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ORCID:

SG: 0000-0003-3417-7800

NP: 0000-0002-8270-2991

GG: 0000-0003-0740-3454

How does weather impact on beehive productivity in a Mediterranean island?

SOFIA GOUNARI¹, NIKOLAOS PROUTSOS^{1,*}, GEORGIOS GORAS²

¹ *Institute of Mediterranean Forest Ecosystems, Hellenic Agricultural Organization "DEMETER", Greece*

² *Faculty of Crop Science, Agricultural University of Athens, Greece*

*Corresponding author. E-mail: np@fria.gr

Abstract. Bee productivity is an essential factor affecting, not only the production of honey or other beehive products but also food security due to the very important role of bees as pollinators. The behavior of the bees and thus their productivity is highly affected by the weather fluctuations. In the present study, five years (2015-2019) of beehive weight data were analyzed to assess the impact of the prevailing weather conditions at an east Mediterranean island, on the productivity of bees. The results indicate that temperature and water-related parameters, significantly affect beehive productivity. Specifically, temperature optimum values of 17°C in spring and 26°C in summer, are associated with higher daily relative changes of the beehive weight, while bee productivity enhances at daily temperatures between 14 and 28°C, presenting negative values beyond this range. The effects of temperature, windspeed, diurnal temperature range, vapor pressure deficit, saturation vapor pressure, and the duration of hot and dry periods, on beehive productivity are strong and negative, whereas the effect of relative humidity is also significant but positive. The results of the study enhance the knowledge of the weather impacts on beehive production especially under the climatic conditions of a small east Mediterranean island, with applications in beekeepers scheduling and hive designing, to maximize beehive productivity.

Keywords: temperature, vapor pressure, diurnal temperature range DTR, vapor pressure deficit VPD, relative humidity, weather, beehive productivity, Greece, Mediterranean island.

1. INTRODUCTION

Honey production is an important sector for the world's economy (Cieśla, 2002; Gallai et al., 2009), rapidly growing in the last decades (Aizen and Harder, 2009). Even though the main role of beekeeping is honey production (Aizen and Harder, 2009; Morse and Calderone, 2000), the maintenance of honey bees significantly contributes to pollination activity. Honeybees as pollinators, provide valuable services to agricultural (Freitas and Paxton, 1996; Ricketts et al., 2004; Roubik, 1995, 2002) and natural ecosystems with significant impact on biodiversity and food security (Allen-Wardell et al., 1998; Ortiz-Caraballo, 2007).

Climate change is considered a major factor affecting honeybees' behavior and productivity with major consequences in both honey and agricultural production (Łangowska et al., 2017). Many research studies express serious concerns about the mass losses of bee colonies and the role of bees as pollinators (Cressey, 2014; Polce et al., 2014; Potts et al., 2010), while others underline important issues for the impact of climate change on honeybee abundance and honey yields (Crane, 1990; Le Conte and Navajas, 2008; van Engelsdorp et al., 2008). The impact of the changing climate is anticipated to be serious in the region of East Mediterranean and the Middle East since positive warming trends and increasing aridity is identified by many research studies (Proutsos et al., 2010; 2020; Tanarhte et al., 2012; Tsiros et al., 2020). Small islands are even more vulnerable regarding agricultural production and trade under the current climate change scenarios (Poonyth and Ford, 2004).

Even though the impacts of the warming climate and the weather conditions on honeybees are generally acknowledged, there is limited research on the connection of honeybees biology, behavior, and productivity with the climatic or weather changes (Gordo and Sanz, 2006; Henneken et al., 2012; Łangowska et al., 2017; Scheifinger et al., 2005; Sparks et al., 2010), whereas data from field experiments (apiaries) are also quite rare.

Bees' activity and honey yields are highly affected by climate and weather at different spatial scales, as shown by the effects of geographical attributes such as latitude (Crane, 1990; Gerlach, 1985; Holmes, 2002; Spivak, 1992) and elevation (Spivak, 1992) on honey yields and bee activity. Temperature, solar radiation or sunshine, wind, and precipitation, are considered as most influential for bee's productivity (Delgado et al., 2012; Łangowska et al., 2017; Puškadija et al., 2007; Vicens and Bosch, 2000) and are used as predictors for honey production, at specific geographical and time-frame scales (Rocha and Dias, 2017).

The precise relations of the meteorological factors with honeybees' behavior and productivity are still not thoroughly investigated. Despite the many negative reports and the documented climate change impacts on honeybees, there are many research studies indicating the opposite effect, when meteorological factors are analyzed under specific timesteps and regions. Łangowska et al. (2017) found strong negative relationships between honey bee spring activity (dates of first cleansing flight and first hive inspection) and temperature, with, however, high variability in timing from year to year. However, in the same study, the authors investigated the temperature influence on honey production, considering annual hive yields for more than 40 years (1965-2010) in

southern Poland and the southern UK and found a significant positive relation between annual yield and April-August temperature, suggesting that an increase of 1°C is associated with 8.97 kg and 8.71 kg increases in yields in southern Poland and the southern UK, respectively. They, also mention a positive relationship between June temperature and yield, suggesting that an increase of 1°C is associated with a 3.7 kg increase in yield. Clarke and Robert (2018) investigated the relationship between honeybee foraging activity and local weather conditions and found a strong connection of bees' activity with temperature and solar radiation. Burrill and Dietz (1981) also studied the effect of meteorological variables of temperature and solar radiation on bee foraging effort and found a positive correlation with temperature. They also found a positive correlation with solar radiation, but only up to a certain threshold of 460 W m⁻², since at higher radiation flux densities the correlation was negative.

Relative humidity is also considered as an influential factor for honey productivity and bees' survival since its values inside the hive affect honey maturation and define egg hatching (Doull, 1976; Li et al., 2016). Joshi and Joshi (2010), however, found a weak impact of RH on flight activity. In an interesting work by Abou-Shaara et al. (2017), the authors reviewed the impacts of both temperature and relative humidity on the honeybees' activities, presenting also specific thresholds and optimum values.

Precipitation may have an impact on beebehavior. de Mattos et al. (2018) in Southeastern Brazil, detected that summer rainfall and cloud cover is strongly and positively related to pollen foraging, whereas bees enhance the foraging effort the day before a heavy rainfall (He et al., 2016).

Relevant research studies assessing the impact of small islands climate on bees' productivity are very rare. Delgado et al. (2012) performed a comparison between contemporary (1998-2005) and historical (1910-1974) honey yield data in the island of Puerto Rico in the Caribbean and found that suitable areas for honey production and honey yields are anticipated to decrease in the future, considering the scenarios of climate change. They also assessed the effect of bioclimatic parameters on honey production concluding that temperature seasonality and mean temperature of the wettest quarter of the year have a negative effect, whereas precipitation of the wettest month and minimum temperature of the coldest month were positively correlated.

Additionally to the effects of weather on honeybee behavior, meteorological factors can affect honey yields, by impacting on vegetation dynamics or even on other insects that control honey production. The availability

of food (pollen, nectar, or honeydew produced by other insects) for the bees is critical and highly influenced by climate and weather. Pollen and nectar availability is sensitive to drought (Waser and Price, 2016) and other abiotic and biotic factors as temperature, water availability, nutrients, herbivory of leaves etc (Kenoyer, 1917; Huber, 1956; Shuel, 1967; Pleasants and Chaplin, 1983; Vasek et al., 1987; Devlin, 1988; Stephenson et al., 1992; Turner, 1993; Lau and Stephenson, 1994; Quesada et al., 1995; Petanidou et al., 1999). Corbet (1990) identified that weather affects pollinator activity, by altering the quantity and sugar concentration of nectar in flowers. Also, Petanidou et al. (1999) found that nutrient and water availability affected nectar production and nectary structure in Labiate species, whereas Devlin (1988) suggested that reduced light availability induced decrease in the amount of nectar of flowers, but not affected the pollen grain number. Quesada et al. (1995) identified the natural herbivory by beetles as a significant factor affecting negatively the production of staminate flowers and pollen grains per flower. Additionally, Vasek et al. (1987) suggested that higher nutrient levels in the soil resulted in the development of higher number of flowers and also advanced the flowering period of the plants.

