



# Understanding seasonal and inter-annual variability in ecosystem CO<sub>2</sub> exchange from temporal variations of leaf traits

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## SUMMARY

1. Ecosystem CO<sub>2</sub> exchange is highly variable in seasons and across years. Such seasonal and inter-annual variability in ecosystem CO<sub>2</sub> exchange is mainly attributed to numerous climate drivers. However, ecological functions and processes behind climate drivers are keys to understand mechanisms of temporally fluctuated ecosystem productivity in natural ecosystems.

2. In this study, we sampled grass and oak leaves in a woody savanna and open grassland in California, USA. Sample were collected at weekly to monthly intervals from 2001 - 2007, including leaf nitrogen concentration (N), leaf mass per unit area (LMA), leaf carbon concentration (C), and leaf carbon stable isotope discrimination (Δ).

3. We also measured ecosystem-level photosynthetic rates of annual grasses ( $A_{grass}$ ) and oak tree canopy ( $A_{canopy}$ ) were deduced from eddy covariance towers over the 7-year study period.

4. By defining the grass community age or tree canopy age, we compared ecosystem-level photosynthetic rates under various combinations of climatic variables. The photosynthetic rates were up to 1–2 gC m<sup>-2</sup> day<sup>-1</sup> inter-annually as annual grasses and oak trees experienced wide ranges of inter-annual climate fluctuations: up to 5 °C in daily mean soil temperature, 15% in soil moisture, and 10 mol m<sup>-2</sup> day<sup>-1</sup> in photosynthetically active radiation (PAR).

5. The multi-year time series of grass and oak leaf traits showed that leaf traits varied seasonally and inter-annually. Multi-year means of grass leaf N, C, D, and LMA were 2.3%, 40.8%, 22.6% and 71.3 g m<sup>-2</sup>, respectively; multi-year means of oak leaf N, C, D, and LMA were 1.9%, 45.1%, 20.5% and 132 g m<sup>-2</sup>, respectively.

6. The analysis of variance shows that seasonal and inter-annual terms were associated with  $A_{grass}$  or  $A_{canopy}$  up to 90% or 81%. On the other hand, variations in leaf N, LMA, C, Δ, and their interactions could statistically explain about 53% and 26% of variations in  $A_{grass}$  and  $A_{canopy}$ , respectively.

7. We discussed possible biological and ecological processes involved in regulating seasonal and inter-annual variability in ecosystem-level photosynthesis. Clearly, seasonal and inter-annual variation in ecosystem photosynthesis was strongly associated with the dynamics of leaf traits.

Notice: This topic has been published as: Ma et al. 2011. Are temporal variations of leaf traits responsible for seasonal and inter-annual variability in ecosystem CO<sub>2</sub> exchange. *Functional Ecology* 2011, 25, 258–270

## RESULTS

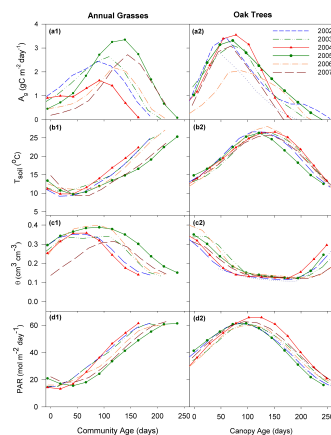


Fig. 1. Seasonal and interannual patterns of daily integrated ecosystem-level photosynthetic rate of annual grassland ( $A_{grass}$ ) and oak canopy ( $A_{canopy}$ ), soil temperature at 4 cm depth ( $T_{soil}$ ), soil volume moisture ( $\theta$ ), and incoming photosynthetically active radiation (PAR) at the savanna.

