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Soil as a capacitor: Considering soil water content improves temporal models of productivity

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ABSTRACT

Above-ground net primary production (ANPP) in arid and semiarid ecosystems is mainly explained by precipitation (ppt). However, when this relationship is evaluated taking into consideration data from different years in the same site (i.e. temporal models of productivity) the relation is weak, and sometimes it does not exist. In spite of this, the inclusion of previous year's ppt and/or ANPP frequently improves temporal models. In this study we analyze if considering NDVI and mean annual soil water content or transpiration (instead of different combinations of current-year ppt and previous year's ppt or ANPP) improves temporal models of productivity in the Southern Monte (Argentina). Current-year ppt only explained 39.7% of variation in ANPP, while mean soil water content explained 85.3%. The remaining models, which include current-year ppt together with previous-year's ppt or previous-year's ANPP, improve the first model; but the explanatory power of the model based only on mean soil water content is never reached. Our results also show that water losses exceed annual ppt in dry years, whereas the opposite occurs during years with above-average ppt. This carryover effect of soil water indicates that soil acts as a capacitor, accumulating water during wettest years and releasing it during following years.

1. Introduction

Precipitation (ppt) is the most important control of aboveground net primary production (ANPP) in arid and semiarid ecosystems. Studies relating mean ANPP and mean ppt of different sites have reported a linear relationship with slopes ranging from 0.48 to 0.85 $g\ m^{-2}\ mm^{-1}\ yr^{-1}$ (Sala, 2001). In contrast, when this relationship is evaluated taking into consideration data from different years in the same site (i.e. temporal models of productivity) the relation is weak, and sometimes it does not exist (Paruelo et al., 1999). However, the low predictive power of temporal models can be improved by including data from previous year's ppt and/or ANPP (Oesterheld et al., 2001), considering seasonal ppt instead of annual ppt (Fabricante et al., 2009; Robinson et al., 2013) and/or taking into consideration other climatic variables such as temperature (Wiegand et al., 2004). In that sense, Reynolds et al. (2004) found that productivity following particular rainfall pulses in deserts is not a direct response to rainfall, but rather to soil water availability. Accordingly, different authors (e.g. Knapp et al., 2002; Muldavin et al., 2008; Nippert et al., 2006) have compared the explanatory power of annual ppt and mean annual soil water content as predictors of annual ANPP, with contrasting results.

A crucial limitation to study temporal variation of ANPP as well as its relationship with precipitation is the lack of long term data (Fabricante et al., 2009). Fortunately, several works have shown that NDVI (Normalized Difference Vegetation Index) is correlated with ANPP (e.g. Jobbágy et al., 2002), and this approach has been widely used in recent years, particularly in Patagonian ecosystems (e.g. Fabricante et al., 2009; Paruelo et al., 1998). This approach was also used in this study. Some authors have highlighted that NDVI and ANPP may or may not be directly correlated, depending on the particular relationship among NDVI, the fraction of photosynthetically active radiation absorbed by vegetation (FAPAR), the photosynthetically active radiation (PAR) and radiation use efficiency (RUE) (Piñeiro et al., 2006). However, this limitation is severe when the objective of the study is to evaluate seasonal productivity and much less problematic in whole-year studies (Piñeiro et al., 2006).

We hypothesize that the low predictive power of current-year ppt in temporal models is consequence of the fact that plants do not respond directly to precipitation events, but rather to the influence of those precipitation events on water content in soil

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layers where roots are present. So, bulk precipitation could be a poor predictor of ANPP if a substantial fraction of precipitation is lost by evaporation, run-off and/or deep drainage, or if soil accumulates significant amounts of water which is consumed by plants with some delay after precipitation allowing carryover effects from one year to the following. In this study we analyze if considering NDVI and mean annual soil water content or plant transpiration (instead of different combinations of current and previous year's precipitation and NDVI) improves temporal models of productivity in a site representative of the Southern Monte (Argentina).

