

Rainfall distribution is the main driver of runoff under future CO₂-concentration in a temperate deciduous forest

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Abstract

Reduced stomatal conductance under elevated CO₂ results in increased soil moisture, provided all other factors remain constant. Whether this results in increased runoff critically depends on the interaction of rainfall patterns, soil water storage capacity and plant responses. To test the sensitivity of runoff to these parameters under elevated CO₂, we combine transpiration and soil moisture data from the Swiss Canopy Crane FACE experiment (SCC, 14 30–35 m tall deciduous broad-leaved trees under elevated CO₂) with 104 years of daily precipitation data from an adjacent weather station to drive a three-layer bucket model (mean yearly precipitation 794 mm). The model adequately predicts the water budget of a temperate deciduous forest and runoff from a nearby gauging station. A simulation run over all 104 years based on measured sap flow responses resulted in only 5.5 mm (2.9%) increased ecosystem runoff under elevated CO₂. Out of the 37 986 days (1 January 1901–31 December 2004), only 576 days produce higher runoff in the elevated CO₂ scenario. Only 1 out of 17 years produces a CO₂-signal > 20 mm a⁻¹, which mostly depends on a few single days when runoff under elevated CO₂ exceeds runoff under ambient conditions. The maximum signal for a double preindustrial CO₂-concentration under the past century daily rainfall regime is an additional runoff of 46 mm. More than half of all years produce a signal of < 5 mm a⁻¹, because trees consume the 'extra' moisture during prolonged dry weather. Increased runoff under elevated CO₂ is nine times more sensitive to variations in rain pattern than to the applied reduction in transpiration under elevated CO₂. Thus the key driver of increased runoff under future CO₂-concentration is the day by day rainfall pattern. We argue that increased runoff due to a first-order plant physiological CO₂-effect will be very small (< 3%) in a landscape dominated by temperate deciduous forests, and will hardly increase flooding risk in forest catchments. Monthly rainfall sums are unsuitable to realistically model such CO₂ effects. These findings may apply to other ecosystems with comparable soil water storage capacity.

Keywords: bucket model, catchment hydrology, FACE, soil moisture, stomata

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Introduction

Global runoff in the 21st century will be affected by anthropogenic activities in three ways: (1) by climate change through radiative forcing (2) by land use change (change in land cover), and (3) by physiological and structural responses of plants to increasing CO₂-concentrations. Any changes in runoff will affect mankind

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critically (Jackson *et al.*, 2001). Generally, runoff is predicted to increase particularly in high latitudes (Stocker & Raible, 2005; Wu *et al.*, 2005), and models based on land cover, actual runoff and theory on vegetation responses confirm the trends for the 20th century (Peterson *et al.*, 2002; Labat *et al.*, 2004; Gedney *et al.*, 2006). However, the validity of the underlying data set of the latter two studies has been challenged (Peel & McMahon, 2006). Even if global runoff increased during the past century, it is questionable whether this is explained mainly by an assumed reduction of plant transpiration in response to increasing CO₂ as was suggested by Gedney *et al.* (2006). Piao *et al.* (2007) for

example find that both direct effects of climate change through radiative forcing as well as land use change have a stronger impact on increasing runoff than the physiological CO₂-effect. Huntington (2008) summarizes evidence for globally increased actual evapotranspiration during the 20th century, strongly arguing against a physiological CO₂-effect on runoff. A recent modelling study investigates the interacting effects of CO₂, temperature and precipitation on runoff in seven different climatic zones (Luo *et al.*, 2008). They find a small increase in runoff driven by the physiological effect of CO₂ alone. Importantly, any reduction in stomatal conductance and eventually transpiration hinges on underlying photosynthesis models in combination with possible structural plant responses. Generally, when scaling up from leaf to ecosystem level, the effect on transpiration from stomatal responses diminishes and there is a danger of overestimating savings in ecosystem-scale transpiration under elevated CO₂ (McNaughton & Jarvis, 1991; de Pury & Farquhar, 1997). First-principle stomatal responses have been shown to be wrong for conifers (Ellsworth, 1999) and much smaller than expected for deciduous forest trees (Wullschlegel & Norby, 2001; Keel *et al.*, 2007). Medlyn *et al.* (2001) find 22% decreased stomatal conductance in a review of tree-responses, but this mean value was mainly derived from young trees, often seedlings, thus probably overestimating mature forest tree responses (Körner *et al.*, 2007). Even for graminoids, responses vary between no response and 50% reduction in stomatal conductance under elevated CO₂ (Lauber & Körner, 1997; Owensby *et al.*, 1997). Initial reductions in stomatal aperture under elevated CO₂ may translate into reduced ecosystem evapotranspiration of 0–10% in trees and rarely >20% in grassland (Ellsworth, 1999; Morgan *et al.*, 2004; Leuzinger & Körner, 2007). A further reduction of net ecosystem water savings in a future climate can be expected by atmospheric feedback (drier air upon stomatal downregulation causes an increase in transpiration, Jacobs & de Bruin, 1997; Douville *et al.*, 2000) and likely structural adaptation by vegetation (increased LAI and land cover, Leipprand & Gerten, 2006; Piao *et al.*, 2007), although LAI at steady state canopy development may actually be lower under elevated CO₂ (Körner & Arnone, 1992; Hättenschwiler *et al.*, 1997; Körner *et al.*, 2005).

