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Soil Moisture and Black Truffle Production Variability in the Iberian Peninsula

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Abstract: The relationship between modelled root zone soil moisture (SM) and black truffle production in the Iberian Peninsula was studied. Previous works have investigated the influence that precipitation exerts on truffle yield highlighting the importance of water for the growth of black truffle. However, SM had not been used until now due to the lack of suitable databases. The SM series from the LISFLOOD hydrological rainfall–runoff model was used in this study. Annual black truffle yield series from 175 locations in Spain was correlated with SM for the period 1991–2012. For this, different approaches were applied considering daily, weekly and monthly temporal scales. The same analysis was carried out using precipitation data to compare the behaviors of both variables related to truffle production variability. The results obtained show critical periods in terms of soil water content in summer (June–September) and during October–November months. Moreover, a clear delay between precipitation and SM influence on black truffle was observed. The results obtained in this study highlight the importance of SM for black truffle production, since this variable truly expresses the available water for this fungus, which completes its entire life cycle living below ground.

Keywords: soil moisture; precipitation; *Tuber melanosporum*; black truffle production

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1. Introduction

Black truffle (*Tuber melanosporum*) is an ectomycorrhizal hypogeous ascomycete fungus. It is a very important economic resource in many Mediterranean forests of southern Europe, although it is currently cultivated in many other countries around the world [1]. Black truffle production is mostly located in northeastern Spain, southern France, and central and northern Italy, where the soils and climate produce favorable conditions for their production [2].

In the 1950s, the exploitation of wild black truffles began to gain popularity in the Iberian Peninsula, and in the late 1990s, black truffle plantations began to grow in abundance [3]. With a Mediterranean climate and calcareous substrate soils with low organic matter content, the Iberian Peninsula is one of the few places worldwide with a vast number of natural locations for black truffle production [4].

Many studies have evaluated the influence that climatic factors exert on the different truffle fruitbody formation stages and therefore, on black truffle production [5–8]. Black truffle fruitbodies develop in the soil from late spring, when mating occurs, until November, when the truffle fruitbody starts to ripen; these truffles are harvested between November and March [7]. Furthermore, the fruitbody depends on carbon allocated by the symbiont tree to the root tips, where the plant–fungus association takes place [9]. Therefore, truffle yields can be influenced by the vegetative growth of the fungus or the symbiont tree, mostly in the early spring. Due to such a long lifespan, fruitbody production is affected by climate variations, especially those involved in the water balance [10].

Büntgen et al. [5] studied the impact of precipitation and maximum temperature on black truffle production in France, Italy and Spain. They found a positive relationship between truffle production and precipitation in summer, when temperatures showed a negative influence. Le Tacon et al. [6] suggested that truffle yield is affected by the number of days with minimum temperature below −5 °C. In addition, several studies have analyzed the possible effects of climate change on black truffle production, focusing on precipitation and temperature [11,12]. These variables have an impact on soil dynamics and soil water content; therefore, soil conditions can influence truffle growth. This confirmed what [13] and [14] suggested years ago: that summer soil water content is a key factor in black truffle productivity. Despite the practical interest in studying the role of soil moisture (SM) in truffle yield, it has not been possible until now because of the large-scale SM network's scarcity to monitor that variable in truffle-producing regions [10].

It has been shown that SM is a key variable in the interaction between land and atmosphere due to its role in the water, energy and carbon cycle [15]. It is also a crucial variable in processes such as drought [16,17] or floods [18,19], as well as in agricultural applications [20]. Additionally, in recent years, the influence of SM on tree growth in water-limited environments has been demonstrated [21,22]. This has a particular interest as truffle-host trees growth is closely linked to the growth and production of black truffles [10]. However, the relationship between SM and black truffle production has not yet been studied, except for one short plot-scale experiments [14].

The monitoring and estimation of SM can be carried out in three different ways, including in situ measurement networks, remote sensing or modelling [23]. The first in situ measurement networks date back to the 1960s, but it was in the 2000s that SM monitoring networks began to gain importance in hydrological and meteorological observations [24]. Although long-term time series can be obtained with this method, they provide site-specific measurements. Since 2010, when SM was considered one of the essential climate variables by the Global Climate Observing System [25], much progress has been made to measure and estimate this variable. Two satellite missions were launched to specifically observe surface SM from the space, the Soil Moisture and Ocean Salinity (SMOS) from the European Space Agency (ESA) [26] and Soil Moisture Active Pasive (SMAP) from the National Aeronautics and Space Administration (NASA) [27]. Another example of this kind of project is the Climate Change Initiative Soil Moisture (CCI SM) database, which includes all the satellites that have estimated SM to date [28]. Although global measurements are acquired with this method, the spatial resolution at which SM is estimated is still too coarse in some cases for certain applications. An alternative approach is the estimation of SM through modelling. Hydrological models can potentially estimate SM at different spatial and temporal resolutions and at different depths, including root zone SM, over large areas [23].

