

Whole ecosystem metabolic pulses following precipitation events

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Summary

1. Ecosystem respiration varies substantially at short temporal intervals and identifying the role of coupled temperature- and precipitation-induced changes has been an ongoing challenge. To address this challenge we applied a metabolic ecological theory to identify pulses in ecosystem respiration following rain events. Using this metabolic framework, precipitation-induced pulses were described as a reduction in metabolic activation energy after individual precipitation events.
2. We used this approach to estimate the responses of 237 individual events recorded over 2 years at four eddy-covariance sites in southern AZ, USA. The sites varied in both community type (woody and grass dominated) and landscape position (riparian and upland). We used a nonlinear inversion procedure to identify both the parameters for the pre-event temperature sensitivity and the predicted response of the temperature sensitivity to precipitation. By examining multiple events we evaluated the consistency of pulses between sites and discriminated between hypotheses regarding landscape position, event distributions, and pre-event ecosystem metabolism rates.
3. Over the 5-day post-event period across all sites the mean precipitation effect was attributed to 6.1 g CO₂ m⁻² of carbon release, which represented a 21% increase in respiration over the pre-event steady state trajectory of carbon loss. Differences in vegetation community were associated with differences in the integrated magnitude of pulse responses, while differences in topographic position were associated with the initial peak pulse rate. In conjunction with the differences between sites, the individual total pulse response was positively related to the drying time interval and metabolic rates prior to the event. The quantitative theory presented provides an approach for understanding ecosystem pulse dynamics and helps characterized the dependence of ecosystem metabolism on both temperature and precipitation.

Key-words: eddy-covariance, precipitation, pulse, respiration, semi-arid

Introduction

Quantifying ecosystem metabolic responses to environmental changes is a key challenge for understanding the constraints to biologic functioning and the feedbacks of terrestrial systems to atmospheric gas composition and climate variability (Canadell *et al.* 2000; Schimel *et al.* 2001). Extensive research has focused on the temperature sensitivity of ecosystem respiration (Kirschbaum 1995; Allen, Gillooly & Brown 2005; Knorr *et al.* 2005; Enquist *et al.* 2007). However, precipitation variability introduces substantial uncertainties in the functioning of terrestrial ecosystems (McClain *et al.* 2003; Huxman *et al.* 2004b; Jenerette & Lal 2005; Siqueira *et al.*

2006). A concise theoretical framework is needed to couple ecosystem temperature and precipitation responses to allow for meaningful comparisons, test alternative hypotheses, and improve ecological modelling capabilities.

To broadly understand the effects of temperature on ecological variability a general metabolic theory of ecology has been developed (Brown *et al.* 2004). While much of this theory has focused on understanding geometric constraints to metabolism, recent studies have also addressed metabolic temperature sensitivities (Allen *et al.* 2006; Anderson *et al.* 2006; Anderson-Teixeira, Vitousek & Brown 2008). Central to metabolic theory is the quantitative model of metabolic responses to temperature variation described by the Arrhenius equation (Lloyd & Taylor 1994; Gillooly *et al.* 2001; Enquist *et al.* 2003; Allen *et al.* 2005):

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$$R = Ae^{\frac{-E_a}{kT}} \quad \text{eqn 1}$$

R is respiration (commonly measured in units of $\mu\text{mol C m}^{-2} \text{ s}^{-1}$). A (has same units as R) is a normalization constant that depends primarily on the amount of available substrate. E_a is the activation energy (eV) and is a joint property of both enzymatic and substrate characteristics. T is temperature (measured in Kelvin) and k is Boltzman's constant (eV K^{-1}). The mechanistic interpretation of the Arrhenius model is based on a statistical mechanical, estimation of the fraction of organic molecules whose kinetic energy is $> E_a$ for the production of CO_2 , (i.e. the exponential term in Eq. 1). E_a A main critique of research examining biological temperature sensitivities has highlighted the dynamic temperature sensitivity of biologic systems (Luo *et al.* 2001; Clarke & Fraser 2004; Yuste *et al.* 2004; Davidson, Janssens & Luo 2006).

