Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Biogeosciences Discussions

Impact of annual and seasonal precipitation and air temperature on gross primary production in Mediterranean ecosystems in Europe

Svenja Bartsch[1], Bertrand Guenet[1], Christophe Boissard[1], Juliette Lathiere[1], Jean-Yves Peterschmitt[1], Annemiek Stegehuis[1], Ilja-M Reiter[2], Thierry Gauquelin[3], Virginie Baldy[3], Catherine Fernandez[3]

[1]Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-OVSQ, Université Paris-Saclay, F-91191 Gif-sur-Yvette, France.

[2]Fédération de Recherche Ecosystèmes Continentaux et Risques Environnementaux CNRS FR3098 ECCOREV, Domaine du Petit Arbois Avenue Louis Philibert, Bâtiment du CEREGE - BP 80, 13545 Aix-en-Provence Cedex 04, France

[3]Aix Marseille Université, Avignon Université, CNRS, IRD, IMBE (Institut Méditerranéen de Biodiversité et d'Ecologie marine et continental), 3 Place Victor Hugo, 13331 Marseille, France

Corresponding author: Bertrand.Guenet@lsce.ipsl.fr

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Biogeosciences Discussions Open Access EGU

Abstract

Mediterranean ecosystems are significant carbon sinks but are also particularly sensitive to climate change but the carbon dynamic in such ecosystem is still not fully understood. An improved understanding of the drivers of the carbon fixation by plants is needed to better predict how such ecosystems will respond to climate change. Here, for the first time, a large dataset collected through the FLUXNET network is used to estimate how the gross primary production (GPP) of different Mediterranean ecosystems was affected by air temperature and precipitation between the years 1996 and 2013. We showed that annual precipitation was not a significant driver of annual GPP. Our results also indicated that seasonal variations of air temperature significantly affected seasonal variations of GPP but without major impact on inter annual variations. Inter-annual variations of GPP seemed largely controlled by the precipitation during early spring (March-April), making this period crucial for the future of Mediterranean ecosystems. Finally, we also observed that the sensitivity of GPP in Mediterranean ecosystems to climate drivers is not ecosystem type dependent.

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

1. Introduction

Mediterranean land ecosystems are of particular interest for research because their outstanding biodiversity is one of the most important after the tropical regions (Cowling et al., 1996). This remarkable diversity is due to a combination of biogeographical and environmental factors (soil types, precipitation, temperature) but also the presence of human activities for millennia (Lavorel et al., 1998; Rey Benayas and Scheiner, 2002). It has been hypothesized that these ecosystems could be severely affected by global climate change in the future, that includes modification of temperature and precipitation regime (Giorgi and Lionello, 2008; Polade et al., 2014). CO_2 increase may also become an important driver of species distribution within these regions (Keenan et al., 2011). Mediterranean ecosystems supply numerous services to people including clean water, flood protection and carbon sinks with a comparable amount of carbon uptake as other European forests (Janssens et al., 2003). For instance, Vayreda et al., (2012) and Pereira et al., (2007) observed a net ecosystem exchange (NEE) of 1.4 Mg C ha^{-1} yr^{-1} in a Spanish and Portuguese forest, and of 1.9 Mg C ha^{-1} yr^{-1} for a grassland in Portugal, while an NEE of 2.7 Mg C ha-1 yr-1 was found for forest ecosystems from the EUROFLUX network throughout Europe (Janssens et al., 2003)

Over the last decade considerable effort has been made to investigate the effect of precipitation and air temperature on biomass production (Goerner et al., 2009; Valladares et al., 2008). So far however, most of this research was carried out using single site experiments (e.g. rain exclusion device (Limousin et al., 2009, 2010; Martin-Stpaul et al., 2013)), or using only a few sites with a single ecosystem type (Reichstein et al., 2002). Consequently, contrasting results are reported in the literature. For instance, Reichstein *et al.*, (2002) observed a high sensitivity to drought

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

for three Mediterranean evergreen forests (two dominated by *Quercus Ilex* and one by *Juniperus phoenicea)* whereas Grünzweig *et al.*, (2008) reported that another Mediterannean species (*Quercus calliprinos*) was well adapted to drought. Sabaté *et al.*, (2002) pointed out that Mediterranean oak forests (*Quercus Ilex*) were particularly sensitive to summer drought whereas Allard *et al.*, (2008) observed an absence of response to summer drought for another Mediterranean oak forest composed also by *Quercus Ilex*. Moreover, Maselli, (2004) suggests that spring precipitation is the most important factor controlling inter-annual variations of vegetation stress. To allow broader conclusions, satellite monitoring on normalized difference vegetation index has been performed (Maselli et al., 2014). However, the link between a vegetation index and gross primary production (GPP) is not straightforward and there is a substantial spread between different satellite products (Garrigues et al., 2008).

Up to now, we are not aware of any other study that has investigated the impact of annual and seasonal precipitation and air temperature on the primary production of Mediterranean ecosystems using a large collection of sites, under different climatic conditions and different vegetation types. Model projections yet indicate that the Mediterranean region will be strongly affected by future climate change (Giorgi and Lionello, 2008; Guiot and Cramer, 2016; Polade et al., 2014). Our approach might therefore be of great importance, providing general regional information for modeling exercises, and enabling to improve future biomass projections on a regional scale. A decrease in precipitation and an increase in temperature, both associated with large spatial variability, are expected for the next decades (Dubrovsky et al., 2014). This makes the Mediterranean region one of the most vulnerable regions to climate change (Nissen et al., 2014) worldwide. In this context, understanding the response of Mediterranean ecosystems to changes in temperature and precipitation is of major importance.

The main goal of this study is to identify the impact of annual and seasonal precipitation (PPT) and air temperature (T) on GPP throughout the European Mediterranean region, based on a multi-sites analysis. To do so, we applied ANOVAs and linear mixed effect models to the GPP obtained from 23 different FLUXNET sites in the European Mediterranean area, representing 5 different ecosystem types.

2. Material and Methods

2.1. Data set & data organization

We used the FLUXNET database (http://www.fluxdata.org), which contains flux measurements (CO_2, water, etc.) based on the eddy covariance method (Baldocchi et al., 2001) and meteorological measurements at a high temporal resolution (up to 30-min intervals). The database covers more than 500 registered sites worldwide and is partly freely available under a Fair-Use policy. All data provided by the international FLUXNET network are processed according to standardized formats and data processing protocols (Moffat et al., 2007; Papale et al., 2006; Reichstein et al., 2005).