2. Methods and material

2.1. Study site

This study was carried out in Estancia San Luis, a site representative of the Southern Monte, Patagonia, Argentina (42°39′S, 65°23′W, 115 m a.s.l.). Vegetation is dominated by evergreen shrubs (*Larrea divaricata*, *Chuquiraga erinacea* spp. *hystrix*, *Atriplex lampa*, among others), although deciduous shrubs (*Prosopidastrum globosum*, *Bougainvillea spinosa*, etc.) and grasses (e.g. *Nassella tenuis*, *Pappostipa speciosa*) are common mostly at lightly grazed areas. Plant cover is low, varying from 15% to 40% according to grazing disturbance (Bisigato et al., 2005). Most roots are concentrated near soil surface, but evergreen-shrub roots can reach depths of 1 m or more (Campanella and Bertiller, 2008). Mean annual precipitation is 235.9 mm, evenly distributed along the year. Different plant species can growth at different moments throughout the year (Campanella and Bertiller, 2008), whenever soil moisture is appropriated, making Southern Monte the physiognomic region with the lowest intra annual variation in NDVI across Patagonia (Paruelo et al., 1998). This study site was selected because the availability of a 16 year-long (1994–2009) meteorological database on a daily basis.

2.2. NDVI

NDVI values were obtained from AVHRR/NOAA images, 8 × 8 km spatial resolution, from Global Land Cover Facility (Tucker et al., 2004; http://glcf.umiacs.umd.edu/data/gimms/). We selected an area of 3 × 3 pixels around the study site and obtained annual mean NDVI by averaging 15-days NDVI composites of every year (1994–2006).

2.3. Soil water model

Annual mean soil water depth (wd) and total annual soil water losses (wl = evaporation + transpiration + drainage) were estimated using a soil water balance model developed for Southern Monte and validated against field observations (Bisigato and Lopez Laphitz, 2009). The required inputs are daily meteorological data (precipitation, maximum and minimum air temperature and solar radiation), vegetation attributes (plant cover and proportion of roots in each soil layer, taken from Bisigato et al., 2005 and Rodríguez et al., 2007, respectively) and soil characteristics (texture and gravel content, taken from Rostagno and del Valle, 1988; Rostagno et al., 1991). This one-dimensional model calculates, on a daily basis, soil water depth in four soil layers (1 m total depth) and losses by evaporation, transpiration and drainage. As Patagonian Monte ecosystems are characterized by flat landscapes and soils are coarse textured, the model does not take in account surface run-off. Losses by evaporation are only computed from the upper layer. Water lost by transpiration is a function of the potential evapotranspiration and the effective available water, which is the sum of the available water of each soil layer weighted by the root proportion in each soil layer. Flow from the last soil layer downward corresponds to deep drainage. Plant cover is kept constant throughout the simulation. This is a reasonable assumption due to low intra annual variation in NDVI in Austral Monte communities. Plant cover was set at 25%, a representative value of most of the study area (Bisigato et al., 2005).

2.4. Statistical analysis

The relationship between annual means of NDVI, precipitation, plant transpiration and soil water depth were inspected by linear regression. We also evaluated if the inclusion of the two previous year's ppt and NDVI significantly improved the models. We evaluated the following seven models:

$$\begin{aligned}
\mathrm{M1:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{ppt}_{(t)} \\
\mathrm{M2:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{ppt}_{(t)} + \mathrm{c}\cdot\mathrm{ppt}_{(t-1)} \\
\mathrm{M3:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{ppt}_{(t)} + \mathrm{c}\cdot\mathrm{ppt}_{(t-1)} + \mathrm{d}\cdot\mathrm{ppt}_{(t-2)} \\
\mathrm{M4:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{ppt}_{(t)} + \mathrm{c}\cdot\mathrm{NDVI}_{(t-1)} \\
\mathrm{M5:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{ppt}_{(t)} + \mathrm{c}\cdot\mathrm{NDVI}_{(t-1)} + \mathrm{d}\cdot\mathrm{NDVI}_{(t-2)} \\
\mathrm{M6:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{wd}_{(t)} \\
\mathrm{M7:}\ \mathrm{NDVI}_{(t)} &= \mathrm{a} + \mathrm{b}\cdot\mathrm{transp}_{(t)}
\end{aligned}$$