In contrast to the continuous response of ecosystem respiration to temperature, a growing number of studies have suggested ecosystem respiration has a pulsed response to precipitation events (Noy-Meir 1973; Huxman *et al.* 2004b; Lee *et al.* 2004; Xu, Baldocchi & Tang 2004; Jarvis *et al.* 2007). Because terminology varies in the literature (Reynolds *et al.* 2004), we explicitly use 'pulse' in reference to the ecological response and precipitation event in reference to the trigger (Noy-Meir 1973). Pulse responses are hypothesized to result from both rapid changes in the biological demand for energy, effectiveness of enzymes, and the availability of highly labile organic matter substrates. Microbial activity can increase rapidly following precipitation with up to 40% increases in microbial cell counts observed within 2 days of a precipitation event (Saetre & Stark 2005). The increased effectiveness of enzymes and consequent reduction in E_a following hydration has been established in several enzyme systems (Affleck *et al.* 1992; Daniel *et al.* 2003; Eppler *et al.* 2006). Soil wetting increases the reactivity and availability of labile soil organic compounds through microbial lysis (Kieft, Soroker & Firestone 1987), the release of stored cytoplasmic solutes (Fierer & Schimel 2003), or the disruption of physically protective soil (Denef *et al.* 2001). Several experiments using soils from a range climatic regions support the importance of each mechanism (Birch 1958; Fierer & Schimel 2003; Huxman *et al.* 2004a; Saetre & Stark 2005; Tang *et al.* 2005b; Yuste, Janssens & Ceulemans 2005; Sponseller 2007); however, few whole ecosystem studies have been conducted (Lee *et al.* 2004; Xu *et al.* 2004).

Here we ask two question at the scale of whole ecosystems: are precipitation induced pulses consistently observed and how do these pulses vary? For whole ecosystems the magnitude and duration of respiration pulses may be related to landscape position, community structure, precipitation event patterns, and ecosystem metabolic activity prior to the event (Huxman *et al.* 2004b; Xu *et al.* 2004). Landscape position along a topographic continuum from upland to riparian sites may influence pulse response by (1) elevated availability of organic matter in riparian sites leading to increased responses or (2) the availability of near surface groundwater may mute the

sensitivity of riparian sites to individual precipitation events. Lee *et al.* (2004) suggested upland topographic regions may be particularly sensitive to precipitation induced pulses. Similarly, differences in vegetation community may influence pulse responses where (1) grassland dominated systems may be more responses to environmental fluctuations (Knapp & Smith 2001) leading to larger pulses or (2) the increased organic matter commonly associated with woodlands may lead to larger pulses. Contrasting hypotheses suggest pulse magnitude may be related to the size of the precipitation event, with (1) events lasting longer because the soils are wetter (Misson *et al.* 2006), or (2) precipitation acts as a trigger where the response is independent of the size of the event and the decay of the pulse is much faster than the evaporation rate (Huxman *et al.* 2004b; Potts *et al.* 2006; Sponseller 2007). If the decay of the pulse response is related to water availability, the decay rate is predicted to follow a square root decay function (Baldocchi, Law & Anthoni 2000; Denmead & Shaw 1962), while if the pulse length is substrate limited the decay rate is predicted to be steeper. The dry-time interval before an event may influence the pulse response, with (1) larger pulse responses resulting from the build-up organic matter substrate during the dry-time or (2) smaller pulse responses due to limited available of recent photosynthate, which often contributes to ecosystem respiration (Hogberg *et al.* 2001; Tang *et al.* 2005a; Baldocchi, Tang & Xu 2006) and photodegradation on the surface, which may reduce labile carbon pools (Austin & Vivanco 2006). Ecosystem metabolic activity prior to the event has been hypothesized to affect the pulse response as nonlinear state-shifts between quiescent and active states result in an inverse relationship between pulse size and antecedent ecosystem metabolic activity (Huxman *et al.* 2004b; Xu *et al.* 2004; Potts *et al.* 2006).

