Review paper

MELLIFEROUS POTENTIAL OF WEEDY HERBACEOUS PLANTS IN CROP FIELDS OF ROMANIA FROM 1949 TO 2012

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A b s t r a c t

Intensive farming systems have led to reduced food availability for honey bees which could be related to their current decline. A global tool is needed in order to assess the melliferous potential of plant species that could be developed as crops or companion plants in such systems. This review is based upon a survey from an extensive dataset collected in Romania over the last sixty years to record the nectar production of 153 weedy species. While there was considerable variation among these plants, we found that the melliferous potential of such large families as the Brassicaceae was low, that of the Apiaceae, Asteraceae and Fabaceae at an intermediate level, and that of the Lamiaceae and Boraginaceae the highest. High nectariferous potential was found to be an important feature of perennial ruderal species. Within the main flowering season, perennials provided much more nectar than annuals. These results could help to develop new agricultural practices more compatible with honey bee colony survival and honey production, as some of these plant species could provide a solution to enable agriculture and beekeeping to coexist in a sustainable way.

Keywords: agricultural habitat, food supply, honey yield, nectar, sugar secretion, weed

INTRODUCTION

A large part of the European honey harvest is derived from the mass flowering of herbaceous crops such as oilseed rape (*Brassica napus*), sunflower (*Helianthus annuus*), lavender (*Lavandula angustifolia*) and coriander (*Coriandrum sativum*). Yet the discontinuous flowering of such crops over the season may result in an inhospitable environment for honey bees in between short periods of abundant resources (Williams, 2002; Decourtye et al., 2011; Requier et al., 2015). Indeed, intensive farming leads to overall low nectar collection over the season with a concomitant reduced honey production and slow development of honey bee colonies, making them more susceptible to stressors (Holzschuh et al., 2007; Bretagnolle & Gaba, 2015; Alaux et al., 2017).

The communities of herbaceous plants in agricultural habitats depend on crop management and agricultural practices. Weedy plant species can interfere with farming activities, but some may play important ecosystem functions (Carvalheiro et al., 2011; Gaba et al., 2017). Indeed, some are melliferous plants that provide an essential component of the food resource for honey bees at the landscape scale (Bretagnolle & Gaba, 2015; Requier et al., 2015). A melliferous plant is defined as a plant that provides resources commonly collected by honey bees and in such amounts that it can provide a honey crop (Crane, 1975). This review will address only floral nectar secretion. This nectar secretion, both from a quantitative and a qualitative standpoint, is driven by environmental and genetic factors

(Davis, 2001; Radhika et al., 2010; Nedić, 2013). Nectar is also heavily dependent upon the intensity of photosynthesis, for instance. However, the stable ranking of the melliferous potential over a large spectrum of species and environmental conditions indicates that intrinsic factors drive a large part of nectar secretion (Jabłoński & Kołtowski, 2002).

Melliferous species have evolved under a wide range of environmental factors, such as climate, soil and biotic factors, and present today a large variability in their value as food supply for honey bees. Their abundance and diversity in agricultural habitats depend on their intrinsic functional traits as well as land-use management. Weedy herbaceous plant communities in agricultural habitats comprise species which are not directly linked with the crop produced and can occur in three vegetation groups: (i) crop plants (feral populations), (ii) segetal weed plants in arable land, (iii) ruderal weed plants in adjacent sites.

There is evidence that the floral diversity and the abundance of weeds plays a key role in agroecosystem regulation as it helps maintain pollination services that are profitable to crop production (Carvalheiro et al., 2011; Denisow & Wrzesień, 2015). Recent surveys have assessed the ability of ecosystems to provide food for pollinators, thanks to the pollen or nectar that some habitats provide (Janssens, Bruneau, & Lebrun, 2006; Jaric et al., 2013; Baude et al., 2016). Melliferous flora can also contribute to wild bee abundance and to crop yields through enhanced floral diversity (Rollin et al., 2013; Hevia et al., 2016). Flowering weeds are heavily foraged by honey bees in semi-natural elements and crops alike (Odoux et al., 2012; Requier et al., 2015), which stresses the importance of mixed habitats in providing resources for the honey bee diet. However, wild flower strip cropping has been shown in orchards not to compete for insect pollination services (Lundin et al., 2017).

The melliferous properties of crops are generally not considered by farmers as a potential source of income and the melliferous properties of weeds are not taken into account either. European public policies encourage schemes for more complex landscape structure in croplands, but results have varied (Wratten et al., 2012). The FAO of the UN has delivered a protocol to assess pollination deficits in crops (Vaissière, Freitas, & Gemmill-Herren, 2011), but references are still needed to compare the ability of plants to provide food for the pollinator fauna.

