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Ecological controls on net ecosystem productivity of a seasonally dry annual grassland under current and future climates: Modelling with *ecosys*

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ABSTRACT

Net ecosystem productivity (NEP) of seasonally dry grasslands in Mediterranean climate zones is determined by the duration and intensity of rainy *vs.* dry seasons. Precipitation in these zones is expected to decline with climate change during the next century, possibly reducing NEP. Ecosystem models used to study climate change impacts on grasslands in these zones need first to simulate effects of soil wetting and drying on the duration and intensity of net C uptake and emission during rainy and dry seasons under current climate. Continuous eddy covariance (EC) measurements of CO_2 and energy exchange provide well constrained tests of such models. In this study, hourly CO_2 and energy exchange from the ecosystem model *ecosys* were tested against EC measurements recorded over an annual grassland at Vaira Ranch, CA in a Mediterranean climate zone during eight years (2001–2008) with variable rainy seasons. Variation in measured CO_2 and latent heat fluxes was sufficiently well simulated during each year of the study ($0.7 < R^2 < 0.9$) that most of the variation unexplained by the model could be attributed to uncertainty in the measurements. Interannual variation in NEP from the model was also correlated with that from EC measurements ($R^2 = 0.75$). Annual NEP from both the model and EC were correlated with the duration of net C uptake, but not with the amount of precipitation, during the rainy seasons. Average annual NEP of the grassland modelled from 2001 to 2008 was $29\,g\,C\,m^{-2}\,y^{-1}$ with an interannual variation of $\pm 110\,g\,C\,m^{-2}\,y^{-1}$ caused by that in the duration of net C uptake. During climate change (SRES A1fi and B1 under HadCM3), changes in modelled NEP were determined by changes in duration and intensity of net C uptake in rainy seasons *vs.* net C emission in dry seasons. In years with briefer rainy seasons, modelled NEP rose because rates of net C uptake increased with higher temperature and CO_2 concentration, while the duration of net C uptake remained limited by that of the rainy season. However in years with longer rainy seasons, modelled NEP declined because the duration of net C uptake was reduced when warming hastened phenological development and caused maturity of annual plants to be reached before the end of the rainy season. As climate change progressed, declines in annual NEP gradually exceeded rises, causing the small C sink modelled under current climate to be almost completely lost after 90 years under SRES A1fi ($2 \pm 103\,g\,C\,m^{-2}\,y^{-1}$) and B1 ($6 \pm 95\,g\,C\,m^{-2}\,y^{-1}$).

1. Introduction

Seasonally dry annual grasslands are an important ecosystem type in Mediterranean climate zones. Those in California alone occupy more than 4.4 Mha or 20% of the area of the state (Huntsinger et al., 2007). Net ecosystem productivity (NEP) of these grasslands is thought to be determined by the duration and intensity of precipitation in the rainy season during which soils are wet enough to sustain net C uptake by plants (Ma et al., 2007). This net C uptake is offset by slow net C emission during the dry season when grasslands have senesced, by rapid, rainfall-induced pulses of net C emission at the start of the next rainy season before grasslands regrow, and sometimes by rapid net C emission at the end of the rainy season if grassland growth terminates before the start of the following dry season. At an annual time scale, net C uptake during the mid rainy season may or may not exceed net C emission during the dry season and during the start and end of the rainy season, so that these grasslands may be either sinks or sources of C.

These ecological controls on net C uptake *vs.* emission in seasonally dry grasslands have been demonstrated with eddy covariance (EC) measurements. Xu and Baldocchi (2004) attributed annual NEP of a northern California grassland to the timing of rain events that determined the duration of net C uptake in the rainy season, rather than to the total amount of rainfall received during the year. Ma et al. (2007) found that changes in the duration of net C uptake with precipitation caused this grassland to alternate between a sink

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or source of C. Pereira et al. (2007) made a similar finding for a Mediterranean grassland in Portugal.

The climatic signals initiating and terminating net C uptake in seasonally dry grasslands are therefore important ecological controls on NEP. Botta et al. (2000) used an index derived from modelled relative soil water content (RSWC) to estimate leafout in tropical deciduous ecosystems. Jolly and Running (2004) used precipitation *vs*. potential evapotranspiration and soil water potential *vs*. net C uptake to estimate dates of leafout and leafoff respectively in drought deciduous ecosystems. However a definitive method has not yet been developed for estimating dates on which C uptake is initiated and terminated in seasonally dry grasslands. For annual grasslands, this method needs also to account for initiation and termination of net C uptake with seed germination and plant maturity.

Understanding the ecological controls on net C uptake *vs*. emission in seasonally dry grasslands is essential to reduce uncertainties in predicting climate change impacts on NEP. These impacts may be particularly adverse in Mediterranean climate zones because precipitation in these zones is generally expected to decline (Christensen et al., 2007). In model projections of climate change impacts in Europe, NEP in Mediterranean regions was expected to be adversely impacted by increasing drought and disturbance (Lindner et al., 2010). Net primary productivity (NPP) in these regions was expected to increase little, and in some cases to decrease, under climate change, so that many ecosystems may change from sinks to sources of C by 2100, mainly from drying caused by declining precipitation *vs*. rising evapotranspiration (Morales et al., 2007).