In this study we used level 4 data (L4, daily time-steps) of GPP, PPT and T from the La Thuile collection (see also http://www.fluxdata.org). We selected sites that are located within the Mediterranean region with the following vegetation types: shrubs (S), grasslands (G), deciduous broadleaf trees (DBT), evergreen needle trees (ENT) and evergreen broadleaf trees (EBT). We only focused on the European region. From the site-year files we calculated the annual mean and sum values of GPP, PPT and T. We also included the corresponding vegetation types. To be able to investigate the impact of different seasons in a rather precise way, we split the year into six parts using a bi-monthly time step (January & February (JF), March & April (MA), May & June (MJ), July & August (JA), September & October (SO), November & December (ND)) (cf. Tab. 2 subset S0-S6).

We only considered the site-year files where at least 90% of the needed data per year or bi-monthly time step were available. This selection process resulted in 23 sites in three different countries (France, Italy, Spain) as presented in table 1.

2.2. Statistical methods

The statistical analyses were performed using RStudio (version 0.99.473, 2009-2015 RStudio). The impact of annual and seasonal PPT, T and the vegetation type on annual and seasonal GPP was investigated by employing a linear mixed effect model ANOVA. The sites were used as random effect, which enabled us to take potential site-dependency effects into account. Because of non-normality, data were rank-transformed before analysis, as previously done by e.g. Guenet *et al.* (2014).

We tested seven different subsets (Tab. 2, S0-S6). We first investigated if the annual mean PPT, T and/or vegetation type significantly affected the annual mean GPP (Tab. 2, S0, case A). Then, we analyzed the annual GPP using bi-monthly mean instead of annual mean PPT and T values (Tab. 2, S1-S6, case A). Note that we investigated the impact of PPT and T on the average annual GPP of the subsequent year rather than on the actual year for the ND subset, because in this time of the year the actual climatic factors hardly control the total growing strength of the actual year (Tab. 2). In a next step all tests were repeated using the total annual and bi-monthly sum, instead of mean values for GPP and PPT (Tab. 2, S0-S6, case B). As we applied several hypotheses on one single data set, we faced the problem of multiple

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

comparisons minimizing the probability of receiving a Type I error. Accordingly, we corrected the original significance level ($p = 0.05$) by applying the Holm-Bonferroni method (Holm, 1979). In a last step, we investigated if the PPT and T of specific seasons (bi-monthly time periods) significantly affected the GPP of the corresponding seasons (Tab. 2, S1-S6, case C). In the latter case, applying the Holm-Bonferroni method was not necessary as we used an independent data set for every season and subset.

To interactively explore which predictors provided a good fit, we applied a stepwise regression in all cases, which conducts an automatic stepwise model selection by the AIC (Akaike information criterion).

3. Results

3.1. Inter-annual GPP variability

Over the selected sites, the vegetation faced a typical Mediterranean climate, with usually hot and dry summers as well as mostly mild and moist winters (Fig. 1). T ranged from -0.1 to 28.4°C (Fig. 1C, bi-monthly averages) and the seasonal PPT from 0 to 11.4 mm d^{-1} (Fig. 1D, bi-monthly averages). GPP values for shrubs were lowest but show the highest variability across the different sites (Fig. 1A). For trees (ENT, DBT, EBT) the GPP values were rather similar to each other. For grassland only two suitable sites were available (Tab. 1, Fig. 1A).

Surprisingly no significant correlation was found between annual GPP and annual T or annual PPT across sites and years. A general trend over the vegetation types was observed but this was not significant according to the Holm-Bonferroni corrected threshold (Tab. 3). Furthermore, the relationships between the applied climatic factors and vegetation types were never found to be significant (Tab. 3). We did not obtain a clearly relationship between annual and seasonal PPT and annual GPP, or between annual and seasonal T and annual GPP by simply applying linear regression models (Fig. 2-5). Nevertheless, annual GPP averages could be explained (significant p-values) by both precipitation during early spring (MA) and air temperature during early winter (ND), when using bi-monthly averages or the sum as explaining variables in the linear mixed effect model (Tab. 3, Fig. 2 & 4). Furthermore, we found that the annual GPP was not significantly affected by climate conditions in summer (MJ & JA), even though this time period is the hottest and the driest for all sites (Fig. 1). Finally, we noticed that none of the interactions between the explaining variables, vegetation type, T (bi-monthly & annual) and PPT (bi-monthly & annual), significantly impacted the annual average of GPP (Tab. 3).

3.2. Intra-annual GPP variability

We observed that GPP was low at the beginning of the year (JF) and increased till MJ (highest median value 6.8 gC m^{-2} d^{-1}), when looking at the bi-monthly distribution of GPP (Fig. 1B). During the summer GPP slowly decreased until the lowest median value in ND (2.2 gC m^{-2} d^{-1}). The highest variability in GPP was observed in JA and dominated by broadleaf trees.

During all time periods the bi-monthly average T significantly affected the bi-monthly average GPP (Tab. 3). In general we observed a positive relationship between seasonal T and seasonal GPP. The only exception occurred in JA, when the increasing air temperature caused a decrease in GPP. From May to August the bi-monthly average GPP was additionally significantly affected by the bi-monthly average of PPT. Finally, as observed for the inter-annual variations of GPP, none of

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

the interactions between the seasonal PPT, seasonal T and vegetation types was significantly correlated to the bi-monthly average of GPP.

4. Discussion

Interestingly, neither the annual T nor the annual PPT was found to be a major control on annual biomass production in the Mediterranean region. This underlines the importance of applying seasonal (or intra-annual) approaches rather than mere inter-annual studies when investigating potential effects on biomass production within the Mediterranean region. This result is in contradiction with Jongen *et al.*, (2011) who observed a positive correlation between annual precipitation and GPP for a Portuguese grassland. However, we only had data for two grassland sites, hence the observed trends were largely controlled by forests and shrublands. Our results are however in accordance with Allard *et al.* (2008) who observed that the seasonal averages of precipitation, more than the annual average, were important drivers for GPP.

The rainfall during the early spring months (MA) had an important impact on annual GPP. PPT over the other time periods however, did not significantly affect annual GPP. During MA, when the growing season starts, the rainfall (Fig. 1D) is high enough to support vegetation growth, whereas the air temperature is not yet too high to reduce C fixation (Fig. 1C). Hence, early spring does not only provide good growing conditions, it can also control the soil moisture conditions before extremely dry and hot summer months (see Fig. 1B & C). The highest GPP values as well as the highest GPP variability were observed in the summer months (MJ, JA; Fig.1B). MA can thus be seen as a decisive time period in the year in controlling the annual biomass production. Allard *et al.*, (2008) concluded that a decrease of precipitation in

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

April-June would have a large effect on annual net ecosystem production (NEP), whereas the impact of decreasing precipitation in July-September on NEP would be minimal. Our results are also consistent with the work of Maselli (2004), who reported that normalized difference vegetation index was mainly affected by spring precipitation. These results highlight the importance of the distribution of precipitation within a year, rather than the annual precipitation sum.