Where: NDVI: Annual normalized difference vegetation index, ppt: Annual precipitation, wd: Mean annual water depth in soil profile (0–100 cm), transp: annual transpiration, 0: current year, 1: previous year, 2: second previous year, and a, b, c, and d are constants.

As we had no information about the initial soil water content, we were unable to include the years 1994 and 1995 in the analysis. However, a precipitation event occurred during 1995 wetted the whole soil profile irrespective of the initial soil water content included in the simulation. So, 11 years (1996–2006) were used to test the models.

Finally, we also evaluated the relationship between wl and ppt by regression analysis. This analysis allows us to determine the magnitude of carryover effects (i.e. transference of soil water from a year to the following year) and their relationship with annual ppt.

3. Results

3.1. Temporal models of ANPP

M1 explained 39.7% of total variance in NDVI (Fig. 1 and Table 1). This model can be improved by including previous year's ppt, but the inclusion of two previous year's ppt did not further improve the model (r^2 51.2% and 52.0%, M2 and M3 respectively, Fig. 1 and Table 1). In contrast, M1 cannot be enhanced by considering previous year's NDVI (r^2 40.8%, M4), but it was greatly improved when the two previous year's NDVI were included (r^2 71.4%, M5 in Fig. 1 and Table 1). The best model was M6 (Fig. 1 and Table 1), which only includes current-year mean soil water depth (r^2 85.3%). Finally, the model including plant transpiration explained 71.2% of variance in NDVI.

3.2. Water losses and their relationship with annual precipitation

Water losses increased with annual precipitation but, as the slope of the regression was <1 and the *y*-intercept >0, it represents a different proportion of ppt as ppt increases (Fig. 2). During the driest year of the series (which had 35.8% of long term average precipitation), wl exceed annual precipitation by more than 20%. In contrast, in the wettest year wl accounted by 96% of annual precipitation. Finally, years with precipitation in the range 185–

