CrossMark

Temporal trends in the enhanced vegetation index and spring weather predict seed production in Mediterranean oaks

Marcos Fernández-Martínez · **Martin Garbulsky** · **Josep Peñuelas** · **Guille Peguero** · **Josep Maria Espelta**

Abstract The extremely year-to-year variable production of seeds (*masting*) is an extended plant reproductive behaviour important for forest dynamics and food webs. The dependence of these episodes of massive seed production on recently or long-term photosynthesised carbohydrates, however, remains controversial. In this paper, we explore whether vegetation (tree canopy) changes, detected using EVI as a proxy of leaf area and photosynthetic capacity, can provide a reliable estimation of seed production. To complete this analysis, we also explored the effect of weather both in the trends of EVI and in acorn crop size. To this end, we compared the trends of the EVI and acorn production over 10 years (2000–2009) in five stands of *Quercus ilex* L. in Barcelona (Catalonia, NE Spain). We found that acorn production was mainly driven by a combination of: (i) a minimum initial threshold in the EVI values, (ii) an increase in EVI in the 9 ± 4 months prior to reproduction, and (iii) appropriate weather conditions (low water stress) during spring. These results indicated, apparently for the first time, that reproduction in masting species could be detected and partly predicted by remotely sensed vegetative indices. Our results suggested that this particular reproductive behaviour in Mediterranean oaks was driven by a combination of two factors, i.e. good and improving vegetation conditions, as shown by a minimum initial threshold and the increase in EVI needed for large seed crops, and the need of wet weather conditions during spring. Moreover, our results fully supported recent studies that have associated short-term photosynthate production with seed production.

Communicated by Joy Nystrom Mast.

M. Fernández-Martínez (✉) · J. Peñuelas · G. Peguero
CSIC, Global Ecology Unit, CREAF-CSIC-UAB,
Cerdanyola del Vallés, 08193 Barcelona, Catalonia, Spain
e-mail: m.fernandez@creaf.uab.cat

M. Fernández-Martínez · J. Peñuelas ·
G. Peguero · J. M. Espelta
CREAF, Cerdanyola del Vallés, 08193 Barcelona,
Catalonia, Spain

M. Garbulsky
Cátedra de Forrajicultura, Facultad de Agronomía,
University of Buenos Aires, IFEVA/CONICET, Av. San
Martín 4453, C1417DSE Buenos Aires, Argentina

Introduction

The synchronous but erratic year-to-year production of seeds, i.e. *masting*, is a widely geographically and taxonomically extended reproductive behaviour (Kelly and Sork 2002). Masting events have cascading effects on several forest functions and processes (Ostfeld and Keesing 2000) such as seedling establishment (Negi et al. 1996; Espelta et al. 2009), the

regulation of the populations of seed consumers (McShea 2000; Espelta et al. 2008), and the propagation of diseases [e.g. lyme disease (Ostfeld 1997)]. Notwithstanding this, what drives this phenomenon is one of the most puzzling questions about the dynamics of forest ecosystems (Koenig and Knops 2005).

Whether seed production in masting species is controlled by recently acquired or accumulated resources (e.g. carbohydrates and nutrients) remains controversial (Koenig and Knops 2000; Kelly and Sork 2002; Sala et al. 2012). On the one hand, the *resource matching* hypothesis (Sork et al. 1993; Kelly and Sork 2002) states that plants produce large or poor seed crops in direct response to the immediate availability of resources, i.e. more favourable weather conditions for photosynthesis would lead to larger harvests (e.g. Espelta et al. 2008, 2009). On the other hand, the *resource budget model*, or the *resource accumulation* hypothesis (Sork et al. 1993; Isagi et al. 1997), suggests that plants produce extraordinary seed crops when a resource threshold is reached after several years of progressive accumulation. This latter hypothesis predicts that plant resources are depleted to sustain the masting episode, so that flowering and seed production are expected to be very low or absent in the next growing season, causing a negative autocorrelation between consecutive seed crops (Koenig and Knops 2000). The consequences of resource depletion after a masting episode may include signs such as a reduction in the leaf area due to self-thinning (Camarero et al. 2010) or a decrease of nitrogen and phosphorous concentrations in branches (Sala et al. 2012).

Recent studies based on carbon isotopes suggest that seed production in several tree species in temperate forests depends only on the carbohydrates photosynthesised during the months prior to seeding (Ichie et al. 2013; Hoch et al. 2013). Unfortunately, the measurement of resource availability at a plant level is time-consuming and expensive and so is difficult to perform at broad spatial and temporal scales. Conversely, remotely sensed vegetation indices may be useful proxies for monitoring the fluctuations of trees resources at large temporal and spatial scales. Indeed, spectral indices such as the normalised difference vegetation index (NDVI) and the enhanced vegetation index (EVI) provide good descriptions of the state of green vegetation (e.g. crown cover, leaf area index, and greenness) and its temporal dynamics. These

indices have thus been widely used to monitor the functional traits involved in the carbon cycle (Garbulsky et al. 2008) and also as annual integrators of carbon uptake in forests (Garbulsky et al. 2013). Few studies, however, have yet applied remotely sensed vegetation indices to predict seed crop production in forest ecosystems, particularly in masting species (but see Camarero et al. 2010). In this sense, a successful methodology to predict seed crops would allow managers to better plan management actions in the near future (e.g. wildlife conservation strategies).

The aim of this study was to explore whether the pattern of seed production in Mediterranean oak (*Quercus* spp.) forests could be governed by the temporal dynamics of tree canopies, assessed by means of remote sensing indices. We hypothesise that vegetation changes, detected using EVI, represent a reliable proxy of the tree resources available for seed production. Therefore, if an accumulation of resources (e.g. carbohydrates and nutrients) for several years is a prerequisite for a masting event, EVI should progressively increase during that period of accumulation. Similarly, if a severe depletion of resources occurs after a masting episode, EVI should decrease due to the self-thinning of the canopy. In addition, given the nature of the Mediterranean climate, we hypothesise that weather conditions (e.g. drought) must be an important driver of the temporal dynamics of both EVI and acorn crop size. To address these questions, we used a dataset comprising 12 years (1998–2009) of acorn production in five oak stands in Collserola Natural Park (Catalonia, NE Spain) and 11 years (2000–2010) of EVI data derived from MODerate Resolution Imaging Spectroradiometer (MODIS) images of each forest stand.

