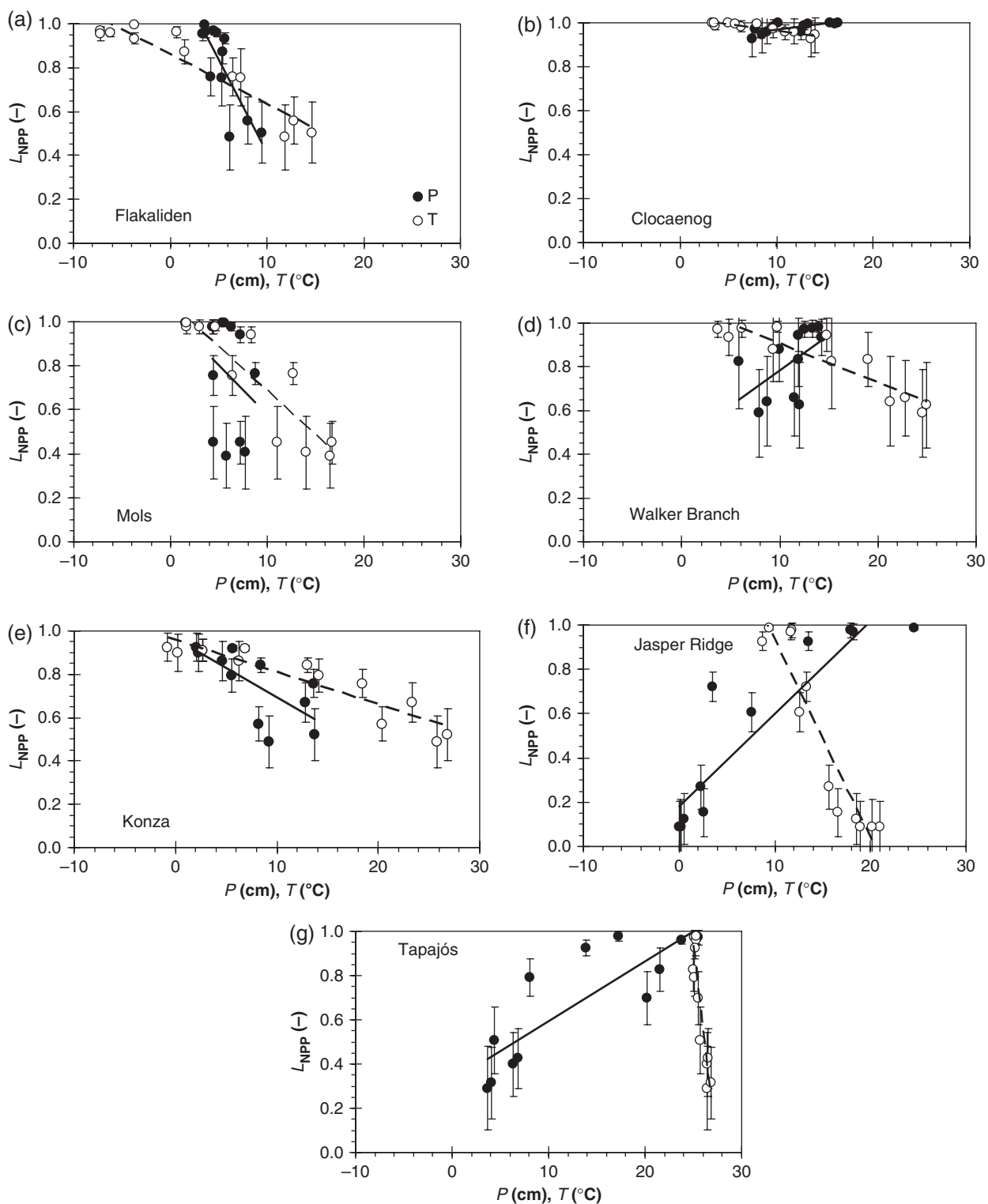
#### *Effects of $P$ change under moderate to strong water limitation*

Under water-limited conditions, the magnitude of NPP change was simulated to be substantially higher – by a factor of up to about five – than under the less limited