Testing these hypotheses have been challenging because an effective theory has not been available to couple available data with predictions from the diversity of fine scale mechanisms responsible for pulse responses. At the microbe-soil-substrate interface pulses result from multiple processes requiring large numbers of parameters not readily identifiable in field or laboratory conditions. Our solution to this problem describes these multiple processes as an ecosystem scale decrease in the E_a of respiration. A dynamic ecosystem E_a does not suggest changes in organic matter availability are unimportant, in contrast it provides an effective description of the multiple changes in substrate-enzyme interactions and in part reflects changes in organic matter availability. This extension to general metabolic theory provides the opportunity to test hypotheses regarding the trajectory of whole ecosystem pulses in terms consistent with many ecosystem models and fine scale mechanisms.

Methods

To explore the coupled metabolic-pulse theory and evaluate pulse response hypotheses we examined whole ecosystem respiration observations over 2 years in four contrasting sites in southern Arizona, USA varying in vegetation composition and topographic position.

Two of the sites (riparian woody and riparian grassland) are riparian bottomland communities with access to groundwater and the others (upland Savanna and upland grassland) are solely dependent on precipitation. This matrix of sites allows for an examination of both topographic effects (upland and riparian) and vegetation effects (grass and woody dominated). These sites are representative of Sonoran desert climate (hot and dry) and vegetation (shrub-grass desert with lush riparian areas). The Sonoran desert has a bimodal precipitation distribution, with both a summer and winter rainy season with concomitant summer and winter growing seasons. Annual precipitation during the period analysed was within 30% of the long-term average for the region. The precipitation was distributed characteristically for the region, with many small events and drying time intervals and few large events and drying intervals (see Huxman *et al.* (2004b) for detailed analysis).

To measure whole ecosystem respiration we used data from eddy-covariance systems (Goulden *et al.* 1996; Baldocchi 2003). Scott *et al.* (2004, 2006) have described the riparian sites, instrumentation and data processing. The upland sites were constructed and are maintained using the same methods used at the riparian sites. Data from years 2004 and 2005 are analysed here. All towers were operating throughout both years except the upland grassland site, which was installed in early spring 2004. Briefly, an open-path infra-red gas analyser and a sonic anemometer were mounted on a tower above the top of the plant canopy. From these instruments, measurements of atmospheric CO₂ concentration and meteorological conditions were obtained at 10 Hz. The covariance between the vertical wind speed and CO₂ concentrations were computed over a 30 min interval, from which estimates of CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) were generated. Data processing included coordinate rotation, addition of the 'wpl' term, removal of data for non-stationary periods, accounting for changes in storage by using the concentration changes measured by the IRGA, and the removal of observations with low atmospheric turbulence (Scott *et al.* 2006). Estimates of ecosystem metabolic activity were obtained by examining night-time fluxes, when there was no photosynthetic uptake. The instrumentation and numerical algorithms are within the standard protocols of the Ameriflux eddy-covariance network and the half-hourly data have been archived in this network <<http://public.ornl.gov/ameriflux/>>. Additional long-term meteorological data throughout the region can be acquired from the Arizona Meteorological Network <<http://ag.arizona.edu/azmet/.html>>.

From each site all precipitation events over the two year study period were identified from the meteorological station located at each tower. Air temperature and night-time carbon fluxes were extracted from the preceding 5 days of each event, the pre-event period, and the following 5 days, the post-event period. The parameters of the Arrhenius model were identified for each pre-event period using a nonlinear maximum likelihood-based inversion procedure (Richardson & Hollinger 2005). Similar procedures have been widely used in ecology and particularly for understanding eddy-covariance derived fluxes (Braswell *et al.* 2005; Richardson & Hollinger 2005; Sacks, Schimel & Monson 2007; Wang *et al.* 2007). As a check on the suitability of the identified parameters, a linear regression analysis was conducted between the observed and modelled fluxes; events where a significant ($P < 0.05$) pre-event model could not be identified were excluded from further analysis.