The extent to which a reduction in ecosystem transpiration and therefore increased soil moisture leads to increased runoff critically depends on the soil water storage capacity and the daily rainfall pattern. However, modelling studies often apply monthly means of precipitation (Cramer *et al.*, 2001; Piao *et al.*, 2007) or disaggregated rainfall sums by means of random number algorithms (Leipprand & Gerten, 2006;

Betts *et al.*, 2007). The present study examines specifically the sensitivities of CO₂-driven runoff changes to the day by day precipitation over the last 104 years and the variation in key model parameters for a temperate deciduous forest under elevated CO₂. Importantly, this study does not use future scenarios for rainfall and temperature. The biological baseline data on stomatal and sap flow responses were taken from a long term experiment at the Swiss Canopy Crane (SCC) research site near Basel, Switzerland (Leuzinger & Körner, 2007). The use of actual response data from mature trees and detailed long-term precipitation data allows us to explore conditions under which the physiological (stomatal) effect of elevated CO₂ leads to increased runoff.

Materials and methods

A three-layer bucket model was constructed based on the combination of three sources of data: (1) sap flow and soil moisture measurements under ambient and elevated atmospheric CO₂ (hereafter referred to as a/e CO₂) at the SCC experimental site in Hofstetten, Switzerland (Leuzinger *et al.*, 2005; Leuzinger & Körner, 2007); (2) daily weather data from the weather station of the Swiss Federal Office of Meteorology in Binningen, Switzerland, 12 km north of the experimental site (Tank *et al.*, 2002); and (3) standard astronomical data for the SCC site for the calculation of light intensities according to Duffie & Beckman (1991). This approach contrasts previous studies which quantified the water balance of vegetation under elevated CO₂ via theoretical effects on transpiration derived from leaf photosynthesis models that are scaled up to the vegetation cover. Our model evaluates the water balance in a top to bottom approach, using the canopy interception layer, including litter (*I*) and two soil layers (*s*₁ and *s*₂) to calculate runoff (*RO*) in daily increments (January 1 1901 to December 31 2004, 104 years) for both the ambient and the elevated CO₂ scenario. All variables and constants used in the model are summarised in Table 1. Transpiration (*Tr*) is modelled directly on the basis of sap flow and soil moisture measurements at the SCC site, where 12 deciduous, mature trees (for the present analysis, three treated and three control trees of the following species were used: *Quercus pubescens*, *Fagus sylvatica* and *Carpinus betulus*) are subjected to 540 ppm CO₂ and compared with a set of control trees at ambient CO₂ (see Leuzinger & Körner, 2007 for details). Therefore, the physiological CO₂-effect simulated in our model corresponds approximately to the years 2060–2080 relative to the year 2000. Sap flow is considered equal to *Tr* (on a daily basis), the storage terms between days are assumed zero. Transpiration under a/e CO₂ (*Tr*_a, *Tr*_e) is modelled using daily means of sap

flow-vapour pressure deficit (*sapflow- v_{pd}*) measurements (Leuzinger & Körner, 2007):

$$Tr_a = \text{sapflow}_a = \frac{\phi_{1,a} + (\phi_{2,a} - \phi_{1,a})}{\exp(-\exp(\phi_{3,a})v_{pd})} \quad (1)$$

$$Tr_e = \text{sapflow}_e = \frac{\phi_{1,e} + (\phi_{2,e} - \phi_{1,e})}{\exp(-\exp(\phi_{3,e})v_{pd})}, \quad (2)$$

with ϕ_1 to ϕ_4 the respective fitted coefficients for a/e (subscripts a and e). The ratio $(1 - Tr_e/Tr_a) \times 100$, referred to as $Tr\%$ is thus the percentage of reduced transpiration under elevated CO₂. The value for $Tr\%$ across all trees for the SCC FACE site as measured by (Leuzinger & Körner, 2007) is 14%. However, that study did not cover long enough dry periods and thus both overall transpiration and the CO₂-effect on transpiration would have been overestimated during dry spells, had we applied Eqns (1) and (2) year-round. We therefore introduced two thresholds for dry (thr_1) and very dry (thr_2) conditions, which were determined according to soil moisture measurements at the SCC experimental site (thr_1 after ca. 10 days of sunny weather, see also Fig. 3 in Leuzinger & Körner, 2007, thr_2 after ca. 30 days of sunny weather, see also Fig. 1 in Leuzinger *et al.*, 2005). If soil water content of soil layer 2, SWC_{s_2} falls below thr_1 , transpiration under elevated CO₂ (Tr_e) equals transpiration under