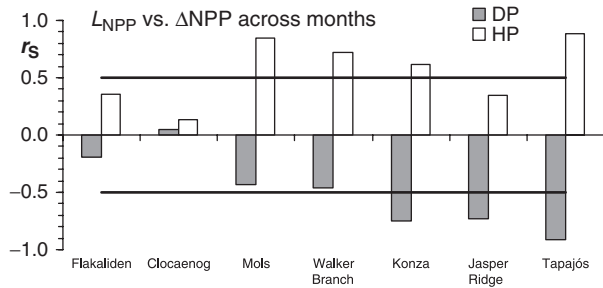
conditions, at all sites and in each of the scenarios studied (Figs 3 and 5). The higher percentage increases in the water-limited seasons were not artefacts arising out of low initial levels of NPP, because at most sites NPP peaked during those periods (compare Fig. 1).

Specifically, in the circumstance of water limitation, halving of  $P$  amount was found to decrease NPP by more than 30% at four out of the seven sites (Fig. 5a), whereas during water-unlimited periods, the decrease in NPP was usually lower and sometimes nil, as described in the previous section. This is also reflected in the SP scenario, in which the percentage NPP losses were significantly higher in the dry season (when  $P$  was reduced) than the percentage gains in winter (when  $P$  was added) (Fig. 5c). However, at most sites, NPP benefited in spring from the additional winter rain or snow (data not shown).

As in the water-unlimited season, NPP responded stronger to  $P$  reductions (HP, SP) than to  $P$  increases (DP) (Fig. 5), which highlights the nonlinear response of NPP to changes in the water cycle. The only exception was Jasper Ridge, where HP produced a stronger decline in NPP in the water-unlimited season (because  $P$  was already negligible in the water-limited season).



**Fig. 3** Scatterplots of monthly precipitation (closed circles) and air temperature (open circles) against NPP water limitation ( $L_{NPP}$ ) for each of the study sites. The error bars indicate the standard deviation across the four models. The thick lines represent the linear regression lines (solid,  $L_{NPP}$  vs.  $P$ ; dashed,  $L_{NPP}$  vs.  $T$ ).



**Fig. 4** Partial Spearman correlations ( $r_s$ , average of the four models) between monthly values of  $L_{NPP}$ ,  $\Delta NPP_{DP}$  and, respectively,  $\Delta NPP_{HP}$ . The straight lines indicate significance at the  $P < 0.05$  level.

Again, responses were generally weakest in the scenarios in which only  $P$  frequency and intensity were changed (Df and Hf; Table 4).

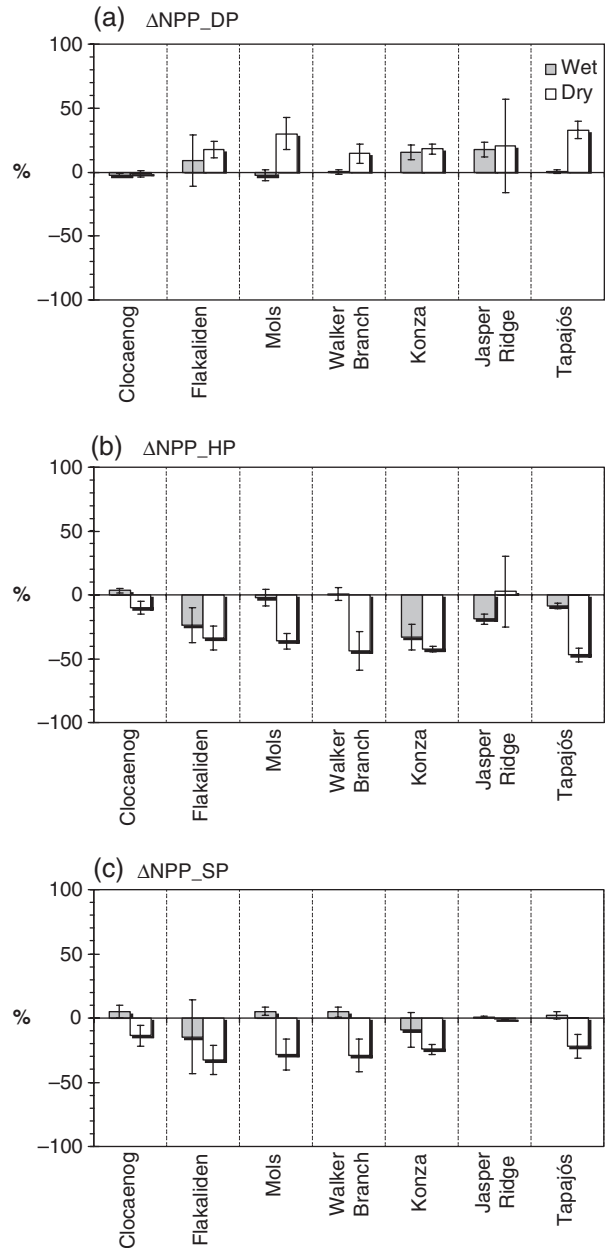
Overall, the simulation results show that NPP responses followed a gradient with largest changes in moderately to strongly water-limited months (except for very dry months – Jasper Ridge in summer) and smallest changes in nonwater-limited months (see also correlations in Fig. 4).