Materials and methods

Study area and species

This study was conducted in the Collserola massif (41°26′N, 02°06′E), whose vegetation is dominated by *Q. ilex*. The study area has a Mediterranean climate and a mean annual temperature of 15.7 ± 1.4 °C. January is the coldest month (8.5 ± 0.6 °C) and August the warmest (24.3 ± 0.7 °C). Mean annual precipitation reaches 613.8 ± 34.0 mm (coefficient of variation (CV) = 0.25; values from the Fabra

Observatory at 415 m.a.s.l. for the current climatological standard normal period, 1991–2010). We selected forest stands of *Q. ilex* because it is the most abundant tree species in Collserola, has a strong masting behaviour (Espelta et al. 2008; Fernández-Martínez et al. 2012), and has evergreen leaves that allow continuous monitoring using remotely sensed vegetative indices. Regarding *Q. ilex* fruiting phenology, the pollination period normally starts during the first week of April and pollen release reaches its maximum during May (Fernández-Martínez et al. 2012). Pollinated flowers are then ripened until mid-September, when the harvest begins. We selected five 10 m radius stands (plots A–E), distributed along the Collserola massif, of nearly pure *Q. ilex* stands to maximise the accuracy of estimates of leaf area (more than 72 % of the trees were *Q. ilex* in all plots) being representative of the nearby area. The selected forests were very dense (coppiced stands of 1357 ± 219 *Q. ilex* stems per hectare), mostly resulting from resprouting and relatively young (ca. 40–60 years), presenting 10.5 ± 0.4 cm as mean diameter at breast height and around 3–4 m of height.

Experimental design and sampling

Acorn crop data

Acorn production was monitored from 1998 to 2009. Fifteen trees per plot were tagged, and the number of branches per tree was estimated using a regression model between crown projection and the number of branches previously determined for a subsample of trees (see Espelta et al. 2008). Acorn production on four branches per tree was recorded each September, i.e. at the peak of seed production in holm oaks before acorns were ripe enough to fall or to be harvested in appreciable number by birds (see Abrahamson and Layne 2002). The total number of acorns produced per tree was estimated by multiplying the mean acorn production per branch by the number of branches per tree (see Espelta et al. 2008 for further details). Since aborted and infested seeds usually fall much before maturation happens, insect-infested or aborted acorns do only consume a small amount of the tree resources, mostly insignificant in comparison with those needed in a mast year. Therefore, we did not take these acorns into account.

Estimates of canopy cover: satellite data

The NDVI and the EVI can be used to monitor temporal and spatial changes in leaf area and in the fraction of photosynthetically active radiation (fPAR) intercepted by the canopy (Myneni et al. 2002; Fensholt et al. 2004; Sprintsin et al. 2007). Both indices provide similar information, but we decided to use the EVI because (i) the NDVI saturates earlier at high levels of greenness (Huete et al. 2002) and our forests were very dense and (ii) because it has been recently demonstrated to successfully monitor biomass in Mediterranean holm oak (Ogaya et al. 2015). We thus used the EVI values as surrogates of photosynthesising leaf area and the available resources of the trees. Data were extracted from the Terra MOD13Q1 product of MODIS for the period between 18 February 2000 and 19 December 2010, with a 16-day periodicity and a spatial resolution of 250×250 m^2 (pixel size $=$ 6.25 ha), for the pixels that covered each forest stand. The pixels selected were almost entirely homogeneous with regard to vegetation type and crown cover, thus coinciding with the features of the sampled trees.

Meteorological data

Acorn crop size in Collserola is highly controlled by weather conditions (Fernández-Martínez et al. 2012). We thus gathered meteorological data from the Fabra Observatory (41°25′N, 02°07′E) to calculate the standardised precipitation-evapotranspiration index (SPEI, Vicente-Serrano et al. 2010) on a monthly basis and for the whole time series for time scales of 1, 3, 6, 9, and 12 months using the SPEI package (Beguería and Vicente-serrano 2012) of R (R Core Team 2013). Positive values of the SPEI indicate above-average wet periods, and negative values indicate drought. Since vegetation may present a lagged responses to prolonged drought periods (Vicente-Serrano et al. 2013) SPEI was calculated for different time scales to determine the influence of weather conditions on acorn production and the EVI signal for different periods of time.

Data analysis

We first calculated mean acorn production per tree for each plot and year. Then we described the masting

behaviour of our holm oak populations using the most common metrics (Kelly and Sork 2002): (i) the CVs of seed production as measures of interannual variability at the population (CV_p) and the individual (CV_i) levels, (ii) Spearman's r coefficients as measures of synchrony in seed production among plots (r_p) and among individual trees within a plot (r_i), and (iii) the mean temporal autocorrelation of seed production of the trees within a plot using simple and partial autocorrelation functions (ACF and PACF, respectively) to the fourth time lag. We also calculated these metrics for the mean annual EVI values to check for similarities in the time series of both acorn production and the EVI. Standard errors of these variables were calculated using the bootstrap method (Efron 1987).

Testing the effect of weather on EVI time series

We tested the effect of weather on the EVI by two methods. (i) We first calculated the standardised and deseasonalised monthly EVI time series using an additive seasonal decomposition. These time series indicated whether a particular month (e.g. January 2000) was above or below the mean for that month (January) in units of standard deviations (SDs). We then smoothed the EVI time series using local regressions (LOESS, Cleveland 1979) to remove noise and identify trends or low-frequency periodicities in the time series. This methodology would also help deal with potential noise addition in the estimation of EVI as a consequence of the flowering intensity (Shen et al. 2014). Finally, we correlated the smoothed EVI time series with the SPEI time series (1, 3, 6, 9, and 12) using Pearson correlations. (ii) We calculated the seasonally averaged EVI and SPEI values (e.g. winter EVI: mean EVI from January to March) for each year to correlate with each other (EVI vs. SPEI) to identify the season in which the SPEI was better correlated with the EVI. Spearman correlations were used for this procedure. To avoid increasing false discovery rate, P values were adjusted using the Bonferroni correction.