Until now, the interest in studying the influence of the variables that are involved in the dynamics of SM on truffle production has been evident. However, it is now possible to directly use SM to analyze its specific relationship with truffle production variability. For this reason, in this work, the relationship between SM and black truffle production in the Iberian Peninsula, one of the most important areas worldwide for black truffle cultivation, has been studied. The study was addressed using the SM database from the LISFLOOD hydrological rainfall-runoff model. At the same time, a comparative analysis was performed with precipitation, which has been the most commonly analyzed water-related variable in this kind of studies. For this study, a database for annual black truffle production from 1991 to 2012 was used. To take advantage of the data availability and to study patterns on different time scales influencing the production of black truffles, this research was carried out on three different time scales: daily, weekly and monthly.

2. Materials and Methods

2.1. Study Area and Black Truffle Production Dataset

The Iberian Peninsula is one of the areas where more black truffle is produced [1]. The area is characterized by a Mediterranean climate, with dry and hot summers and mild and humid winters. Truffle production is located in forested mountain areas in the eastern part of the Iberian Peninsula (Figure 1). In this region, 175 locations where black truffle has been naturally produced and commercialized were considered [29]. These locations are a meaningful representation of black truffle production in Spain until 2012, period in which wild production was largely dominant. The fact that truffles from these locations were commercially harvested indicates the likelihood of high truffle-fruiting yield [4].

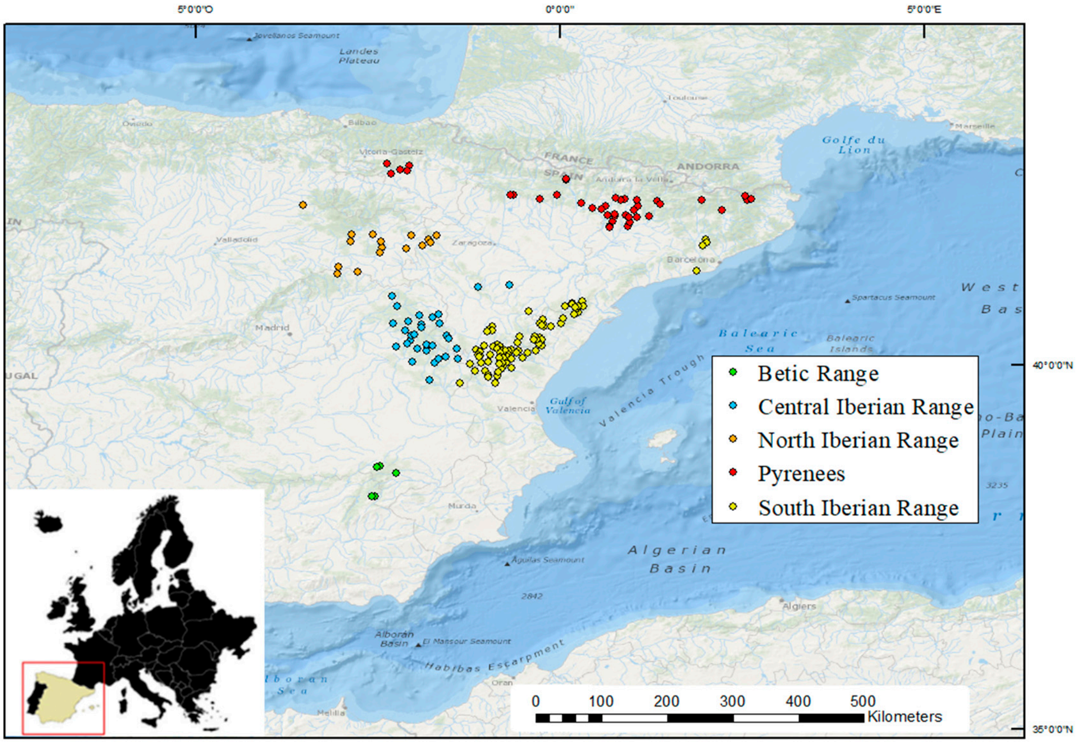

Figure 1. Black truffle production locations.

To characterize the study area (Table 1), three databases were considered. These include the SPREAD and STEAD 5 km daily databases [30,31], from which precipitation, maximum and minimum temperature were obtained, respectively, and the SoilGrids 250 m soil database, from ISRIC [32].

Table 1. Climate variable and soil characteristics values for the study area. *IR corresponds to Iberian Range.

	Tmax (°C)	Tmin (°C)	Rainfall (mm)	Clay (%)	Sand (%)	Silt (%)	OM (%)
Mean	16.6	5.6	773	23.73	35.85	40.42	2.41
Betic Range	18.2	6.1	909	19.55	42.12	38.33	2.46
Pyrenees	16.8	5.6	992	26.70	32.12	41.17	3.12
North IR.	16.1	4.6	702	24.81	37.08	38.11	2.06
Central IR.	16.2	4.4	773	20.94	37.28	41.78	2.27
South IR.	16.8	6.2	675	23.43	36.45	40.12	2.21

For the whole sampling area, the mean annual maximum temperature value for the study period was 16.6 °C, while the minimum temperature was 5.6 °C. In turn, the mean annual precipitation was 773 mm (Table 1), ranging between 400 and 1800 mm. de

Luis et al. [33] found that available water was scarce from May to August, while it was more balanced between March and April and between September and October, according to the seasonal precipitation peaks and conditions of the Mediterranean climate in Spain. Regarding the soil root-zone profiles (0–100 cm), Table 1 shows how all the soils tend to be loamy or clayey, without significant differences between the 175 locations. The organic matter values did not exceed 3% in any case, with an average of 2.41% for the 175 points.