Apart from the impact of weather on the availability of pollen and nectar, critical is its influence on the honeydew-producing insects, since honeydew is a significant food source for honeybees, highly affecting honey production. The honeydew producers, mainly Coccoidea or Aphidoidea, are insects with highly modified mouthparts and digestive system (Kunkel, 1997). They produce droplets of honeydew as they feed from the phloem sap of mainly forest trees. Specifically, for pines (*Pinus* spp.), the main honeydew producing insect is *Marchalina hellenica* (Hemiptera: Coccoidea, Marchalinidae). Honeydew honey is the final product of a biological system, elements of which are: the tree, the honeydew insect, the honeybee, the beekeeper and the unpredictable factor, which affects all previous i.e. the weather conditions (Gounari, 2010). In Greece, honeydew pinehoney represents more than 60% of the country's annual honey production (Thrasylvoulou and Manikis, 1995). More specifically, the honey production of the island of Rhodes is characterized as pine honeydew honey with a percentage of about 20-30% nectar honey, depending of the year (Moschidis et al., 2019). Consequently, adverse weather conditions are expected to impact honey production by affecting honeybees' behavior, the phenology and the sap flow of trees, and the behavior and phenology of the honeydew-producing insects.

Aim of the present work is to study the impact of the weather in a small island in the eastern Mediterrane-

an basin, on the honeybees' productivity, by assessing a great number of temperature, humidity, wind, and other related biometeorological variables. Such results would be useful for honey production weather-based prediction models and also for assessing the impacts of climate change in the highly vulnerable regions, as are the small islands or the eastern part of the Mediterranean basin.

2. MATERIALS AND METHODS

2.1 Sites description

The island of Rhodes is located in southeastern Greece and is surrounded by the Aegean Sea, part of the east Mediterranean basin. It covers an area of about 1400 km² with altitudes ranging from 0 to 1215 m a.s.l. and a coastline of 220 km. In the north-east and central west part of the island two experimental apiaries were established in the areas of Sianna (36° 9' 58.88" N, 27° 45' 9.02" E) and Kallithies (36° 20' 47.53" N, 28° 10' 23.92" E) depicted in Fig. 1 and an aspect of each site is presented in Fig. 2. The sites are located either inside (Sianna) or quite near (Kallithies) to protected areas of the Natura 2000 network (sites codes: GR4210029, GR4210005, GR4210030). The sites selection was performed considering their importance for beekeeping, due to the enhanced biodiversity and the increased flora richness concerning important plant species in beekeeping, as *Pinus brutia*, *Pistacia lentiscus*, *Coridothymus capitatus*, *Cistus* spp, *Erica verticillata*, *Ceratonia siliqua*, *Satureja Cf thymbra*, *Smilax aspera* L, *Eucalyptus* spp., *Myrtus communis*, *Echium* spp, etc. The nectar produced by these plants along with the honeydew from the pines trees determine both the qualitative and quantitative characteristics of local honey production which, on an annual basis ranges from 200 to 250 tons of exceptional honey, mainly honeydew pine honey with 20-30% of polyflora honey, with distinctive organoleptic characteristics (Moschidis et al, 2019).

The flowering period of the plants and the life-cycle of the honeydew producing insects, control the honey production in the region. In Table 1, the flowering period of the main plant species for honey production in the island of Rhodes is presented (Moschidis et al., 2013). During the cold winter period December-February, the food availability for the bees is reduced, whereas nectar and pollen are abundant in spring and remain available, in smaller quantities in summer and autumn.

The insect *Marchalina hellenica* produces honeydew secretions from late June to late March or April of the next year. The period which honey bees can store honey is from August to November with two pauses, one at the

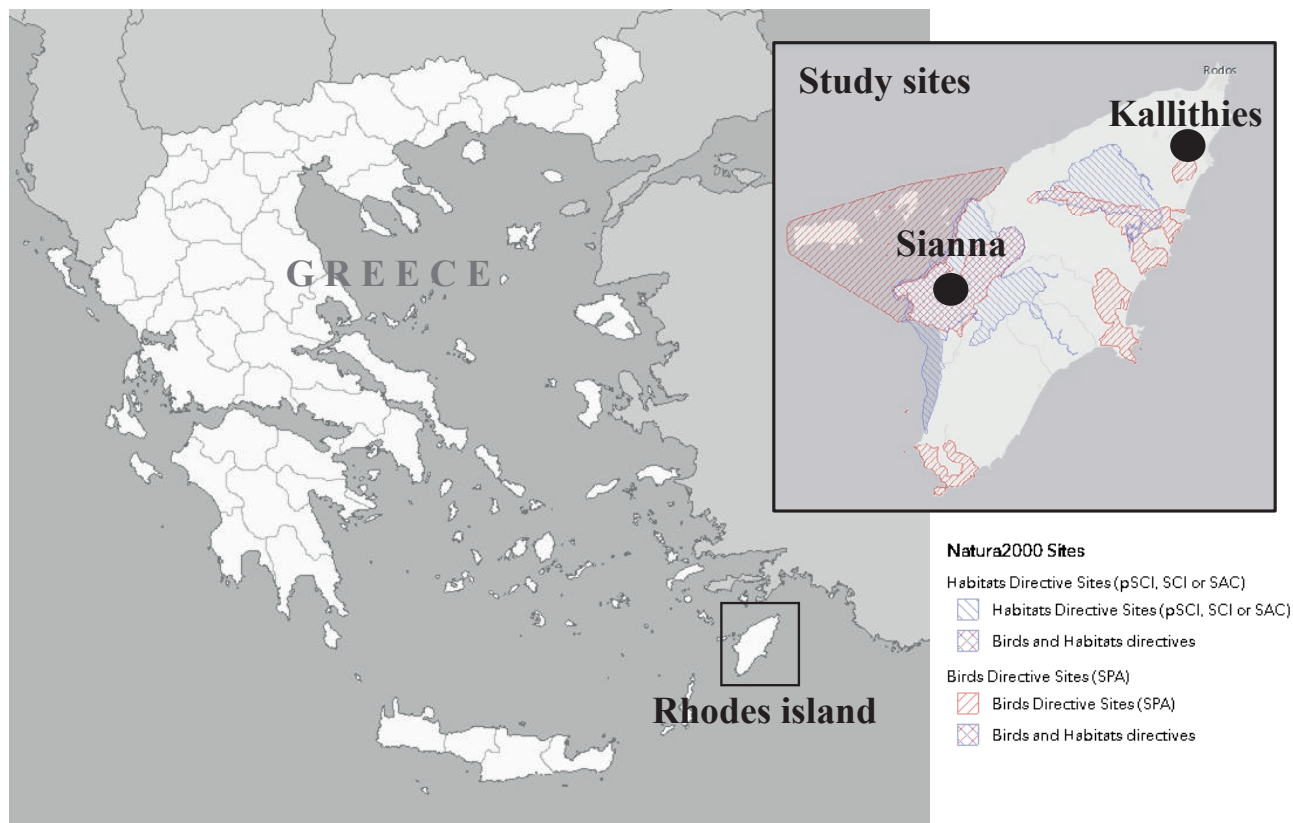


Fig. 1. Sites where apiaries were established on the island of Rhodes. The hives were placed in forest openings inside (Sianna) or near (Kallithies) sites of the Natura 2000 network.