If climate change would affect early spring precipitation, the effect on GPP might be highly significant, whereas if precipitation would change during the other periods, the effect on GPP of Mediterranean ecosystems might be limited. Polade et al., (2014) showed that Mediterranean climate regions would face a dryer climate in the future. Using a multi-scenario and a multi-model ensemble, Goubanova & Li (2007) suggested that the precipitation over the Mediterranean region will be reduced throughout the 21st century during spring, summer and autumn. Moreover, Toggweiler & Key (2001) showed that the intensity of precipitation will mostly be reduced from February to May, using downscaling statistics. Taken together, these results indicate that the effect of climate change on the GPP of Mediterranean ecosystems might be very important, leading to a reduction of total carbon storage from those ecosystems. It furthermore suggests that the effects of climate change should be estimated using mechanistic models with a fine time resolution or with statistical models based on precipitation distribution at a seasonal time scale.

Interestingly, the winter T also controls the annual GPP (Tab. 3). Lowest GPP values were associated to lower air temperatures. Most Mediterranean vegetation is well adapted to heat and water stress, but not all species might be able to survive low winter temperatures (Aranda et al., 2005; Ferrio et al., 2003; Karavatas and Manetas, 1999; Larcher, 2000; Llorens et al., 2003). These can induce photoinhibition that cannot be reversed during periods with more favorable temperatures (Camarero et al., 2012; Ogaya et al., 2011). Furthermore, below-zero temperatures may induce freezing-induced embolism, which can only be partly restored (Cochard et al., 2001; Nardini et al., 2000). These factors can predispose trees to drought and heat stress that are often occurring during summer in the Mediterranean region (Peguero-Pina et al., 2011). Bansal *et al.*, (2015), and Sohn et al., (2012) found that winter conditions are most likely more decisive for plant growth than summer aridity in some parts of the Mediterranean region. However, they may also be partly favorable for reducing summer stress, as they may influence the genetic variation in drought-resistance because traits of drought- and freezing-resistance can be co-occurring (Bansal et al., 2015; Blödner et al., 2005; Gimeno et al., 2009) However, future climate projections suggest an increase of air temperature over the Mediterranean regions (Goubanova and Li, 2007), reducing the impact of cold winter temperatures on GPP. For air temperature and precipitation it is interesting to note that interactions with vegetation types were never significant, suggesting that the observed responses are not dependent on the vegetation types.

Our results also illustrate that summer PPT as well as summer T (for both MJ & JA) significantly influenced summer GPP (see Tab.3C). In particular, increasing JA T caused a decrease in GPP. Allard *et al.*, (2008) presented the Mediterranean region as an area characterized by a long growing season that is often interrupted during late summer, when water stress is getting too high (see also Reichstein *et al.*, (2002)). The authors suggested that under these extreme drought conditions, GPP and ecosystem respiration (R_{eco}) are partly decoupled, most likely due to stomatal closure. Our results slightly support this finding. We observed a negative correlation between T and GPP during JA (Fig. 5, second line, right-side plot). Hence, if T reaches a certain threshold,

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Biogeosciences Discussions Open Access EGU

GPP starts to decrease. In general, seasonal T seems to control the equivalent seasonal GPP, which indicates that seasonal T, and not the PPT as expected, generally has a major effect on seasonal GPP in the Mediterranean regions. However, the seasonal effect of T on GPP during the same season seems not to directly affect the annual GPP.

5. Conclusions

In this study we investigated the response of the GPP of Mediterranean ecosystems to different climatic variables. We used the largest collection of sites over the Mediterranean region that has been considered so far. We showed that seasonal variations of T significantly impacted seasonal variations of GPP, but without a major impact on the variation of inter annual GPP. Our results suggest that variations of inter annual GPP are largely controlled by early spring precipitation, making this period crucial for the future of Mediterranean ecosystems. Interestingly, we did not observe an effect of vegetation type, indicating that the response of GPP of Mediterranean ecosystems to climate drivers is not vegetation-type dependent.

Unfortunately, the studied sites were only located in Europe. To broaden our conclusions more data would be needed from other non-European parts of the Mediterranean region. Nevertheless, we showed that in the future, the reduction of spring precipitation will have a major impact on carbon storage of many different Mediterranean ecosystems.

Acknowledgments:

This work was supported by the French National Agency for Research (ANR-12-BSV7-0016-01, SECPRIME2).

REFERENCES

Allard, V., Ourcival, J. M., Rambal, S., Joffre, R. and Rocheteau, a: Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France, Glob. Chang. Biol., 14, 714–725, doi:10.1111/j.1365-2486.2008.01539.x, 2008.

Aranda, I., Castro, L., Alía, R., Pardos, J. a and Gil, L.: Low temperature during winter elicits differential responses among populations of the Mediterranean evergreen cork oak (Quercus suber)., Tree Physiol., 25(8), 1085–1090, doi:10.1093/treephys/25.8.1085, 2005.

Baldocchi, D., Falge, E., Gu, L. H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X. H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., U, K. T. P., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., Paw, U. K. T., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K. and Wofsy, S.: FLUXNET: A New Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon Dioxide, Water Vapor, and Energy Flux Densities, Bull. Am. Meteorol. Soc., 82(11), 2415–2434, doi:10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2, 2001.

Bansal, S., Harrington, C. A., Gould, P. J. and St.Clair, J. B.: Climate-related genetic variation in drought-resistance of Douglas-fir (Pseudotsuga menziesii), Glob. Chang. Biol., 21(2), 947–958, doi:10.1111/gcb.12719, 2015.

Blödner, C., Skroppa, T., Johnsen, Ø. and Polle, A.: Freezing tolerance in two Norway spruce (Picea abies [L.] Karst.) progenies is physiologically correlated with drought tolerance, J. Plant Physiol., 162(5), 549–558, doi:10.1016/j.jplph.2004.09.005, 2005.

Camarero, J. J., Olano, J. M., Arroyo Alfaro, S. J., Fernández-Marín, B., Becerril, J. M. and García-Plazaola, J. I.: Photoprotection mechanisms in Quercus ilex under contrasting climatic conditions, Flora Morphol. Distrib. Funct. Ecol. Plants, 207(8), 557–564, doi:10.1016/j.flora.2012.06.003, 2012.

Cochard, H., Lemoine, D., Améglio, T. and Granier, a: Mechanisms of xylem recovery from winter embolism in Fagus sylvatica., Tree Physiol., 21, 27–33, doi:10.1093/treephys/21.1.27, 2001.

Cowling, R. M., Rundel, P. W., Lamont, B. B., Arroyo, M. K. and Arianoutsou, M.: Plant diversity in mediterranean-climate regions, Trends

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Ecol. Evol., 11(9), 362–366, doi:10.1016/0169-5347(96)10044-6, 1996.

