



Start of the dry season as a main determinant of inter-annual Mediterranean forest production variations



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ABSTRACT

Recent investigations have highlighted the dependence of Mediterranean forest production on spring rainfall. The current work introduces the concept of the start of the dry season (SDS) and performs a three-step analysis to determine the effect of SDS on Mediterranean forest production.

Seven forest zones of Tuscany (Central Italy), which present differently pronounced Mediterranean features, are considered. First, a statistical analysis investigates the influence of spring water budget on forest Normalized Difference Vegetation Index (NDVI) inter-annual variations during July–August. The analysis is then extended to assess the impact of inter-annual SDS variability on forest gross primary production (GPP) simulated by a NDVI driven parametric model, modified C-Fix. These simulations lead to rank the considered forest types according to the relevance of SDS in regulating inter-annual GPP variations. The application of similar statistical analyses to detrended tree ring-width time series of typical Tuscany forests confirms the existence of an eco-climatic gradient in the functional relevance of SDS. The influence of SDS on tree growth is attenuated moving from Mediterranean arid to temperate humid environments. These findings are examined and interpreted from an eco-physiological viewpoint taking into consideration the peculiarity of Mediterranean forest ecosystems. Next, relevant implications are discussed in view of the possible consequences of ongoing climate change.

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1. Introduction

The Mediterranean climate is typically characterized by the occurrence of mild, humid winters and hot, dry summers (Bolte et al., 2006). The coincidence of the dry season with the period of maximum temperature and solar irradiation creates problems for vegetation growth, which is mainly limited by water availability (Scarascia-Mugnozza et al., 2000; Ma et al., 2007). Challenging conditions particularly derive from the high inter-annual variability of spring-summer rainfall, which results in variable onset, length and intensity of the dry period (Cotrufo et al., 2011). Most flat and hilly areas in the Mediterranean basin are characterized by

these eco-climatic conditions, which become less pronounced with increasing latitude and altitude.

Although the control exerted by water on Mediterranean vegetation is a well-known phenomenon, the exact timing and intensity along the mentioned gradients are still a matter of debate (Bolte et al., 2006; Vicente-Serrano et al., 2010; Garbulsky et al., 2010). In general, the vegetation of dry Mediterranean ecosystems is adapted to utilize the variable spring water availability and to cope with the subsequent summer water shortage (Scarascia-Mugnozza et al., 2000). A strategy commonly adopted is the dominance of evergreen or semi-deciduous species, which allows proper growth during the mild winter period and variable photosynthetic activity during summer depending on seasonal dryness. Spring rainfall is, therefore, expected to be decisive in determining annual forest production. Investigations based on different techniques have supported this expectation, showing that summer photosynthetic activity and growth of Mediterranean forests

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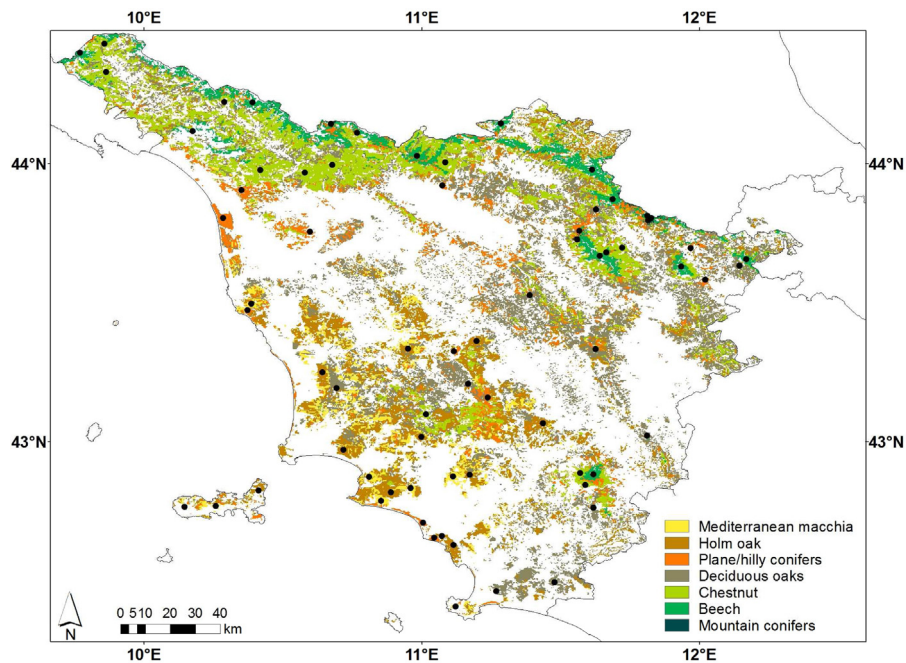


Fig. 1. Spatial distribution of the seven forest types considered in Tuscany with superimposed 70 selected sites (dots). The map is obtained from those of Arrigoni et al. (1998) and Maricchiolo et al. (2004) (see text for details).

are strongly influenced by spring rainfall. In particular, Maselli (2004) highlighted the influence of early spring rainfall on summer Normalized Difference Vegetation Index (NDVI) inter-annual variations of Mediterranean dry forests. More recently, investigations conducted by the analysis of flux tower data (Allard et al., 2008) and tree ring-widths (Lebourgeois et al., 2012) have confirmed the influence of spring rainfall on annual forest production in Mediterranean semi-arid areas.

The general validity of this phenomenon, however, has not been fully defined, as is the modality of its attenuation moving toward more humid, temperate areas (Prieto et al., 2009; Garbulsky et al., 2010). This is due to the complex and diversified effects of increased rainfall and reduced temperature in different environmental conditions. Warming can have a direct effect during winter by extending growth periods and raising photosynthetic rates (Peñuelas and Filella, 2001). This positive effect during the cold and wet season, however, can be counterbalanced by a lower availability of water in summer, by shortening the growth period and extending the duration of dry spells. Indeed, the effects of warming in semi-arid environments, such as Mediterranean areas, appear related to the indirect effect of decreasing soil-water content, adding to temperature-induced changes in phenological shifts (Peñuelas et al., 2004). This reinforces the importance of quantifying the varying timing and intensity of climate control on vegetation growth in dependence on major environmental gradients.