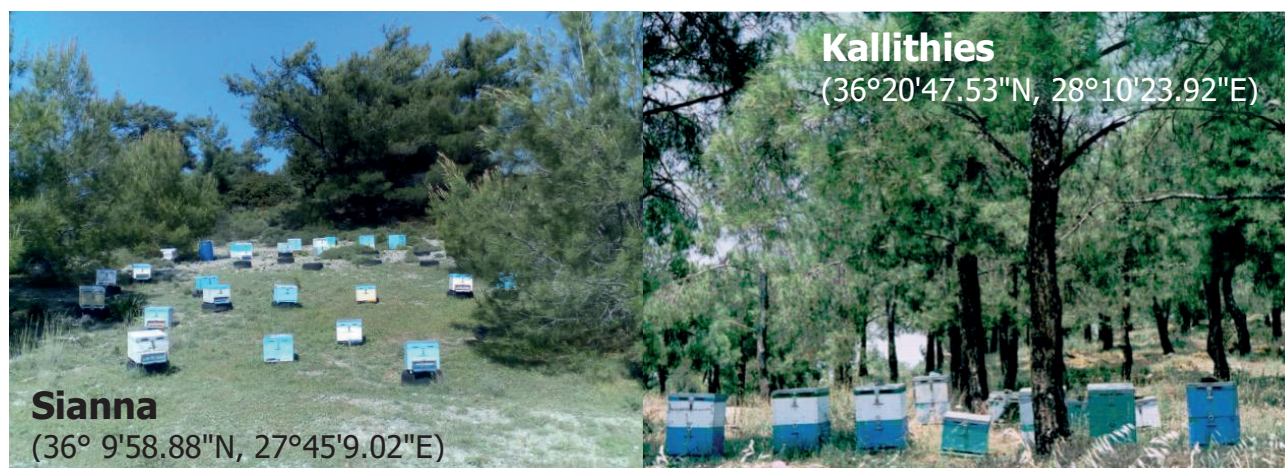


Fig. 2. Aspects of the experimental apiaries in Sianna and Kallithies sites.

end of August and the other at the beginning of October and in spring from late February to the end of March or until the female adult appears. In general, insects' adult appearance and the ovulation time occur from 25 March

– 25 April, depending on the weather conditions. By mid-June all the first stage nymphs are attached to the branches of the pine trees, under the scales, they form colonies and the first honeydew drops appear. The insect

Table 1. Flowering period of the main plant species for honey production in Rhodes island. The period of honeydew production on pines by the insect *Marchalina hellenica* is also presented.

Plant Species	Flowering period (Month)											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Ceratonia siliqua</i>												
<i>Cistus</i> spp.												
<i>Coridothymus capitatus</i>												
<i>Echium</i> spp.												
<i>Erica verticillata</i>												
<i>Eryngium campestre</i>												
<i>Eucalyptus</i> spp.												
<i>Inula viscosa</i>												
<i>Lavandula stoechas</i>												
<i>Lithodora hispidula</i>												
<i>Myrtus communis</i>												
<i>Oxalis pes-caprae</i>												
<i>Pistacia lentiscus</i>												
<i>Satureja Cf thymbra</i>												
<i>Salvia officinalis</i>												
<i>Sinapis arvensis</i>												
<i>Smilax aspera</i>												
<i>Trifolium repens</i>												
<i>Urginea maritima</i>												
<i>Vitex agnus-castus</i>												
Insect	Honeydew production period											
<i>Marchalina hellenica</i>												

hibernates as a 3rd stage nymph, producing honeydew secretions, which honeybees cannot collect during the winter due to bad weather conditions.

The climate of the region is Mediterranean type. Considering the available climatic data, obtained from the local meteorological station which was installed by the Hellenic Meteorological Service (lat. 36° 40' N, long 28° 28' E, alt. 35m), the area belongs to the humid (H) climate zone according to Climatic Zone Classification of UNEP (UNEP, 1992), with Thornthwaite's Aridity Index (AI) values presenting to decrease from 0.77 (during the period 1930-1960) to 0.74 (for the period 1960-1997), indicating that more arid conditions persist nowadays compared to the past (Tsiros et al., 2020). The annual precipitation is 703 mm, unevenly distributed mainly in winter (58.7%) and autumn (23.5%) and less in summer (only 0.4%) and spring (17.4%). In general, the summer months in Rhodes are extremely dry, with August and July being the driest (0.2 and 0.4 mm, respectively).

The annual temperature in the region is 19.1°C, while its average minimum and maximum values are

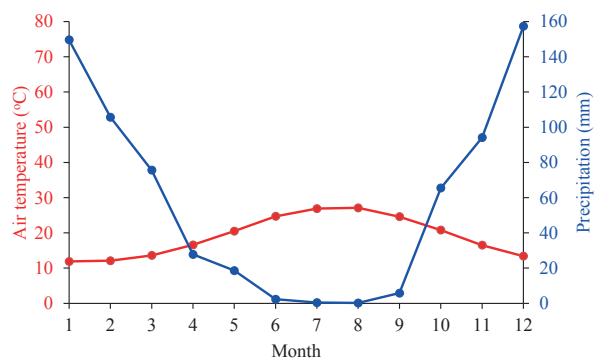


Fig. 3. The Pluvio Diagram for the city of Rhodes derived from meteorological data of the period 1955-2017.

22.5 and 15.2°C, respectively. The seasonal temperature averages vary from 12.5°C in winter to 26.2°C in summer, with intermediate values of 16.9°C and 20.6°C in spring and summer, respectively. The warmer month is August (27.1°C) and the cooler is January (11.9°C). According to the pluvio diagram (Fig. 3), the dry season occurs from mid-April until September.

2.2 Hive productivity data

According to Meikle et al. (2008), the weight of the hive indicates colony size and food reserves. The beehive productivity in the present study was assessed by studying the relative daily mass changes, expressed as percentages of the change of each hive's mass (% or hive's mass daily change per total mass of the hive), of two hives placed in different sites at the north and southwest parts of the Rhodes island. The field experiment was conducted during years 2015 (March to December), 2016 (February to November), 2017 (February to July), 2018 (March to December) and 2019 (January to September). A total number of 894 daily mass records from the first hive and 693 from the second were recorded during the 5-year period, distributed mainly in summer (38.7%) and spring (34.9%) and less in autumn (21.0%) and winter (5.4%). The analysis was performed for the first hive and the second was used for crosschecking the results. From the dataset, all values recorded during hive maintenance for honey extraction works were excluded to avoid inconsistencies.

Commonly in the region, beekeepers transport their beehives into pine forests for pine honey harvest twice a year, in spring (March) and summer (late August). However, for the needs of this study, the hives remained in the same sites throughout the year. In order to ensure that our data are representative, all hives used in this

work had sisters queens and similar brood and population growth characteristics. The usual seasonal manipulations were carried out in the beehives, while the rate of infestation by *Varroa* and *Nosema*, the main diseases of bees in Greece, was also monitored. All beehives were maintained by the same beekeeper, under the supervision of the authors.

2.3 Meteorological data and analysis

Weather data were obtained from the local meteorological station of the Athens National Observatory (36° 24' N, 28° 12' E, elev. 95 m a.s.l., <https://meteosearch.meteo.gr>) which operates on the island of Rhodes since 2012. Specifically, daily values of air temperature T and relative humidity RH attributes (daily average, minimum and maximum), wind speed WS and daily wind gust WS_{gust} , wind direction WD , and precipitation P were used in this study for the years 2015 to 2019. Air humidity-related parameters were also estimated: vapor pressure at saturation e_s , by employing Tetens' (1930) formula (Eq. 1), actual vapor pressure e_a (Eq. 2), and vapor pressure deficit VPD , which is an index for evaluating atmospheric dryness estimated by Eq. 3.

$$e_s = 0.61078 e^{\frac{17.27 T}{237.3+T}} \text{ in kPa} \quad (1)$$

$$e_a = \frac{RH}{100} 0.61078 e^{\frac{17.27 T}{237.3+T}} \text{ in kPa} \quad (2)$$

$$VPD = e_s - e_a \quad (3)$$

Additionally, the diurnal temperature range $DTR = T_{max} - T_{min}$, expressing mainly the temperature range on a daily basis, was also employed.