Dubrovsky, M., Hayes, M., Duce, P., Trnka, M., Svoboda, M. and Zara, P.: Multi-GCM projections of future drought and climate variability indicators for the Mediterranean region, Reg. Environ. Chang., 14(5), 1907–1919, doi:10.1007/s10113-013-0562-z, 2014.

Ferrio, J. P., Florit, A., Vega, A., Serrano, L. and Voltas, J.: Δ13C and tree-ring width reflect different drought responses in Quercus ilex and Pinus halepensis, Oecologia, 137(4), 512–518, doi:10.1007/s00442-003-1372-7, 2003.

Garrigues, S., Lacaze, R., Baret, F., Morisette, J. T., Weiss, M., Nickeson, J. E., Fernandes, R., Plummer, S., Shabanov, N. V., Myneni, R. B., Knyazikhin, Y. and Yang, W.: Validation and intercomparison of global Leaf Area Index products derived from remote sensing data, J. Geophys. Res. Biogeosciences, 113(2), doi:10.1029/2007JG000635, 2008.

Gimeno, T. E., Pas, B., Lemos-Filho, J. P. and Valladares, F.: Plasticity and stress tolerance override local adaptation in the responses of Mediterranean holm oak seedlings to drought and cold, Tree Physiol., 29(1), 87–98, doi:10.1093/treephys/tpn007, 2009.

Giorgi, F. and Lionello, P.: Climate change projections for the Mediterranean region, Glob. Planet. Change, 63(2–3), 90–104, doi:10.1016/j.gloplacha.2007.09.005, 2008.

Goerner, A., Reichstein, M. and Rambal, S.: Tracking seasonal drought effects on ecosystem light use efficiency with satellite-based PRI in a Mediterranean forest, Remote Sens. Environ., 113(5), 1101–1111, doi:10.1016/j.rse.2009.02.001, 2009.

Goubanova, K. and Li, L.: Extremes in temperature and precipitation around the Mediterranean basin in an ensemble of future climate scenario simulations, Glob. Planet. Change, 57(1–2), 27–42, doi:10.1016/j.gloplacha.2006.11.012, 2007.

Grünzweig, J. M., Carmel, Y., Riov, J., Sever, N., McCreary, D. D. and Flather, C. H.: Growth, resource storage, and adaptation to drought in California and eastern Mediterranean oak seedlings, Can. J. For. Res., 38(2), 331–342, doi:10.1139/X07-152, 2008.

Guenet, B., Danger, M., Harrault, L., Allard, B., Jauset-Alcala, M., Bardoux, G., Benest, D., Abbadie, L. and Lacroix, G.: Fast mineralization of land-born C in inland waters: First experimental evidences of aquatic priming effect, Hydrobiologia, 721(1), 35–44, doi:10.1007/s10750-013-1635-1, 2014.

Guiot, J. and Cramer, W.: Climate change , the Paris Agreement thresholds and Mediterranean ecosystems, Science (80-.)., 4532(October), 4528–4532, doi:10.1126/science.aah5015, 2016.

Hertig, E. and Jocobeit, J.: Assessments of Mediterranean precipitation changes for the 21st century using statistical downscaling techniques, Int. J. Climatol., 28, 1025–1045, doi:10.1002/joc, 2008.

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Janssens, I. a, Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., Schlamadinger, B., Hutjes, R. W. a, Ceulemans, R., Schulze, E.-D., Valentini, R. and Dolman, a J.: Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO2 emissions., Science, 300(5625), 1538–42, doi:10.1126/science.1083592, 2003.

Jongen, M., Pereira, J. S., Aires, L. M. I. and Pio, C. A.: The effects of drought and timing of precipitation on the inter-annual variation in ecosystem-atmosphere exchange in a Mediterranean grassland, Agric. For. Meteorol., 151(5), 595–606, doi:10.1016/j.agrformet.2011.01.008, 2011.

Karavatas, S. and Manetas, Y.: Seasonal patterns of photosystem 2 photochemical efficiency in evergreen sclerophylls and drought semi-deciduous shrubs under Mediterranean field conditions, Photosynthetica, 36(1–2), 41–49, doi:Doi 10.1023/A:1007010502269, 1999.

Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M. and Sabate, S.: Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters!, Glob. Chang. Biol., 17(1), 565–579, doi:10.1111/j.1365-2486.2010.02254.x, 2011.

Larcher, W.: Temperature stress and survival ability of Mediterranean sclerophyllous plants, Plant Biosyst. - An Int. J. Deal. with all Asp. Plant Biol., 134(3), 279–295, doi:10.1080/11263500012331350455, 2000.

Lavorel, S., Canadell, J., Rambal, S. and Terradas, J.: Mediterranean terrestrial ecosystems : research priorities on global change effects, Glob. Ecol. Biogeogr., 7(3), 157–166, doi:10.1046/j.1466-822X.1998.00277.x, 1998.

Limousin, J. M., Misson, L., Lavoir, A. V., Martin, N. K. and Rambal, S.: Do photosynthetic limitations of evergreen Quercus ilex leaves change with long-term increased drought severity?, Plant, Cell Environ., 33(5), 863–875, doi:10.1111/j.1365-3040.2009.02112.x, 2010.

Limousin, J. M., Rambal, S., Ourcival, J. M., Rocheteau, A., Joffre, R. and Rodriguez-Cortina, R.: Long-term transpiration change with rainfall decline in a Mediterranean Quercus ilex forest, Glob. Chang. Biol., 15(9), 2163–2175, doi:10.1111/j.1365-2486.2009.01852.x, 2009.

Llorens, L., Penuelas, J. and Estiearte, M.: Ecophysiological responses of two Mediterranean shrubs, Erica multiflora and Globularia alypum, to experimentally drier and warmer conditiions, Physiol. Plant., 119(Ipcc 2001), 231–243, doi:10.1034/j.1399-3054.2003.00174.x, 2003.

Martin-Stpaul, N. K., Limousin, J. M., Vogt-Schilb, H., Rodríguez-Calcerrada, J., Rambal, S., Longepierre, D. and Misson, L.: The temporal response to drought in a Mediterranean evergreen tree: Comparing a regional precipitation gradient and a throughfall exclusion experiment, Glob. Chang. Biol., 19, 2413–2426, doi:10.1111/gcb.12215, 2013.

Maselli, F.: Monitoring forest conditions in a protected Mediterranean coastal area by the analysis of multiyear NDVI data, Remote Sens. Environ., 89(4), 423–433, doi:10.1016/j.rse.2003.10.020, 2004.