The effect of precipitation was identified using residuals from the observed post-event respiration rates and the pre-event derived model parameters. The residual error provides a direct estimate ($\mu\text{mol C m}^{-2} \text{s}^{-1}$) of the instantaneous variation in respiration caused by the precipitation event. To transform the observed change in respiration rates into changes in ecosystem E_a , we rearranged the Arrhenius equation to algebraically solve for E_a :

$$E_a = -kT(\ln(R_{\text{observed}}) - \ln(A)) \quad \text{eqn 2}$$

This algebraic rearrangement of the Arrhenius equation reduced E_a when the pre-event model underestimates post-event respiration. The trajectory of ecosystem E_a following a precipitation event was quantified as an exponential decay function:

$$\Phi = -\Delta e^{-\Lambda d} \quad \text{eqn 3}$$

Φ is the precipitation induced reduction in E_a through time following rainfall, Δ is the initial maximum reduction in E_a , Λ is the decay rate of the precipitation effect, and d is the number of days since the most recent rain event. The nonlinear inversion approach used to estimate the Arrhenius temperature sensitivity was also used to identify the parameters of Eq. 3. An integrated 5-day precipitation effect was estimated by computing the difference between the respiration model using only the pre-event parameters and the precipitation event altered ecosystem E_a for the entire post-event meteorological record. These event statistics were computed individually for each precipitation event. The data describing pulse trajectories derived from these analyses were used to test predictions of pulse responses.

Results

Pulse responses of ecosystem respiration were readily identified following precipitation events (Fig. 1a). By

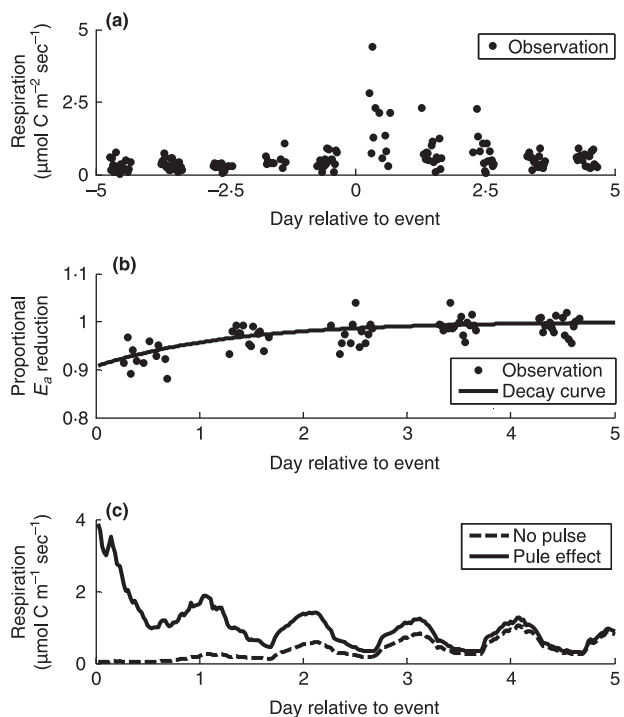


Fig. 1. An example of precipitation pulse dynamics from an early-summer event in the upland woodland. The observed fluxes both from 5 days before the event and 5 days after the event show the pulse of respiration following the precipitation event. The error in activation energy (eV) from the pre-event model and the resulting exponential decay model describe the trajectory of respiration dynamics (b). The gaps in data (a and b) result from exclusion of daytime values. The resulting modelled fluxes over 5 days after the event showing both the pre-event parameters and the precipitation model (c).