The annual black truffle production database, the most consistent and useful data record of black truffle production among all Spanish statistical sources, was obtained from the Spanish Federation of Truffle Growers Associations (FETT), [3]. This database provided a single annual black truffle production dataset, which corresponded to the black truffles collected in the 175 selected locations from 1970 to 2012. This annual time series was detrended using a General Additive Model (GAM) with a normal distribution and thin plate regression splines [34], later checking that the time series did not show a significant autocorrelation. The application of this methodology was justified by the fact that the black truffle harvests for the period between 1970 and 2012 showed a significant positive temporal trend, as explained in [8]. Then, the anomalies from the detrended time series were calculated.

A regional analysis was included to analyze whether differences in the pattern of the relationship between SM and truffle production occur. Therefore, the 175 locations were divided by geographic location into 5 regions partially according to [29]: the Pyrenees with 40 locations; the Betic Range with 5 locations; the Northern Iberian Range with 16 locations; the Central Iberian Range with 33 locations; and the South Iberian Range with 81 locations (Figure 1). The climate and soil characteristics of each area are shown in Table 1.

2.2. Soil Moisture and Precipitation Databases

The SM database used in this study is provided by the LISFLOOD hydrological model [35]. It is a rainfall-runoff model developed by the floods group of the Natural Hazards Project of the Joint Research Center (JRC) of the European Commission and used by the European Drought Observatory (EDO) monitoring system [36]. The model provides SM for three depth layers, with a spatial resolution of 5 × 5 km. For this study, the database generated by the European Flood Awareness System (EFAS) was used [37]. It provides series with a time resolution of 6 h from 1991 to present. The data of the first two soil layers, corresponding to depth 0–100 cm, and the two time 00- and 12-h, were used. The four data were averaged to obtain the SM in a site and at a day.

This SM database was preferred over other available ones because it was considered the most suitable for the study objectives. On the one hand, it was previously validated over Europe [38] and applied satisfactorily in different studies over the Iberian Peninsula [22,39]. On the other hand, its spatial resolution was adjusted for applications in related topics where spatially restricted sampling was used [21]. There are other available SM databases from modelling [40] and remote sensing [41] that could have been considered. However, either their spatial resolution was too coarse [42] or, having finer spatial resolution, the length of their series of observations was not long enough [43] for this type of study.

The precipitation data were obtained from the SPREAD database, which has a spatial resolution of 5 × 5 km over the Iberian Peninsula and a daily temporal resolution from 1950 to 2012 [30]. Due to its spatial distribution and large temporal coverage, SPREAD has been widely applied in studies over the Iberian Peninsula [22,44].

After obtaining the time series for the study period (1991–2012), only the pixels from the locations corresponding to the black truffle database were chosen, obtaining 175 different time series, one for each sample. These time series were rescaled to weekly and monthly scales, and in turn, a 30-day moving average was applied to the original daily time series following the methodology in [21]. Therefore, three different time scales were obtained for each database and for each pixel.

2.3. Statistical Analysis

To analyze the relationship between soil water content and black truffle yield variability, the Spearman correlation coefficient (R) and the *p* value were calculated. Black truffle annual series were correlated with SM daily, weekly and monthly series by comparing each day, week and month with annual truffle yield data. In other words, for example and for daily data, SM values of every 1st of January were correlated with annual values of truffle production, and so on with each day of the corresponding harvest year, like in [21]. Same strategy was applied to weekly and monthly series.

Two statistical approaches were applied for each temporal scale of analysis. On the one hand, we computed the average of the SM and precipitation series of all the samples selected for the study. Thus, just one series of the water related variables was confronted to the truffle production series. We will refer to this strategy as the samples-average approach. A single R and *p* values for each day, week or month was obtained following this approach. On the other hand, the time series of SM and precipitation of each sample was individually correlated with the truffle production series. Therefore, 175 R and *p* values were obtained, one for each sample, enabling the calculation of a percentage of sites with statistical significance. We will refer to this strategy as the sample-by-sample approach.

Finally, the obtained statistical parameters for each approach were analyzed, first considered all together the 175 locations (the whole sampling area), and second, by each of the five regions defined in this study (Figure 1). This was made in order to analyze whether geographical differences in the pattern of the relationship between SM and truffle production occur.

3. Results and Discussion

The results obtained from the comparison between SM and the black truffle production database using the samples-average approach, show significant coefficients of correlation greater than 0.6 in the summer months (July–August–September) (Figure 2a and Table 2). This fact can be observed in the three time scales used, even with R reaching 0.74 in the daily scale. A period with significant R values lower than −0.4 was also found in October–November. These results indicated that high water content in the soil during the summer can have a positive influence on the development of the black truffle, whereas high soil water content in October–November can have a negative influence on the production.

Table 2. Maximum correlation coefficient values between soil moisture and black truffle production obtained in the Iberian Peninsula with the two approaches. For the sample-by-sample approach, Rmax refers to the median (med) values, and the corresponding percentage of R significant ($p < 0.05$) values is also included. * Time (day, week or month) at which the maximum value is reached.