## Discussion

### *NPP responsiveness of sites and seasons depends on water limitation status*

Using NPP as a key ecosystem process, this modelling study demonstrated that ecosystem response to altered precipitation amount or frequency depends mainly on the degree of water limitation ( $L_{NPP}$ ) to which the process under consideration was subjected before the  $P$  change.  $L_{NPP}$  varied not only among the sites but also in the course of a year at a given site. Therefore, the sensitivity of NPP to any change in  $P$  varied considerably among seasons, in that responses were most pronounced in time periods that were already water limited and least pronounced or absent in nonwater-limited periods. Hence, it is not only the magnitude but also the seasonal timing of a change in  $P$  that is crucial for the response of an ecosystem, as has been suggested in previous studies for any climate change signal in both terrestrial and aquatic ecosystems (e.g. Adrian *et al.*, 2006).

The present modelling results are supported by local experimental observations from the sites under study here as well as by other modelling studies. For example, an experimental  $P$  increase of 33% at Walker Branch under already wet conditions produced only little impact on transpiration and, thereby probably also on NPP (which is closely linked to transpiration as both



**Fig. 5** Modelled 14-year averages of NPP changes from the Ctrl run (%) for the dry and wet season of the different sites, under the DP (a), the HP (b) and the SP scenario (c). The error bars represent the standard deviation across models. The Df and Hf scenarios produce little response (cf. Table 4) and are therefore not shown here.

processes occur simultaneously through the plants' stomata), whereas extended droughts had a substantially larger impact (Wullschlegel & Hanson, 2006). Our finding that supplemental water had a minor effect in the absence of water limitation (in winter) is furthermore supported by earlier findings for Walker Branch

**Table 4** Directions of change in NPP under the different *P* scenarios, for the seven sites and, respectively, the water-limited ('Lim.') and water-unlimited seasons ('Unlim.') defined as in Table 1

Scenario	Season	Flakaliden	Clocaenog	Mols	Walker Branch	Konza	Jasper Ridge	Tapajós
DP	Lim.	↑ ↓ ↑ ↓	• • • •	• • ↓ ↓	• • • •	↑ ↑ • •	• • ↑ ↑	• ↑ • •
	Unlim.	↑ • ↑ ↑	• • • •	↑ ↑ • ↑	↑ • • ↑	↑ ↑ ↑ ↑	↓ ↑ ↑ ↑	↑ • ↑ ↑
HP	Lim.	↓ ↓ ↓ ↓	• • • •	• ↓ ↓ ↓	↑ • • ↓	↓ ↓ • ↓	• • ↓ ↓	• ↓ ↓ •
	Unlim.	↓ ↓ ↓ ↓	• ↓ • ↓	↓ ↓ ↓ ↓	↓ ↓ ↓ ↓	↓ ↓ ↓ ↓	↑ ↓ • ↓	↓ ↓ ↓ ↓
Df	Lim.	↓ ↑ • •	• • • •	• ↑ ↓ •	• • • •	• • • •	• • • ↑	• ↑ ↑ •
	Unlim.	• • • ↑	• • • •	• ↑ • •	• • • ↑	• • • •	↓ ↑ ↑ ↑	↑ ↑ ↑ ↑
Hf	Lim.	• • • •	• • • •	• • • •	• • • •	• • • •	• • • •	• • • •
	Unlim.	• • • •	• • • •	• • • •	• • • •	• • • •	• • • •	• • ↑ •
SP	Lim.	↓ ↓ ↑ ↓	• ↑ • •	↑ • • ↓	↑ • • ↓	↑ ↓ ↓ ↓	• • • •	• • • •
	Unlim.	↓ ↓ ↓ ↓	• ↓ • ↓	↓ ↓ • ↓	↓ ↓ • ↓	↓ ↓ ↓ ↓	• ↓ • •	↓ • • ↓

↑, ΔNPP ≥ +10%; ↓, ΔNPP ≤ -10%; •, +10% < ΔNPP < -10%. For each case, the results from the four models are indicated (order: LPJ, ORCHIDEE, TECO, DayCent).