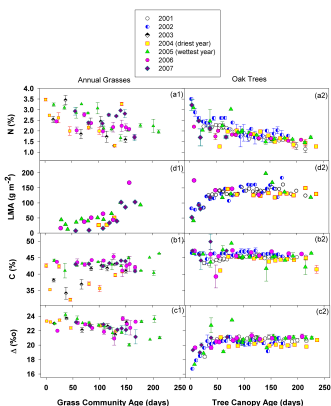


Fig. 2. Relationships between ecosystem-level photosynthesis ( $A_{grass}$  for annual grasses;  $A_{canopy}$  for tree canopy) and leaf nitrogen concentration (N), and relationships between leaf N and leaf mass per area (LMA) for annual grasses and oak trees, respectively, compared with a global dataset (in gray dots) adapted from Reich, Walters & Ellsworth (1997).

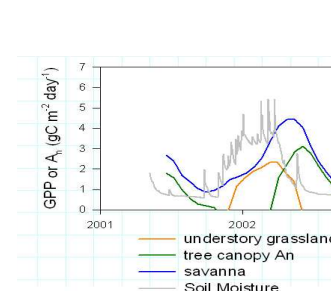
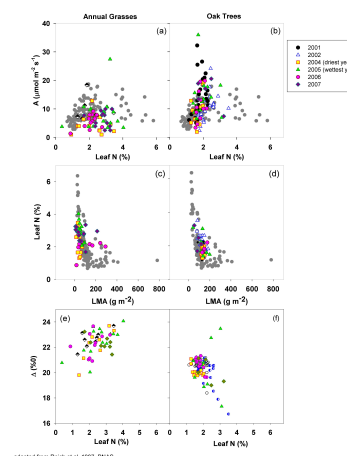
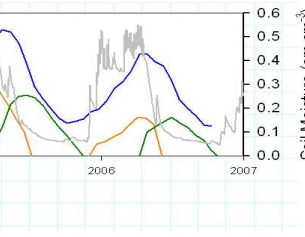
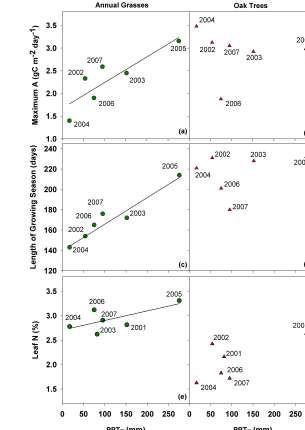


Fig. 3. Effects of precipitation during the second phenol-phase (PPT<sub>II</sub>) on maximum photosynthetic rates ( $A_{grass}$  for annual grasses;  $A_{canopy}$  for tree canopy) and lengths of growing season, illustrating water conditions of a given hydrological year. Notice that the solid lines represent the linear regression lines with  $R^2$  equal to 0.93 and 0.75 in (a) and (c), respectively. The dash lines represent the general trends in (b) and (d).



adapted from Reich et al. 1997, 1998.



## DISCUSSION

### Ecosystem-level photosynthesis and climate fluctuations

- The concepts of grass community age and tree canopy age are ecosystem-level concepts.
- Annual grasses and oak trees experience a wide range of climate fluctuations during their ontogeny, but multi-year climate data are comparable only when plant phenological events are considered.
- Seasonal photosynthetic capacity (daily maximum  $A_{grass}$  or  $A_{canopy}$ ) is higher in wetter years and lower in drier years.

### Ecosystem mechanisms behind seasonal and inter-annual variability in ecosystem-level photosynthesis

- Seasonal trends in ecosystem CO<sub>2</sub> fluxes result from evolutionary adaptation, whereas inter-annual trends illustrate more about how ecosystems plastically respond to environmental changes, especially climate fluctuations from years to decades and from decades to hundreds of years.
- Within one growing season, leaf-level investment-cost tradeoff is supported by our ecosystem-level data.
- Across multiple years, the relationships between photosynthetic capacity and leaf N and between leaf N and LMA are reversed.
- The interactions among vegetation groups at the ecosystem level are important.
- Ecosystem also follows "sink-source" regulation of the whole plant.

### Implication for future research

- Temporal variability in ecosystem CO<sub>2</sub> fluxes does not arise from a single process or function but from ecosystem integration.



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