The current paper investigates this issue in a Region of Central Italy (Tuscany), where forests are widespread along a range of eco-climatic conditions. The relevance of spring meteorology in determining inter-annual production variations of Mediterranean forests is investigated for seven forest types representative of an environmental gradient from Mediterranean dry to temperate humid climatic conditions. The study starts with a statistical analysis of meteorological and satellite data to assess the impact of spring meteorological conditions on summer NDVI values of the seven selected forest types. Next, the concept of the start of the dry season (SDS) is introduced as the spring period during which potential evapotranspiration (PET) begins to exceed rainfall computed over a two-month time step. The analysis is then extended to

consider the relationships between inter-annual variations of SDS and forest production simulated by a NDVI-driven parametric model (modified C-Fix). The results obtained are finally substantiated by applying further statistical analyses to dendrochronological data series collected in ecologically diversified forest areas throughout Tuscany. A discussion section provides an eco-physiological interpretation of these results, whose implications are analyzed in the context of the current debate on the effects of global change.

2. Materials and methods

2.1. Study area

Tuscany (9–12° E Long., 42–44° N Lat.) has extremely heterogeneous morphological and land cover features (Fig. 1). Its climate ranges from Mediterranean to temperate warm or cool following the altitudinal and latitudinal gradients and the distance from the sea (Rapetti and Vittorini, 1995). Forests cover about half of the region and are mostly placed in the inner hilly and mountainous areas. The dominant forest species are various oaks, both evergreen (*Quercus ilex* L.) and deciduous (*Q. pubescens* Willd. and *Q. cerris* L.), Mediterranean pines (*Pinus pinaster* Ait., *P. pinea* L.), chestnut (*Castanea sativa* Mill.), beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.). Mediterranean macchia is mainly widespread in the most arid zones near the coast and on the islands.

2.2. Study data

2.2.1. Forest map

The spatial distribution of Tuscany forests was mostly derived from the map of Arrigoni et al. (1998). The 18 classes reported by this map were grouped into six main forest types following the eco-physiological criteria proposed by Chiesi et al. (2007). The distribution of Mediterranean macchia was derived from the CORINE Land Cover 2000 map (Maricchiolo et al., 2004). The seven forest types finally considered are listed in Table 1, and their distribution is shown in Fig. 1.

Table 1

Main characteristics of the 70 sites selected in Tuscany (10 per forest type). The forest types are listed following a gradient of decreasing xeric condition (i.e., decreasing annual Cws, see Fig. 3a). For each FT the minimum and maximum values of elevation, mean annual temperature and total annual precipitation estimated by DAYMET over the 10 sites are provided.

Class number	Forest type (FT)	Elevation (m a.s.l.)	Mean annual temperature (°C)	Annual precipitation (mm)
1	Mediterranean macchia	67–436	13.9–15.9	590–739
2	Holm oak	121–482	13.6–15.4	701–923
3	Plain/hilly conifers	2–576	12.2–15.7	642–1182
4	Deciduous oaks	165–915	10.5–15.0	703–1551
5	Chestnut	420–888	10.7–12.6	949–2013
6	Beech	904–1540	6.6–10.7	994–1709
7	Mountain conifers	934–1364	6.6–10.0	1213–2067

2.2.2. Meteorological data

Daily minimum and maximum temperatures and precipitation for the decade 2001–2010 were derived from existing weather stations spread all over Tuscany. In particular, daily maximum and minimum temperatures and daily total precipitation were collected from 139 and 179 stations, respectively (see Chiesi et al., 2007, for details).

Additional long-term daily meteorological data were used to characterize the six study sites for which dendrochronological data were available (Table 2); these data were derived from six stations belonging to the regional meteorological network.

2.2.3. Satellite data

Moderate Resolution Imaging Spectroradiometer (MODIS) imagery collected by TERRA and AQUA sensors was obtained from the NASA Land Processes Distributed Active Archive Center (LP DAAC) (<https://lpdaac.usgs.gov/>) as 10-degree tiles in a sinusoidal projection. The present work uses the Nadir BRDF Adjusted Reflectance (NBAR) NDVI derived from the MODIS MCD43 product. As deriving BRDF requires merging multiple looks at each pixel, the NDVI is provided every 16 days, with 500 m spatial resolution. All images of the tile corresponding to Central Italy were downloaded from the NASA website for the same ten years as above (2001–2010). An example of these images is shown in Fig. 2.

2.2.4. Dendrochronological data

Table 2 summarizes the main features of the six Tuscany study sites where dendrochronological measurements have been taken during the last few years (Fig. 2). These sites encompass most eco-climatic variability that characterizes Tuscany forests, ranging from dry Mediterranean areas (Maremma) to temperate humid mountain zones (Mugello and Sasso Fratino). All tree ring-width data series were collected and pre-processed following standard protocols, as fully described in Battipaglia et al. (2010).

2.3. Pre-processing of meteorological and satellite data

The daily minimum and maximum temperature and precipitation data collected in the ground stations from 2001 to 2010 were extended over the Tuscany surface by applying the DAYMET interpolation procedure (Thornton et al., 1997). Daily global solar radiation for the same period was then estimated through the MT-CLIM model (Thornton et al., 2000) and converted into Photosynthetically Active Radiation (PAR) by a constant coefficient (0.464; Iqbal, 1983).

The NDVI time series was filtered using the local method LOESS (aka LOWESS) (Cleveland and Devlin, 1988) in order to remove undesirable day-to-day variability (noise) resulting from cloud, ozone, dust, and other aerosols, which generally decreases the near-infrared reflectance and leads to spurious drops in NDVI data. This

Table 2

Main environmental (a) and dendrochronological (b) characteristics of the dendrochronological sites considered in the study (E = evergreen, D = deciduous).