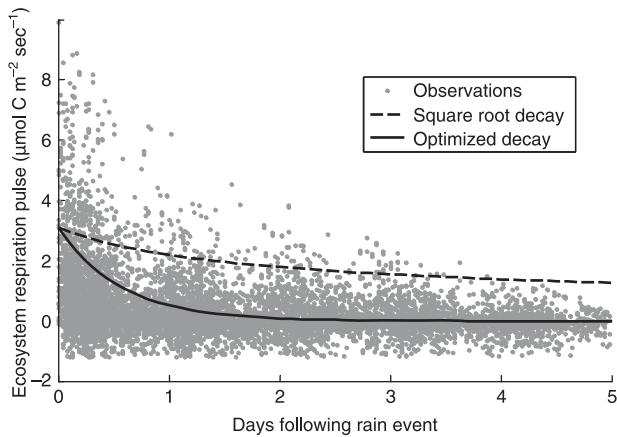


Fig. 2. Observed pulse effect on respiration ($\mu\text{mol C m}^{-2} \text{s}^{-1}$) following all rain events over two years at four sites. This is a direct measurement of ecosystem metabolic activity attributable to a precipitation event, that has been normalized by the pre-event temperature sensitivities. The solid line shows the best fit decay function. The dashed line shows the square root decay function, which would be predicted from soil drying alone.

converting the post-event pulse flux rates to reductions in E_a , an exponential decay function described the trajectory of ecosystem temperature sensitivity (Fig. 1b). The event dependent dynamics of ecosystem E_a allowed for an integrated pulse response to be estimated and its expected pattern through time to be predicted (Fig. 1c). This example event highlights how pulses were identified, described and integrated over 5 day periods.

Across all four sites and for 2 years 237 precipitation events were identified and a range of ecosystem responses were observed following the events (Fig. 2). Overall, an immediate increase in respiration was generally observed and this effect decreased following an exponential decay that was substantially steeper than a square root decay expected based on evaporation (Denmead & Shaw 1962). The mean precipitation induced change in metabolic activity resulted in a reduction of the pre-event E_a by 3.8% from a mean pre-event E_a across all events of 0.57 (eV). Over the 5-day post-event period the mean precipitation effect was attributed to a 6.1 ($\text{g CO}_2/\text{m}^2$) of carbon release, which represented a 21% increase in respiration compared to pre-event rates of carbon loss. Caution is warranted in scaling this effect to an annual contribution to ecosystem respiration – current respiration estimates are an uncertain combination of pulse and non-pulse dynamics – a simple multiplication of pulse effect by precipitation events would have unknown uncertainties and biases.

Vegetation community and topographic position showed different responses of total pulse induced changes in respiration (Fig. 3). Larger 5-day integrated inductions of metabolic activity were seen in grassland communities as compared to woody dominated communities (ANOVA with Bonferonni adjusted *post hoc* tests $P < 0.05$). Differences in topographic position were related to differences in the initial magnitude, Δ , of change in metabolic state (ANOVA with Bonferonni adjusted *post hoc* tests $P < 0.05$); in this case, upland sites were more responsive than riparian sites (Fig. 3). In addition to differences between sites, both metabolic and precipitation characteristics