For assessing the effect weather parameters on the hive productivity, post-processing analysis was performed by grouping the data according to the meteorological parameter each time examined. The values of weather parameters were grouped in appropriate bin classes per 1°C for the temperature T attributes (T_{mean} , T_{min} and T_{max}) and DTR , per 10% for the RH attributes (RH_{mean} , RH_{min} and RH_{max}), per 0.2 kPa for the e_s , e_a and VPD , per 1 km/h for average wind speed (WS), per 5 km/h for gust windspeed (WS_{gust}) and 16 wind direction classes (WD).

Correlation analysis was additionally performed to identify the relations between beehive productivity and weather variables. For this purpose, the Pearson's correlation coefficient was calculated and the significance levels were determined. Pearson's correlation coefficient is a parametric measure of the strength and direction of the linear relationship between paired

values of continuous variables. Its values are dimensionless and range between -1 and +1. The negative or positive values of the coefficient indicate respectively a negative or positive relationship between the examined variables, whereas its absolute magnitude shows the strength of the linear relationship (Yeager, 2021). The IBM SPSS Statistics software package was used for conducting the statistical analysis (<https://www.ibm.com/analytics/spss-statistics-software>).

3. RESULTS

3.1 Prevailing weather conditions

From the analysis of the meteorological data for the period 2015-2019, year 2017 was the cooler and 2019 the warmer in terms of mean, maximum and minimum temperature. Also, 2019 was the wetter year with higher values of mean and maximum relative humidity, less days without rain and extremely higher annual precipitation, though 2018 presented higher minimum relative humidity and actual vapor pressure and lower vapor pressure deficit. The drier year was 2016 with less annual precipitation, increased days without rain and vapor pressure deficit values and reduced relative humidity values (mean, minimum and maximum). However, 2017 presented the lower actual vapor pressure values. Specific annual values of various meteorological and biometeorological parameters for the study years are presented in Table 2.

The meteorological data analysis for the period from April to June, which is the common period with available beehive productivity data among the years of this study, indicates that 2018 (April to June) presented the higher temperatures (22.1°C for T_{mean} , 25.3°C for T_{max} and 19.5°C for T_{min}), vapor pressure deficit (0.785 kPa) and number of dry days (82) and lower precipitation (22.8mm) as well, while in 2015 were recorded the lowest temperatures (19.9°C for T_{mean} , 23.3°C for T_{max} and 17.3°C for T_{min}) but also the lowest mean and minimum relative humidity (69.3% and 54.2%, respectively) and actual vapor pressure (1.65 kPa) values. Year 2019 could be considered as the wetter for the specific period of the year, since it has the higher RH mean and minimum values (71.6% and 57.3% respectively), higher precipitation (94.6mm) and lowest vapor pressure deficit (0.712 kPa) and number of dry days (75).

3.2 Beehive productivity rates and yields

The relative beehive weight changes, in the island of Rhodes, are presented per year and season in Fig. 4.

Table 2. Mean values and standard deviations SD for the meteorological parameters and attributes during years 2015 -2019.

Parameter	2015		2016		2017		2018		2019	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
T _{mean} (°C)	19.5	5.6	19.5	5.6	19.2	5.6	20.2	5.2	19.7	5.4
T _{max} (°C)	22.5	6.1	22.4	6.0	22.0	6.0	22.8	5.6	22.5	5.8
T _{min} (°C)	17.2	5.5	17.2	5.5	17.0	5.4	18.0	5.1	17.4	5.2
DTR (°C)	5.3	1.5	5.2	1.4	5.0	1.3	4.8	1.3	5.1	1.4
RH _{mean} (%)	69.6	9.1	68.9	9.5	70.0	9.4	72.2	8.4	72.3	8.2
RH _{max} (%)	82.6	8.4	82.2	9.2	82.6	8.7	84.4	7.3	85.0	7.0
RH _{min} (%)	56.6	11.5	55.6	11.7	57.5	11.7	60.0	11.2	59.7	11.2
e _s (kPa)	2.39	0.80	2.39	0.79	2.35	0.81	2.47	0.77	2.41	0.79
e _a (kPa)	1.67	0.59	1.66	0.59	1.63	0.55	1.77	0.54	1.73	0.54
VPD (kPa)	0.72	0.33	0.73	0.32	0.71	0.36	0.70	0.34	0.68	0.35
WS (km/h)	7.6	3.4	8.0	3.3	7.9	3.3	8.1	3.3	7.8	3.5
WSgust (km/h)	31.8	10.5	32.8	10.0	31.2	9.5	32.6	10.2	32.2	11.6
Precipitation (mm)	568		316		479		631		1198	
Spring T _{mean} (°C)	16.9	3.2	17.9	2.6	17.1	2.7	19.1	3.3	17.1	2.9
Spring WS (km/h)	7.43	3.30	8.09	3.47	7.51	2.79	8.08	3.36	7.53	3.38
Spring e _s (kPa)	1.95		2.07		1.97		2.25		1.98	
Spring e _a (kPa)	1.36		1.43		1.43		1.61		1.41	
Spring VPD (kPa)	0.59		0.64		0.54		0.64		0.56	
Spring DTR	5.51		5.55		5.33		5.26		5.33	
No of spring days with T _{mean} >20°C	20		19		13		38		16	
No of summer days with T _{mean} >25°C	59		75		71		69		68	
No of summer days with WS>10 km/h	23		44		41		40		27	
No of spring days without rain	67		70		74		79		68	
No of days without rain	287		308		295		287		266	

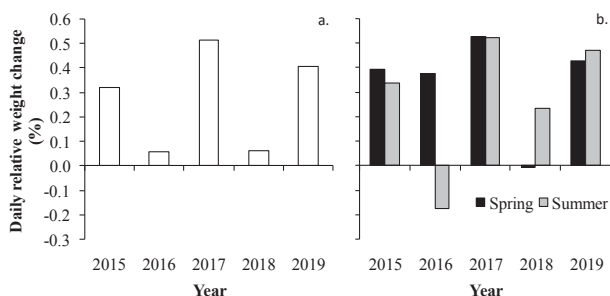


Fig. 4. Relative changes of diurnal beehive productivity (%) during the experimental periods of years 2015, 2016, 2017, 2018 and 2019, derived from (a) all data and (b) spring and summer values.

The productivity in years 2016 and 2018 is reduced and in years 2019 and 2017 increased. Specifically, year 2016 present an intermediate weight gain in spring, whereas in summer it was very low presenting negative average values. On the other hand, year 2018 had a relatively small productivity in summer and it even smaller in spring, presenting almost zero average weight change.

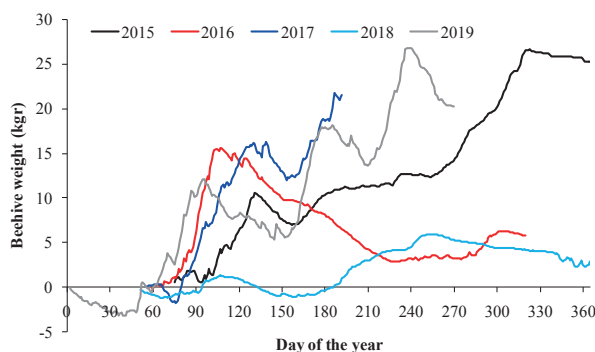


Fig. 5. Cumulative beehive production per day in kgr during the years 2015, 2016, 2017, 2018 and 2019.

The day by day changes of the beehive weight is presented per year in Fig. 5, appear negative rates in winter, starting to increase in early spring. Beehive weight reaches its maximum in spring, at dates that differ from year to year. Thereafter, productivity starts decreasing, until the end of spring or the beginning of summer. During

summer, an increasing rate persists with duration that also depends on the year. The above pattern, generally describes the beehive weight changes for most years. However, it appears that in 2016, the summer increase in productivity was not accomplished. Also, during the spring season of the year 2018, the maximization of beehive productivity didn't reach satisfactory values.