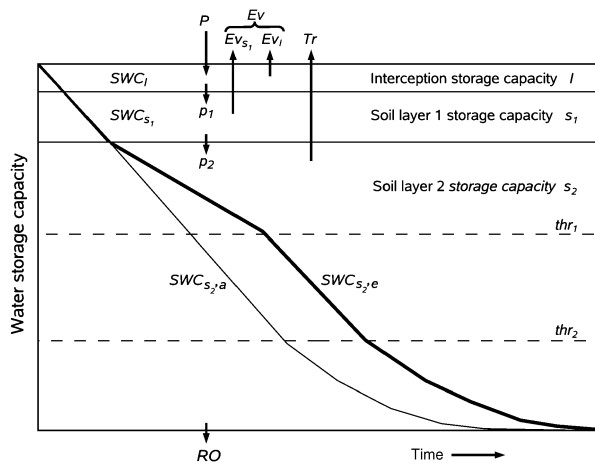


Fig. 1 Model structure. The vertical axis represents the storage capacity of the three compartments interception I , soil layer 1 s_1 and soil layer 2 s_2 . A hypothetical, completely dry spell is shown where I and s_1 drain first, then s_2 . Threshold 1 (thr_1) and threshold 2 (thr_2) divide s_2 into three modes of transpiration (Tr), each modelled according to experimental data: above thr_1 , Tr is lower under the elevated CO₂ scenario, between the thresholds, Tr_a is equal to Tr_e , and below thr_2 , Tr decreases asymptotically in both scenarios. Precipitation and the throughflow to lower compartments are denoted P , p_1 and p_2 respectively. Evaporation Ev consists of evaporation drawn from s_1 and I (Ev_{s_1} and Ev_I). The shown time period corresponds to ca. 30 days.

ambient conditions (Tr_a , Eqn (3), according to Fig. 2 in Leuzinger & Körner, 2007). This reflects the result of initial water savings under elevated CO₂, which, at a later stage of a dry period, permit more generous water use than under ambient conditions. Below thr_1 , it is therefore possible that initial water savings (difference between $SWC_{s_2,a}$ and $SWC_{s_2,e}$) are subsequently lost by soil-status dependent transpiration (Figs 1 and 2, cf. Leuzinger & Körner, 2007). If further soil drying takes place and $SWC_{s_2} < thr_2$, both transpiration under elevated and ambient CO₂ are decreasing asymptotically. During these very dry spells, Tr under both ambient and elevated CO₂ is modelled according to soil moisture measurements (moisture availability in soil layer 2 s_2 , see Table 1) during the centennial drought at the experimental site in 2003 (Leuzinger *et al.*, 2005):

$$Tr_e = Tr_a = \phi_1 \exp(-\exp(\phi_2)SM) + \phi_3 \exp(-\exp(\phi_4)s_2) \quad (3)$$

again with ϕ_1 to ϕ_4 the respective fitted coefficients and the subscripts a and e for ambient/elevated CO₂. Note

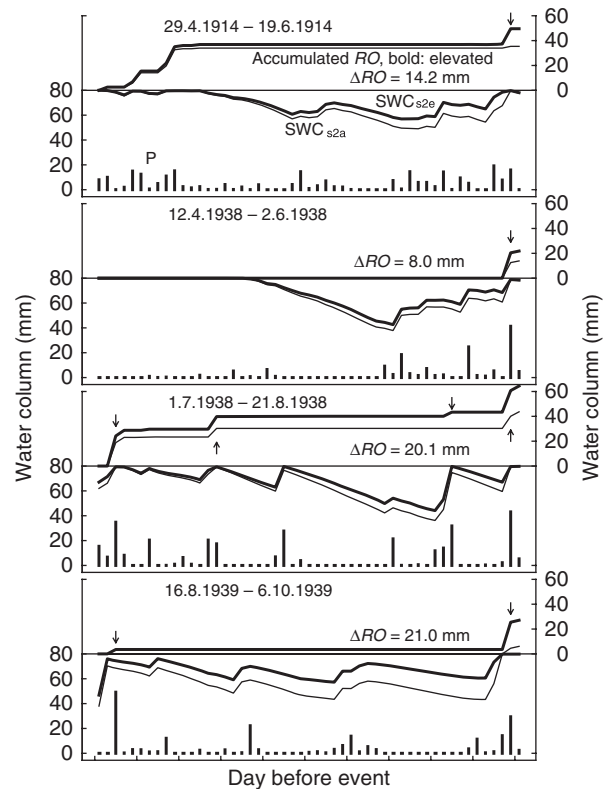


Fig. 2 Increased runoff due to elevated CO₂: shown are the four periods of 50 days each out of all 104 years with the highest additional runoff. Soil water capacities of the a/e scenarios ($SWC_{s_2,a}$, $SWC_{s_2,e}$) as well as accumulated runoff (right axis, RO) are shown with fine and bold lines respectively, arrows indicate days when $\Delta RO > 1$ mm. The bars show precipitation events during the indicated periods.