(Hanson *et al.*, 2005) and Jasper Ridge as well (Dukes *et al.*, 2005). In addition, Emmett *et al.* (2004) found for the very wet Clocaenog site that substantial ecological effects will only occur if relative soil moisture fell below 60%; this is reflected in our result that NPP at that site only increased in the SP and HP scenarios, which both imply a very strong decrease in soil moisture. The present results generally suggest that presently water-unlimited periods and sites would require *P* declines of >50% for a significant change in NPP to occur, as was also found in other studies for the humid tropics. The modelling study of Cowling & Shin (2006) found that for a larger part of the Amazon basin, a ~50% reduction in *P* would lower NPP by only ~10–20% as found in the present study, and that substantial reductions would occur only when *P* declines by ~80%.

Sowerby *et al.* (2005) furthermore reported that drought effects on enzyme activity and nutrient mineralization were far less pronounced at Clocaenog than at more water-limited locations in the Netherlands and in Denmark (including Mols). Their conclusion was that at intermediate levels of water limitation, small changes in soil moisture will have greater consequences (in either direction) for ecosystem processes than at very dry or very wet sites. This is in line with our general result that effects of *P* change were weakest not only at low water limitation (found for most sites, Fig. 4a) but also when water limitation was very severe (Jasper Ridge in the dry season), while sites like Walker Branch that are moderately water limited in summer responded strongest (Fig. 4b). The modelled drastic declines in NPP under HP and SP in the dry season in particular are corroborated by observational evidence from many ecosystems that underwent expanded summer droughts (e.g. Reichstein *et al.*, 2007), including the Tapajós site (Asner *et al.*, 2004; Nepstad *et al.*, 2007).

In sum, we found that the NPP of terrestrial ecosystems responded relatively weakly to changes in *P* amount in nonwater-limited cool and humid regions/periods but strongly in water-limited warm and dry regions/periods. We noted that the present analysis was restricted to a few sites (though these are located in different climatic zones). Nonetheless, the finding that NPP responses to *P* changes follow water limitation appears to be a general principle applicable at larger scales, as the spatial pattern of NPP water limitation – and, thus, the pattern of vulnerability toward *P* change – reported in global modelling studies (Gerten *et al.*, 2005, 2007), as well as global data-based analyses (Nemani *et al.*, 2003) basically correspond to the differences among the systems demonstrated here. For example, Gerten *et al.* (2005) found that the *P* increase projected for high northern latitudes will not significantly affect NPP in these regions, while *P* decreases in presently water-limited regions may strongly reduce NPP through decreased soil moisture. Such effects of *P* decreases can be dramatic (potentially including large-scale vegetation diebacks) (e.g. in parts of the Amazon region that according to some climate models will be prone to higher drought frequency later this century (Cox *et al.*, 2004; Cramer *et al.*, 2004).

However, Gerten *et al.* (2005) found that concurrent changes in temperature, CO<sub>2</sub> concentration and related changes in vegetation structure and physiology will modify the *P* impact in many regions. For example, increased CO<sub>2</sub> may decrease transpiration at the leaf level and, thereby attenuate adverse hydrologic effects on NPP of decreased *P* and increased *T*. While changes in vegetation composition were suppressed in the present analysis, changes in plant phenology in response to *P* changes are inherent to our simulation results, in that e.g. increased NPP in response to higher water avail-

ability in spring was reflected in advanced leaf build-up (data not shown). Individual and combined effects of changes in  $T$  and  $\text{CO}_2$  relative to the  $P$  effects reported here are analysed in a companion paper (Luo *et al.*, 2008).