Testing the effect of weather and the EVI on seed production

We performed a two-step analysis to determine the relationships among weather, the EVI, and acorn production. First, we explored the relationships of seasonally averaged SPEI and EVI time series with acorn production to identify the season when SPEI has the largest effect on EVI. Then, we tested the correlation between acorn production and the seasonally averaged time series of SPEI and EVI. We used Spearman correlations for this procedure because the acorn production data were not normally distributed. Second, we used the smoothed EVI time series to test whether tree resources increased before large seed crops (i.e. masting events) by looking for evidence of an increasing EVI prior to masting. We identified all changes in the trends (e.g. from increasing to decreasing EVI) of the smoothed time series and considered an EVI trend to be the period between two of these points of change (peaks or valleys). We chose not to calculate trends for fixed periods of time because weather drives the phenology of these trees from year to year (Fernández-Martínez et al. 2012), and the periods of resource accumulation might thus occur during slightly different periods depending on the particular meteorological characteristics of the year. Then we assigned each trend to the most plausibly influenced harvest, starting at least 5 months (spring) before the harvest season (October). We also calculated the initial and final EVI values (EVI_i and EVI_f, respectively, units in SD) and the increment in the EVI (i.e. $\Delta EVI = EVI_f - EVI_i$) of each trend.

To test the influence of weather, the EVI, and previous acorn harvests on acorn production, we constructed a generalised linear mixed model (GLMM) fitted using the negative binomial distribution, using the natural logarithm as the link function, to correct for overdispersion. The model included the plot as a five-level random factor. The fixed effects were an SPEI variable (best correlated with acorn production), ΔEVI, EVI_i, EVI_f, and the acorn production of the previous year as covariates. We also included the interaction of ΔEVI with EVI_i and EVI_f to test for possible synergic effects of an increasing EVI and the initial or final level reached in the EVI. The inclusion of the acorn production of the previous year allows the testing for a negative autocorrelation in seed production that would suggest a depletion of resources after mast years (Sork et al. 1993). The minimum adequate model was achieved by deleting all non-significant predictors and minimising the Akaike information criterion. The models were fitted using the R package *lme4* (Bates et al. 2013).

Testing for the reduction of leaf area after large seed crops

To test whether the crowns of trees were self-thinned after mast seeding, we analysed the entire 16-day EVI time series with the breaks for additive seasonal and trend (BFAST) methodology using the R package *bfast* (Verbesselt et al. 2010a, b). We used this technique due to its ability to integrate the decomposition of time series into trend, seasonal, and residual components with methods for detecting changes in trends and seasonal behaviour. We configured BFAST to detect one break per year because we expected to find breaking points in the deseasonalised EVI time series after episodes of mast seeding.

Results

Synchrony, interannual variability, and temporal autocorrelation in acorn production and the EVI

Two clear mast seeding episodes occurred in our experimental plots, in 2002 and 2008 (Figs. 1, 2). Another masting event of extremely high acorn production occurred in plot D in 2004, but the other stands produced moderate amounts of acorns, so that we could not clearly define 2004 as a mast year for our holm oak plots (Fig. 2). The time series of acorn production in all forest stands, however, presented a typical masting profile: high synchrony (r_i among trees and r_p among plots), high interannual variability at the individual (CV_i) and the population (CV_p) levels, and

negative temporal autocorrelation (Table 1). No significant differences were found for r_p, r_i, CV_p, CV_i, and temporal autocorrelation among plots (using bootstrapped standard errors of the means). The average synchrony (r_p) in the mean annual EVI was 0.68 ± 0.03 (Table 1). The CVs of the EVI values were very low (~ 0.05) and did not differ from zero (were not significant) due to error propagation, although the r values were quite high.

Effects of weather and an increasing EVI on acorn production

Droughts and wet periods (i.e. negative and positive SPEI9 values—SPEI for a 9-month window) were correlated with low and above-average EVI values, respectively (Fig. 1). The correlation analysis confirmed that the EVI could be driven by the cumulative effect of weather conditions during the previous nine months ($r = 0.50$, $P < 0.001$; Table 3). Additionally, acorn crops were larger after wetter seasons and when they were preceded by larger increases in the EVI during the previous months (Figs. 1, 2). Acorn crop sizes, however, were still very low when these periods of increasing EVI began from very low EVI values and did not reach above-average values (Figs. 1, 2).

The selected periods of increasing or decreasing EVI values (Fig. 2, shaded periods) lasted, on average, 9 ± 4 months (range: 4–16 months). Most of these periods began during the summer or autumn of the previous year or during the winter of the year in which acorns were produced, and they ended mostly in summer (Fig. 2). Acorn crop size was positively
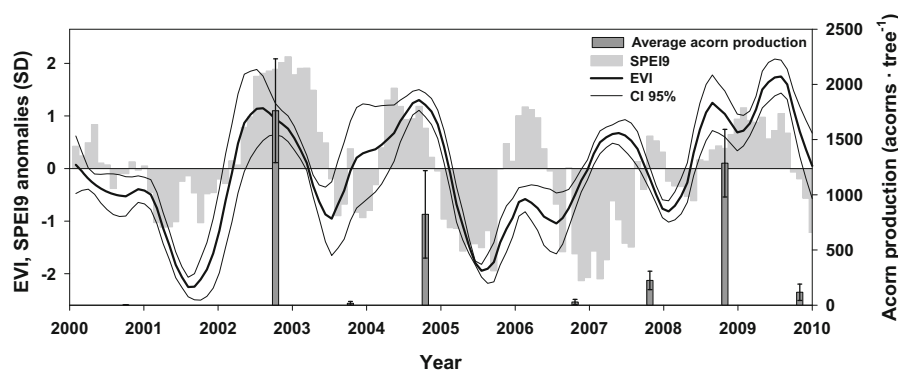
Fig. 1 Smoothed and deseasonalised anomalies of EVI time series averaged for all five plots overlaid to SPEI9. Humid periods (positive SPEI9) lead to positive anomalies in the EVI