Table 1 Model variables

Variable	Description
<i>Input variables</i>	
<i>P</i>	Daily precipitation sum 1901–2004 (mm day ⁻¹)*
<i>T</i>	Daily mean temperature 1901–2004 (°C) [†]
<i>SS</i>	Daily sunshine hours [†] (h), used to calculate PET
<i>RH</i>	Relative humidity of the air [†] , used to calculate PET
<i>Rad</i>	Actual radiative energy input, combining <i>SS</i> and <i>rad_{pot}</i> (Wm ²)
<i>PET</i>	Potential evapotranspiration, calculated from above parameters (mm day ⁻¹) [‡]
<i>Tr_a</i> , <i>Tr_e</i>	Transpiration estimated from sap flow measurements (under a/e CO ₂ , mm day ⁻¹) [§]
<i>Constants [range used for sensitivity analysis in brackets]</i>	
<i>Tr_%</i>	(1– <i>Tr_e</i> / <i>Tr_a</i>) × 100, percent decreased transpiration under elevated CO ₂ , default = –14% [–17.5, –5]
<i>I</i>	Interception capacity of both canopy and litter, assumed constant (mm), default = 2 mm [1,3]
<i>s₁</i>	Water storage capacity of soil layer 1 (mm), default = 10 mm [5,15]
<i>s₂</i>	Water storage capacity of soil layer 2 (mm), default = 80 mm [80,280]
<i>thr₁</i>	Threshold within <i>s₂</i> below which on transpiration savings under elevated CO ₂ cease (mm), default = 0.7 <i>s₂</i> [0.6 <i>s₂</i> , 0.8 <i>s₂</i>]
<i>thr₂</i>	Threshold within <i>s₂</i> below which transpiration under both ambient and elevated CO ₂ decreases asymptotically according to field measurements (mm), [¶] default = 0.2 <i>s₂</i> [0.1 <i>s₂</i> , 0.3 <i>s₂</i>]
<i>sat</i>	Forced reset of soil moisture to field capacity in January, true/false, default = true [true,false]
<i>α</i>	Sweep parameter for calculation priority, 0 ≤ <i>α</i> ≤ 1; <i>α</i> = 0 <i>Ev</i> calculated first, <i>α</i> = 1 <i>p₁</i> , <i>p₂</i> and <i>RO</i> calculated first, default = 0.5 [0,1]
<i>Output variables, a/e CO₂ denoted with subscript a/e [range used for sensitivity analysis in brackets]</i>	
<i>Ev_{I,a}</i> , <i>Ev_{I,e}</i>	Interception (evaporation from interception layer, mm day ⁻¹)
<i>Ev_{s₁,a}</i> , <i>Ev_{s₁,e}</i>	Evaporation from soil layer 1 (mm day ⁻¹)
<i>Ev_a</i> , <i>Ev_e</i>	Total evaporation, (<i>Ev_I</i> and <i>Ev_{s₁}</i> combined, mm day ⁻¹)
<i>p_{1,a}</i> , <i>p_{1,e}</i>	Throughfall from interception to soil layer 1 (mm day ⁻¹)
<i>p_{2,a}</i> , <i>p_{2,e}</i>	Input soil layer 1 to soil layer 2 (mm day ⁻¹)
<i>Int_a</i> , <i>Int_e</i>	Water content of interception layer (mm)
<i>SWC_{s₁,a}</i> , <i>SWC_{s₁,e}</i>	Soil water content of soil layer 1 (mm)
<i>SWC_{s₂,a}</i> , <i>SWC_{s₂,e}</i>	Soil water content of soil layer 2 (mm)
<i>RO_a</i> , <i>RO_e</i>	Runoff (mm day ⁻¹)
<i>ΔRO</i>	Difference between runoff under ambient and elevated CO ₂ , <i>RO_e</i> – <i>RO_a</i>

*Tank *et al.* (2002).

[†]Duffie & Beckman (1991).

[‡]Monteith (1965).

[§]Leuzinger & Körner (2007).

[¶]Leuzinger *et al.* (2005).

that the above functions are first fit to the experimental data and then used for predicting transpiration during the 104 years of the model run. This results in a long term average of decreased transpiration under elevated CO₂ (*Tr_e*) of 14% compared with transpiration under ambient conditions (*Tr_a*). The percentage of reduced transpiration *Tr_%* was varied outside the experimentally measured value of 14% in order to test the sensitivity of runoff to this parameter. Transpiration is always drawn from *s₂*, never from the top soil layer *s₁*. This is compensated by transpiration of understorey vegetation, which is not considered otherwise. Preliminary runs showed that this simplification did not affect the model outcome. Total evapotranspiration (*Ev* + *Tr*) is limited to potential evapotranspiration (*PET*) as calculated from weather and astronomical data (Table 1, Fig. 1). Evaporation is drawn