Maselli, F., Cherubini, P., Chiesi, M., Gilabert, M. A., Lombardi, F., Moreno, A., Teobaldelli, M. and Tognetti, R.: Start of the dry season as a main determinant of inter-annual Mediterranean forest production variations, Agric. For. Meteorol., 194(2014), 197–206, doi:10.1016/j.agrformet.2014.04.006, 2014.

Moffat, A. M., Papale, D., Reichstein, M., Hollinger, D. Y., Richardson, A. D., Barr, A. G., Beckstein, C., Braswell, B. H., Churkina, G., Desai, A. R., Falge, E., Gove, J. H., Heimann, M., Hui, D., Jarvis, A. J., Kattge, J., Noormets, A. and Stauch, V. J.: Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, Agric. For. Meteorol., 147(3–4), 209–232, doi:10.1016/j.agrformet.2007.08.011, 2007.

Nardini, A., Salleo, S., Lo Gullo, M. A. and Pitt, F.: Different responses to drought and freeze stress of Quercus ilex L. growing along a latitudinal gradient, Plant Ecol., 148(2), 139–147, doi:10.1023/A:1009840203569, 2000.

Nissen, K. M., Leckebusch, G. C., Pinto, J. G. and Ulbrich, U.: Mediterranean cyclones and windstorms in a changing climate, Reg. Environ. Chang., 14(5), 1873–1890, doi:10.1007/s10113-012-0400-8, 2014.

Ogaya, R., Peñuelas, J., Asensio, D. and Llusià, J.: Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change, Environ. Exp. Bot., 73(1), 89–93, doi:10.1016/j.envexpbot.2011.08.004, 2011.

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T. and Yakir, D.: Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation, Biogeosciences, 3(4), 571–583, doi:10.5194/bg-3-571-2006, 2006.

Peguero-Pina, J. J., Alquézar-Alquézar, J. M., Mayr, S., Cochard, H. and Gil-Pelegrín, E.: Embolism induced by winter drought may be critical for the survival of Pinus sylvestris L. near its southern distribution limit, Ann. For. Sci., 68(3), 565–574, doi:10.1007/s13595-011-0068-0, 2011.

Pereira, J. S., Mateus, J. a., Aires, L. M., Pita, G., Pio, C., David, J. S., Andrade, V., Banza, J., David, T. S., Paço, T. a. and Rodrigues, a.: Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems – the effect of drought, Biogeosciences, 4(5), 791–802, doi:10.5194/bg-4-791-2007, 2007.

Polade, S. D., Pierce, D. W., Cayan, D. R., Gershunov, A. and Dettinger, M. D.: The key role of dry days in changing regional climate and precipitation regimes., Sci. Rep., 4(4364), 8pp, doi:10.1038/srep04364, 2014.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M.,

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, Glob. Chang. Biol., 11(9), 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x, 2005.

Reichstein, M., Tenhunen, J. D., Roupsard, O., Ourcival, J. M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G. and Valentini, R.: Severe drought effects on ecosystem CO2 and H2O fluxes at three Mediterranean evergreen sites: Revision of current hypotheses?, Glob. Chang. Biol., 8(10), 999–1017, doi:10.1046/j.1365-2486.2002.00530.x, 2002.

Rey Benayas, J. M. and Scheiner, S. M.: Plant diversity, biogeography and environment in Iberia: Patterns and possible causal factors, J. Veg. Sci., 13(2), 245, doi:10.1658/1100-9233(2002)013[0245:PDBAEI]2.0.CO;2, 2002.

Sabaté, S., Gracia, C. A. and Sánchez, A.: Likely effects of climate change on growth of Quercus ilex, Pinus halepensis, Pinus pinaster, Pinus sylvestris and Fagus sylvatica forests in the Mediterranean region, For. Ecol. Manage., 162(1), 23–37, doi:10.1016/S0378-1127(02)00048-8, 2002.

Sohn, J. A., Kohler, M., Gessler, A. and Bauhus, J.: Interactions of thinning and stem height on the drought response of radial stem growth and isotopic composition of Norway spruce (Picea abies), Tree Physiol., 32(10), 1199–1213, doi:10.1093/treephys/tps077, 2012.

Valladares, F., Zaragoza-Castells, J., Sanchez-Gomez, D., Matesanz, S., Alonso, B., Portsmuth, A., Delgado, A. and Atkin, O. K.: Is shade beneficial for Mediterranean shrubs experiencing periods of extreme drought and late-winter frosts?, Ann. Bot., 102(6), 923–933, doi:10.1093/aob/mcn182, 2008.

Vayreda, J., Martinez-Vilalta, J., Gracia, M. and Retana, J.: Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests, Glob. Chang. Biol., 18(3), 1028–1041, doi:10.1111/j.1365-2486.2011.02606.x, 2012.

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

List of Figures

Fig. 1: Boxplots showing A) the general GPP distribution of the different vegetation types (ENT = evergreen needle trees; DBT = deciduous broadleaf trees; EBT = evergreen broadleaf trees; G = grasslands; S = Shrubs; numbers in the brackets indicating the numbers of sites per vegetation type) and (B) the GPP distribution C) the air temperatures (T) and D) the precipitation distribution observed during the different bi-monthly time periods (JF = January & February, MA = March & April, MJ = May & June, JA = July & August, SO = September & October, ND = November & December).

Fig. 2: Seasonal mean PPT versus the annual mean GPP for the different vegetation types and over the different bi-monthly time periods. See Fig. 1 for the abbreviations. A simple trend line & R-squared value (including all vegetation types) was added to those plots where a significant p-value was obtained during our statistical tests (see Tab. 3).

Fig. 3: Seasonal mean PPT versus the seasonal mean GPP for the different vegetation types and over the different bi-monthly periods. See Fig. 1 for the abbreviations. Trend lines & R-squared values (including all vegetation types) were added to those plots where a significant p-value was obtained during our statistical tests (see Tab. 3).

Fig. 4: Seasonal mean T versus the annual mean GPP for the different vegetation types and over the different bi-monthly time periods. See Fig. 1 for the abbreviations. A simple trend line & R-squared value (including all vegetation types) was added to

those plots where a significant p-value was obtained during our statistical tests (see Tab. 3).

Fig. 5: Seasonal mean T versus the seasonal mean GPP for the different vegetation types and over the different bi-monthly time periods. Trend lines & R-squared values (including all vegetation types) were added to those plots where a significant p-value was obtained during our statistical tests (see Tab. 3). See Fig. 1 for the abbreviations.