Approach		Daily	Weekly	Monthly
samples-average	Rmax	0.74	0.60	0.66
	Time *	12-August	33 (August)	August
sample-by-sample	Rmax(med)	0.55	0.51	0.52
	%	74.3	70.3	81.7
	Time *	1-August	32 (August)	August

When we applied this samples-average approach regionally, the results of positive R with statistical significance were again obtained in the months of July, August and September in all the zones (exceeding the values of R = 0.5 in all cases, even reaching 0.7 in the Southern Iberian Range) except for the most rainy area, the Pyrenees (Figure 2b–f). For this region significant R values were obtained only for August and September. The negative influence of SM between October and November is now just observed in the Pyrenees and the North Iberian Range, also with statistical significance at the daily and weekly scales, and always with lower values than those obtained in summer.

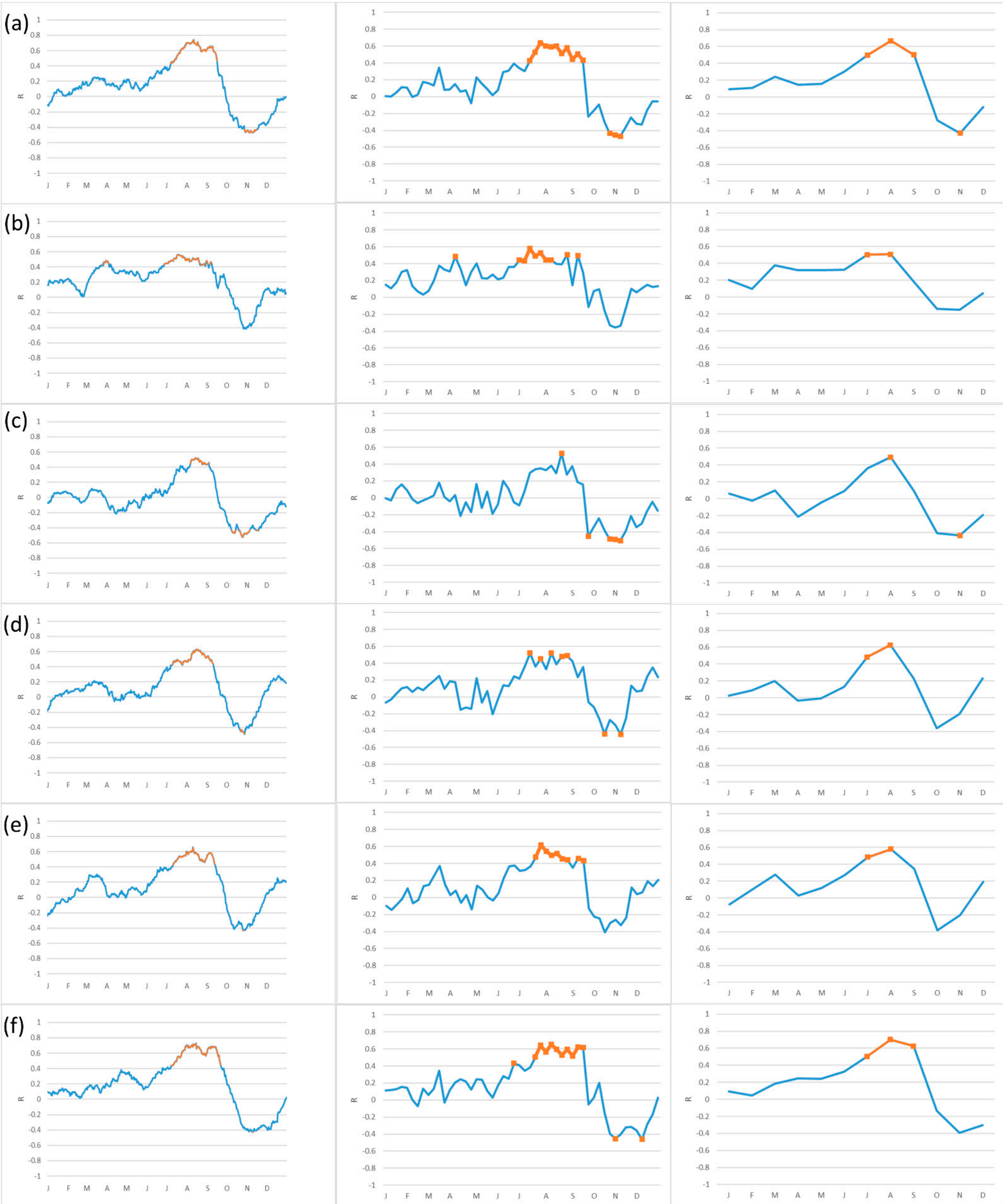

Figure 2. Temporal evolution of correlation coefficient values obtained with the samples-average approach between SM and black truffle production for daily data (left column), weekly data (middle column) and monthly data (right column). (**a**) Iberian Peninsula; (**b**) Betic Range; (**c**) Pyrenees; (**d**) North Iberian Range; (**e**) Central Iberian Range; (**f**) South Iberian Range. Orange points are R values with p value < 0.05.