exclusively from the interception layer (*I*) and *s₁*, never from *s₂*. The interception layer *I* was assumed to be constant, as more litter in winter approximately compensates for missing canopy leaves. Since no information on the within-day rain and sunshine pattern was available, a parameter *α*, which regulates the evaporation/throughfall priority was introduced (see Table 1). For example, when *α* = 0, evaporation is deducted from the water balance after input to the next lower storage compartment (*p₁*, *p₂*, Fig. 1). This simulates a day on which rain occurs first, followed by dry weather. On the other hand, if *α* = 1, evaporation is deducted first, simulating a day on which several rain events, interrupted by dry spells, take place. As *α* varies from 0 to 1, random within-day rain/sunshine patterns are simulated. This allows to test the sensitivity of runoff to different within-day rainfall distribution

Table 2 Model run summary, average and standard errors over all 104 years (mm a⁻¹)

Variable	This study (mean)		SE		Mean of seven studies of temperate deciduous forests*	SE
	Ambient	Elevated	Ambient	Elevated		
Precipitation (<i>P</i>)	794		13.6		818	78
Interception (<i>Ev_I</i>)	192		2.2		167	26
Evaporation from <i>s</i> ₁ (<i>Ev_{s1}</i>)	188		2.6		136	20
Transpiration (<i>Tr</i>)	221	216	2.8	2.7	315	20
Evapotranspiration (<i>Ev_{s1}</i> + <i>Tr</i>)	409	404	3.8	3.7	451	39
Runoff (<i>RO</i>)	193	199	9.4	9.7	200	71

*Lösch (2001).

The last column shows an average of seven studies on temperate deciduous forests. Numbers rounded to nearest integers, except for SE.

patterns. The initialization of the model was carried out assuming saturated soil layers (*s*₁ and *s*₂) but test runs with lower initial saturation proved that this is not critical for the model outcome. The model was first run over all 104 years with all model constants set to what was thought is the best estimate for the SCC site or to the best estimate from the literature where available (Walthert *et al.*, 2004, called the 'default settings' hereafter, see Table 1). These settings also coincide with the best correlation of the calculated runoff with river discharge data from an adjacent catchment. Maximum canopy and litter interception (*I*) was set to 2 mm. Soil water storage capacity of soil layers 1 and 2 (*s*₁ and *s*₂) was set to 10 and 80 mm respectively (based on a soil profile at a close-by site, Walthert *et al.*, 2004). There is no explicit assumption on maximum tree rooting depth, *s*₂ represents the total soil water which is available to trees. This is a comparatively shallow accessible soil profile for this type of forest, the effect of a deeper soil were explored by varying *s*₁ from 5 to 15 and *s*₂ from 80 to 280 mm. The actual rooting depth is much deeper, as illustrated by tree water relations during a three month drought period (Leuzinger *et al.*, 2005). The remaining parameters were chosen as follows: *thr*₁ = 0.7*s*₂, *thr*₂ = 0.2*s*₂, *sat* = true and $\alpha = 0.5$. The sensitivity analysis involved varying these parameters over a wide range (indicated in square brackets in Table 1). The free software package 'R', version 2.6.0 (R Development Core Team, 2007) was used for all data processing, programming, statistical analyses and graphics.

Results

General model validation and performance

On average, the ca. 800 mm annual precipitation are distributed approximately equally between interception, evaporation, transpiration and runoff (Table 2). We also find a good correlation ($R_{adj}^2 = 0.65$) of the calculated runoff with 71 years of river discharge of an adjacent catchment. Forced saturation of the lower soil layer in

January (*sat*) only decreases ΔRO (runoff under elevated CO₂ – runoff under ambient CO₂) by 0.2 mm a⁻¹, which shows that the model is in equilibrium and field capacity is reached at least once every year.

Reduced transpiration under elevated CO₂

Over the whole 104-year period, the reduced transpiration under assumed CO₂-enrichment (540 ppm) yields an increase in runoff of only 5.5 mm (2.9%, with default settings, which represent the most plausible estimates based on the literature, see 'Materials and methods' section). Out of the 37 986 days (1 January 1901–31 December 2004), only days 576 (1.5%) produce higher runoff in the elevated CO₂ scenario ($\Delta RO > 0$). On 4337 out of 37 986 days (11.4%), there is runoff, but with no difference between the low and high CO₂ scenario. The largest value of ΔRO for one single day is 17.4 mm. The analysis of the history of four events with the highest increased runoff due to elevated CO₂ shows that relatively long periods (> 25 days) with moderate rain events (< 20 mm) are necessary to produce a substantial ΔRO -effect (Fig. 2). Very long, dry periods cause the initial effect to disappear, as transpiration reduces in response to dry soil in both (a/e) scenarios. During very wet periods, differences in soil moisture between the scenarios remain small and a ΔRO -effect cannot build up.