Site	Position	Elevation (m a.s.l.)	Reference weather station	Period of weather data	T (°C)	P (mm)	Species
(a)							
Lajatico (E)	43.43° N–10.7° E	210	Saline	1963–1997	14.1	887	<i>Quercus ilex</i>
Lajatico (D)	43.43° N–10.7° E						<i>Quercus cerris</i> ; <i>Q. pubescens</i>
Maremma	42.65° N–11.07° E	5	Alberese	1959–2001	14.4	686	<i>Pinus pinea</i>
Mugello	44.05° N–11.45° E	1020	Razzuolo	1959–2001	9.7	1274	<i>Fagus sylvatica</i>
Radicondoli	43.14° N–11.04° E	500	Larderello	1951–1999	13.1	949	<i>Quercus cerris</i> ; <i>Q. pubescens</i>
San Rossore	43.73° N–10.28° E	10	Pisa F. Agraria	1963–2002	15.3	872	<i>Pinus pinaster</i>
Sasso Fratino	43.84° N–11.79° E	1550	Camaldoli	1970–1994	8.8	1530	<i>Fagus sylvatica</i>
Site	Number of stands	Total number of samples	Period of dendrochronological data	Reason for the possible exclusion of some years	Period selected for correlation analysis		
(b)							
Lajatico (E)	1	70	1951–1997		1977–1996		
Lajatico (D)	1	100	1951–1997		1977–1996		
Maremma	3	32	1968–2003	Parasitic attack at the beginning of '90es (Moriondo et al., 1995)	1971–1990		
Mugello	4	48	1952–2002		1981–2000		
Radicondoli	2	20	1951–2002	Conversion of coppice to high forest at the end of 1980s (Ceppatelli, personal communication)	1970–1989		
San Rossore	5	60	1963–2002		1982–2001		
Sasso Fratino	1	15	1827–2008		1974–1993		

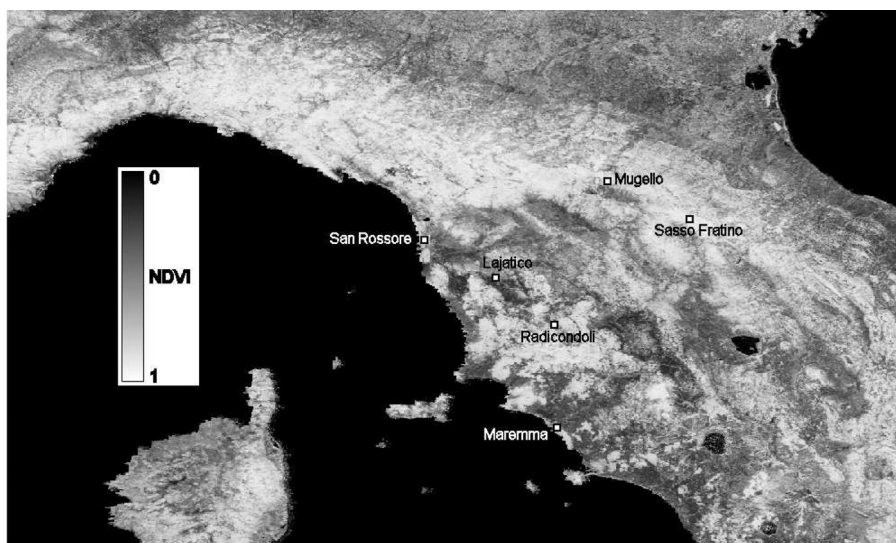


Fig. 2. MODIS NDVI image of mid-August 2003 showing the position of the six sites where dendrochronological measurements were collected. Forest areas have generally NDVI higher than agricultural and urban lands.

procedure smoothes the temporal profile as a function of time in a moving fashion analogous to how a moving average is computed for time-series. However, a locally weighted quadratic regression was used for the smoothing rather than a simple average. Finally the data were linearly interpolated to estimate missing values and obtain the NDVI product on a daily basis using the filtered series (see Moreno et al., 2012, for details).

2.4. Simulation of forest GPP

Within each of the seven forest types considered, ten sites of about 1 km² were selected representative of relevant eco-climatic conditions (see Chiesi et al., 2007, for details). A summary of the main environmental features of these sites is reported in Table 1. The meteorological and NDVI data of these 70 sites were extracted from corresponding pixels and used to drive an NDVI based parametric model, modified C-Fix (Maselli et al., 2009a).

C-Fix is a Monteith type model driven by temperature, radiation and the fraction of absorbed photosynthetically active radiation (fAPAR), quantified through its generalized relationship with NDVI (Veroustraete et al., 2002, 2004). Maselli et al. (2009a) proposed a modification of C-Fix aimed at improving the model performance in Mediterranean areas, which are characterized by a long summer dry season during which vegetation growth is limited by water availability (Bolle et al., 2006). This version includes an additional water stress factor, which is computed by using meteorological data and limits photosynthesis in case of short-term water stress (Maselli et al., 2009a). The factor, Cws, is obtained as:

$$Cws = 0.5 + 0.5 \frac{AET}{PET} \quad (1)$$

where AET and PET are actual and potential evapotranspiration, respectively, both cumulated over a two-month period. AET is assumed to equal precipitation when this is lower than PET. Consequently, Cws can vary between 0.5 (when short-term water shortage reduces photosynthesis to half of its potential value) and 1 (when there is no water shortage and photosynthesis reduction). Modified C-Fix therefore predicts the forest GPP of day *i*, GPP_{*i*}, as:

$$GPP_i = \varepsilon \cdot Tcor_i Cws_i fAPAR_i PAR_i \quad (2)$$

where ε is the maximum radiation use efficiency (1.2 g C MJ⁻¹), Tcor_{*i*} is the MODIS temperature correction factor of each forest type (Heinsch et al., 2003), Cws_{*i*} is the water stress factor, fAPAR_{*i*} is the

fraction of absorbed PAR, and PAR_{*i*} is the incident solar radiation between 400 and 700 nm, all referred to day *i*.

Modified C-Fix was applied to simulate the daily GPP of the 70 selected forest sites for the whole study period (2001–2010). The meteorological data needed to drive the model (minimum and maximum temperatures, precipitation and PAR) were extracted from the 1-km pixels of the study sites and used to predict PET by the method of Jensen and Heise (1963). The NDVI data were extracted from the corresponding 500-m pixels and converted into fAPAR using the generalized linear equation proposed by Myneni and Williams (1994).