The relatively low productivity, recorded in 2016 is probably associated with the stronger winds prevailing this specific year, during most of the days of the summer period. Compared to the other years, the number of summer days with average windspeeds greater than 10 km/h is much higher, i.e. 44 days, while in other years the respective numbers vary between 23 days (2015) and 41 days (2017). Additionally, during the summer of 2016, the persistence of relative hot days was more common compared to the other years of the study. Specifically, a number of 75 days with daily temperatures greater than 25°C was recorded during the summer of 2016, when the respective values for the other years were much lower ranging from 59 days (2015) to 69 days (2018). It should be also noted that the year 2016 has also the greater number (308 days) of dry days i.e. days without rainfall, while all other years have smaller respective numbers (266-295 days).

The small productivity during the spring of 2018 is probably due to the prevailing warmer weather conditions. More specifically, in the summer of 2018, the average temperature is much higher (19.1°C) compared to the other years (ranging from 16.9°C in 2015 to 17.9°C in 2016). These hot conditions persisted during most of the days of the spring season, since the number of days with $T_{\text{mean}} > 20^\circ\text{C}$ was 38 in 2018, much increased compared to the other years (range from 13 days in 2017 to 20 days in 2015). Additionally, in spring 2018, e_s and VPD were increased (2.25 and 0.64 kPa, respectively) and DTR decreased (5.26°C), whereas the number of days without rain was the highest (79 days).

3.3 Assessing the impact of meteorological factors on beehive productivity

3.3.1 Effect of air temperature and temperature-related attributes

Air temperature appears to affect beehive productivity presenting two optimum values as clearly depicted in Fig. 6. At low temperatures, the diurnal hive production rate takes negative values indicating that the bees consume more honey inside the hive compared to the food collection from outside. The rates remain negative though increasing to about 14°C. Thereafter, the

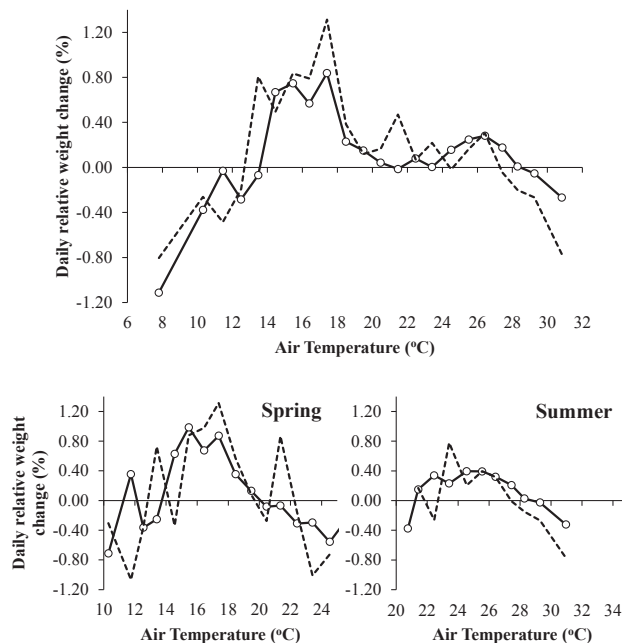


Fig. 6. Relative changes of diurnal beehive productivity (%) under different daily air temperature T values grouped in 1°C bin classes, using annual and seasonal (spring and summer) data. The dashed line presents the respective changes of a second beehive for cross-checking.

increasing pace is sustained and the beehive productivity becomes positive and maximizes (+0.838%) when the daily temperature reaches about 17°C. An additional temperature increase results in productivity reduction, which reaches zero values at about 21°C. As temperatures increase further, the productivity rates remain positive but low, presenting however a minor positive increasing trend. This, results in a second though lower maximum (+0.304%) at temperatures around 26°C. The slightly increasing productivity cannot be sustained in warmer weather conditions. The productivity rates start reducing at temperatures higher than 26°C. For extremely warm conditions (temperatures above 28°C) the productivity becomes negative.

The two optimum values of air temperature for the highest rates in beehive productivity described above appear to have a seasonal connection as also depicted in Fig. 5, where spring and summer changes of beehive productivity are examined in conjunction with the respective daily temperatures. Considering that the double optimum temperatures are related to different seasons (mainly spring and summer), the higher hive productivity appears to be associated with the food availability and more specifically with the availability of nectar and pollen produced by the plants mainly during the

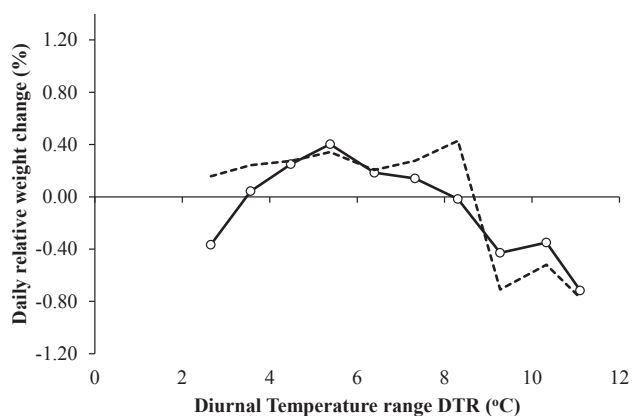


Fig. 7. Changes of diurnal beehive productivity (in kgr/d) under different diurnal temperature range DTR values grouped in 1°C bin classes. The dashed line presents the respective changes of a second beehive used for crosschecking.

spring period and with the availability of honeydew produced by the insect *Marchalina hellenica*. This is in line with the flowering periods of the plants in the region and also with the phenological stages of the insect since in spring most of the plant species on the island are in their flowering stage and also in spring *Marchalina hellenica* adults dominate and produce high quantities of honeydew (Gounari, 2006).

The impact of the diurnal temperature range DTR on the beehive daily production is presented in Fig. 7. In general, DTR expresses the diurnal changes of temperature i.e. the difference between daytime and night temperatures. In many studies, DTR is associated with atmospheric cloudiness, with its higher values indicating clear skies and the lower overcast sky conditions. As depicted in Fig. 7, very low values of DTR (around 3°C) are connected with negative or low positive productivity rates of the hive. As DTR increases, reaching intermediate values (greater than 3°C but lower than 5°C), the beehive productivity becomes positive and increasing, reaching a maximum at DTR=5°C.

At the optimum DTR value of about 5°C, the relative diurnal beehive weight change is maximized to +0.342%. Higher DTR results in diminished but positive productivity rates, which become negative at DTR values greater than 8°C. The negative productivity rates can reach -0.772% when DTR becomes equal to about 11°C.

The pattern mentioned above can be explained by considering DTR as an indirect index of the sky clearness, suggesting that at lower or higher DTR values (overcast or clear skies, respectively), the beehive productivity is reduced, reaching negative to low positive productivity rates.

It should be noted, that the above-mentioned DTR values are rather small compared to other regions, even of the Greek peninsula. This is rather expected for a Mediterranean island, where hot and dry conditions generally persist both during daytime and nighttime. Thus the above thresholds may differ to other e.g. mountainous regions.

3.3.2 Effect of air humidity and other water-related attributes

Relative humidity RH presents a more sound effect on the beehive productivity daily rates, presenting to increase with RH by an average rate of +0.237% change per 10% increase of RH_{mean} . Similar patterns also present the RH_{min} and RH_{max} values but with different changing rates (+0.137% per 10% increase of RH_{min} and +0.242% per 10% increase of RH_{max}), as illustrated in Fig. 8a.