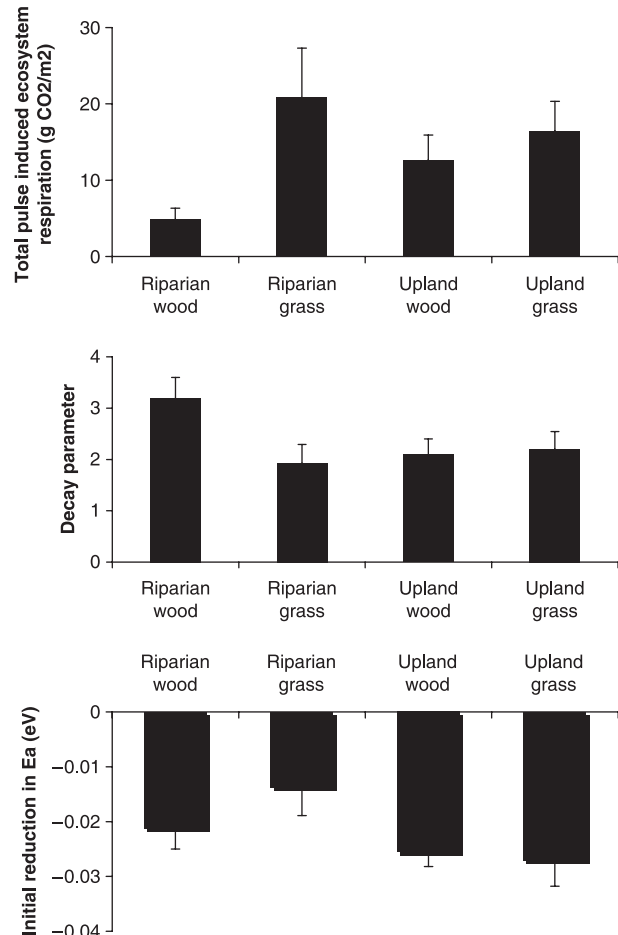


Fig. 3. Precipitation response dynamics including the total estimated respiration flux, (b) the initial maximum reduction in activation energy (b), and the decay factor (c). These are site means and standard errors of all precipitation events for 2 years.

associated with each event were related to the pulse responses. The total precipitation effect after 5 days was positively related to dry time interval before the event and negatively related to the prior metabolic activity (Fig. 4). A positive effect of antecedent metabolic activity and a negative effect of event size were related to the initial component of the pulse, the immediate reduction in E_a (Fig. 5) (linear regression $P < 0.05$). The effect of pre-event ecosystem metabolic activity on the initial pulse was associated with variation in the pre-event ecosystem E_a and not the normalization constant (linear regression $P < 0.05$). When the ecosystem had a higher E_a and therefore lower metabolic activity, the initial pulse response to precipitation was larger.

Discussion

Coupling a theory of ecosystem metabolic temperature dependence to a pulse dependent precipitation response allowed for quantification, comparison and hypothesis testing of pulse events. Understanding both continuous and discontinuous factors that govern ecosystem dynamics and sources of variability is important for producing a predictive framework for understanding ecosystem dynamics in varying