2.5. Statistical analyses

As previously explained, Cws is a simplified water stress indicator, which in Mediterranean areas approaches the potential maximum (Cws = 1) during winter and drops toward the minimum (Cws = 0.5) during the summer dry season. This is due to the concomitant action of increasing temperature and radiation associated to the seasonal evolution and of decreasing precipitation typical of the climate type. Consequently, Cws shows maximum inter-annual variations in a period around the Mediterranean spring, when the transition from high to low Cws occurs depending on seasonal dryness (Maselli et al., 2009a). In order to assess the effect of spring water availability on inter-annual summer NDVI variations inter-annual correlations over the ten study years were computed between Cws of each day from March to July and mean NDVI of July–August (NDVI_{07–08}) for the 70 forest sites. The period from March to July includes the described transition from humid to dry conditions in a wide range of Mediterranean climates. The two summer months coincide with the peak of Mediterranean summer, when forest NDVI is strongly controlled by water availability (Maselli, 2004). Similar correlation analyses were then repeated considering Cws aggregated on a monthly basis.

For the reasons given above, the value of Cws computed over the period from March to July (Cws_{03–07}) can be taken as an indicator of SDS in all Tuscany environmental conditions. More precisely, Cws_{03–07} can be used as a weight to express SDS in day of year (DOY) through the following equation:

$$SDS = 59 + 153 \frac{Cws_{03-07} - 0.5}{0.5} \quad (3)$$

where 59 are the days of January–February (when the dry season cannot start and Cws is assumed to be always equal to 1) and 153 are the days from the beginning of March to the end of July (peak of the Mediterranean dry season).

The value of SDS as a climatic indicator of humidity was first assessed by analyzing the meteorological data of the 70 forest sites. This was done by confronting the SDS of these sites computed over the ten years considered with the respective mean humidity defined as the difference between annual rainfall and PET. Next, the previous correlation analysis was extended to assess the influence of SDS on annual GPP simulated by modified C-Fix (GPP_{Ann}). More precisely, inter-annual correlations were computed between SDS and GPP_{Ann} simulated by C-Fix for each examined forest site.

Finally, similar correlation analyses were performed between SDS and tree ring-widths measured in the six sites of Fig. 2 over different time periods. These analyses are based on the consideration that, after proper treatment, ring-widths are proportional to the biomass accumulated by trees during corresponding growing seasons, i.e., to annual NPP; since in a first approximation the ratio between annual forest NPP and GPP can be considered constant (Waring et al., 1998), ring-widths can be expected to be indicative also of annual GPP (Rodolfi et al., 2007).

A SDS series was computed for each site using daily meteorological data derived from the most adjacent station (see Table 1). Before performing the correlation analyses, the measured ring-widths were detrended to remove the possible influence of different tree ages (Chiesi et al., 2012). The detrending was carried out following the method already used in Rodolfi et al. (2007), i.e., by applying the following operation to the ring-width series:

$$DRW = \frac{RW - RW_{AV}}{RW_{SD}} \quad (4)$$

where DRW is the detrended ring-width, RW the original ring-width and RW_{AV} and RW_{SD} are the ring-width moving average and standard deviation computed using a window of order 3. The same detrending was applied to the SDS data series (DSDS). The correlation between the two detrended data series was finally computed for each site and main forest type previously defined. More precisely, one forest type was considered for each site of Maremma, Mugello, Radicondoli and San Rossore (Table 2), while two forest types (evergreen and deciduous oaks) were considered for the Lajatico site.

3. Results

3.1. Simulation of forest GPP

Fig. 3 shows the annual profiles of Cws (a), NDVI (b) and simulated GPP (c) obtained by averaging the data of the ten sites for each forest type over the period 2001–2010. The mean profiles of Cws show the mentioned gradient in humidity from macchia to fir, which involves both a general increase of mean Cws and a shortening of the dry season, mostly due to a delay of SDS.

As regards the inter-annual variability, clear Cws minima are observed for all seven FTs in the hottest and driest year of the decade (2003), while the maxima are more irregular. Most of this variability is concentrated at the beginning of the dry season, particularly for the driest forest types. More precisely, the inter-annual variation of Cws_{03-07} accounts for most of the total annual Cws variation for macchia, Holm oak, plain/hilly conifers, deciduous oaks and chestnut (coefficient of determination r^2 ranging from 0.50 to 0.64), while these values drop slightly for beech and mountain conifers (r^2 around 0.45).

The annual NDVI profiles show more complex patterns related to the presence of evergreen and deciduous species. The three evergreen forest types of plain-hilly areas (macchia, Holm oak

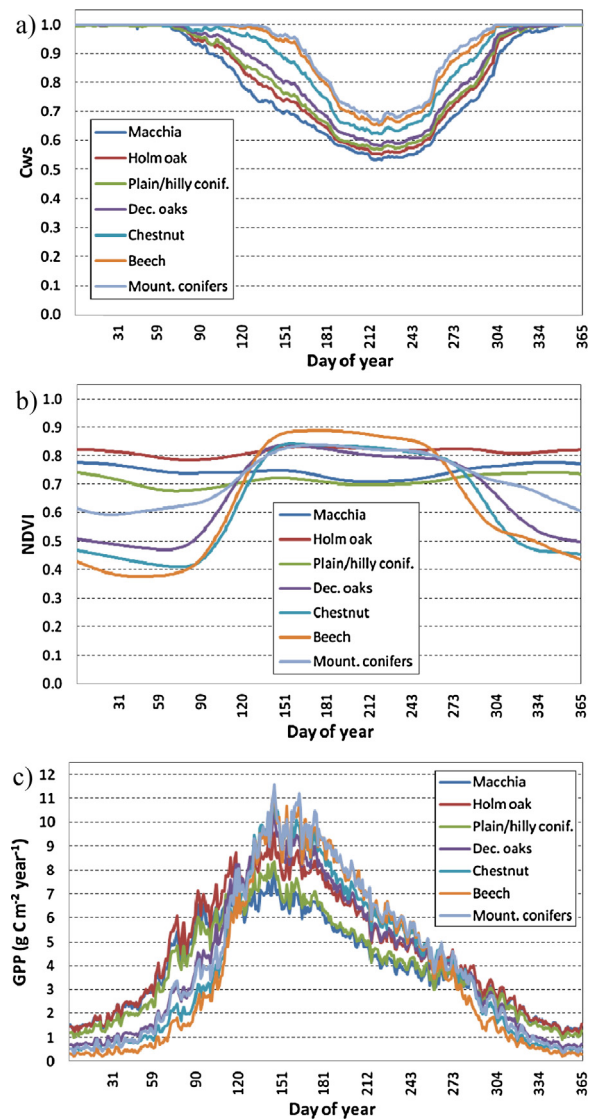


Fig. 3. Average annual profile of Cws (a), NDVI (b) and GPP (c) computed for the seven forest types over the study period (2001–2010).

and plain/hilly conifers) show an almost flat profile, while certain seasonality is visible for evergreen mountain conifers due to winter thermal limitation. This seasonality is obviously more pronounced for the deciduous forest types (oaks, chestnut and beech); the last forest type, which is typical of mountain zones, shows the most peaked NDVI profile. The inter-annual variations of NDVI follow those of Cws only for the driest FT (macchia, $r^2 = 0.38$). More generally, the inter-annual NDVI variability is limited, and both minima and maxima are observed in different years.