Since RH is an indirect (relative) measure of the humidity content of the air, the actual vapor pressure e_a and the vapor pressure at saturation e_s were also employed to detect the effect of air humidity on beehive productivity (Fig. 8c and d). The hive productivity increases with e_a for values lower than 1.3 kPa present-

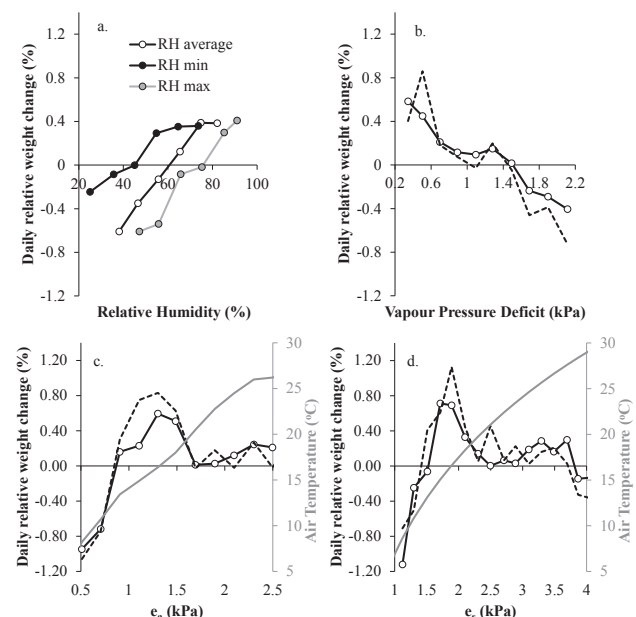


Fig. 8. Relative changes of diurnal beehive production (%) under different daily values of (a) mean, maximum, and minimum relative humidity RH, grouped in 10% bin classes, (b) vapor pressure deficit VPD, (c) actual vapor pressure e_a and (d) saturation vapor pressure e_s , grouped in 0.2 kPa bin classes. The dashed line presents the respective changes of a second beehive and the respective air temperature values are also presented (grey line).

ing, however, negative values at e_a less than 0.8 kPa. The e_a value of 1.3 kPa can be considered as an optimum for beehive productivity rate since at higher e_a values the daily hive production reduces becoming almost zero at very humid weather conditions i.e. for e_a greater than 1.7 kPa. The reduction of the productivity when e_a increases more than 1.3 kPa may be attributed to the higher temperatures (about 17°C) which, as reported above, are connected with decreasing hive productivity.

The pattern mentioned above refers to spring, whereas the respective distribution for all-season data indicates that for e_a values greater than 1.7 (mainly prevailing in summer), does not result in negative productivity rates. This indicates that in summer, other parameters, beyond e_a , may also affect the beehive productivity.

The pattern of e_a is also similar to the respective pattern of e_s as depicted in Fig. 8c, but with different thresholds. Here the optimum e_s value for maximum beehive productivity rates is 1.9 kPa.

A significant variable for assessing atmospheric dryness is the vapor pressure deficit VPD, which expresses the demand of the atmosphere for water vapor and combines the effects of e_a and e_s , (i.e. RH and T). Its effect on the beehive productivity is sound as presented in Fig. 8b. As VPD increases i.e. the atmosphere becomes drier, the diurnal beehive productivity reduces. The reduction occurs with an average rate of +0.507% per kPa. Negative productivity is identified at VPD values greater than 1.5 kPa.

In order to assess the impact of air dryness on beehive productivity, the length of the periods with extremely dry conditions (consecutive days with VPD greater than 1.5 kPa) was also investigated. The results shown in Table 3, indicate that the impact of the persistence of extremely dry days with VPD greater than 1.5 kPa, on beehive productivity, is rapid resulting in negative production rates even if the length of the dry period is only one day.

Table 3. Relative diurnal beehive production changes (%) for different duration of extremely dry periods (number of consecutive days with VPD>1.5 kPa).

Consecutive days with VPD>1.5 kPa	Relative diurnal beehive production (%)					
	Colony 1			Colony 2		
	N	mean	SD	N	mean	SD
1	11	-0.032	0.565	8	-0.160	0.545
2	13	-0.127	0.606	10	-0.123	0.571
3	7	-0.483	0.428	5	-0.623	0.406
4	1	-0.139	0.294			

3.3.3 Wind effect

The wind, in terms of its speed, also appears to affect beehive productivity (Fig. 9), probably because strong winds can affect the bees' flights. Daily average windspeed values lower than 7 km/h seems to favor the productivity of the hive. At such wind conditions the productivity rates are maximized (average rate +0.372%). As winds become stronger, the productivity rates appear to reduce with a pace of -0.080% per 1 km/h increase of the daily average windspeed values. Notably, beehive productivity becomes negative only at very high windspeeds (above 14 km/h), suggesting that only under extremely strong winds, the bees stop flying and remain inside the hive. Similarly, is the pattern for the maximum daily windspeed (Fig. 9b). Wind gust greater than 40 km/h is associated with zero productivity, which becomes negative as maximum windspeed increases.

Wind direction does not appear to have a direct effect on beehive production (Fig. 10). Its rather increased values, identified under NNE and SSE winds, whereas at NNW and E winds the productivity is minimized.

3.4 Correlations between beehive productivity and meteorological variables

To further the significance and the impact of the temperature and temperature-related parameters, a correlation analysis was performed by employing Pearson correlation coefficient r . The respective r values and their significance from the correlation between the relative daily weight changes of the two beehives and the different meteorological temperature-related variables are presented in Table 4.

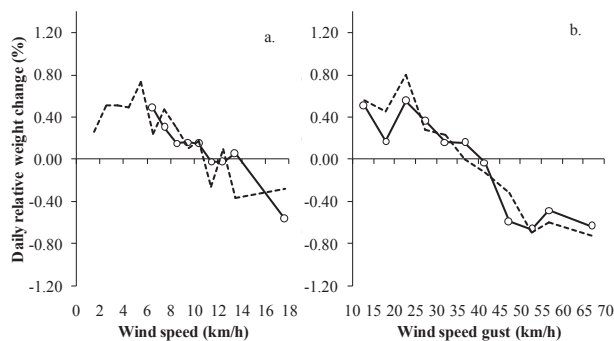


Fig. 9. Relative changes of diurnal beehive production (%) under different daily average (a) and gust (b) wind speed WS values grouped in 1 km/h and 5 km/h bin classes, respectively. The dashed line presents the respective changes of a second beehive for cross-checking.

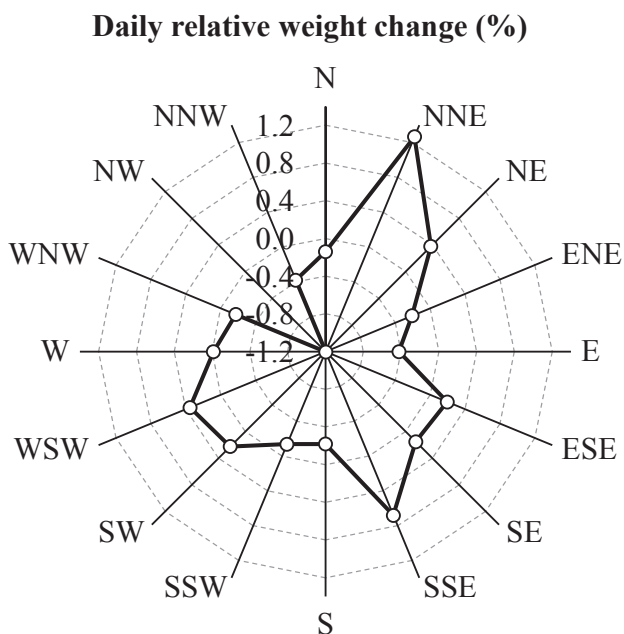


Fig. 10. Changes of diurnal honey production (in kgr/d) under different wind directions.

From the analysis of data from the two hives, significant negative correlations are identified between beehive productivity and all temperature attributes (T_{mean} ,

T_{max} , and T_{min}), indicating the strong influence of temperature. More specifically T_{mean} is significantly related to hive productivity both on an annual basis ($r=-0.135$, $p<0.01$) and for all seasons ($r=-0.232$, $p<0.01$ for spring, $r=-0.118$, $p<0.05$ for summer; $r=-0.253$, $p<0.01$), except winter. T_{max} plays a significant role mainly in spring ($r=-0.212$, $p<0.01$) and summer ($r=-0.146$, $p<0.01$), negatively affecting annual production ($r=-0.130$, $p<0.01$), whereas T_{min} effect is significant and negative only in spring ($r=-0.229$, $p<0.01$), affecting also the annual productivity ($r=-0.128$, $p<0.01$). DTR effect on beehive productivity is negative and strong ($r=-0.169$, $p<0.01$) during summer, however not affecting annual productivity.