#### *Differential response to changes in P amount vs. P frequency and intensity*

A consistent pattern across models and sites was that effects of halved  $P$  frequency (Hf scenario) on NPP were mostly negligible (Table 4). Doubled  $P$  frequency (Df) induced somewhat more pronounced changes, particularly at seasonally dry sites (Jasper Ridge, Tapajós) that obviously benefited in the short term from the additional water pulses. Similar sensitivities have been reported by other authors. For example, in a simulation resembling our Hf scenario, Porporato *et al.* (2006) found small effects for a dry site, but a  $\sim 10\text{--}20\%$  decrease in annual NPP for Konza. In  $P$  manipulation experiments at the same site – which also resemble our Hf scenarios – Knapp *et al.* (2002) found NPP to be reduced by  $\sim 10\%$  as compared with the ambient rainfall pattern. These effects are larger than those in the present study, which may be due to differences in the exact treatment of rainfall pattern; for instance, it may be that the periods of relative dryness were longer in those studies than in ours.

We conclude that effects of altered  $P$  frequency and depth are not zero, and that scenarios of increased frequency in particular merit consideration in future modelling and experimental studies. However, we furthermore suggest that the changes in NPP induced by altered  $P$  frequency were much weaker than those induced by altered  $P$  amounts (either Df or Hf), though one has to note that the DP and HP scenarios represent rather extreme cases (see 'The scenarios').

#### *Model robustness*

In almost all cases, the four ecosystem models used here agreed surprisingly well in terms of the direction of NPP changes under the various scenarios, indicating that these overall trends are robust against different model designs and parameterizations. Model discrepancies are, however, sometimes large as regards the magnitudes of change. These discrepancies are partly attributable to the fact that levels of NPP differed already in the Ctrl model run (see error bars in Fig. 1), such that the percentage changes inevitably differed even if the absolute changes were the same. Additional analyses of daily simulation results (data not shown) revealed that the seasonal course and especially the absolute values of soil moisture and  $L_{\text{NPP}}$  were not

always synchronized among models, which led to model differences in NPP and which can be explained by the different treatment of the related processes in the models used here (see 'The models' and Table 2). We, thus support the conclusion by Morales *et al.* (2005) that the way how models simulate water stress or stomatal conductance (via atmospheric stress and/or soil moisture stress) is crucial, particularly for water-limited sites.

Overall, changes in  $P$  can substantially affect ecosystem processes, and may well leave a traceable signature not only locally but also globally, if  $P$  is to change over large geographical domains (IPCC, 2007). This renders monitoring and both model and experimental studies of  $P$  effects on representative ecosystems all the more important. As a potential guideline for experimental studies, the results of the present modelling study suggest that precipitation manipulation experiments should be focussed more on changes in  $P$  amounts, including seasonal amounts, than on changes in  $P$  frequency or intensity, as the former are likely to have more dramatic consequences. Our results also suggest that  $P$  experiments should be designed so as to capture water-limited periods (which are not necessarily the periods with lowest  $P$ , as for example, high  $T$  may also produce water limitation).

#### **Conclusion**

Based on scenario analyses for a range of ecosystem types in different climatic zones, the present modelling study found that the degree of change in key ecosystem processes in response to altered precipitation amount or frequency/intensity critically depends on the (seasonally varying) water limitation of the ecosystems. Changes in NPP and other ecosystem processes usually were strongest in moderately to strongly water-limited ecosystems. Furthermore, doubled or halved  $P$ , or a drought in the middle of the growing season, usually produced significantly stronger responses than altered  $P$  frequency and intensity at constant annual amounts.

We recognized that the nature of climatic changes will differ among the sites and will include combinations of changes in  $P$  amount and frequency that were not explicitly addressed here. Therefore, it would be useful to investigate responses of individual ecosystems under ensembles of different climate models and, as is the case for the sites studied here (e.g. Dukes *et al.*, 2005), to set up manipulation experiments that explore effects of  $P$  change either in isolation or in combination with changes in other (atmospheric) drivers. Effects of changed  $T$  and  $\text{CO}_2$  – both in isolation and coupled with the  $P$  scenarios analysed here – are studied in detail in a companion paper (Luo *et al.*, 2008). In that study, we also analyse ecosystem processes other than NPP

(including heterotrophic soil respiration) that are likely to be influenced by *P* changes.

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