The differences in annual GPP profile among the seven forest types are mainly determined by Cws and fAPAR, being PAR relatively similar for all FTs and T_{cor} effective only for mountain FTs during the growing season. The three evergreen forest types of plain-hilly areas show an early start of the growing season and a clear summer decline due to water stress. The two mountain forest types (beech and mountain conifers) show the shortest and most peaked growing season. Globally, the highest GPP estimates are obtained for the evergreen Mediterranean species (Holm oak, around $1700 \text{ g C m}^{-2} \text{ year}^{-1}$) and the lowest for the deciduous mountain species (beech, around $1400 \text{ g C m}^{-2} \text{ year}^{-1}$). The inter-annual variations of GPP are mainly determined by Cws; clear minima in 2003 and irregular maxima are observed for all FTs. More

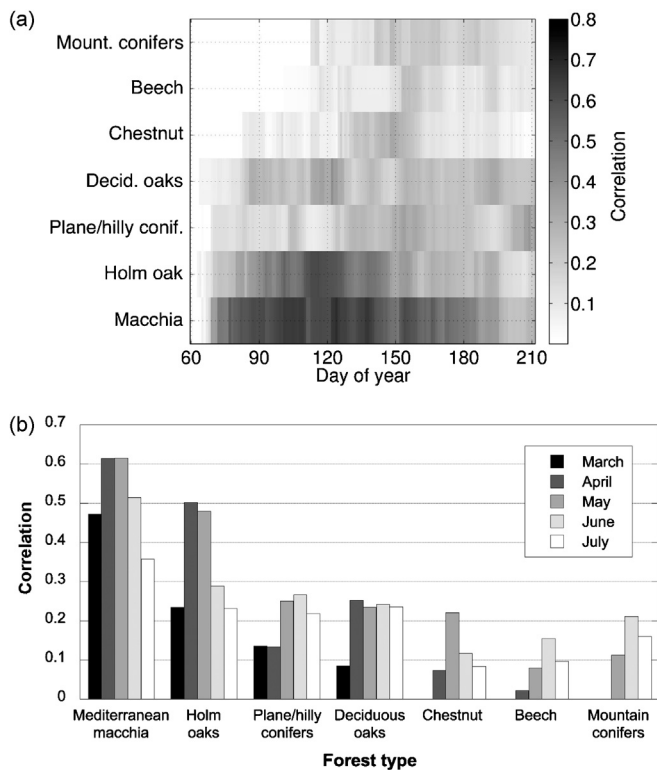


Fig. 4. (a) Mean inter-annual correlation coefficients computed for the seven FTs between the daily SDS values from 1st March (day 60) to 31st July (day 212) and the NDVI values of July–August for the ten study years (2001–2010). (b) The same mean correlation coefficients computed aggregating Cws on a monthly basis. In both cases negative correlations, whose absolute values are all lower than 0.16, are set to 0.

precisely, the coefficient of determination between annual Cws and GPP values is higher than 0.7 for all FTs with the usual exception of beech and mountain conifers.

3.2. Statistical analyses

The results of the inter-annual correlation analyses between spring Cws and summer NDVI values are summarized in Fig. 4a and b. More precisely, Fig. 4a shows the mean correlations of the seven forest types computed on a daily basis. The described increase in humidity involves both a decrease in mean correlations and a shift in the correlation maxima from March–April (for macchia and Holm oak) to June to July (for beech and mountain conifers).

Both these patterns are even more evident in the histogram of Fig. 4b, which shows the same mean correlations computed on a monthly basis. The month of maximum correlation moves from April to May–June following the described humidity gradient. The same gradient is influent on relevant correlation intensity; the maximum inter-annual correlations are reduced from 0.6–0.7 to 0.1–0.2 going from macchia/Holm oak to mountain forest types. For the former forest types the correlations remain moderate also for one-two months following the early spring maximum. The correlations of plain/hilly conifers and deciduous oaks, which cover very diversified eco-climatic conditions (Table 1), are quite irregular. Those of beech are very low or even negative.

Fig. 5 shows the mean SDS of the seven forest types versus the described humidity index. As expected, SDS accounts for virtually all humidity variation, ranging from DOY 140 (mid-May) in the driest ecosystem (macchia), where annual PET strongly exceeds rainfall, to DOY 188 (beginning of July) in the most humid ecosystem (mountain conifers), where the opposite is the case.

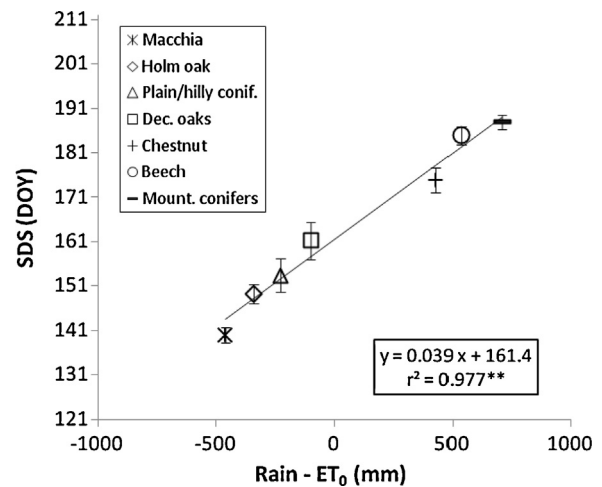


Fig. 5. Linear regression of mean SDS versus mean site aridity (Rain-ET₀) for the seven forest types considered (see text for details). The bars indicate the inter-site standard errors of the estimates (**highly significant correlation, $P < 0.01$).