($r = 0.50$, $P < 0.001$). *Grey bars* indicate the average annual acorn production of the five plots. *Error bars* indicate standard errors. *SD* standard deviation, *CI* confidence interval
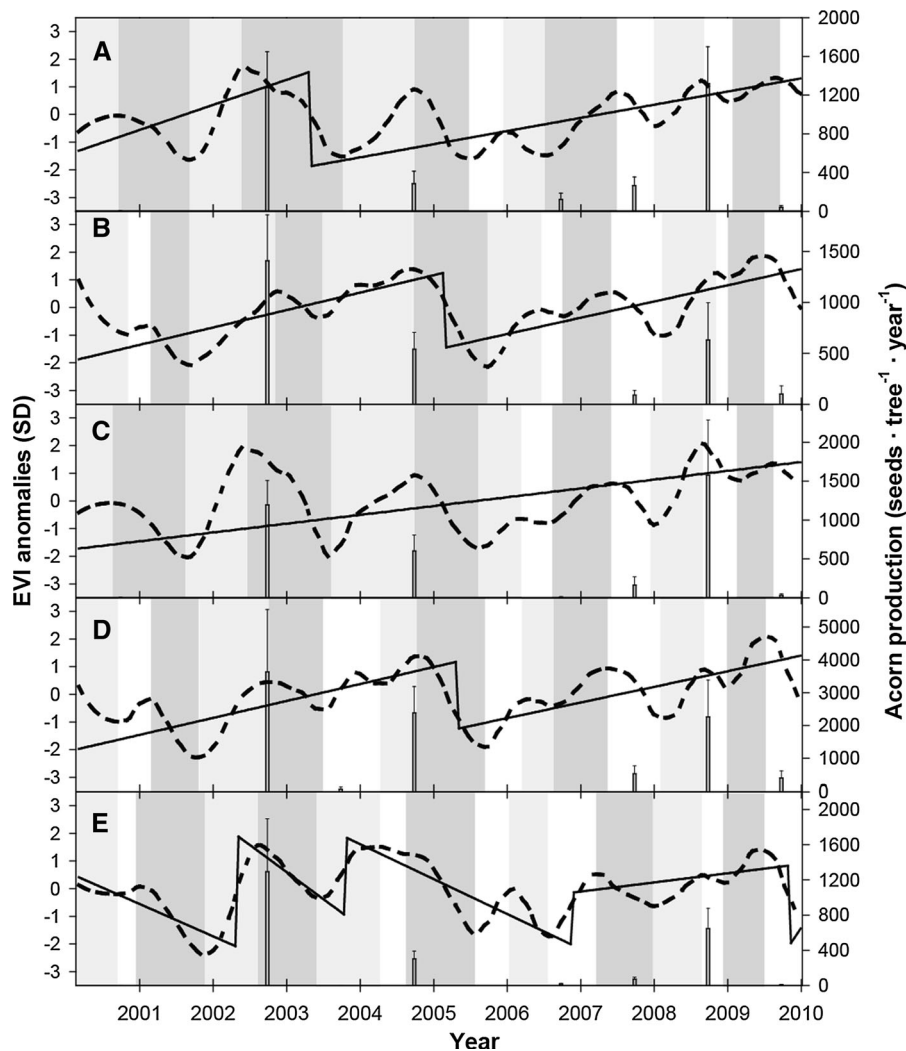
Fig. 2 Temporal dynamics of the EVI time series anomalies, BFAST trends identified in the EVI time series, and acorn production from 2000 to 2010 for each forest stand (**a–e**). *Dashed lines* represent the deseasonalised, smoothed EVI anomalies, *solid lines* show the BFAST trends of the series, and *bars* indicate annual acorn production. *Light and dark* *shading* indicate the periods used to calculate ΔEVI. Unshaded periods were not used to calculate these increments (see "Testing the effect of weather and the EVI on seed production" section for information about the selection of periods). *Error bars* indicate standard errors

correlated with SPEI6$_{Jn}$, EVI$_i$, and ΔEVI (Table 2). The best model predicting acorn production included SPEI6$_{Jn}$ (i.e. SPEI comprising 6 months from January to June), EVI$_i$, ΔEVI, and a positive interaction between EVI$_i$ and ΔEVI. In this model, the effect of acorn production in the previous years was negligible. These results confirmed the visual inspection of Figs. 1 and 2: large acorn crops were correlated with both wet spring periods and a previous trend of increasing EVI but depended on the values at which

this trend started. Interestingly, the positive interaction between EVI$_i$ and ΔEVI on acorn production (Table 2; Fig. 3) highlighted the importance of reaching an initial EVI threshold before the beginning of the increasing EVI period.

Effects of masting events on crown condition

The BFAST methodology failed to identify a clear pattern of abrupt decreases in the trend of the EVI after

Table 1 Synchrony (r_p among plots and r_i among trees), variability at the population (CV_p) and individual (CV_i) levels, and temporal autocorrelation [simple and partial (P)] of acorn production and EVI time series (mean ± SE)