Ecosystem models used to study climate change impacts on seasonally dry grasslands need first to be tested for their ability to simulate ecological controls on NEP by simulating those on its component fluxes gross primary productivity (GPP) and ecosystem respiration (R_e) under highly variable rainfall. Of particular importance in this regard are the climatic and phenological signals initiating and terminating GPP and hence plant C uptake at the start and end of rainy seasons, and the effects of soil wetting and drying on C uptake and emission during rainy and dry seasons. In this study, we used the ecosystem model *ecosys* (Grant and Flanagan, 2007; Grant et al., 2006, 2007a,b,c, 2008, 2009) to test algorithms for:

(1) the climatic and phenological signals that induce germination during soil wetting at the start of the rainy season, and senescence during soil drying at the end of the rainy season, thereby setting the duration of GPP which enables sustained productivity by annual plants in seasonally dry climates,
(2) a soil–root–canopy–atmosphere hydraulic scheme by which soil and atmospheric water status determine plant water status, and hence GPP during soil wetting and drying between germination and senescence (Grant and Flanagan, 2007), and
(3) the stimulation or suppression of heterotrophic respiration (R_h) during wetting or drying of surface residues and soil (Grant and Rochette, 1994), thereby simulating the precipitation-driven pulses that characterize C emissions in seasonally dry ecosystems (Huxman et al., 2004).

CO_2 and energy fluxes modelled with these algorithms in *ecosys* were tested against those from continuous EC measurements recorded over an annual grassland from 2001 to 2008 in a Mediterranean climate zone at Vaira Ranch in California. Varying intensity and duration of rainy seasons recorded during this period provided a strong test of model robustness. These algorithms were then used to project changes in CO_2 fluxes and hence NEP for this grassland under different climate change scenarios projected for the next 100 years in California.

2. Methods

2.1. Model development

2.1.1. General

The key algorithms governing the modelling of ecological controls on NEP in *ecosys* are described in the Supplement to this article, in which equations and variables referenced in the Results below are described and listed in Appendices A, B, C and D. All model parameters in *ecosys* are derived from independent experiments and so remain unchanged in this study from those used in earlier studies (e.g. Grant et al., 2007b,c, 2008, 2009) as given in the Supplement. However these algorithms have not yet been tested under the more variable hydrological conditions encountered in Mediterranean ecosystems.

Algorithms (1), (2) and (3) above are described in more detail below.

2.1.2. Algorithm (1): initiation and termination of gross primary productivity in seasonally dry climates

Leafout and leafoff in cold-deciduous plant functional types (PFT) in *ecosys* occur when requirements for time accumulated at plant temperatures above or below set thresholds have been met under lengthening or shortening photoperiods respectively (e.g. Grant et al., 2009). Here we adapt this approach to leafout, or germination in annual plants, and senescence in drought-adapted PFTs by setting requirements for time accumulated at plant water potential above or below set thresholds to be met during earlier and later plant growth stages respectively. For this study time requirements and thresholds were set at 480 h above −0.2 MPa for germination, and 240 h below −2.0 MPa for senescence. These requirements were set to avoid premature germination or senescence and hence wastage of resources during false starts or ends to the rainy season. In the model, plant water potential is represented by canopy water potential (ψ_c), calculated from coupled equations by which root water uptake is equilibrated with canopy transpiration [B14]. When the canopy is absent before leafout in perennials or seed germination in annuals, ψ_c is determined by soil water potential (ψ_s) at seeding depth and so responds to rainfall events that maintain high ψ_s for long enough to meet the accumulated time requirements specified for the PFT.

During the growing season, ψ_c is determined by ψ_s throughout the rooted soil profile, and by transpirational demand imposed by vapor pressure deficit *D*. Therefore sustained declines in ψ_c that meet the time requirements for senescence occur only when most of the rooted soil profile is dry and *D* is large. Sustained declines in ψ_c also induce senescence and litterfall through declining CO_2 fixation and consequent depletion of nonstructural C products by respiration and grain filling. This depletion forces remobilization of metabolic C and litterfall of associated structural C to meet respiration and grain filling requirements. Senescence in the model drives translocation of plant nonstructural C to storage reserves (perennials) or seeds (annuals) that drive regrowth following leafout or germination at the start of the next growing season. These processes for leafout and senescence were designed in the model to maximize long-term productivity of drought-adapted plants under variable rainfall. This was accomplished by using nonstructural C during favourable growing conditions to grow and maintain structural C required to produce storage or seed C, while limiting wastage of nonstructural C during unfavourable growing conditions to grow and maintain structural C that does not produce storage or seed C.

Senescence modelled in annual plants may also be induced by phenological maturity following completion of their annual life cycle if this occurs before the senescence requirement for time accumulated at ψ_c below the set threshold has been met. The life