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Figures

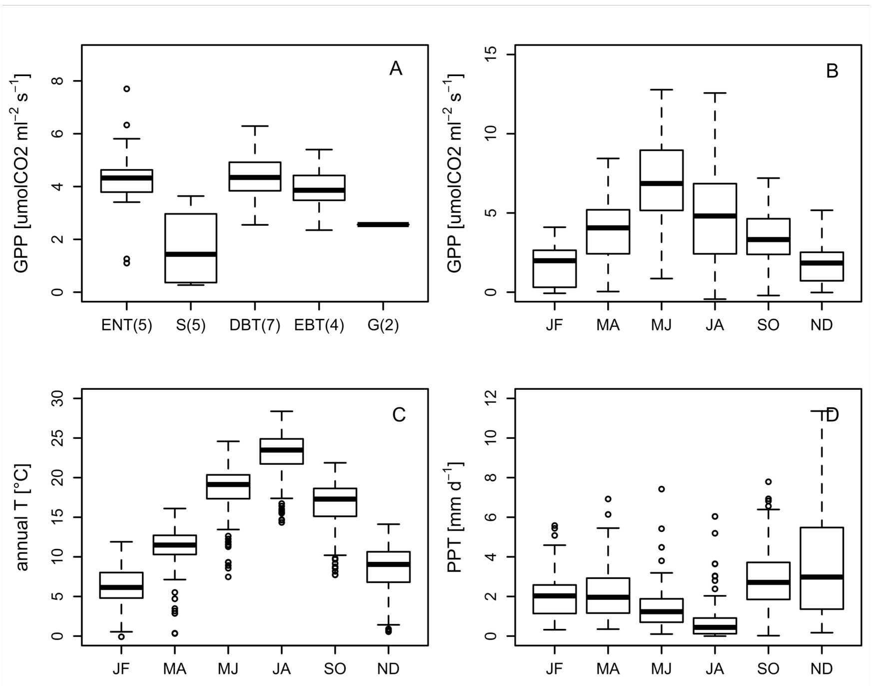
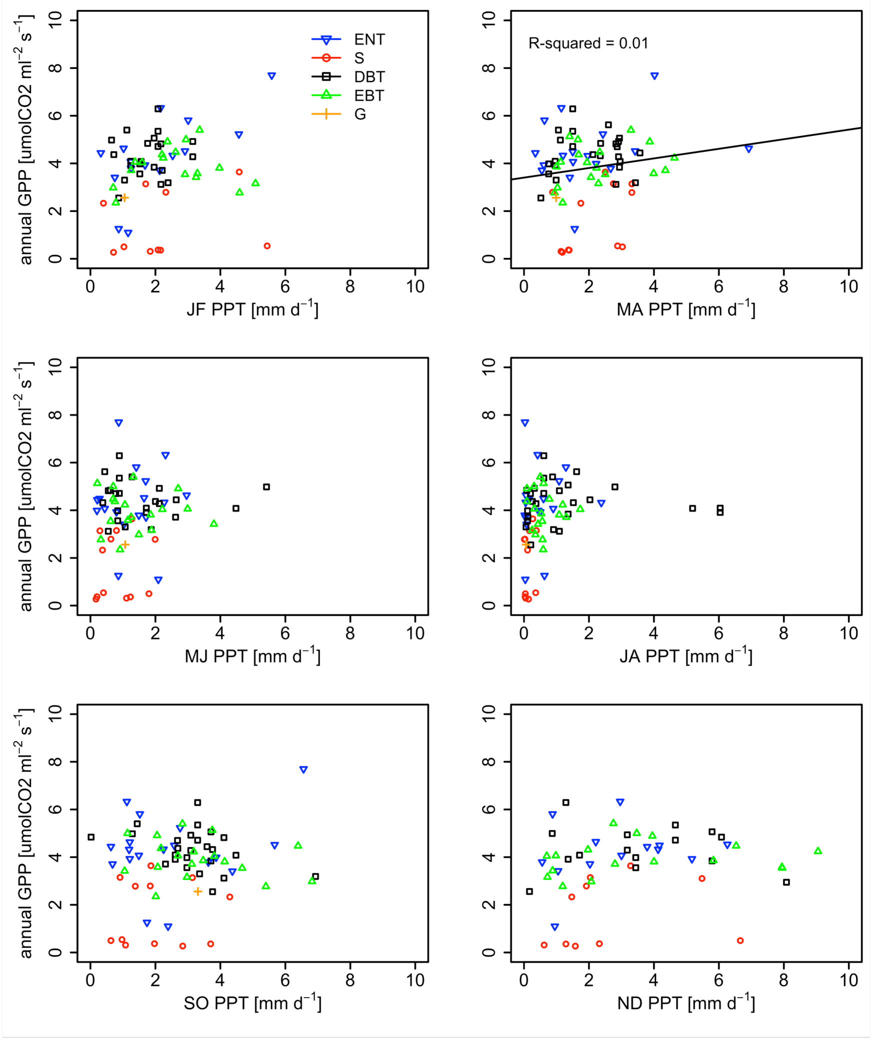