| Plot		r_p	r_i	CV_p	CV_i	Lag 1	Lag 2	Lag 3	Lag 4	Lag 2 (P)	Lag 3 (P)	Lag 4 (P)
Acorns	A	**0.89 ± 0.26**	**0.64 ± 0.08**	**1.74 ± 0.42**	**2.26 ± 0.14**	**−0.16 ± 0.03**	−0.05 ± 0.03	**−0.17 ± 0.02**	**−0.09 ± 0.02**	**−0.09 ± 0.03**	**−0.19 ± 0.02**	**−0.20 ± 0.03**
	B	**0.85 ± 0.29**	**0.69 ± 0.10**	**1.86 ± 0.49**	**2.17 ± 0.12**	**−0.24 ± 0.02**	0.03 ± 0.04	**−0.15 ± 0.03**	**−0.17 ± 0.03**	−0.03 ± 0.04	**−0.16 ± 0.04**	**−0.29 ± 0.03**
	C	**0.91 ± 0.21**	**0.62 ± 0.06**	**1.77 ± 0.48**	**2.27 ± 0.13**	**−0.20 ± 0.02**	0.02 ± 0.04	**−0.17 ± 0.02**	**−0.11 ± 0.04**	−0.03 ± 0.04	**−0.18 ± 0.01**	**−0.22 ± 0.05**
	D	**0.84 ± 0.28**	**0.66 ± 0.06**	**1.61 ± 0.47**	**2.06 ± 0.17**	**−0.20 ± 0.02**	0.02 ± 0.04	**−0.17 ± 0.02**	**−0.11 ± 0.04**	−0.03 ± 0.04	**−0.18 ± 0.01**	**−0.22 ± 0.05**
	E	**0.89 ± 0.25**	**0.73 ± 0.10**	**2.03 ± 0.52**	**2.12 ± 0.14**	**−0.16 ± 0.04**	0.00 ± 0.04	**−0.18 ± 0.02**	−0.06 ± 0.03	−0.05 ± 0.03	**−0.18 ± 0.03**	**−0.17 ± 0.04**
	Mean	**0.87 ± 0.01**	**0.65 ± 0.02**	**1.80 ± 0.07**	**2.18 ± 0.04**	**−0.19 ± 0.01**	0.00 ± 0.01	**−0.17 ± 0.01**	**−0.11 ± 0.02**	**−0.05 ± 0.01**	**−0.18 ± 0.01**	**−0.22 ± 0.02**
EVI	A	0.70 ± 0.41		**0.05 ± 0.01**		0.32 ± 0.30	−0.04 ± 0.33	−0.20 ± 0.33	−0.32 ± 0.34	−0.16 ± 0.30	−0.15 ± 0.30	−0.24 ± 0.30
	B	0.73 ± 0.49		**0.05 ± 0.01**		0.22 ± 0.30	−0.25 ± 0.32	−0.18 ± 0.33	−0.05 ± 0.34	−0.31 ± 0.30	−0.05 ± 0.30	−0.08 ± 0.30
	C	0.57 ± 0.58		**0.04 ± 0.01**		0.06 ± 0.30	0.08 ± 0.30	−0.39 ± 0.31	−0.06 ± 0.35	0.08 ± 0.30	−0.40 ± 0.30	−0.01 ± 0.30
	D	0.76 ± 0.42		**0.05 ± 0.01**		0.32 ± 0.30	−0.15 ± 0.33	−0.04 ± 0.34	0.00 ± 0.34	−0.29 ± 0.30	0.14 ± 0.30	−0.10 ± 0.30
	E	0.64 ± 0.55		**0.04 ± 0.01**		0.17 ± 0.30	−0.41 ± 0.31	−0.48 ± 0.36	0.00 ± 0.41	−0.45 ± 0.30	−0.39 ± 0.30	−0.06 ± 0.30
	Mean	**0.68 ± 0.03**		**0.05 ± 0.01**		**0.22 ± 0.05**	**−0.16 ± 0.08**	**−0.26 ± 0.08**	**−0.09 ± 0.06**	**−0.23 ± 0.09**	−0.17 ± 0.10	**−0.10 ± 0.04**

No significant differences were found among plots

Values different from zero are in bold type

Table 2 Output of the generalised linear mixed model using a negative binomial distribution ($\theta = 0.4013$) relating acorn crop size, SPEI6$_{Jn}$, EVI$_i$, and ΔEVI, with plot as a random effect

Groups	Name	Variance	SD
Random effects			
Plot	Intercept	0.1203	0.3469
Residual		0.7708	0.8779

	Estimate	SE	t value	P value
Fixed effects				
Intercept	4.31	0.30	14.48	<0.0001
ΔEVI	1.12	0.26	4.38	<0.0001
EVI$_i$	−0.47	0.41	−1.15	0.2515
SPEI6$_{Jn}$	1.01	0.46	2.20	0.0278
ΔEVI × EVI$_i$	0.45	0.13	3.52	0.0004

SD standard deviation, *SE* standard error
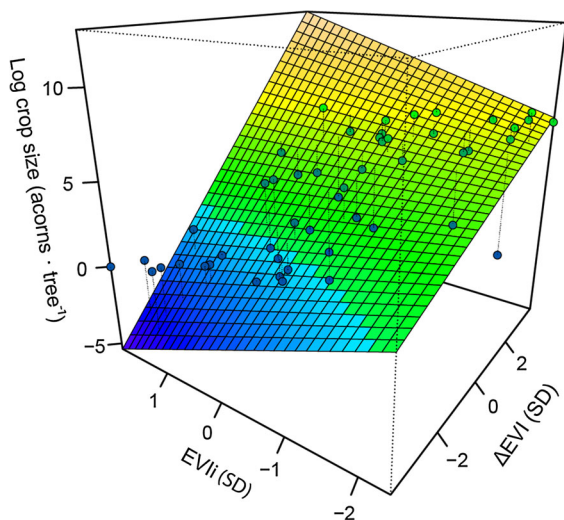
Fig. 3 3D representation of the response surface of acorn production to changes in ΔEVI and EVI$_i$. EVI units are standard deviations (SD)

the two observed masting events (Fig. 2). Two stands (B and D) presented a break during 2005, and one plot (A) presented a break after 2003, possibly associated with the severe droughts that occurred in those years. Another plot (C) did not present any breaks during any time series, and only two of the five plots (A and E) presented one break that could be associated with the masting episode of 2002.

Discussion

To our knowledge, we report for the first time that mast seeding events can be detected and, to some extent, predicted using remotely sensed vegetative indices such as the EVI. The masting events observed in this study followed an average period of increase in the EVI (a surrogate of potential photosynthetic capacity) of 9 ± 4 months but also required favourable weather conditions in spring (low levels of water stress, SPEI6$_{Jn}$). In addition to these two factors, the initial EVI value at the start of an EVI increase period was also important, i.e. a large increase in the EVI did not lead to a masting event unless it departed from a minimum EVI$_i$ threshold (Table 2; Figs. 1, 2, 3). This initial EVI threshold may suggest the need of a minimum amount of previously stored resources to produce buds before a mast seeding event, while the importance of the seasonal increase in the EVI and the favourable weather conditions in spring supports the relevance of the immediate availability of resources for triggering the masting episode. Our results thus fully agree with those recently found for deciduous trees in studies that applied isotopic analyses to show that the main photosynthates spent in the production of seed crops were those accumulated during the last growing seasons (within 17 months) (Ichie et al. 2013; Hoch et al. 2013).