On a yearly basis, only 1 out of 17 years produces a CO₂-signal of $\Delta RO > 20$ mm a⁻¹ and this result depends on average on four rain events (days) per year. The maximum ΔRO due to the physiological CO₂-response is 46 mm a⁻¹ for the rainfall pattern of the year 1938. The average ΔRO for years that produce a difference in runoff due to CO₂ ($\Delta RO > 0$) is 8.9 and 13.6 mm a⁻¹ for years with $\Delta RO > 5$ mm.

Sensitivity of increased runoff to model parameters

Runoff effects of elevated CO₂ (ΔRO) averaged over all 104 years are nine times more sensitive to changes in

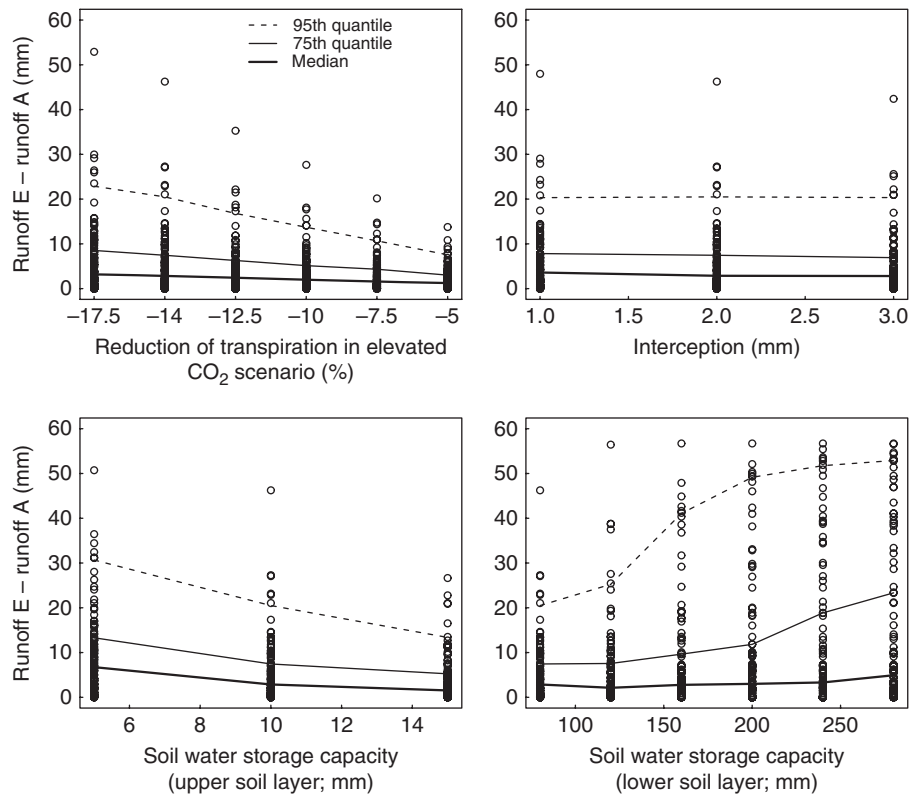


Fig. 3 Sensitivity of % decreased transpiration under elevated CO_2 ($Tr\%$), Interception (I), soil water capacity of soil layer 1 (s_1), and soil water capacity of soil layer 2 (s_2 , top left to bottom right). The other model constants are held constant at default values (see text) for each box plot. Each year is represented by a dot, the bold line shows the median, the thin line the 75th, and the dashed line the 95th percentile of all 104 years. The majority of years only show a small difference ($> 10 \text{ mm a}^{-1}$) between the a/e scenario as parameters change. The conspicuous outlier corresponds to year 1938.

rain pattern (ΔRO between 0 and 46.3 mm a^{-1} , Fig. 3 top left panel, at a reduction in transpiration of 14%) than to changes in soil water storage capacity (ΔRO between 1.2 and 6.7 mm a^{-1} , Fig. 3 bottom left panel, bold line). Note that in Fig. 3, the data points represent individual years and thus different rain patterns, while the bold, fine and dashed lines indicate the median, 75th and 95th percentile of all years. The difference in runoff, ΔRO , does not exceed 9 mm a^{-1} (median of all years) in any combination of the model parameters. Varying the storage capacity of the upper and lower soil layer (s_1 and s_2) from 5 to 15 and from 80 to 280 mm have the second largest (5.2 and 2.0 mm a^{-1}) effect on the median of ΔRO . The sensitivity of ΔRO to changes in the purely technical model constants (transpiration thresholds thr_1 and thr_2 , soil saturation in January sat , and the evaporation/throughfall priority parameter α) are generally lower than the sensitivities to the model constants shown in Fig. 3. In more extreme years, i.e. years which produce a higher ΔRO -effect (25 out of 100 years, 75th percentile, thin line; 5 out of 100 years, 95th percentile, dashed line; Fig. 3), the sensitivities generally increase.