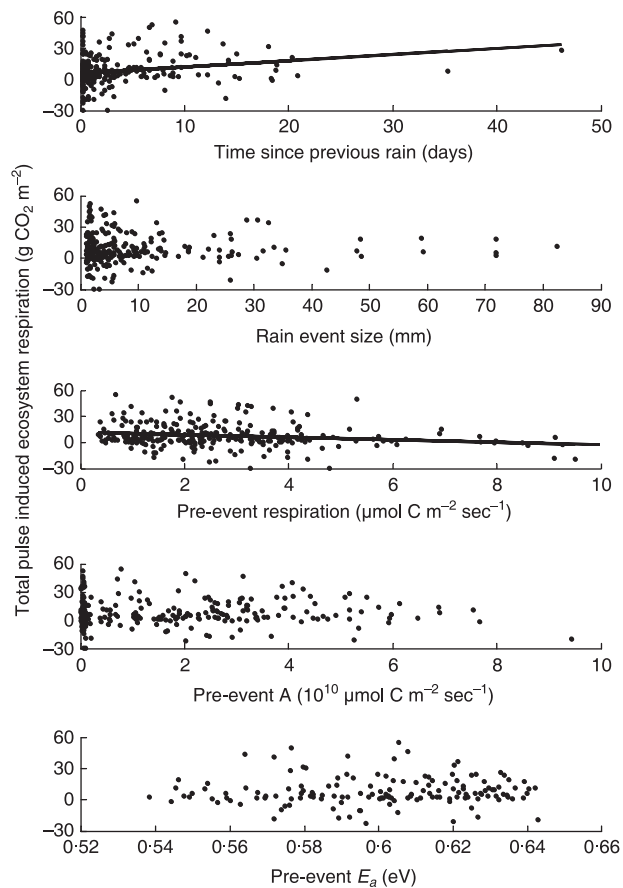


Fig. 4. Sensitivity of the total precipitation pulse response after 5 days to prior metabolic rates and event characteristics. Pre-event metabolic rate characteristics include both parameters of the Arrhenius model and an evaluation of the model at 30 °C. The event characteristics include both the time since the previous rain and the size of the rain event. Lines are included when regression analysis identified a significant relationship ($P < 0.05$).

meteorological conditions. The coupled metabolic and pulse theory generated here was both empirically useful for describing whole ecosystem dynamics and consistent with mechanisms described by micro-scale changes in enzymatic reactivity and substrate availability. Independent model inversions for each of the 237 events allowed us to maintain the mechanistic description of E_a based temperature dependence while generating a comprehensive data base describing pulse variability.

In general, the resulting observations of pulse dynamics followed the hypothesized pulse trajectory response of an initial maximum increase in metabolism followed by a rapid return to the pre-event conditions likely related to substrate limitation rather than soil drying (Fig. 2). These results extend previous controlled experiments and observations of individual events to allow quantitative analyses of whole ecosystem responses to multiple events at multiple sites. As ecosystem pulse responses have been observed in more mesic environments (Yuste *et al.* 2003; Lee *et al.* 2004), our approach provides a succinct framework for understanding pulse variability across broad climate gradients. New experiments identifying the dynamics of temperature sensitivities associated with drying–rewetting cycles are needed to further

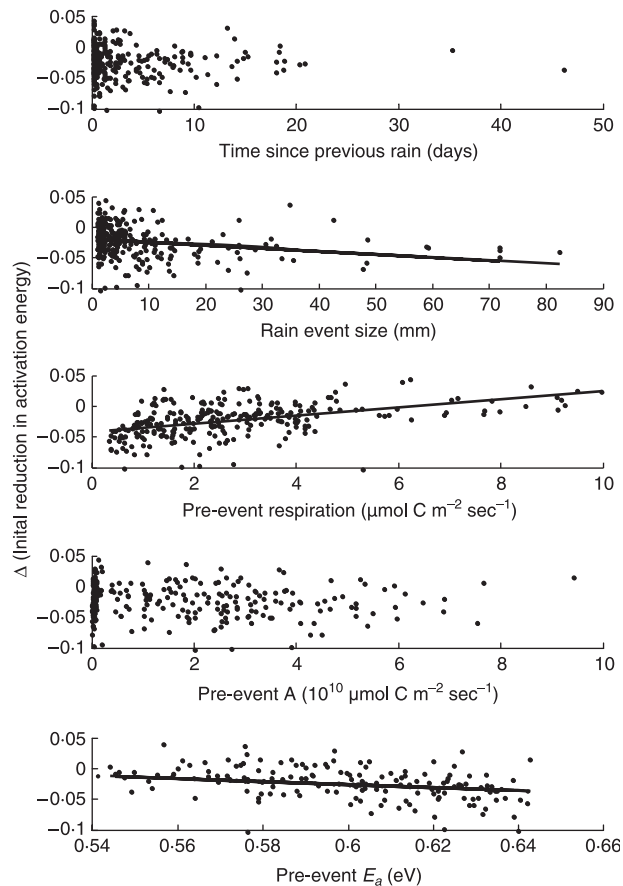


Fig. 5. Sensitivity of the initial precipitation pulse response to prior metabolic rates and event characteristics. Pre-event metabolic rate characteristics include both parameters of the Arrhenius model and an evaluation of the model at 30 °C. The event characteristics include both the time since the previous rain and the size of the rain event. Lines are included when regression analysis identified a significant relationship ($P < 0.05$).