Short-time resource accumulation and masting

The need of a minimum threshold of the EVI to produce large seed crops at the beginning of the increasing or decreasing EVI periods, despite the increase in the EVI during the last months before reproduction, supports the hypothesis that trees require a minimum level of stored resources to produce buds that will eventually ripen and produce seeds (Sork et al. 1993; Isagi et al. 1997; Kelly and Sork 2002). This minimum EVI value is in line with many studies reporting a relevant role of the conditions of the previous years (e.g. canopy growth, bud development, and temperatures) to account for a future masting episode (Alla et al. 2011, Sánchez-Humanes et al. 2011, Kelly et al. 2013). Moreover, the negative autocorrelation coefficients among consecutive acorn crops (Table 1, lags 1, 3, and 4) also support the premise that large crop sizes are driven by endogenous cycles of resource accumulation-depletion. When

Table 3 Correlation coefficients for the SPEI9 and EVI time series, annual acorn production (AP), SPEI6 from June (SPEI6$_{Jn}$), and summer EVI (EVI$_{sm}$)

Plot	EVI versus SPEI9	AP versus EVI$_{sm}$	AP versus SPEI6$_{Jn}$	EVI$_{sm}$ versus SPEI6$_{Jn}$
A	0.48***	0.69*	0.68*	0.74**
B	0.42***	0.85**	0.82**	0.81**
C	0.41***	0.94***	0.74*	0.70*
D	0.36***	0.81**	0.82**	0.72*
E	0.50***	0.75*	0.75*	0.94***

Pearson correlations were used for EVI versus SPEI9 and EVI$_{sm}$ versus SPEI6$_{Jn}$, and Spearman correlations were used for the AP relationships (due to the non-normal distribution of the data)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

taking into account the EVI temporal dynamics and SPEI, however, the negative autocorrelation at lag 1 was not significant (Table 2), which indicates the relatively small importance of these endogenous cycles in comparison with the paramount role of the current year's weather conditions. The BFAST analyses, in contrast to Camarero et al. (2010), did not indicate that leaf area decreased due to crown self-thinning after a masting episode. The lack of such an effect in our oak stands could be due to several reasons: (i) the low number of acorns produced in these moderately young forests (coppiced stands of ca. 40–60 years; see Espelta et al.2008, 2009) relative to the number produced in older forests, ii) oaks in the mild Mediterranean climate of our study area can even photosynthesise in autumn and early winter after the seeding season (Sánchez-Humanes 2009; Ogaya et al. 2014), thus replenishing a certain amount of the resources spent in reproduction and allowing to preserve more leaf area, and (iii) the frequent droughts in our study area (see the values for SPEI9 in Fig. 1) may be a much more relevant factor accounting for the changes in leaf area than the amount of resources invested in acorn production.

Once a minimum threshold of EVI was reached, the increase in EVI during the months (9 ± 4) previous to reproduction also influenced acorn production. The relationship between the leaf area index and gross primary production is well established (Gower et al. 2001; Law et al. 2002; Fernández-Martínez et al. 2014), and the EVI is proficient at estimating forest growth in Mediterranean evergreen forests (Garbulsky et al. 2013), but we cannot determine the part of the increase in the EVI that corresponds to an increase in leaf area or photosynthesis. The increase in leaf area during spring leads to higher rates of carbon fixation,

thus generating the pool of carbohydrates needed to sustain a mast seeding event (Figs. 1, 2). These recently synthesised carbohydrates could be those identified in isotopic studies (Ichie et al. 2013; Hoch et al. 2013). However, since only deciduous species were used in these studies, caution should be taken when extrapolating these conclusions for the evergreen *Q. ilex*. The relatively short-time periods of increasing EVI values (i.e. acquisition of resources) mediated by favourable weather conditions (e.g. low water stress) could be a consequence of drought episodes (see Fig. 1, negative SPEI9 values for years 2005 and 2007) that may often interrupt a more constant accumulation of resources through the years. These results are consistent with the nature of the Mediterranean climate in which the growth of vegetation is mostly limited by severe shortages of water (Kramer et al. 2000). The effect of weather on Mediterranean forests, however, may not only be of relevance for water availability. Precipitation may also increase mineralisation rates in soils (Jarvis et al. 2007) and nutrient availability to plants (Sardans and Peñuelas 2007; Smaill et al. 2011) in Mediterranean areas. The combined pulse of water and nutrient availability may thus produce a synergic effect boosting large seed crops in these forests. Accordingly, the reproductive behaviour of *Q. ilex* would be mostly aligned with that of a *putative* masting species that mimics the behaviour of the weather (sensu Koenig and Knops 2000).

Rethinking the influence of weather on masting behaviour

Previous studies have suggested that weather could rarely be the most important factor driving masting

due to the bimodality usually presented by seed production (Norton and Kelly 1988; Herrera et al. 1998), given the absence of bimodality in weather variables, and due to the higher variability of seed production compared to the variability of weather variables such as rainfall (Kelly and Sork 2002; Koenig and Knops 2005). These assumptions are unquestionably true for linear relationships between weather and seed production but not for non-linear relationships, as a consequence of *Jensen's inequality* (Jensen 1905; Ruel and Ayres 1999). The key role of weather found in this study, presenting a logarithmic relationship with acorn production, suggests that non-linear relationships between weather and seed production might be the cause of these differences in the distribution of seed production and weather data. For example, if seed production can be modelled as an exponential function of rainfall, the variability in seed production will easily be much higher than the variability in rainfall. Similarly, a sigmoid relationship between weather and seed production would lead that bimodality to appear in the data for seed production (e.g. flowering intensity of *Chionochloa* sp. in McKone et al. (1998)). The *Moran Effect* or synchronisation using weather cues (Ranta et al. 1997; Kelly et al. 2013) could also account for this non-linear effect of weather variability and seed production. These exosomatic signals may act as triggers for mobilising stored reserves in plants to produce seeds. We do not suggest (or report) that weather is the only driver of seed production and its extreme variability, but we call for a renewed view of the effect of weather and a reinforcement of its influence in conditioning masting behaviour either as a cue (Kelly et al. 2013) or as providing good conditions for photosynthesis (Fernández-Martínez et al. 2012).

Are remotely sensed vegetative indices suitable for monitoring masting?