On the other hand, interception (I) yields almost identical ΔRO for values between 1 and 3 mm, even in years with considerable ΔRO . As expected, if transpiration in the elevated CO_2 scenario increases (decreasing $Tr\%$), the ΔRO -effect decreases (nearly linearly and to a larger extent in more extreme years). The effect of varying soil water capacities s_1 and s_2 in years with large ΔRO are opposite: ΔRO decreases with larger s_1 and increases with larger s_2 , with the strongest effect for the 95th percentile in s_2 . The conspicuous outlier in all plots of Fig. 3 refers to the year 1938 with its unusual rain pattern (215 rain free days combined with the relatively high yearly precipitation sum of ca. 900 mm). However, the other 5 years with the highest total ΔRO -effect do not show any particularity and are well within the range of the other years in terms of total precipitation vs. rain free days. We tried to characterize years with rainfall distribution patterns that produce the highest ΔRO -effect using the available climate data. A linear discriminant analysis could not successfully isolate the years with the highest ΔRO -effect using eight climate parameters (number of days with rain, rain sum and

mean temperature, mean relative humidity and mean cloud cover for both summer and winter months).

Discussion

Our three-layer bucket model, constructed on the basis of physiological and soil moisture data from a tall tree FACE experiment and driven by 104 years of daily climate data adequately represents the water budget of a temperate deciduous forest. The water balance resulting for the ambient scenario (averaged over all 104 years) is close to the average of seven studies on water relations of deciduous temperate forests (Table 2, Lösch, 2001). The model answers two fundamental questions in forest hydrology under future atmospheric CO₂-concentrations: (1) How does a first-order physiological CO₂-effect on forest transpiration cascade down to an ecosystem runoff-effect? (2) Under which conditions may an extreme rain event under future CO₂-conditions lead to enhanced runoff and possibly cause increased flooding risk?

While most predictions agree that ΔRO is likely to increase in the next 100 years, the separation of the drivers of this process is difficult. Our model is not a mechanistic prediction of runoff under climate change, it elucidates one particular aspect, namely the physiological effect of CO₂ on runoff and the associated hysteresis mechanism (mitigation of the propagation of the initial effect on soil moisture). Nevertheless, we relate our results to previous reports on the physiological CO₂-effect on runoff of more sophisticated models. Our results support the view of Piao *et al.* (2007) that, based on experimental data, the effect may be a lot smaller than estimated based on observational data using statistical methods by Gedney *et al.* (2006), suggesting that other than the assumed stomatal drivers are responsible for the observed changes in continental discharge. Despite a measurable decrease in transpiration under elevated CO₂ (due to partial stomatal closure), there is only limited propagation of this effect down to the level of yearly ecosystem runoff. A first-order CO₂-effect during ample water supply of ca. -14% (Leuzinger & Körner, 2007) translates to a mere 2.9% reduction in yearly ecosystem runoff (ΔRO ; estimates for the year 2070 compared with 2000, based on the rising CO₂-concentration only), provided the model is run with daily resolution. This is lower than most previous studies suggest. Cramer *et al.* (2001) compare six dynamic global vegetation models with a focus on the carbon cycle. They find that on average, global runoff might change between -3% and +47% from 1990 to 2100 due to the assumed physiological CO₂-effect alone. The wide range of estimates between the reviewed models shows the high uncertainty associated with such predictions. Climate warming alone has a marginal effect on runoff

in all reviewed models. More recently, Betts *et al.* (2007) used a global climate model with a vegetation component and predicted a 6% increase in global ΔRO (caused by the physiological CO₂-effect only) for doubled atmospheric CO₂ compared with the preindustrial CO₂ concentration. If the same time horizon as in our study is considered (ca. 2000–2070), the estimate of Betts *et al.* (2007) reduces to ca. 3% increased ΔRO , which is close to what our model predicts.

A fundamental difference between these global vegetation models and the present bucket model for a temperate, deciduous forest is the implementation of the physiological CO₂ effect on plants. Our model, while accurately capturing the basic water budget of a temperate forest, does not rely on a cascade of upscaling steps from a leaf-level stomatal response to elevated CO₂. Instead, this theory-based scaling (which in all models ultimately drives the physiological CO₂-effect on ΔRO) is replaced by experimental sap flow data from a FACE site, which account for aerodynamic coupling and energy balance effects at canopy level. Tall trees' stomatal responses to CO₂ clearly do not follow theoretical predictions (Keel *et al.*, 2007). For conifers (not considered here) such theory-based predictions would fail completely, since no mature conifer has ever been shown to significantly (measurably) reduce stomatal conductance when exposed to elevated CO₂ (Ellsworth *et al.*, 1995; Ellsworth, 1999; Körner *et al.*, 2007). As we will discuss below, however, the net water saving effect, driven by whatever mechanism, may be less decisive for runoff estimates than the future rainfall distribution at a daily resolution.