test and validate the mechanistic appropriateness of this coupled theory. For example, partitioning the overall control of the reduction in E_a between biotic dynamics of microbes and plants that change the availability of enzymatic activity vs. the physical features of soil wetting and drying that control substrate availability will be important in comparing disparate ecosystem types. Coupling these precipitation event driven processes with continuous changes in soil moisture would be a useful direction for future research. While moisture patterns for some of our sites have been previously described (Scott *et al.* 2000; Scott, Cable & Hultine 2008), properly characterizing soil moisture dynamics for terrestrial ecosystems is an ongoing research challenge (Shuttleworth 2007).

Our application of the coupled metabolic–pulse dynamics theory allowed for the examination of multiple hypotheses of pulse dynamics. The larger pulse response in the grassland dominated communities (Fig. 3) supports hypotheses of increased grassland sensitivity to precipitation variability; however, the mechanism for this effect is not clear. The larger immediate pulse response in the uplands are consistent with the hypotheses that near surface ground water mutes riparian ecosystem responses and support the prediction by Lee *et al.*

(2004) suggesting increased effects in upland areas for the initial pulse effect. In addition to site-specific characteristics, pulse dynamics were also associated with event characteristics. The 5-day total pulse effect was related to the drying time before a rainfall event and the metabolic activity of the system prior to the event (Fig. 4). The relationship with drying time supports the hypothesis of an accumulation of organic matter between events. The sensitivity of the initial pulse response to event size (Fig. 5) may be related to either deeper wetting of the soil profile and a concomitant increase in soil and biological components activated, or the contribution of autotrophic components to the initial respiration response. The independence of the total pulse response to the size of the rainfall event (Fig. 4) supports hypotheses of trigger-response initial dynamics and substrate limitation dictating the pulse decay. Further examinations of the precipitation response in conjunction with observed soil moisture dynamics will help resolve the effects of precipitation event size. The inverse relationship between pre-event metabolic state and whole ecosystem pulse response (Figs 4 and 5) was consistent with previous experimental manipulation of rainfall patterns and whole ecosystem observations of precipitation events (Xu *et al.* 2004; Huxman *et al.* 2004b) and supports the general pulse dynamic theory suggested for water limited systems (Noy-Meir 1973; Huxman *et al.* 2004b).

The results and quantitative framework presented here have implications both for a better understanding of the dynamics within ecosystems and the potential for modelling feedbacks to the drivers of ecosystem dynamics. Several new ecological experiments are currently being constructed to identify responses to both discrete events and more gradual trends associated with climate change (Jentsch, Kreyling & Beierkuhnlein 2007). Analyses of these experiments will be aided by clear theoretical predictions of the interactions between changes in trends and changes in events or central tendencies vs. variability. Furthermore, coupling the continuous and discontinuous ecosystem responses to temperature and precipitation variability may provide improved modelling schemes for describing the interactions between climate and soil-vegetation-atmosphere gas exchange. While the research presented here was primarily hypothesis testing, the precipitation response could readily be incorporated into many ecosystem and land-surface models and may also be suitable for linking with statistical rainfall distribution analyses (Scanlon *et al.* 2005; Rodriguez-Iturbe *et al.* 2006). Models of moisture and temperature interactions on respiration have commonly applied moisture stress as a continuous reduction factor on maximum respiration rates (Davidson & Janssens 2006; Sacks *et al.* 2007; Wang *et al.* 2007); no ecosystem model we are aware of includes a pulse response in metabolism following precipitation events. Developing coupled models that include precipitation effects will allow for validation and expanded analyses, such as impulse-response modelling that tracks the cascading effects of events throughout a system (Thompson & Randerson 1999). Understanding whole ecosystem metabolic responses to combinations of temperature and precipitation variability remains an important research

challenge and these results provide a quantitative framework for untangling this complexity.

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