From this point of view, the melliferous potential is useful to compare plant species. The melliferous potential, also called the 'honey potential', is defined as the theoretical quantity of honey (in kilograms/ha) that could be obtained in the course of a season from one hectare of land covered with the focal plant (Crane, 1975). It is calculated for each plant species based on the sugar amount secreted from individual flowers, the duration of the blooming period and the number of flowers per hectare. Three conditions are assumed: 1) optimal growing conditions for the plants, 2) adequate population of worker honey bees to gather the total amount of nectar secreted, and 3) climatic conditions suitable for honey bee foraging. Although in practice these conditions are rarely fulfilled, the melliferous potential provides a useful basis for taxa comparison (Crane, 1975). Extensive studies have been conducted on some major crops, especially in order to provide some knowledge on the relative attractiveness of different varieties, for example on oilseed rape (Pierre et al., 1999, Ion et al., 2012; Nedić et al., 2013) and sunflower (Frank & Kurnik, 1970; Pham- Delègue et al., 1985; Ion et al., 2012).

In order to help beekeepers, farmers, and land managers, some authors have developed lists with a ranking of the melliferous plants for several decades. These references can be global reviews and useful check lists for the melliferous potential of many species (Crane, 1975; de Wilmars, Bruneau, & Evrard, 1989). Others offer a compilation of species, but do not discuss the values of the melliferous potential they report (Janssens, Bruneau, & Lebrun, 2006). Ricciardelli d'Albore and Intoppa (1978) conducted an exhaustive study to assess melliferous plants all over the Mediterranean basin. As a guiding tool for beekeepers, some data on the melliferous potential are also available in apicultural manuals, but the source of the values reported is generally not provided. Additionally, melliferous potential must not be understood by beekeepers as the real honey harvest, due to the presence of other species in the pollinator community the honey bee belongs to and which consume nectar as well.

Only few authors have carried out extensive measurements of nectar secretion under cropping or gardening conditions that resulted in a solid classification of the melliferous potential of plants in a given context (e.g., Kołtowski (2006) in Poland). In addition, they highlighted the method of measurement and stressed the accuracy of the capillary method (Jabłoński & Szklanowska, 1979). Jabłoński & Kołtowski (2002) showed that the melliferous potential can be similar over a period of forty years for some species. Other surveys also concern some specific phylogenetic or economic groups of plant species, e.g., spontaneous Lamiaceae or medicinal plants in Romania (Ion & Ion, 2007; Bășa et al., 2008). More recently, Baude et al., (2016) assessed the nectar production at a countrywide scale by looking at a large range of species and combining several methods of empirical measurements and calculated estimates.

Many data on the melliferous potential are available in the scientific literature, but few of them deal with a wide range of plants and allow comparison of species under similar environmental conditions. Yet the development of a large database on the melliferous potential recorded over a long time period under natural conditions and over a large range of plant species in the same region still remains a necessary and fundamental basis for the solid assessment of the potential honey production and beekeeping potential of a given area. Indeed, to our knowledge, no study to date has dealt specifically with the large herbaceous plant community found in cropping habitats. Also, the few studies that have addressed these plant taxa have done so with a range of methods. The objective of our survey was to synthesize a large body of data obtained with a standard method to assess the melliferous potential of weedy species depending on i) their botanical traits, and ii) their ecological traits, namely their flowering period, their life cycle, and their habitat to better understand the causes of variability of this potential and identify the most interesting species.

MATERIAL AND METHODS

Acquisition and preparation of the data set

This review is based upon a survey of many studies conducted in Romania over the last sixty years on the melliferous potential of herbaceous species from various habitats. We surveyed data reported within about 1000 publications at the library of the Beekeeping Research and Development Institute in Bucharest (ICDA Bucharest), mainly from former and current scientists from this institute. Excluding the reports without methodological information, we exclusively collected data which were obtained with a common method, i.e., the capillary method. Even though some factors of variation can exist between different measurement sessions (due to, for example, season, stage of flower development, sampling hour, and blooming phenology), we considered these data as suitable for our work, and data accumulated over several generations on various species could be viewed together as a long-term study. In addition, for each species reported, we noted botanical, biological and ecological features (family, biological type and life cycle, preferred habitat, type of inflorescence, flower colour and blooming month) which might be associated with their melliferous potential. To this end, we used the data freely available on the Tela Botanica database (www.tela-botanica.org) and the Apibotanica database (http://apibotanica.inra.fr).