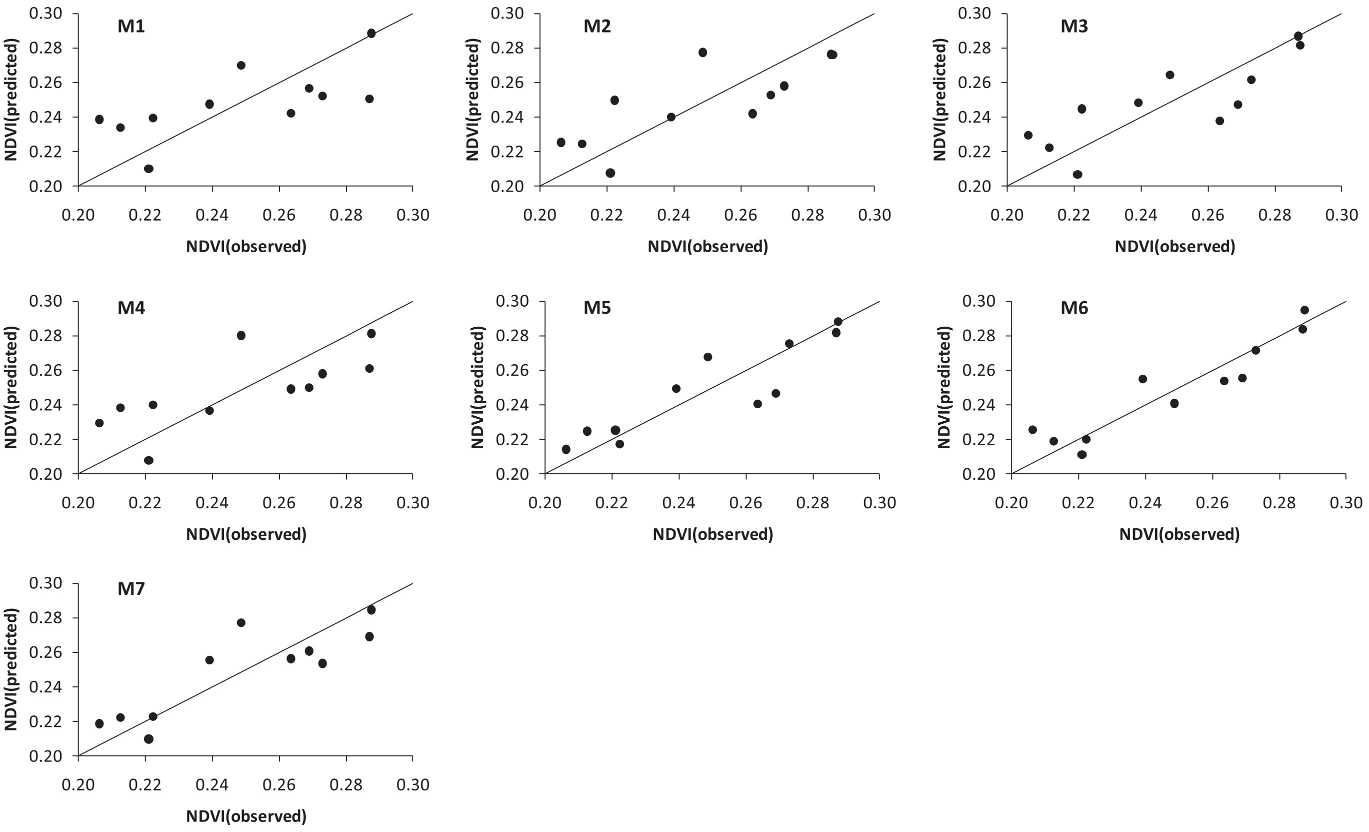

Fig. 1. Observed and predicted NDVI values according the models 1–7 (M1 to M7). Diagonals indicate the 1:1 line.

260 mm (which includes mean long term average, 235.9 mm) showed a variable response.

4. Discussion

Our results indicate that mean soil water depth throughout the year accounted for 85.3% of variation in NDVI, twice the amount of variation explained by current-year ppt (39.7%). This seems reasonable since plant growth does not respond directly to precipitation; it is a function of water availability in soil layers where roots are present. Thus, instead of bulk precipitation, what it really matters is effective precipitation, that is the amount of water available to plants after subtracting evaporation, runoff and drainage losses (Fernández, 2007). As several characteristics of precipitation events such as moment of the year, size and duration as well as antecedent conditions can affect the partitioning between different losses (Golluscio et al., 1998), bulk precipitation is a poorer predictor of ANPP that average soil water depth. Similarly, considering annual precipitation does not take into consideration the date when particular events took place, what can strongly affect ANPP (Swemmer et al., 2007). For example, it does not discriminate between two events of similar size occurring in January or December, although most of the water infiltrated during the last event could be hardly ever transpired this year. In this sense, our results show that soil acts as a capacitor, accumulating water during wettest years and releasing it during following years. This

Table 1
Alternative models that account for the interannual variation in current year mean NDVI of the study site in Estancia San Luis. ppt indicates annual precipitation (mm); wd indicates mean water depth in the soil profile (mm); transp indicates total transpiration (mm); (t), ($t-1$), and ($t-2$) indicate the current year, first-previous year, and second-previous year, respectively. Bold indicates that the model was significant.