The duration of hot conditions, expressed by the number of consecutive days with temperatures greater than 20°C, present a strong negative correlation with beehive productivity during the transitional seasons of spring ($r=-0.194$, $p<0.01$) and autumn ($r=-0.242$, $p<0.01$), affecting also the total annual production ($r=-0.119$, $p<0.01$).

Relative humidity (RH) mean, maximum and minimum attributes are positively related to beehive productivity on an annual basis with high significant levels ($p<0.01$) as presented in Table 5. The seasonal values show strong positive correlations in spring and summer. The e_s values present a strong negative correlation with the beehive productivity for all seasons, except winter, whereas VPD presents similar results. The e_a is negatively correlated with productivity in autumn but positively

Table 4. Pearson correlation coefficients (r), number of values (N), and significance levels from the correlation between the relative daily weight changes of the two beehives and the meteorological variables of the mean (T_{mean}), maximum (T_{max}), and minimum (T_{min}) temperature, diurnal temperature range (DTR), and number of cold days with $T_{mean}>20$ °C, on an annual and seasonal basis.

Variable	Hive No	Annual		Spring		Summer		Autumn		Winter	
		N	r	N	r	N	r	N	r	N	r
T_{mean} (°C)	all	894	-0.135**	312	-0.232**	346	-0.118*	188	-0.253**	48	0.207
	1	807	-0.086*	289	-0.232**	302	-0.066	171	-0.119	45	0.262
	2	452	-0.147**	150	-0.145	184	-0.181*	86	-0.321**	32	0.331
T_{max} (°C)	all	894	-0.130**	312	-0.212**	346	-0.146**	188	-0.227**	48	0.226
	1	807	-0.085*	289	-0.222**	302	-0.096	171	-0.098	45	0.318*
	2	452	-0.138**	150	-0.118	184	-0.174*	86	-0.302**	32	0.335
T_{min} (°C)	all	894	-0.128**	312	-0.229**	346	-0.056	188	-0.239**	48	0.188
	1	807	-0.079*	289	-0.227**	302	-0.003	171	-0.113	45	0.223
	2	452	-0.139**	150	-0.126	184	-0.155*	86	-0.290**	32	0.329
DTR (°C)	all	894	-0.052	312	-0.059	346	-0.169**	188	-0.042	48	0.144
	1	807	-0.050	289	-0.087	302	-0.158**	171	0.007	45	0.302*
	2	452	-0.051	150	-0.045	184	-0.094	86	-0.163	32	0.052
No c.d. $T>20$ °C (days)	all	894	-0.119**	312	-0.194**	346	-0.011	188	-0.242**	na	na
	1	807	-0.085*	289	-0.173**	302	0.002	171	-0.171*	na	na
	2	452	-0.118*	150	-0.168*	184	-0.007	86	-0.133	na	na

*Correlation is significant at the 0.05 level. **Correlation is significant at the 0.01 level.

Table 5. Pearson correlation coefficients (r), number of values (N), and significance levels from the correlation between the relative daily weight changes of the two beehives and the meteorological variables of the mean (RH_{mean}), maximum (RH_{max}), and minimum (RH_{min}) relative humidity, actual (e_s), and saturation (e_s) vapor pressure, and vapor pressure deficit (VPD), on an annual and seasonal basis.

Variable	Hive No	Annual		Spring		Summer		Autumn		Winter	
		N	r	N	r	N	r	N	r	N	r
RH _{mean} (%)	all	894	0.186**	312	0.212**	346	0.227**	188	0.044	48	0.192
	1	807	0.201**	289	0.259**	302	0.174**	171	0.026	45	0.241
	2	452	0.182**	150	0.194*	184	0.236**	86	0.073	32	0.262
RH _{max} (%)	all	894	0.196**	312	0.239**	346	0.174**	188	0.048	48	0.199
	1	807	0.204**	289	0.255**	302	0.150**	171	0.036	45	0.241
	2	452	0.195**	150	0.227**	184	0.203**	86	0.078	32	0.243
RH _{min} (%)	all	894	0.148**	312	0.158**	346	0.226**	188	0.035	48	0.156
	1	807	0.166**	289	0.218**	302	0.163**	171	0.015	45	0.215
	2	452	0.139**	150	0.129	184	0.221**	86	0.060	32	0.233
e _s (kPa)	all	894	-0.139**	312	-0.250**	346	-0.125*	188	-0.263**	48	0.186
	1	807	-0.090*	289	-0.250**	302	-0.075	171	-0.125	45	0.244
	2	452	-0.160**	150	-0.166*	184	-0.187*	86	-0.335**	32	0.315
e _a (kPa)	all	894	-0.055	312	-0.102	346	0.110*	188	-0.166*	48	0.200
	1	807	-0.005	289	-0.078	302	0.105	171	-0.072	45	0.267
	2	452	-0.079	150	-0.029	184	0.061	86	-0.189	32	0.309
VPD (kPa)	all	894	-0.207**	312	-0.292**	346	-0.221**	188	-0.199**	48	-0.070
	1	807	-0.181**	289	-0.325**	302	-0.169**	171	-0.107	45	-0.102
	2	452	-0.221**	150	-0.252**	184	-0.241**	86	-0.237*	32	-0.092

*Correlation is significant at the 0.05 level. **Correlation is significant at the 0.01 level.

Table 6. Pearson correlation coefficients (r), number of values (N), and significance levels from the correlation between the relative daily weight changes of the two beehives and the meteorological variables of average (WS) and maximum (WSgust) windspeed, on an annual and seasonal basis.

Variable	Hive No	Annual		Spring		Summer		Autumn		Winter	
		N	r	N	r	N	r	N	r	N	r
WS	all	894	-0.162**	312	-0.250**	346	-0.031	188	-0.131	48	-0.295*
	1	807	-0.179**	289	-0.319**	302	-0.047	171	-0.095	45	-0.316*
	2	452	-0.168**	150	-0.177*	184	-0.086	86	-0.047	32	-0.383*
WSgust	all	894	-0.174**	312	-0.244**	346	0.005	188	-0.193**	48	-0.313*
	1	807	-0.199**	289	-0.302**	302	0.009	171	-0.179*	45	-0.400**
	2	452	-0.176**	150	-0.187*	184	-0.105	86	-0.038	32	-0.407*

*Correlation is significant at the 0.05 level. **Correlation is significant at the 0.01 level.

in summer, indicating that increased water content in the atmosphere results in increased productivity in summer and decreased productivity in autumn.

Spring and winter average and maximum windspeeds are strongly and negatively correlated with beehive productivity, affecting also the annual production of the hives as indicated by the respective values of the Pearson correlation factor (Table 6).

4. DISCUSSION

The microenvironment inside the beehive is strictly regulated. This implies that the honeybees dedicate much of their effort and energy to regulate beehive's narrow-ranged micrometeorological conditions (Ellis, 2009). Outside the hive, foraging can occur between a wide temperature range from 10 to 40°C (Abou-Shaara,

2014). At lower temperatures, bees reduce the foraging trips (Joshi and Joshi, 2010), which in general start when the average temperature reaches 6.57°C and are maximized at 20°C (Tan et al., 2012). It is also worth noting that honeybees at high altitudes (above 1,000 m a.s.l.) perform foraging flights to harvest water or pollen, even at ambient temperatures lower than 5°C, according to authors' unpublished research data and field observations in Greece. However, Woyke et al. (2003) mention that 10°C is the threshold for foraging initiation, and the number of foragers increases 10fold at 12°C. Blažytė-Čereškienė et al. (2010) observed the minimum forage activity at 43°C. In the present work, we found an optimum value of the ambient temperature of about 17°C where beehive productivity reaches its maximum rates. On a seasonal basis, average daily temperatures between 14 and 18°C are associated with the highest rates of bee productivity, which is maximized at 17°C. In summer, the respective range is between 22 and 27°C and the optimum summer temperature is 25°C.