Fig. 6 shows the linear regression of the mean correlations SDS/GPP_{Ann} versus the humidity index for the seven samples considered. Also these correlations vary in dependence on annual humidity. In the driest ecosystems (macchia, Holm oak) more than 60% of simulated inter-annual GPP variability is accounted for by SDS. This percentage is reduced to 20–30% for mountain forest types (beech and mountain conifers). While examining this pattern the partially spurious nature of these correlations should be kept in mind, which is due to the contribution of CWS_{03–07} to C-Fix simulation of annual GPP (see discussion for details).

The correlation analyses between detrended SDS and tree ring-widths could theoretically dispose of different continuous periods covered by both meteorological and dendrochronological data series for each site. In two cases (Maremma and Radicondoli) these periods were limited by the effects of management operations or parasitic attacks, as summarized in Table 2. Moreover, the first and last years of the common series had to be excluded to avoid the consideration of incorrect moving statistics within Eq. (4). Finally, a common length of the series was chosen for all six sites in order to enhance the comparability of the obtainable correlation

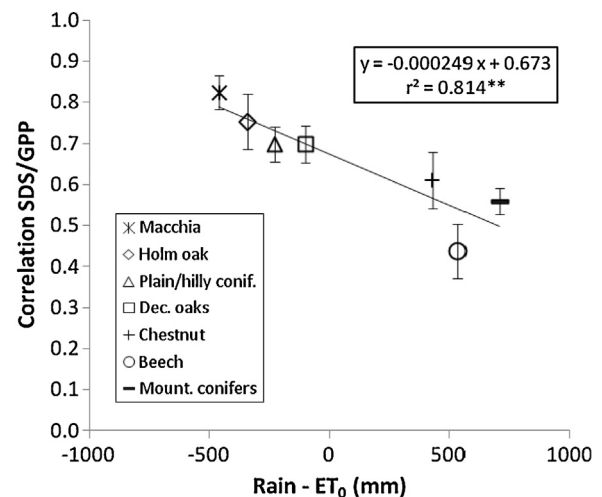


Fig. 6. Linear regression of mean inter-annual correlations SDS/GPP_{C-Fix} versus mean site aridity for the seven forest types considered (see text for details). The bars indicate the inter-site standard errors of the estimates (**highly significant correlation, $P < 0.01$).

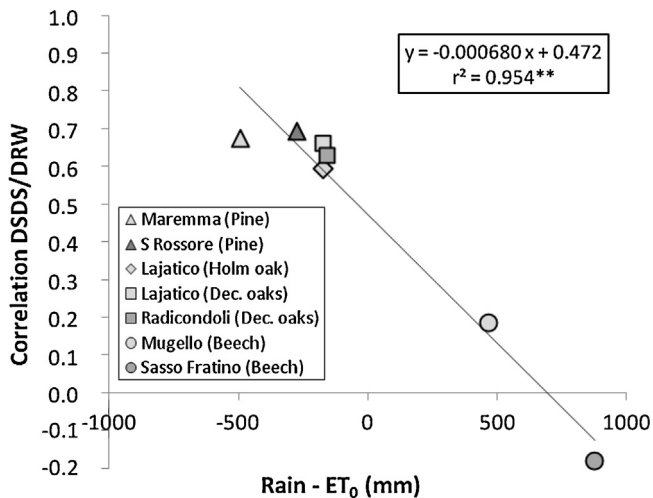


Fig. 7. Linear regression of mean inter-annual correlations DSDS/DRW versus mean site aridity for the six sites and forest type considered (see text for details) (**highly significant correlation, $P < 0.01$).

statistics. The most recent ring-width series of 20 years were therefore selected in all cases (Table 2).

Fig. 7 shows the linear regression of the correlations DSDS/DRW versus the humidity index for the seven ecosystems considered. The coefficient of determination and the slope of the regression are higher than the corresponding statistics of Fig. 6, mostly due to the consideration of the two humid sites (Mugello and, above all, Sasso Fratino), where the correlation DSDS/DRW is low or even negative. The two regressions, however, show a similar negative trend, which supports the existence of the described eco-climatic gradient in the effect of SDS on Mediterranean forest growth.

4. Discussion

4.1. The concept of SDS

Quantifying the effects of climate change on tree growth requires the development of specific indices that describe the causal relationship between main environmental drivers and plant responses. The control exerted by rainfall on the phenology and functions of water-limited forest ecosystems is a well-known phenomenon whose characteristics have been examined in a number of studies (Worbes, 1999; Cotrufo et al., 2011; Toledo et al., 2011; Misson et al., 2011). In particular, both eco-physiological considerations and experimental evidences indicate that the precipitation occurring early in the growing season has a strong impact on the primary production potential of dry Mediterranean forests (Cherubini et al., 2003; Maselli, 2004; Allard et al., 2008; Wu et al., 2012), the onset of radial growth being delimited by the occurrence of plant rehydration and the increase of air temperature (Cocozza et al., 2012).

The current study investigates this topic considering seven main forest types that are in quasi-equilibrium with relevant environmental conditions along a gradient from Mediterranean dry to temperate humid zones in Central Italy. The first statistical analyses confirm the importance of spring water budget in determining inter-annual summer NDVI variations of typical Mediterranean dry forests. The effect of spring dryness on summer NDVI becomes more rapid and less intense moving toward more temperate humid conditions.

The study then introduces the concept of SDS, which is computed on the basis of a simplified water budget considering all months when the transition from humid to dry meteorological

conditions may occur in a variety of Mediterranean eco-climatic situations (March–July). SDS is defined as the day of year when potential evapotranspiration exceeds rainfall, both accumulated over a period that is most influential on forest primary production (two months, see Maselli et al., 2009a). Climatically, SDS is characterized by an extreme spatial and temporal (inter-annual) variability, which tends to increase with increasing aridity (Bolle et al., 2006).

4.2. Influence of SDS on simulated GPP

The investigation proceeds by analyzing the influence of SDS on forest GPP simulated by a NDVI-driven parametric model, modified C-Fix. The accuracy of this model in Mediterranean areas has been recently demonstrated through comparison with eddy covariance flux measurements (Maselli et al., 2009b, 2010; Chiesi et al., 2011). These studies indicated that modified C-Fix is capable of reproducing both inter- and intra-year variations of Mediterranean forest GPP.