Figure 1



522

523 **Figure 2**

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

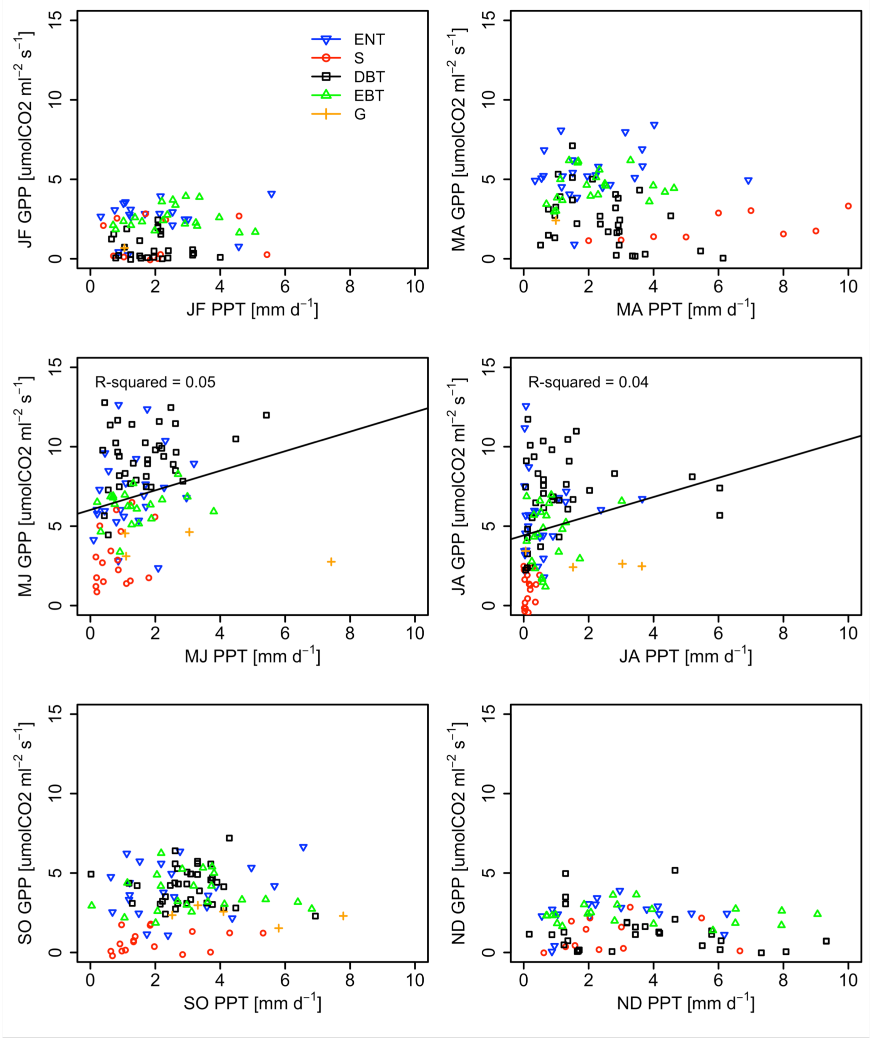
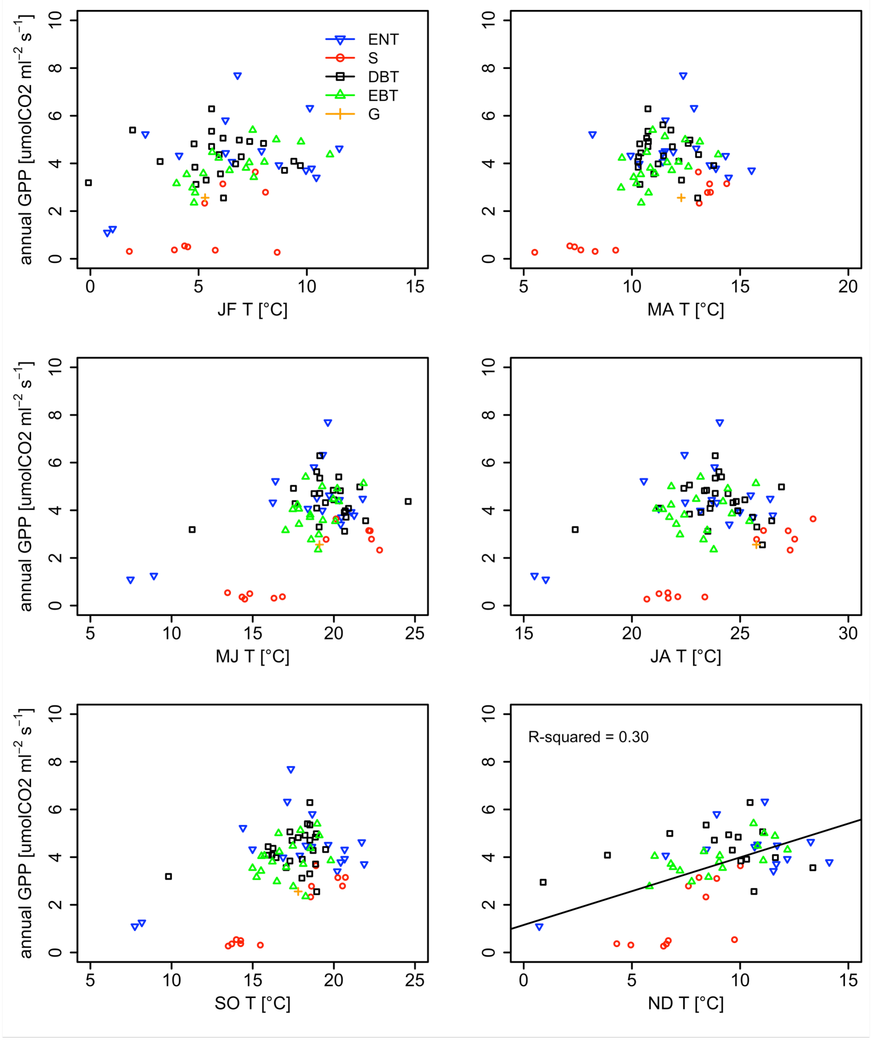