Our results clearly indicate that mast seeding events in *Q. ilex* can be detected by the analysis of trends in remotely sensed vegetative indices such as the EVI. According to our results, large seed crops in *Q. ilex* might be anticipated when detecting large increasing trends in the deseasonalised EVI, mostly since the winter prior to seed harvest, especially if the trend begins at high EVI values and weather conditions during spring are mostly wet. Other authors have suggested that remotely sensed vegetative indices could predict yields in annual agricultural crops (Zhao et al. 2007), but to our knowledge, this study is the first to demonstrate that seed production in forest ecosystems can also be detected using satellite imagery and weather data. Nevertheless, the study of species with different cycles of flowering, pollination, and maturation of seeds (e.g. red oaks that require more than 1 year from the onset of flowering to seed maturation), may require a different approach. Likewise, the study of deciduous forests may also require different methodologies, because these species may respond differently. For example, a drastic reduction in crown cover was detected in two birch species (*Betula alleghaniensis* and *B. papyrifera*) during a mast year (Gross 1972), and *Fagus* sp. has also shown drastic reductions in crown conditions due to large seed harvests (Innes 1992; Ferretti et al. 1998; Han et al. 2008; Vicca et al. 2014). In these kinds of forests, masting could be detected after substantial decreases in the EVI not explained by weather conditions (Vicca et al. 2014). Various approaches may thus be needed to monitor and predict seed production in different plant species according to their contrasting functional and life-history traits. Establishing a reliable methodology for predicting masting events in forest ecosystems for extensive and remote areas will help improve pest controls, wildlife management, and hunting policies.

References

Abrahamson W, Layne J (2002) Relation of ramet size to acorn production in five oak species of xeric upland habitats in south-central Florida. Am J Bot 89:124–131

Alla AQ, Camarero JJ, Maestro-Martínez M, Montserrat-Martí G (2011) Acorn production is linked to secondary growth but not to declining carbohydrate concentrations in current-year shoots of two oak species. Trees 26:841–850. doi:10.1007/s00468-011-0658-3

Bates D, Maechler M, Bolker B, Walker S (2013) lme4: linear mixed-effects models using Eigen and S4

Beguería S, Vicente-serrano SM (2012) SPEI: calculation of the standardised precipitation-evapotranspiration index. R package version 1.1

Camarero JJ, Albuixech J, López-Lozano R, Casterad MA, Montserrat-Martí G (2010) An increase in canopy cover leads to masting in Quercus ilex. Trees 24:909–918. doi:10.1007/s00468-010-0462-5

Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. J Am Stat Assoc 74:829–836. doi:10.1080/01621459.1979.10481038

Core Team R (2013) R: a language and environment for statistical computing. R Found Stat Comput 1:409

Efron B (1987) Better bootstrap confidence intervals. J Am Stat Assoc 82:171–185

Espelta JM, Cortés P, Molowny-horas R, Sánchez-humanes B, Retana J (2008) Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. Ecology 89:805–817

Espelta JM, Cortés P, Molowny-Horas R, Retana J (2009) Acorn crop size and pre-dispersal predation determine interspecific differences in the recruitment of co-occurring oaks. Oecologia 161:559–568. doi:10.1007/s00442-009-1394-x

Fensholt R, Sandholt I, Rasmussen MS (2004) Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. Remote Sens Environ 91:490–507. doi:10.1016/j.rse.2004.04.009

Fernández-Martínez M, Belmonte J, Maria Espelta J, Espelta JM (2012) Masting in oaks: disentangling the effect of flowering phenology, airborne pollen load and drought. Acta Oecol 43:51–59. doi:10.1016/j.actao.2012.05.006

Fernández-Martínez M, Vicca S, Janssens IA, Luyssaert S, Campioli M, Sardans J, Estiarte M, Peñuelas J (2014) Spatial variability and controls over biomass stocks, carbon fluxes and resource-use efficiencies in forest ecosystems. Trees Struct Funct 28:597–611. doi:10.1007/s00468-013-0975-9

Ferretti M, Baratozzi L, Cenni E, Cozzi A, Savini P (1998) Crown transparency of beech (Fagus sylvatica L.) in the Northern Appennines (Italy)—status, changes and relationships with site characteristics and other indices of tree condition. Chemosphere 36:1037–1042. doi:10.1016/S0045-6535(97)10168-0

Garbulsky MF, Peñuelas J, Papale D, Filella I (2008) Remote estimation of carbon dioxide uptake by a Mediterranean forest. Glob Chang Biol 14:2860–2867. doi:10.1111/j.1365-2486.2008.01684.x

Garbulsky MF, Peñuelas J, Ogaya R, Filella I (2013) Leaf and stand-level carbon uptake of a Mediterranean forest estimated using the satellite-derived reflectance indices EVI and PRI. Int J Remote Sens 34:1282–1296. doi:10.1080/01431161.2012.718457

Gower STG, Rankina OK, Olson RJO, Apps MA, Inder SL (2001) Net primary production and carbon allocation patterns. Ecol Appl 11:1395–1411

Gross HL (1972) Crown deterioration and reduced growth associated with excessive seed production by birch. Can J Bot 50:2431–2437. doi:10.1139/b72-312

Han Q, Kabeya D, Iio A, Kakubari Y (2008) Masting in Fagus crenata and its influence on the nitrogen content and dry mass of winter buds. Tree Physiol 28:1269–1276. doi:10.1093/treephys/28.8.1269

Herrera C, Jordano P, Guitián J, Traveset A (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. Am Nat 152:576–594

Hoch G, Siegwolf RTW, Keel SG, Körner C, Han Q (2013) Fruit production in three masting tree species does not rely on stored carbon reserves. Oecologia 171:653–662. doi:10.1007/s00442-012-2579-2

Huete A, Didan K, Miura T, Rodriguez E, Gao X, Ferreira L (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens Environ 83(1):195–213. doi:10.1016/S0034-4257(02)00096-2

Ichie T, Igarashi S, Yoshida S (2013) Are stored carbohydrates necessary for seed production in temperate deciduous trees? J Ecol 101:525–531. doi:10.1111/1365-2745.12038

Innes JL (1992) Observations on the condition of beech (Fagus sylvatica L.) in Britain in 1990. Forestry 65:35–60. doi:10.1093/forestry/65.1.35

Isagi Y, Sugimura K, Sumida A, Ito H (1997) How does masting happen and synchronize? J Theor Biol 187:231–239. doi:10.1006/jtbi.1997.0442