The statistical analyses performed show that in the warmest, most arid areas SDS accounts for a large fraction of simulated inter-annual forest production variations. This is due to:

1. The low relevance of the thermal factor in limiting annual GPP (through T_{cor}).
2. The direct effect of spring water availability on spring GPP (through CWS_{03-07}).
3. The previously demonstrated influence of spring water shortage on summer fAPAR (through NDVI).

As fully discussed in Maselli et al. (2009a), the last two factors account for the two-phase response of forest ecosystems to water stress. During the first phase (1–2 months) photosynthesis is mainly limited by rapid and reversible mechanisms (decreases of stomatal and mesophyll conductance, soil-to-leaf hydraulic conductance, cell division and turgor, and cell wall elasticity, among the others), which only marginally imply structural canopy alterations (Field et al., 1995). Within modified C-Fix, these processes are modeled by a reduction of Cws. In the second phase a structural damage of tree canopy occurs due to irreversible mesophyll damage, leaf wilting, yellowing and shedding. This is associated with a reduction of fAPAR, which is observed through a NDVI decrease (Running and Nemani, 1988). Accordingly, NDVI alone cannot be considered as integrative indicator of how photosynthetic capacity is controlled by environmental stress, because it mainly measures plant greenness and can only track decreases in photosynthetic activity when leaf yellowing or shedding occurs (Gamon et al., 1995; Maselli et al., 2009a).

These considerations have particular implications for dry Mediterranean forest ecosystems, in which GPP is only marginally limited by low spring temperatures. As a consequence, most annual GPP can theoretically occur in the months around the summer solstice, i.e., from April to August, which includes around 2/3 of total annual solar radiation. During this period Mediterranean forest GPP is mainly limited by water availability. In the current simulations the effect of SDS on GPP is first mostly direct (in April–June, through CWS_{03-07}) and then mostly indirect (in July–August, through the influence of spring Cws on NDVI/fAPAR).

The same simulations indicate that the relevance of SDS diminishes moving toward more cold-humid eco-climatic zones, where SDS is delayed and less influent. Again, this finding can be attributed to both direct and indirect decreased effects of SDS. Spring water stress is here almost absent and anyway scarcely influent due to the prevalence of thermal limitation. The previously observed lower

influence of spring Cws on summer NDVI/fAPAR completes this pattern concerning the most productive summer months.

4.3. Analyses of tree ring-widths

The results of the previous simulations are confirmed by the statistical analyses of tree ring-widths collected in six sites representative of different Tuscany eco-climatic zones and forest types. Specifically, these analyses support the existence of a clear ecoclimatic gradient of SDS control on forest production. Detrended tree ring-widths of most arid areas are positively strongly correlated with SDS, while this is less the case for temperate humid zones. In the highest and coldest mountain site (Sasso Fratino) a slightly negative effect of SDS has even been found which could be attributed to the reduced air temperature and solar radiation and, consequently, carbohydrate accumulation that are usually associated to abundant rainfall at the beginning of the brief growing season.

The observed gradient in the effect of SDS on forest production can be interpreted in the light of the grouping introduced by Cherubini et al. (2003) for the characterization of tree-ring formation. The driest Mediterranean forest ecosystems show a summer stop in cambial activity due to water stress, which can be reasonably expected to depend on SDS. This pattern becomes less evident moving toward more temperate humid areas, where no clear stop (or two moderate stops in winter and summer) in cambial activity should correspond to a lower relevance of SDS. Finally, a unique winter stop in cambial activity can be found in coldest environments, where SDS has only a minimal influence.

Our analyses do not examine the effects of the meteorology of other seasons (winter, summer and autumn), which, even if of minor importance, may concur to determine tree ring-widths in Mediterranean regions (Cherubini et al., 2003). These effects, and particularly those of summer weather conditions, can be expected to increase along with the reduced influence of SDS, i.e., when moving toward more temperate humid environments. Support to this hypothesis is brought by the results of Piovesan et al. (2008), who found a significant impact of summer drought on the productivity of beech forests in the central Apennines.

4.4. Possible considerations on eddy covariance data

Further support to the current results could be brought by the analysis of medium-long term GPP data series derived from flux tower measurements (Baldocchi, 2003). Such analyses, however, are hampered by the scarcity of long and complete flux tower measurement series, whose consistency is often deteriorated by the effects of instrumental degradations and/or forest disturbances (management operations, parasitic attacks, etc.). In Tuscany there are three eddy covariance towers placed within forest ecosystems: San Rossore, Lecceto and Pianosa. In the San Rossore pine forest an eddy covariance flux tower has been active for about a decade (1999–2009), but only the measurements of a few years are complete and consistent (2001–2005, see Moreno et al., 2012). Among these, the two seasons of 2002 and 2003 show rather extreme and opposite meteorological and GPP patterns (Moreno et al., 2012). The first year, quite humid, was characterized by a late SDS (DOY 154) and high annual GPP ($1964 \text{ g C m}^{-2} \text{ year}^{-1}$). The second year, extremely dry, was characterized by an early SDS (DOY 119) and correspondingly lower annual GPP ($1647 \text{ g C m}^{-2} \text{ year}^{-1}$). Similar results are obtained from the flux tower site of Lecceto, which is covered by a hilly Mediterranean evergreen oak forest (Moreno et al., 2014). During the available three years of measurements (2006–2008), the driest year (2007) was characterized by an early SDS (DOY 149) and low GPP ($852 \text{ g C m}^{-2} \text{ year}^{-1}$), while the most humid year (2008) showed a late SDS (DOY 168) and high GPP

($1142 \text{ g C m}^{-2} \text{ year}^{-1}$). This pattern is even more evident for the “macchia” tower site of the Pianosa Island, which is characterized by the most arid climate (Colom et al., 2004). The first of the two measurement years (2007) was quite dry (SDS = 130 DOY) and showed a low GPP ($1080 \text{ g C m}^{-2} \text{ year}^{-1}$), while the second year (2008) was wetter (SDS = 156 DOY) and showed a higher GPP ($1361 \text{ g C m}^{-2} \text{ year}^{-1}$). Finally, these trends are confirmed by the findings obtained by Allard et al. (2008) regarding six fully recorded years of flux tower measurements taken within a Mediterranean evergreen oak forest in Southern France. A strong negative relationship was found between annual gross and net production and rainfall accumulated during the spring months from March to June.