Code	Model	Adj-r^2	F(df)	P
M1	NDVI$_{(t)}$ = 0.188 + 2.43E-4 ppt$_{(t)}$	0.397	7.571 (1,9)	**0.022**
M2	NDVI$_{(t)}$ = 0.129 + 3.24E-4 ppt$_{(t)}$ + 1.57E-4 ppt$_{(t-1)}$	0.512	6.242 (2,8)	**0.023**
M3	NDVI$_{(t)}$ = 0.156 + 3.59E-4 ppt$_{(t)}$ + 1.18E-4 ppt$_{(t-1)}$ −1.01E-4 ppt$_{(t-2)}$	0.520	4.618 (3,7)	**0.044**
M4	NDVI$_{(t)}$ = 0.123 + 2.42E-4 ppt$_{(t)}$ + 0.264 NDVI$_{(t-1)}$	0.408	4.447 (2,8)	**0.050**
M5	NDVI$_{(t)}$ = 0.211 + 2.78E-4 ppt$_{(t)}$ + 0.415 NDVI$_{(t-1)}$ −0.542 NDVI$_{(t-2)}$	0.714	9.306 (3,7)	**0.008**
M6	NDVI$_{(t)}$ = 0.104 + 1.893E-3 wd$_{(t)}$	0.853	59.083 (1,9)	**<0.001**
M7	NDVI$_{(t)}$ = 0.187 + 0.614E-3 transp$_{(t)}$	0.712	25.704 (1,9)	**0.001**

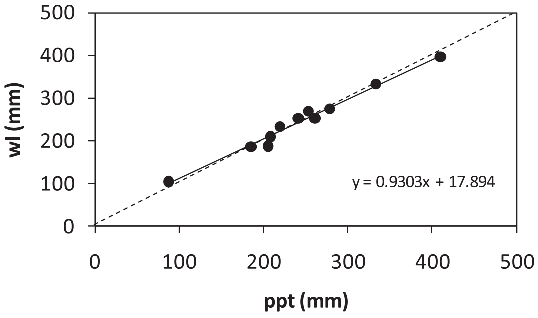

Fig. 2. Relationship between simulated water losses (evaporation + transpiration + deep drainage) and precipitation. Each point corresponds to a year. Dotted line indicates the 1:1 line. Points above the diagonal correspond to years when water losses exceed precipitation.

transference of resources from one year to the other as well as its potential importance to temporal models has been previously proposed by Verón et al. (2005), among others.

Previous attempts to improve temporal models have included a variety of approaches that, in essence, represent simplified soil water balances. For example, the rationale behind considering previous year(s) precipitation (e.g. Oesterheld et al., 2001) could be the existence of carryover effects of soil water. Similarly, considering seasonal instead of annual precipitation (e.g. Robinson et al., 2013) and/or large precipitation events rather than total precipitation (e.g. Swemmer et al., 2007) can be interpreted as an effort to remove evaporation, run-off and/or deep drainage losses from the analysis. In the same way, Wiegand et al. (2004) included in their models temperature, which is the main control of potential evapotranspiration. Finally, the latter authors also calculated memory indexes, which ponder previous-months ppt in an exponentially declining manner. These indexes can also be related to a soil water balance, since the effect of particular events declines with time (Ogle and Reynolds, 2004).

Although our results show that mean soil water depth is a better predictor of annual mean NDVI than different combinations of current and previous year's ppt and NDVI, it may not be appropriate to directly extrapolate our results to different systems since some authors have evaluated this relationship with contrasting results. For example, Nippert et al. (2006) found that both growing season precipitation and modeled soil moisture were significantly and positively related to grass ANPP. In contrast, Muldavin et al. (2008) found that ANPP in a black grama grassland was better predicted by soil moisture than by precipitation, but the reverse was true for a creosote shrubland. Finally, Knapp et al. (2002) did not find a relationship between grassland ANPP and mean soil water content, although ANPP was strongly and negatively related to temporal variability in soil water content. In our opinion, these contrasting results are due to the fact that the relationship between ANPP and soil water can be influenced by climate, soil, type of vegetation and/or sampling method.