In order to evaluate likely constellations for extreme ΔRO -effects in a future climate, we made use of the 104 different rainfall distribution patterns (years) and different combinations of model constants. Random combination of the values for the eight model constants (Table 1, nearly 18000 combinations) yields a maximum of ca. 9 mm a⁻¹ (6.2%) increased runoff under elevated CO₂ across all 104 years. On the other hand, randomly selecting individual years combined with a fixed combination of model constants yields a ΔRO in the range of 0–55 mm a⁻¹ (Fig. 3). With default parameter settings (representing the best estimate available for the non-measurable model constants defined in Table 1), the random selection of a particular year causes a range in ΔRO of 0–46 mm a⁻¹. Therefore, the rainfall distribution pattern is by far the most important determinant of increased runoff due to elevated atmospheric CO₂-concentrations in this temperate deciduous forest. However, years with such rainfall distribution patterns are not easily predicted using standard climate parameters. While the year with the highest ΔRO -effect (1938) shows an exceptionally high total precipitation compared with its number of rain free days, this does

not hold for the other years with a strong ΔRO -effect. Although Fig. 2 shows that moderately long periods with relatively little rain are necessary to produce substantial ΔRO -effects, we could not find general climatic characteristics of years producing larger ΔRO than others. We suggest that the stochastic component of rainfall patterns is ultimately the strongest driver of changes in runoff under future CO_2 -concentrations. Models not using a realistic precipitation distribution pattern are thus severely compromised in the accuracy of their output. In our model, we tried to simulate within-day rainfall distribution with the parameter α , which linearly combines two extreme cases: after rainfall, priority is given either to evaporation (simulating several rain events) or to through fall (simulating a single rain event). Varying α does not cause substantial changes in ΔRO , which suggests that a daily resolution may be sufficient for modelling ΔRO .

While the sensitivity of ΔRO to the model constants is small across all years, this is not the case for years with unusual rainfall patterns (75th and 95th percentile marked in Fig. 3). Increasing water storage capacity in the upper soil layer (s_1 , bottom left panel in Fig. 3) seems to decrease ΔRO , possibly because in the present model, only (CO_2 -insensitive) evaporation is drawn from s_1 , which increasingly buffers the CO_2 -effect as its storage capacity increases. It is likely that the 95th percentile line in the bottom right panel of Fig. 3 would be hump-shaped, had we tested soils with even larger water storage capacity. In fact, soils with zero (e.g. bare rock) as well as infinitely large water storage capacity cannot produce a CO_2 -effect in runoff. Relative to the changes applied to s_1 , the range of values used for interception (I , 1–3 mm) is probably too low to cause noticeable changes in ΔRO (top right panel, Fig. 3). However, it is unlikely that the value for I will be outside the tested range in most vegetation types. In comparison to the effect of reduced transpiration under elevated CO_2 (Fig. 3, top left panel, dashed line), the soil storage capacity term has a much larger effect on ΔRO (Fig. 3, bottom right panel, dashed line). Therefore, although a lot of effort has been put into quantifying reduced transpiration under elevated CO_2 (e.g. Medlyn *et al.*, 2001; Morgan *et al.*, 2004), accurate information on soil water capacities and rainfall patterns may be more important for estimating the water balance of forests under future CO_2 -concentrations. Such data however are often difficult to obtain, and many models have to work with rough assumptions that cannot be verified (Cramer *et al.*, 2001).

To assess the potential of increased flooding risk, maximum daily effects must be known. The maximum daily ΔRO -effect of ca. 17 mm ($17 L m^{-2} days^{-1}$) that we arrived at for the rainfall regime of the past 104 years would certainly be dangerous if it was to coincide with a

peak rainfall event. However, the maximum ΔRO -effects in this study often occurred at the first large precipitation event following a long (20–50 days) period of low to moderate rainfall (Fig. 2). An analysis of the largest flooding events in the Birs catchment (where climate data used here originate from) during the 20th century showed that none of the events would have been amplified substantially by a physiological CO_2 -effect, because they occurred when soils were already saturated. Future precipitation scenarios point towards more intense rain events (Groisman *et al.*, 2005; Tebaldi *et al.*, 2007), which, for the ecosystem modelled here, tends to further reduce a potential CO_2 -effect on runoff. Although our model is constructed and designed for one particular plant functional type (temperate, deciduous forest), the mechanisms behind our finding of a relatively small average ΔRO -effect may be more generally applicable. For grassland, close to the same site where the data for this study originate, ca. 7% reduced transpiration under elevated CO_2 has been found on bright summer days (Stocker *et al.*, 1997). Rainfall distribution will be a key driver for changed runoff in this grassland ecosystem as well, and changes in interception, soil water storage and the amount of reduced transpiration will be secondary in determining ΔRO .

In conclusion, based on our FACE data, we find a yearly net increase in ΔRO due to a physiological CO_2 -effect that is much smaller than expected from leaf level signals and from theory-based assumptions. For a given ecosystem, the exact amount of reduced transpiration under elevated CO_2 seems less important than the temporal distribution of a given amount of rainfall over a test period and water storage capacity in the rooted soil volume.

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