Figure 3

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016



526

527 **Figure 4**

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

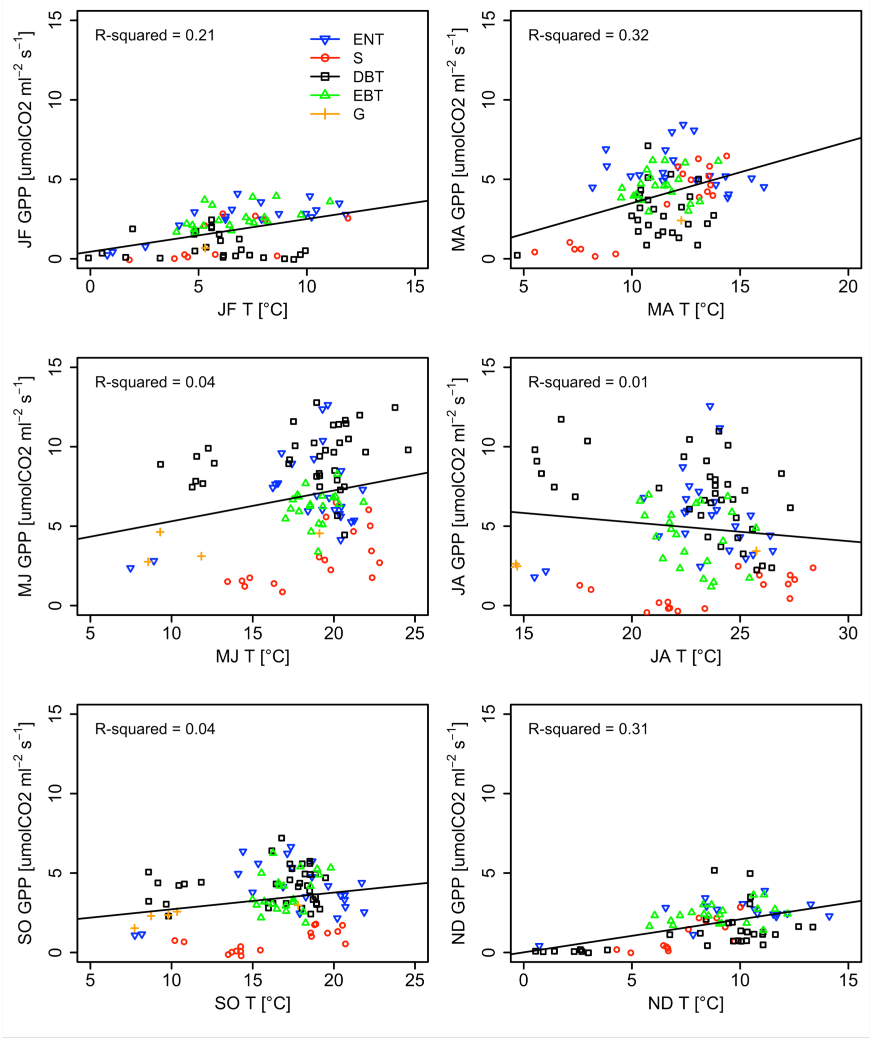


Figure 5

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Biogeosciences Discussions

Tables

Tab. 1: Site description

Nr.	SITE ID	SITE NAME	COUNTRY	COORDINATES (Lat., Long.)	VEGETATION
1	ESES1	El Saler	Spain	39.3460, -0.3188	evergreen needleleaf trees
2	ESLgS	Laguna Seca	Spain	37.0979, -2.9658	evergreen needleleaf trees
3	ESLJu	Llano de los Juanes	Spain	36.9266, -2.7521	shrubs
4	ESLMa	Las Majadas del Tietar	Spain	39.9415, -5.7734	shrubs
5	ESLn1	Lanjaron-Non intervention	Spain	36.9721, -3.4739	shrubs
6	ESLn2	Lanjaron-Salvage logging	Spain	36.9695, -3.4758	shrubs
7	ESVDA	Vall d'Alinya	Spain	42.1522, 1.4485	grasslands
8	FRFBn	Font-Blanche	France	43.2408, 5.6792	evergreen needleleaf trees
9	FRPue	Puechabon	France	43.7414, 3.5958	evergreen broadleaf trees
10	ITBon	Bonis	Italy	39.4778, 16.5347	evergreen needleleaf trees
11	ITCA1	Castel d'Asso1	Italy	42.3804, 12.0266	deciduous broadleaf trees
12	ITCA3	Castel d'Asso2	Italy	42.3772, 12.0260	grasslands
13	ITCol	Collelongo-Selva Piana	Italy	41.8494, 13.5881	deciduous broadleaf trees
14	ITCpz	Castelporziano	Italy	41.7052, 12.3761	evergreen broadleaf trees
15	ITLec	Lecceto	Italy	43.3036, 11.2698	evergreen broadleaf trees
16	ITNon	Nonantola	Italy	44.6902, 11.0911	deciduous broadleaf trees
17	ITPia	Island of Pianosa	Italy	42.5839, 10.0784	shrubs
18	ITRo1	Roccarespampani1	Italy	42.4081, 11.9300	deciduous broadleaf trees
19	ITRo2	Roccarespampani2	Italy	42.3903, 11.9209	deciduous broadleaf trees
20	ITSRo	San Rossore	Italy	43.7279, 10.2844	evergreen needleleaf trees
21	ITTo1	Tolfa wet	Italy	42.1897, 11.9216	deciduous broadleaf trees
22	ITTo2	Tolfa dry	Italy	42.1897, 11.9216	deciduous broadleaf trees
23	ITTol	Tolfa	Italy	42.1897, 11.9216	evergreen broadleaf trees

Tab. 2: Annual and bi-monthly subsets (PPT = precipitation; T = air temperature). Note that for the early winter (ND) subset we studied the impact of the PPT and T on the average annual GPP of the subsequent year rather than on the actual year.

ID	Subset description
S0	mean annual (Jan.-Dec.) PPT, T & vegetation
S1	mean JF (Jan. & Feb.) PPT, T & vegetation
S2	mean MA (Mar. & Apr.) PPT, T & vegetation
S3	mean MJ (May & Jun.) PPT, T & vegetation
S4	mean JA (Jul. & Aug.) PPT, T & vegetation
S5	mean SO (Sept. & Oct.) PPT, T & vegetation
S6	mean ND (Nov. & Dec.) PPT, T & vegetation

(A) Impact on average annual GPP
(B) Impact on total annual GPP (sum)
(C) Impact on average seasonal GPP

Biogeosciences Discuss., doi:10.5194/bg-2016-491, 2016
Manuscript under review for journal Biogeosciences
Published: 15 November 2016

Tab. 3: Results of the statistical analysis. The numbers represent significant p-values ($p < 0.05$) whereas an 'o' represents no significance ($p > 0.05$). The used significance levels are given in brackets. Green numbers are representing p-values that are still significant after the Holm-Bonferroni correction. Red numbers indicate the p-values that lost their significance after the Holm-Bonferroni correction. Black numbers represent the applied significance level without using the Holm-Bonferroni correction (Seasonal Approach).

			seasonal (S2-S7)					
		annual (S0)	Jan & Feb (S2)	Mar & Apr (S3)	May & Jun (S4)	Jul & Aug (S5)	Sep & Oct (S6)	Nov & Dec (S1)
	Nr. of sites	19	19	19	18	19	19	15
	Nr. of years	76	65	74	70	74	75	56
	R^2	0.64	0.70	0.71	0.75	0.69	0.70	0.70
(A) averages	PPT	o	o	0.008 (p < 0.050)	o	o	o	o
	T	o	0.022 (p < 0.008)	0.047 (p < 0.006)	o	o	o	0.011 (p < 0.025)
	vegetation	0.020 (p < 0.010)	0.027 (p < 0.007)	0.016 (p < 0.017)	o	o	0.030 (p < 0.006)	0.019 (p < 0.013)
	PPT:T	o	o	o	o	o	o	o
	PPT:vegetation	o	o	o	o	o	o	o
	T:vegetation	o	o	o	o	o	o	o
	R^2	0.63	0.70	0.70	0.73	0.68	0.69	0.96
(B) sums	PPT	o	o	0.012 (p < 0.025)	o	o	o	o
	T	o	0.020 (p < 0.010)	0.030 (p < 0.006)	o	o	o	0.008 (p < 0.050)
	vegetation	0.016 (p < 0.013)	0.027 (p < 0.007)	0.014 (p < 0.017)	o	o	0.025 (p < 0.008)	0.027 (p < 0.006)
	PPT:T	o	o	o	o	o	o	o
	PPT:vegetation	o	o	o	o	o	o	o
	T:vegetation	o	o	o	o	o	o	o
	R^2	-	0.84	0.67	0.78	0.73	0.63	0.78
(C) seasonal approach	PPT	-	o	o	0.003 (p < 0.050)	0.003 (p < 0.050)	o	o
	T	-	0.001 (p < 0.050)	0.009 (p < 0.050)	0.005 (p < 0.050)	0.005 (p < 0.050)	0.041 (p < 0.050)	0.003 (p < 0.050)
	vegetation	-	o	o	o	o	0.009 (p < 0.050)	o
	PPT:T	-	o	o	o	o	o	o
	PPT:vegetation	-	o	o	o	o	o	o
	T:vegetation	-	o	o	o	o	o	o