Climate can influence the relationship between ANPP and soil water in several ways. For example, season of the year, event size, and rain intensity affect the partitioning among evaporation, run-off, and transpiration (Fernández, 2007). Due to low evaporative demand, winter rainfall is hardly ever lost by direct evaporation. In contrast, evaporative loses during summer are increased, mainly if precipitation events are small and only superficial soil is recharged (Fernández, 2007). Rain intensity determines run-off since these losses occur if rain intensity exceeds soil infiltration rate (Rostagno et al., 1999). Similarly, total precipitation and soil water holding capacity in the rooting zone influence the magnitude of losses by deep drainage because they occur whenever infiltration plus previous soil water content surpass water holding capacity. Type of vegetation can influence the relationship between soil water and ANPP trough root system depth and plant phenology. Water holding capacity is low in plant communities dominated by shallow-rooted species (e.g. grasslands) because the reduced soil volume explored by roots makes deep drainage losses feasible. In these cases ppt must be a worst predictor of ANPP than soil water content. Similarly, those systems whose rainy season is decoupled from the growing season can show non-significant relationships between rain and ANPP (e.g. Jobbágy et al., 2002). Finally, sampling method can affect our ability to find a relationship between ANPP and soil water if the last variable is not measured or estimated at soil layers where plants have most of active roots. For example, the lack of relationship between ANPP and soil water in the creosote shrubland studied by Muldavin et al. (2008) could be consequence of the fact that soil water was evaluated in the 0–30 cm layer, although roots systems of creosote are much deeper (Ogle and Reynolds, 2004).

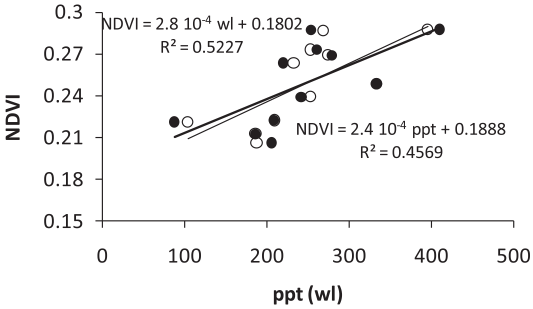

Fig. 3. Relationship between annual NDVI and annual ppt (black symbols, tick line) and simulated annual water losses (wl; white symbols, thin line).

The carryover of water among years could also explain, in part, the differences between the slopes of spatial and temporal models of ANPP reported in sites with mean annual ppt lower than 400 mm (Paruelo et al., 1999). Different mechanisms have been proposed to explain that spatial models have higher slopes than temporal models, and they were collectively called "vegetational constraints" (Lauenroth and Sala, 1992). For example, it was proposed that the species adapted to these environments show drought tolerance traits which limit their ability to respond to increases in ppt (Verón et al., 2002). Similarly, it was suggested that low plant cover limits the response of vegetation during wet years (Golluscio et al., 2009) or during normal years following dry years because plant mortality during the drought (Yahdjian and Sala, 2006). Although these mechanisms were invoked to explain the differences among spatial and temporal models during years with above average ppt (Lauenroth et al., 2000; Sala, 2001; Sala et al., 1996), they are less useful for explaining why the temporal models predict higher ANPP than the spatial model during dry years. However, as the carryover of water results in a transference of water from years with above average precipitation to years showing below average precipitation, the slope of a temporal model taking into consideration the transference of water among years should be greater than that of the model including annual ppt (Fig. 3).

In conclusion, our results suggest that mean soil water depth is a good predictor of annual ANPP in non-seasonal arid ecosystems. In part, it is due to carryover effects of soil water, what could contribute to the lower slope of temporal models of ANPP. The calibration and use of soil water balance models would improve our ability to predict ANPP in arid ecosystems.

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