The results obtained with the sample-by-sample approach (Figure 3a and Table 2) showed a similar pattern as those of the samples-average approach. The median R values for the 175 locations were approximately 0.5 on the three scales for the summer months, being approximately 70% on the daily and weekly scales and 80% on the monthly scale, significant correlations. It was also observed that in the period October-November, the median of the R values was approximately −0.4 for the three temporal scales, and the percentage of results with statistical significance exceeded 30% in the daily and weekly scales. Weaker correlations were obtained in the monthly analysis, where the R median was −0.3 and the percentage of locations with statistical significance only reached 20%. The R value and the percentages of results with statistical significance were much higher (absolute values) in summer than in fall, which indicates that SM is more critical in that period.

Small differences were observed when the results are analyzed regionally (Figure 3b–f). While in the Pyrenees the median value of R and the percentage of significant results were higher (in absolute value) in October–November (R = −0.43 and 55%, respectively) than in the summer months (R = 0.40 and 45%, respectively), in the North Iberian Range it was higher in summer (R = 0.53 and 92%), but similar in October–November (R = −0.4 and 50%). This can be observed for the three time scales. In turn, this last pattern was repeated in the other two areas of the Iberian Range, which was not observed in the samples-average approach. However, these small differences were not very noticeable, owing that production of all truffle sites was provided in a single series instead of having yield series for each location.

The fact that high positive R values with statistical significance were obtained in the summer months in all strategies carried out for the three timescales and for all areas was in agreement with results obtained in previous studies [5,6,8,45]. These works highlighted the importance of water availability in this period for the Mediterranean climate. However, these studies did not analyze SM but instead used different precipitation databases. Considering that during summer months the black truffle fruitbody is already present in the soil and has initiated its development and swelling stage, the results support the hypothesis that more water available in the summer months leads to higher fruitbody survival and growth [7,14]. Negative correlation coefficients with statistical significance have also been observed in November, as in the work carried out by [46], although in their case, the analysis was also made with precipitation. Truffle growers empirically associate the occurrence of heavy autumn rains that result in long periods of soil waterlogging with a decrease in truffle yield and/or an increase in the occurrence of rotten truffles [47].

The results obtained with the samples-average approach for the precipitation analysis considering the 175 locations all together were similar to those obtained with SM, which, to some extent, was expected (Figure 4a and Table 3). Positive significant R values during the summer months were obtained with the three temporal scales, reaching values of 0.8 at the daily scale, and 0.56 and 0.6 at the weekly and monthly scales, respectively. When the results were analyzed by regions, the summer period was also prominently observed at the three timescales for all the regions (Figure 4b–f).