4.5. Eco-physiological relevance of SDS

The spectrum of plant sensitivity to drought is generally governed by alterations in water (i.e., water supply vs. water demand) and carbon (i.e., photosynthesis, respiration and total non-structural carbohydrate use) balances, and by stomatal control strategies in balancing water loss with carbon gain (isohydric vs. anisohydric behaviors; Centritto et al., 2011). All previous observations support the hypothesis that in Mediterranean areas the gradient of SDS relevance is mostly independent of forest types. This would imply that different forest species in the same ecoclimatic condition react in a relatively similar way to the water shortage which is typical of Mediterranean summers. A plausible explanation for this behavior can be provided by the converging ecophysiological and morphological adaptations shown by Mediterranean ecosystems (Cherubini et al., 2003), although different growth forms display specific adjustments in response to water shortage. In a study with six Mediterranean shrubs, Medrano et al. (2002) revealed that, in spite of some marked inter-specific differences, all followed the same pattern of dependence of photosynthetic processes on stomata conductance. It must be pointed out that the similarities in sclerophylly and related traits among species in the Mediterranean vegetation reflect a mix of conserved traits that arose prior to the occurrence of Mediterranean-type climates and more recent adaptive shifts in lineages derived from cooler climates (Ackerly, 2004).

Indeed, despite the convergent behavior with respect to leaf functional and structural traits, Mediterranean shrubs and trees may show species-specific water relationships and hydraulic properties in response to climatic drivers, such as elevated atmospheric CO_2 concentration (Peñuelas et al., 2002; Tognetti et al., 2000, 2001); nevertheless, all these species display an intrinsic growth strategy that highly prioritizes water saving over carbon uptake (Tognetti and Peñuelas, 2003). No matter of the strategy, Mediterranean woody plants are highly tolerant of severe water stress and tissue dehydration despite the damage inflicted by extreme drought, and are adapted to warm and dry climates. These species, however, often operate at the limits of hydraulic safety, which are surpassed under severe droughts, and prolonged climatic stress might predispose them to decline (Tognetti et al., 1998). As previously noted, if stomata closure is the earliest response to decreasing water availability and the dominant limitation to photosynthesis at moderate water stress, progressive down-regulation or inhibition of metabolic processes may prevail at severe drought (Flexas and Medrano, 2002).

Some differences among species in the response to dry periods may be expected due to species-specific water use efficiency and tree structural balance. For example ring-width variability, as well as tree-ring growth in dry years that should be unaffected by stand dynamics, were found higher in *Q. pubescens* than in *Q. cerris*, in central Tuscany (Cermak et al., 2008; Tognetti et al., 2007). In any case the ability to switch quickly between inactive to active

stages is a common feature of Mediterranean woody plants which enables them to restart physiological processes and to cope with typically erratic climatic conditions. Indeed, during early phases of water stress, plant growth declines before photosynthesis, temporarily resulting in a non-structural carbohydrate surplus (e.g., Luxmoore et al., 1995). The drought-induced reduction of photosynthesis increases photosynthate partitioning to storage during the early period of stress, in association with molecular signals that down-regulate growth and respiration and up-regulate carbohydrate flux to storage (e.g., Smith and Stitt, 2007). With progressive drought, however, photosynthesis may decline before (or to a greater extent than) respiration, resulting in depleted carbohydrate reserves through less favorable balance of carbohydrate production and use (McDowell, 2011).

4.6. Expected effects of changing SDS

Many questions remain about the effects of a generally warmer future climate and the impacts on forest productivity, in particular whether plants can acclimate or adapt their growth patterns and resilience mechanisms as quickly as the rate of increase in SDS relevance and drought frequency. Higher air temperature are expected to exacerbate the impact of drought on plant water loss by elevating the vapor pressure deficit (VPD) in the atmosphere, thereby increasing potential transpiration, particularly in the driest Mediterranean forests. Hence, climate-change driven increases in the relevance of SDS and the frequency of droughts might lead to vegetation growth failure and even forest dieback (Centritto et al., 2011). A dramatic increase in temperature during the pre- and early growing season may also exacerbate the soil water limitation by depleting soil water reserves, again reducing tree growth. These results also highlight the important effect of environmental conditions before, and at the very beginning of, the growing season on tree growth and vegetation activity in Mediterranean forests.

Hypotheses regarding carbon starvation (failure to maintain metabolism or fend off biotic agents due to prolonged negative carbohydrate balance) and hydraulic failure (desiccation from failed water transport) have stimulated the recent debate on tree mortality associated with increased temperatures and droughts (McDowell, 2011). Given the potential risks of climate-induced tree mortality (Allen et al., 2010), increased management attention to adaptation options for enhancing stand resistance and resilience to projected climate stress can be envisaged for Mediterranean forests, following climatic indices, such as SDS.

5. Conclusions

The current analyses of ground and remote sensing data descriptive of diversified Mediterranean forest conditions have yielded the following main results:

- The relevance of SDS in controlling inter-annual production variations of dry Mediterranean forests is supported by both remote sensing based model simulations and tree ring-width analyses.
- The eco-physiological bases of this phenomenon have been identified by analyzing the main environmental factors that limit photosynthesis through the down-regulation of radiation use efficiency and fAPAR.
- The control of SDS on forest production becomes less intense and more rapid moving toward more temperate humid eco-climatic zones, which can be also interpreted on the basis of simple eco-physiological considerations.

These findings can have important repercussions on the current debate about the effects of different climate change scenarios on

Mediterranean forest behavior. In particular, the expected increase in annual temperature and the decrease in spring rainfall could have dramatic consequences for the growth of Mediterranean forests. Suggesting possible strategies for the practical management of these forests is a difficult task. Generally, if climate change will result in a significant modification of selection pressure, phenology and growth are major aspects of tree functioning that will need adjusting. Therefore, the conservation of forest biodiversity (with a rich variability in species and genotypes) will be essential to favor the resilience of Mediterranean forests to a changing climate and land use.

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