Since original data was generally not accessible, we examined the data from each reference in order to exclude data with a significant author bias (see below). Finally, we kept the data from thirty-eight papers written by nineteen authors and reporting results from 1949 to 2012 on 153 plant species belonging to 28 botanical families. (Fig. 1) (See references in Annex 1). Preliminary analysis upon the 417 available values led to the

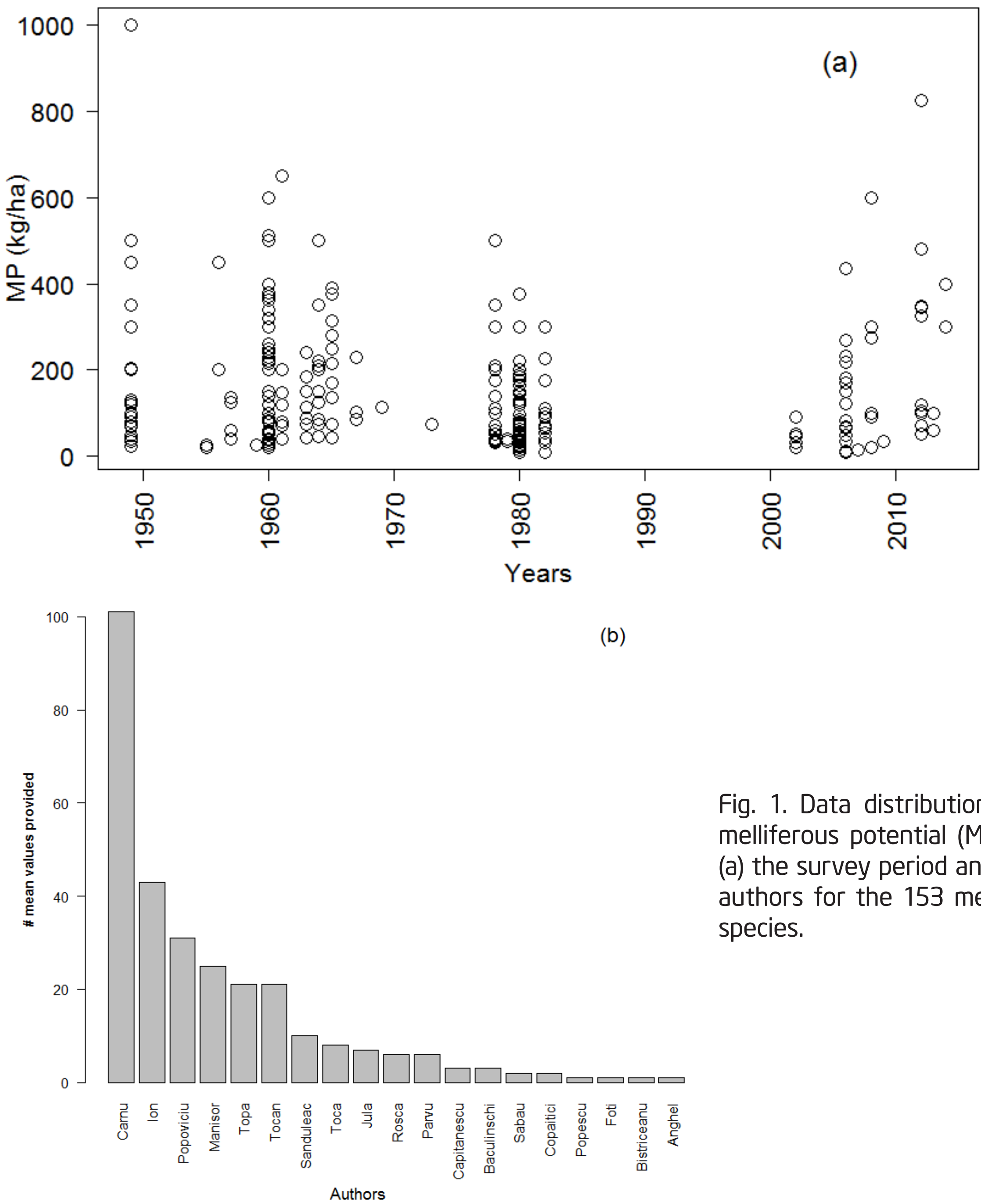

Fig. 1. Data distribution of the melliferous potential (MP) along (a) the survey period and (b) the authors for the 153 melliferous species.

conclusion that there has not been a significant time trend over this long period (lm, $p>0.05$; Fig. 1). It is noteworthy that 52% of the data set were provided by I. Cîrnu, the previous head of the Melliferous Flora Laboratory, who has done a remarkable synthesis of the laboratory works, and the first author of this paper who added and confirmed many former values (217 out of 417 values).

The calculation of the melliferous potential for each botanical species was based on three parameters monitored at the same sampling site: 1) the average sugar mass produced by individual flowers during anthesis; 2) the duration of anthesis, that is the period during which the flowers remained open and foraged (expressed in days); and 3) the flower density, that is the number of open flowers per unit area of land cover (see below).