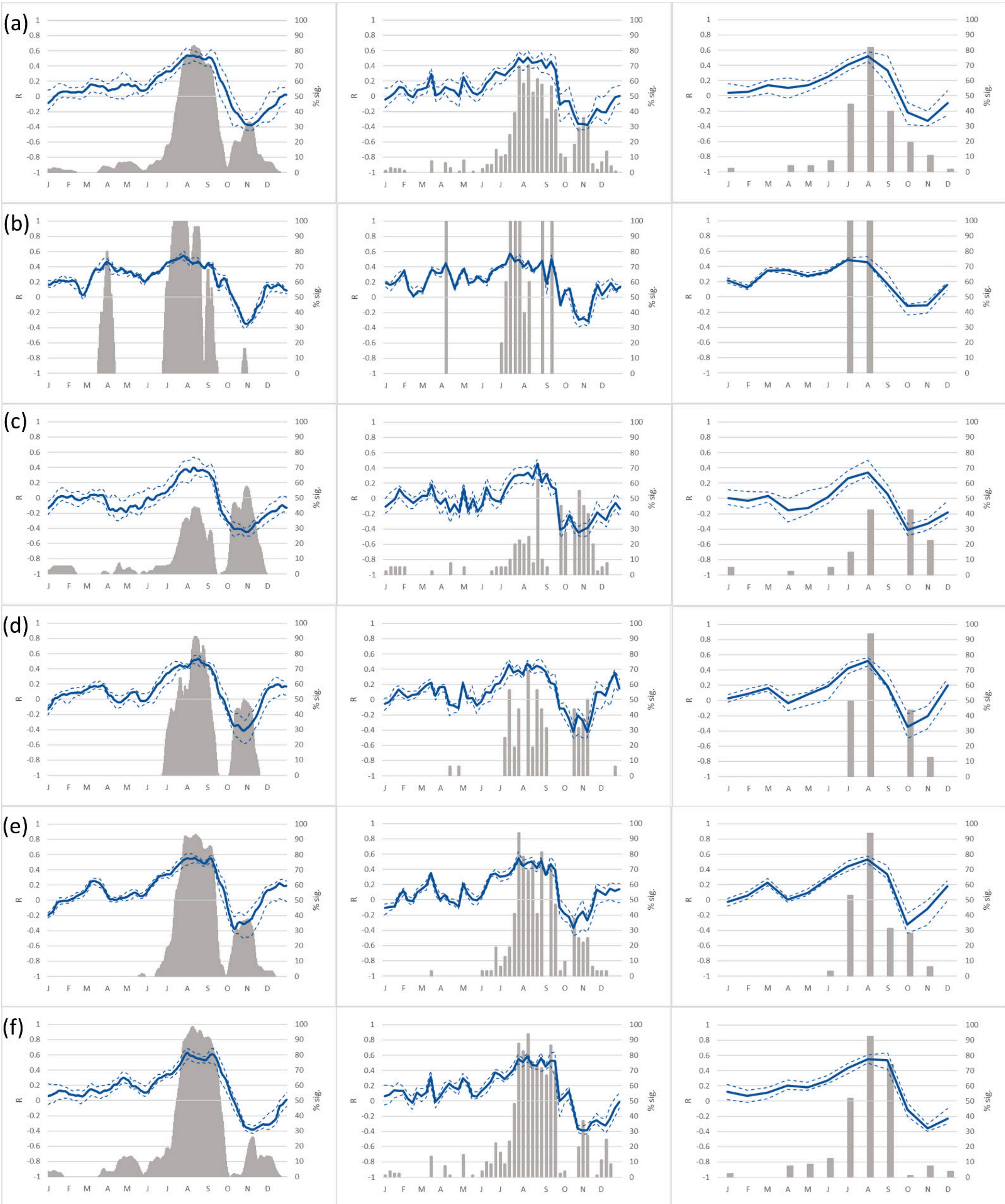

Figure 3. Temporal evolution of percentile 75, percentile 25 (dashed blue lines), median (dark blue line), and percentage of R values with p value < 0.05 (grey bars) obtained with the sample-by-sample approach between SM and black truffle production for daily data (left column), weekly data (middle column) and monthly data (right column). (**a**) Iberian Peninsula; (**b**) Betic Range; (**c**) Pyrenees; (**d**) North Iberian Range; (**e**) Central Iberian Range; (**f**) South Iberian Range.