Jarvis P, Rey A, Petsikos C, Wingate L, Rayment M, Pereira J, Banza J, David J, Miglietta F, Borghetti M, Manca G, Valentini R (2007) Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect". Tree Physiol 27:929–940. doi:10.1093/treephys/27.7.929

Jensen JLW (1905) Sur les fonctions convexes et les inégalités entre les valeurs moyennes. Acta Math 30:175–193

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447. doi:10.1146/annurev.ecolsys.33.020602.095433

Kelly D, Geldenhuis A, James A, Penelope Holland E, Plank MJ, Brockie RE, Cowan PE, Harper GA, Lee WG, Maitland MJ, Mark AF, Mills JA, Wilson PR, Byrom AE (2013) Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. Ecol Lett 16:90–98. doi:10.1111/ele.12020

Koenig W, Knops J (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. Am Nat 155:59–69. doi:10.1086/303302

Koenig W, Knops J (2005) The mystery of masting in trees. Am Sci 93:340–347. doi:10.1511/2005.54.970

Kramer K, Leinonen I, Loustau D (2000) The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. Int J Biometeorol 44:67–75

Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, Berbigier P, Davis K, Dolman AJ, Falk M, Fuentes JD, Goldstein A, Granier A, Grelle A, Hollinger D, Janssens IA, Jarvis P, Jensen NO, Katul G, Mahli Y, Matteucci G, Meyers T, Monson R, Munger W, Oechel W (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric For Meteorol 113:97–120

McKone MJ, Kelly D, Lee WG (1998) Effect of climate change on mast-seeding species : frequency of mass flowering and

escape from specialist insect seed predators. Glob Chang Biol 4:591–596

McShea W (2000) The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81:228–238

Myneni RB, Hoffman S, Knyazikhin Y, Privette JL, Glassy J, Tian Y, Wang Y, Song X, Zhang Y, Smith GR, Lotsch A, Friedl M, Morisette JT, Votava P, Nemani RR, Running SW (2002) Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sens Environ 83:214–231. doi:10.1016/S0034-4257(02)00074-3

Negi ASS, Negi GCSCS, Singh SPP (1996) Establishment and growth of *Quercus floribunda* seedlings after a mast year. J Veg Sci 7:559–564. doi:10.2307/3236305

Norton DA, Kelly D (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Funct Ecol 2:399–408

Ogaya R, Llusià J, Barbeta A, Asensio D, Liu D, Alessio GA, Peñuelas J (2014) Foliar CO2 in a holm oak forest subjected to 15 years of climate change simulation. Plant Sci 226:101–107. doi:10.1016/j.plantsci.2014.06.010

Ogaya R, Barbeta A, Başnou C, Peñuelas J (2015) Satellite data as indicators of tree biomass growth and forest dieback in a Mediterranean holm oak forest. Ann For Sci 72:135–144. doi:10.1007/s13595-014-0408-y

Ostfeld RS (1997) The ecology of Lyme-disease risk. Am Sci 85:338–346

Ostfeld R, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol Evol 15:232–237

Ranta E, Kaitala V, Lindström J, Helle E (1997) The moran effect and synchrony in population dynamics. Oikos 78:136–142

Ruel JJ, Ayres MP (1999) Jensen's inequality predicts effects of environmental variation. Trends Ecol Evol 14:361–366. doi:10.1016/S0169-5347(99)01664-X

Sala A, Hopping K, McIntire EJB, Delzon S, Crone EE (2012) Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytol 196:189–199. doi:10.1111/j.1469-8137.2012.04257.x

Sánchez-Humanes B (2009) Acorn production and growth in Mediterranean oaks: trade-offs and the role of climate modular organization and phenology. Universitat Autonòma de Barcelona, Barcelona

Sánchez-Humanes B, Sork VL, Espelta JM (2011) Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy. Oecologia 166:101–110. doi:10.1007/s00442-010-1819-6

Sardans J, Peñuelas J (2007) Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest. Funct Ecol 21:191–201. doi:10.1111/j.1365-2435.2007.01247.x

Shen M, Chen J, Zhu X, Tang Y (2014) Yellow flowers can decrease NDVI and EVI values: evidence from a field experiment in an alpine meadow. Can J Remote Sens 35:99–106. doi:10.5589/m09-003

Smaill SJ, Clinton PW, Allen RB, Davis MR (2011) Climate cues and resources interact to determine seed production by a masting species. J Ecol 99:870–877. doi:10.1111/j.1365-2745.2011.01803.x

Sork VL, Bramble J, Sexton O (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528–541

Sprintsin M, Karnieli A, Berliner P, Rotenberg E, Yakir D, Cohen S (2007) The effect of spatial resolution on the accuracy of leaf area index estimation for a forest planted in the desert transition zone. Remote Sens Environ 109:416–428. doi:10.1016/j.rse.2007.01.020

Verbesselt J, Hyndman R, Newnham G, Culvenor D (2010a) Detecting trend and seasonal changes in satellite image time series. Remote Sens Environ 114:106–115. doi:10.1016/j.rse.2009.08.014

Verbesselt J, Hyndman R, Zeileis A, Culvenor D (2010b) Phenological change detection while accounting for abrupt and gradual trends in satellite image time series. Remote Sens Environ 114:2970–2980. doi:10.1016/j.rse.2010.08.003

Vicca S, Balzaloro M, Filella I, Veger A, Zhang C, Peñuelas J, Janssens IA (2014) Drought responses in forests of different leaf type and climate: how do remote sensing indicators reflect field measurements? Global vegetation monitoring and modeling conference, Palais des Papes, Avignon, 07 Feb 2014

Vicente-serrano SM, Beguería S, López-Moreno JI (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J Clim 23:1696–1718. doi:10.1175/2009JCLI2909.1

Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI, Azorín-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A (2013) Response of vegetation to drought time-scales across global land biomes. Proc Natl Acad Sci USA 110:52–57. doi:10.1073/pnas.1207068110

Zhao D, Reddy KR, Kakani VG, Read JJ, Koti S (2007) Canopy reflectance in cotton for growth assessment and lint yield prediction. Eur J Agron 26:335–344. doi:10.1016/j.eja.2006.12.001