The impact of temperature is associated with the food availability and bees' phenology. At low daily temperatures, mainly recorded in winter, early spring and late autumn, the available nectar sources are minimum and used for the development of the brood and for the regulation of the inside beehive temperature in the broodnest. As temperatures increase (during spring) the availability of nectar and pollen enhances, and is mainly used for strengthening the colony. If the weather conditions are not favorable during the spring season, the hive will not be able to exploit the available food (nectar, pollen or honeydew). For example in year 2016, strong winds and dry conditions (reduced precipitation during spring) prevented the increase of the beehive productivity, by shortening the flowering period (diminished pollen and nectar production) and reducing sap flows of pine trees (reduced honeydew production). Similarly, in 2018, the very warm spring had similar effects. At high temperatures (above 17°C), occurring mainly in late spring, summer and early autumn, the availability of food (nectar and pollen production) is diminished since the flowering stages of many plants is completed, whereas the pines sap-flow (honeydew production) is also diminished. Under such conditions and as temperatures increase further (mid-summer), food availability and thus beehive productivity reduces. Short flowering periods of few species are available for the bees, allowing a small increase of the hive productivity at daily temperatures around 25°C (second optimum value).

In our study, the correlation of beehive productivity and temperature is generally, negative and strong on an annual basis and for almost all seasons (except win-

ter) for all temperature attributes examined (average, minimum or maximum daily temperature). It should be stated, however, that, regardless of the general trends, at daily average temperatures lower than 17°C (optimum value) the trends are positive, becoming negative for warmer conditions, indicating the non-linear relationship between temperature and beehive productivity. The negative effect of high temperature is attributed to both the reduction of food (nectar, pollen, honeydew availability) and to changes in the colony phenology and bees' behavior. Łangowska et al. (2017), mention also a strong negative relationship between honey bee spring phenology and temperature, stating also that rising temperatures especially in summer can decrease the first harvest production. Delgado et al. (2012) in the island of Puerto Rico found that temperature seasonality and mean temperature of the wettest quarter of the year have negative effects, whereas precipitation of the wettest month and minimum temperature of the coldest month were positively correlated.

DTR appears to have a strong ($p < 0.01$) negative correlation with beehive productivity and can be explained considering that DTR is related to atmospheric cloudiness and solar radiation fluxes, both acknowledged as significant parameters affecting the photosynthetic activity of the plants and their growth (Gimeno et al., 2012; Gu et al., 2003; Proutsos et al., 2019; Proutsos and Tigkas, 2020). High DTR values (clear sky conditions) usually prevailing in summer are also associated with increased temperatures and VPD values. Under such hot and dry conditions, the honey production is negatively affected probably because the bees will either remain in the hive to regulate its temperature by fanning or have to cope with a food deficit. The low food availability is probably due to the diminished nectar outflow from plants, the reduced activity of the honeydew-producing insects (due to the reduction of the sap flow of the trees) or the inability of bees to collect the honeydew droplets (due to the droplets' dehydration which makes them more compact and not easy to be collected). Lower DTR values (partly overcast skies) are associated with higher precipitation and lower evapotranspiration rates (Easterling et al., 1997) and according to the results of this study, also with increased productivity of the beehive, indicating that cloudy and wet weather enhances bees productivity.

Research studies are indicating that RH has a very weak (Joshi and Joshi, 2010) or negative impact on bees flight activity. Vicens and Bosch (2000) found that the activity of the Africanized honeybees was more intense at relatively low RH (around 43.6%) when associated with hot conditions (air temperatures of about 29.4

$\pm 4.9^{\circ}\text{C}$). In our study, RH (all attributes i.e. average, maximum, and minimum daily values) appears to affect beehive productivity and has a strong positive influence, especially during the productive seasons of spring and summer. This is probably because on Rhodes island the honey productivity is highly influenced by the availability of food and especially honeydew, which is more easily collected by honeybees when RH is increased. Similarly, VPD and e_s , which can also be used as atmospheric dryness indices, also present a strong negative correlation with beehive productivity especially during spring, summer, and autumn.

Windspeed (WS) effect on bee productivity is also evident, presenting a negative correlation, especially in spring. Hive productivity is zero when the daily average (or maximum) WS reaches 14 km/h (or 40 km/h) and becomes negative for even higher values. This may be attributed to the wind effect on bees flying ability or the dehydration of honeydew droplets (that cannot be exploited by the bees), contributing to negative impacts on honey yields. Additionally, when strong winds are associated with increased temperatures (as often recorded in the islands of east Mediterranean), plants as pines reduce their sap-flows (reduction in honeydew production), while others, as thyme, stop the production of nectar. The negative wind effect is also assessed by Lundie (1925), who found a negative linear relationship between wind speed and the number of forages. According to the author, honeybees normally fly with windspeeds 29 and 26 km/h, without and with load respectively and their flying speed can reach 32-34 km/h when agitated (without load), but they cannot carry loads upwind against strong winds (greater than 26 km/h).

5. CONCLUDING REMARKS

Weather conditions impact beehive productivity. In the small Mediterranean island, where the present study was conducted, the daily relative weight changes of the beehive were used as an index for assessing bees' productivity. Temperature and its attributes (i.e. T_{mean} , T_{max} , T_{min} , and DTR) are, in general, negatively related to beehive productivity, presenting strong correlations, especially during summer. T_{mean} and T_{max} have a significant negative influence on the hive weight changes in all seasons except winter, while T_{min} only in spring and autumn.

Beehive positive production rates are recorded for average daily temperatures higher than 14°C . The T_{mean} optimum value is 17°C and is associated with an average daily hives change of $+0.838\%$, achieved mainly in

spring. The summer T_{mean} optimum is 26°C and is associated with an average productivity rate of $+0.303\%$. Very high daily temperatures (above 28°C) are connected with negative hive weight changes. The duration of hot periods (i.e. consecutive days with $T_{\text{mean}} > 20^{\circ}\text{C}$) present also a significant and negative correlation with bees' productivity in spring and autumn.

In summer, the effect of DTR is also strong and negative. High DTR (usually associated with hot and clear sky conditions) reduces the productivity rates, whereas intermediate DTR (usually representing partly overcast days) enhances it. A maximum rate of $+0.342\%$ is achieved when DTR is about 5°C .

RH attributes (RH_{mean} , RH_{max} , and RH_{min}) have a positive strong influence on the hive productivity rates, especially in spring and summer. Also, VPD and e_s have significant negative influence in all seasons except winter. For VPD greater than 1.5 kPa the daily changing rates of beehive weight become negative, while as the length of dry periods (consecutive days with $\text{VPD} > 1.5$ kPa) increases, the productivity rates decrease. Additionally, the productivity rates decrease with windspeed, and present strong correlation in spring and summer.

The general findings of this work can be used to enhance existing knowledge concerning the impact of weather variables on bees' behavior and productivity especially at the microenvironment of a relatively small Mediterranean island, with potential applications to beekeepers scheduling for moving apiaries in order to achieve higher beehive product yields. Also, such information can be meaningful in beehive designing. However, further research is necessary to identify the critical weather variables affecting honey production at local level either directly (honeybees' behavior) or indirectly (vegetation dynamics or behavior of honeydew-producing insects). Additionally, it should be noted that the available data presented in this work (5 years) may be considered sufficient to draw some initial conclusions concerning the short-term impact of the meteorological variables on beehive productivity but longer timeseries are necessary in order to assess the impact of climate on bees behavior, activity and honey production. Within this framework, the findings of this paper are part of an ongoing research project aiming to better understand the impact of critical factors (climate, beekeeping manipulations, honeydew-producing insects bioecology) on honey productivity in Greece. Future research may concern the integration of the present work's results in a forecasting honey production model based on the honeydew harvest, to be used as a tool from beekeepers for increasing honey yields and decreasing beekeeping costs.

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