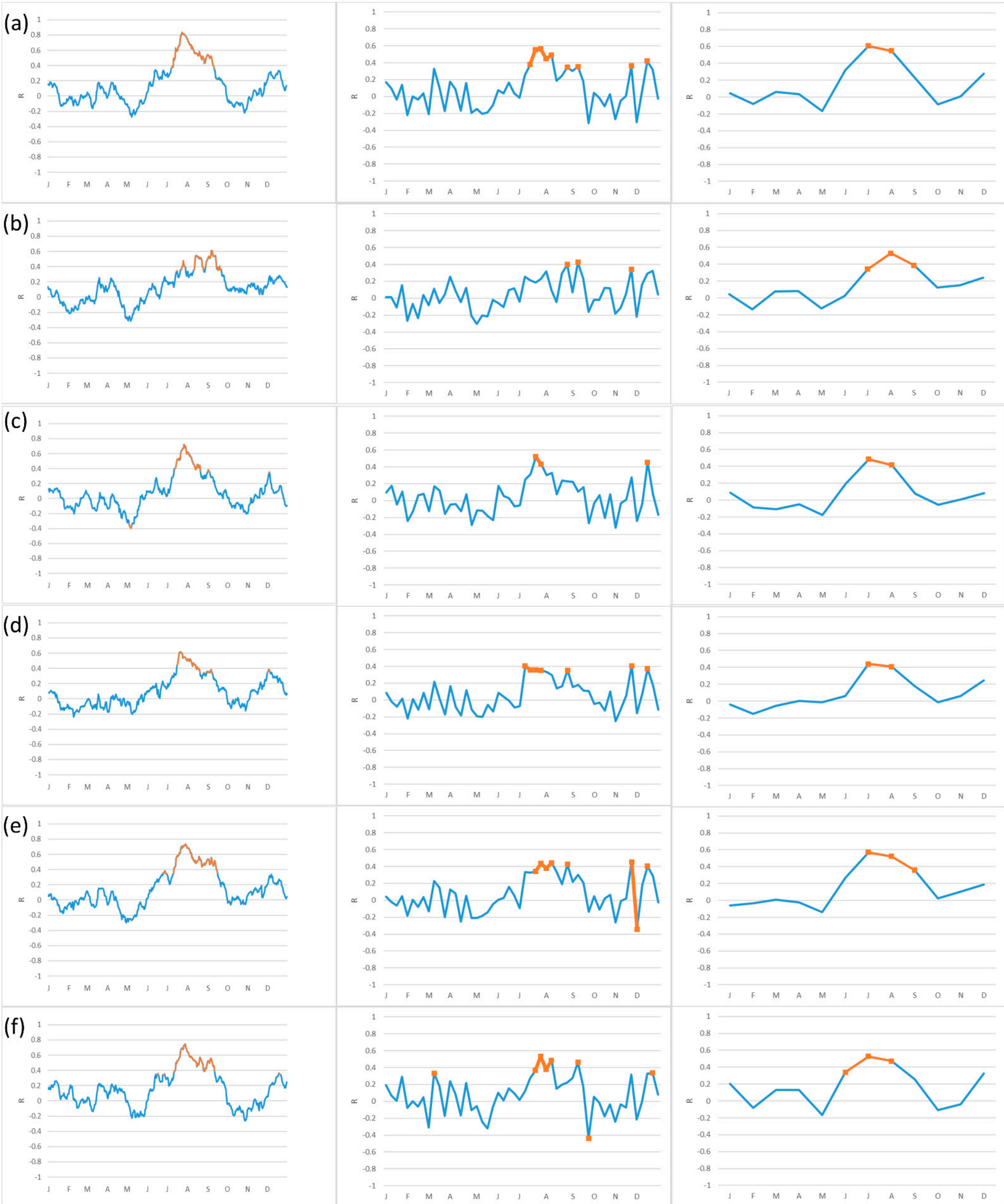

Figure 4. Temporal evolution of correlation coefficient values obtained with the samples-average approach between precipitation and black truffle production for daily data (left column), weekly data (middle column) and monthly data (right column). (**a**) Iberian Peninsula; (**b**) Betic Range; (**c**) Pyrenees; (**d**) North Iberian Range; (**e**) Central Iberian Range; (**f**) South Iberian Range. Orange points are R values with p value < 0.05.

Table 3. Maximum correlation coefficient values between precipitation and black truffle production obtained in the Iberian Peninsula with the two approaches. For the sample-by-sample approach, Rmax refers to the median (med) values, and the corresponding percentage of R significant ($p < 0.05$) values is also included. * Time (day, week or month) at which the maximum value is reached.

Approach		**Daily**	**Weekly**	**Monthly**
samples-average	Rmax	0.83	0.56	0.60
	Time *	25-July	30 (July)	July
sample-by-sample	Rmax(med)	0.53	0.36	0.39
	%	91.4	61.7	78.9
	Time *	29-July	30 (July)	July

The summer period also stood out in the approach by locations both considering all together or by regions (Figure 5). At daily scale, the maximum median R value obtained did not exceed 0.6 in any case, while the percentage of significant correlations exceeded 80% everywhere. In the weekly and monthly scales, the correlation values obtained were lower, around 0.4, and in general, the percentages of significant correlations were also lower. No great differences were observed between results obtained from the different regions, except for the Pyrenees where weaker correlations and less significant results were obtained.

These results obtained for summer months with the precipitation variable are in line with previous studies in the Iberian Peninsula [5,8] and other Mediterranean areas [45,46]. Although they used different databases, the correlation values are very similar. These results are also in agreement with those obtained with the SM database used in this study, thus reinforcing the importance of water availability in the summer period for black truffle production.

The fact that in this case, the critical period of October–November was not observed for precipitation, which stood out with the SM, is very remarkable. In turn, this circumstance has only been observed in the analysis carried out by [46], where precipitation was also correlated with the annual production database of black truffle in Spain. Therefore, the higher relevance of SM compared to precipitation and the potential of its use for truffle cultivation management is highlighted as it allows detecting another critical period in addition to summer, which was not detected using precipitation for the same statistical analysis. Black truffle completes its entire life cycle living within the soil, obligatorily in symbiosis with the roots of a host tree. Since both these trees—and the truffle fruit-body itself—interact with hydrological processes, the soil water content acquires much more prominence because the rainwater does not reach the ground in its entirety due to interception and evapotranspiration processes [48].

Another difference observed between precipitation and SM is the time between the beginning and the end of the critical summer period observed by both databases, as well as the time when the maximum correlation value is reached. Table 4 shows the dates of the beginning, the end and the time at which the maximum value of R is reached, as well as the maximum value of correlation obtained at the daily scale from the approach by locations. In general, the critical summer period begins and ends earlier for precipitation than for SM, and in turn, the maximum correlation value is reached later with SM. It can also be observed how these maximum correlation values are always higher for SM than for precipitation.

Figure 5. Temporal evolution of percentile 75, percentile 25 (dashed blue lines), median (dark blue line), and percentage of R values with p value < 0.05 (grey bars) obtained with the sample-by-sample approach between precipitation and black truffle production for daily data (left column), weekly data (middle column) and monthly data (right column). (**a**) Iberian Peninsula; (**b**) Betic Range; (**c**) Pyrenees; (**d**) North Iberian Range; (**e**) Central Iberian Range; (**f**) South Iberian Range.

Table 4. Dates of the beginning and end of the critical summer period (R statistically significant), maximum value of correlation reached, date on which it was reached and delay between that maximum for soil moisture (SM) and precipitation (P).

		Critical Summer Period	R Max.	Date	Delay (Days)
Iberian Peninsula	SM P	8 July–17 September 14 June–12 September	0.85 0.76	29 July 23 July	+6
Betic Range	SM P	28 June–8 September 16 July–22 September	0.63 0.63	24 July 21 August	−28
Pyrenees	SM P	7 August–4 September 12 July–1 September	0.85 0.68	25 July 20 July	+5
North Iberian Range	SM P	10 July–11 September 08 July–8 September	0.76 0.69	23 July 15 July	+8
Center Iberian Range	SM P	12 July–13 September 25 June–10 September	0.77 0.72	11 August 24 July	+18
South Iberian Range	SM P	8 July–22 September 14 June–12 September	0.79 0.76	1 August 28 July	+14

The delay between the maximum R value for SM and for precipitation (Table 4) is approximately one week for the whole study area. In most of the regions, the critical time of SM is always after that of precipitation, and the delay oscillates between 5 and 18 days. In the case of the Betic Range, the maximum R is almost one month earlier for SM than for precipitation. This specific result could be related to the more meridional position and more stressed climatic conditions of this location and could also be conditioned by the scarce number of sampled points. The delay observed in the other areas is consistent with the functioning of the soil-water-plant–atmosphere system and the decoupling that exists between the atmospheric and the soil system [49]. On the one hand, it is the delay that is related to the transit time between precipitation, infiltration and soil water storage. On the other hand, this result is in line with the interference caused by the tree in the transfer of water from the atmosphere to the soil, mainly due to the interception process.

Quercus ilex and *Quercus faginea* are the most common tree species in Spain, with which black truffles live in obligate symbiosis [10]. Interception in forest oak species is 20.0% on average in Europe [50] and 22.4% in Spain [51]. Specifically, for these two species, the coefficient of interception is 30.0% and 22.1%, respectively, in Spain. Therefore, between a fifth and a quarter of the water that falls on the trees under which the truffle grows does not reach the soil. This is probably exacerbated in summer [52], when water availability is more critical for truffle production, as was found in the present study.

The results obtained in this study, as well as the comparison of these results with those obtained in recent studies on black truffle production, showed that SM was capable of effectively detecting the critical periods for the growth of the black truffle. A closer relationship was also observed than that obtained when the traditional climatic variable for this type of study, such as precipitation, was used.

The increasing availability of SM databases, especially those generated by modelling and remote sensing, which are increasingly accurate and with better temporal and spatial resolutions [43], enables studies that until recently were not feasible. Until now, to perform this type of study, it was necessary to use indirect approaches or resort to the use of proxies. This is the case for studies in forest areas, where it is known that the soil water content plays a fundamental role, especially in water-limited environments [53], both for species above and within the soil [54]. Recent studies have shown that this approach is feasible and gives good results [21,22].

The results of this work can also be a useful contribution to applications such as mushroom yield modelling [55] or forest management for mushroom production [56].

Expected improvements in the spatial resolution of remote-sensing products [57] would allow the application of SM monitoring to truffle cultivation management. In recent years, the black truffle production of Spain has greatly increased due to the spread of plantations and the irrigation of these plantations. However, these plantations are relatively small and scattered, except in a few regions, such as Sarrión (Teruel, eastern Spain). With finer spatial and temporal resolution, which is already available [58], remote sensing could be used to optimize the irrigation regime of these plantations and to predict the annual harvest of the regions with large plantation surfaces.

4. Conclusions

The influence of root zone SM on black truffle growth and production variability over the Iberian Peninsula was analyzed. The time series of this variable was correlated with the time series of annual black truffle production corresponding to 175 locations in eastern Spain. Subsequently, a similar analysis was repeated with precipitation, the climatic variable most often used in this kind of study, and the results obtained for both variables were compared.

From these results, as expected, the importance of available water for truffle production can be inferred, especially during the summer months. The relationship obtained indicates that more water availability in this period leads to higher black truffle production. These results were obtained at daily, weekly and monthly time scales, and with different statistical approaches. The importance of the SM variable in the period of October–November was observed, when excess soil water content negatively affects the truffle production, although this was not the case for precipitation.

In comparing the results obtained with both variables for the summer period, it was also observed that there was a clear delay between precipitation and soil moisture. This delay was very relevant because it emphasized the different dynamics of both variables and the decoupling that existed between the atmospheric and the soil system. This meant that the rainwater did not reach the ground either directly or in its entirety due to relevant processes such as interception and evapotranspiration. Especially in water-limited environments such as the Mediterranean, this process is aggravated in summer, when water availability is more critical for truffle production, as was found in the present study.

The results of this research show that using SM with appropriate temporal and spatial resolution is more suitable to monitor the growth of the black truffle and to analyze the variability in its production than other approaches. SM behaves as a storage variable from the water coming from precipitation and therefore directly expresses the available water content for the black truffle and its environment. However, the fact that black truffle production was provided in a single annual time series for the 175 locations prevents deepening in a greater discrimination of patterns of the relationship between SM and truffle yield. Although the LISFLOOD SM database has been successfully validated in Spain and elsewhere in Europe, it would be wise to delve into applications of this type under different bioclimatic conditions. Therefore, it is necessary to investigate more on this topic in other geographical contexts.

The increase in recent years of available SM databases generated through modelling or remote sensing allows now having suitable SM series for applications as the one performed in this research, which was not possible until recently. Due to the increase in black truffle plantations in many regions, as well as the expansion of irrigation practices, this kind of study acquires great importance. The characterization of the delay found could be important information for implementing irrigation systems in truffle plantations, where interception is lower due to canopy covers of usually less than 30%, especially for those that frequently use micro-sprinkling. These approaches for monitoring and analysis can be used for truffle farm water management, as well as for annual truffle harvest forecasting in regions where this fungus has increasing economic and environmental relevance.

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Data Availability Statement: LISFLOOD database is freely available online (https://cds.climate.copernicus.eu/cdsapp#!/dataset/efas-historical?tab=form accessed on 24 May 2022). SPREAD database is freely available on the web repository of the Spanish National Research Council (CSIC) (https://digital.csic.es/handle/10261/141218 accessed on 24 May 2022). Black truffle database was freely obtained from the Spanish Federation of Truffle Growers Associations.

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