Different methods are commonly proposed to measure the sugar production of individuals flowers: i) rinsing the nectariferous tissues with distilled water and subsequently measuring its sugar concentration, ii) extracting nectar with

Table 1.
Melliferous potential (MP) of twenty-seven plant families determined from the N data sets recorded in thirty-eight papers ranked by decreasing median values

Botanical family	Number of species studied	number of values	number of references	MP range (kg/ha)	MP median (kg/ha)	MP mean (kg/ha)	Coef-ficient of variation SD
Apocynaceae	1	10	5	94 - 600	430	430	-
Lythraceae	1	5	4	100 - 250	206	206	-
Rutaceae	1	3	2	50 - 119	190	190	-
Lamiaceae	40	122	16	10 - 600	145	160	64.9
Boraginaceae	8	30	11	40 - 1000	137	204	89.7
Plantaginaceae	3	5	3	40 - 140	99	86	48.0
Apiaceae	10	26	9	10 - 500	74	122	90.9
Cucurbitaceae	8	18	6	20 - 230	70	87	70.8
Fabaceae	20	67	15	15 - 500	61	101	86.4
Asteraceae	18	43	16	10 - 500	58	96	99.0
Polygonaceae	3	11	8	20 - 150	56	62	57.1
Amaryllidaceae	2	7	5	10 - 150	53	53	115.0
Geraniaceae	1	1	1	50	50	50	-
Polemoniaceae	1	1	1	50	50	50	-
Resedaceae	2	2	1	50	50	50	-
Brassicaceae	10	30	14	20 - 325	43	64	104.9
Malvaceae	7	13	4	30 - 200	40	66	89.6
Rosaceae	1	2	1	30 - 50	40	40	
Asparagaceae	3	2	2	10 - 30	30	23	49.0
Dipsacaceae	2	2	1	10 - 50	30	30	94.3
Solanaceae	1	2	1	20 - 40	30	30	-
Ranunculaceae	4	5	2	20 - 50	23	29	49.95
Colchicaceae	1	2	1	10 - 20	15	15	-
Iridaceae	1	2	1	10 - 20	15	15	-
Papaveraceae	1	2	1	10 - 20	15	15	-
Liliaceae	1	2	2	10 - 10	10	10	-
Linaceae	1	1	1	10	10	10	-
Portulacaceae	1	1	1	10	10	10	-
28	*153*	*417*	*38*	Total			

Based on a sugar content of 80% for honey (Codex Alimentarius CODEX STAN 12-1981, FAO, Rome), the melliferous potential was then calculated as follows:
Melliferous Potential (MP) =
Sugar mass/flower × anthesis duration × flower density × $0.80^{-1} \times 10^{-6}$
where:
MP is expressed in kg honey/ha;
Sugar mass in nectar per flower and per day is expressed in mg/flower/day;
Duration of anthesis is expressed in days;
Flower density is expressed in number of flowers per ha;
0.80^{-1} represents the conversion factor of sugar in honey;
10^{-6} represents the conversion of milligrams to kilograms.

filter paper, and iii) extracting nectar with glass capillaries. When its use is possible, the capillary method followed by nectar mass weighing (mg/flower) and sugar concentration determination (% weightwise) is the most accurate technique to measure the sugar production of flowers and requires simple equipment, in spite of the precaution to insert a glass tube to reach the nectar glands, and the availability of a well-trained staff (Jabłoński, 2002). Sugar mass production has been considered by many authors as a method of standardization because it provides a common currency in which one can express the nutritional contribution of all plant species (Baude et al., 2016).

The manipulation requires only touching the drop of nectar without breaking the drop apart nor damaging the nectariferous glands. In most studies we used, only one operator performed samplings and a potential operator effect was therefore avoided. In this paper, the nectar collection was performed thanks to a capillary device improved at the ICDA laboratory, with a nectar collecting tube (0.3 mm internal diameter) connected to two inflated bulbs, fitted to an appropriate mouthpiece for suction (Fig. 2 a & b). This device thus combines the capillary force applied first where the collecting tube is applied with a sucking force during the suction process. The pipettes were then weighed on a precision scale to record the amount of nectar (Fig. 2c). The sugar concentration was measured in the field using a hand-held refractometer (0-80% sugar; Fig. 2d). The minimum volume of one nectar sample was such that it made the reading possible when placed on the refractometer stage (5 µL), and so it was sometimes necessary to get the nectar from up to fifty single open flowers or florets (e.g. *Helianthus annuus*) to obtain a measurable amount of nectar (one nectar sample) depending on the species and the volume of nectar per flower (an average of ten flowers or florets including those without available nectar were used). Morphological features of the flower/inflorescence were used to select only fresh-looking flowers and have a complete sampling of the flowers throughout all stages of their period of anthesis.

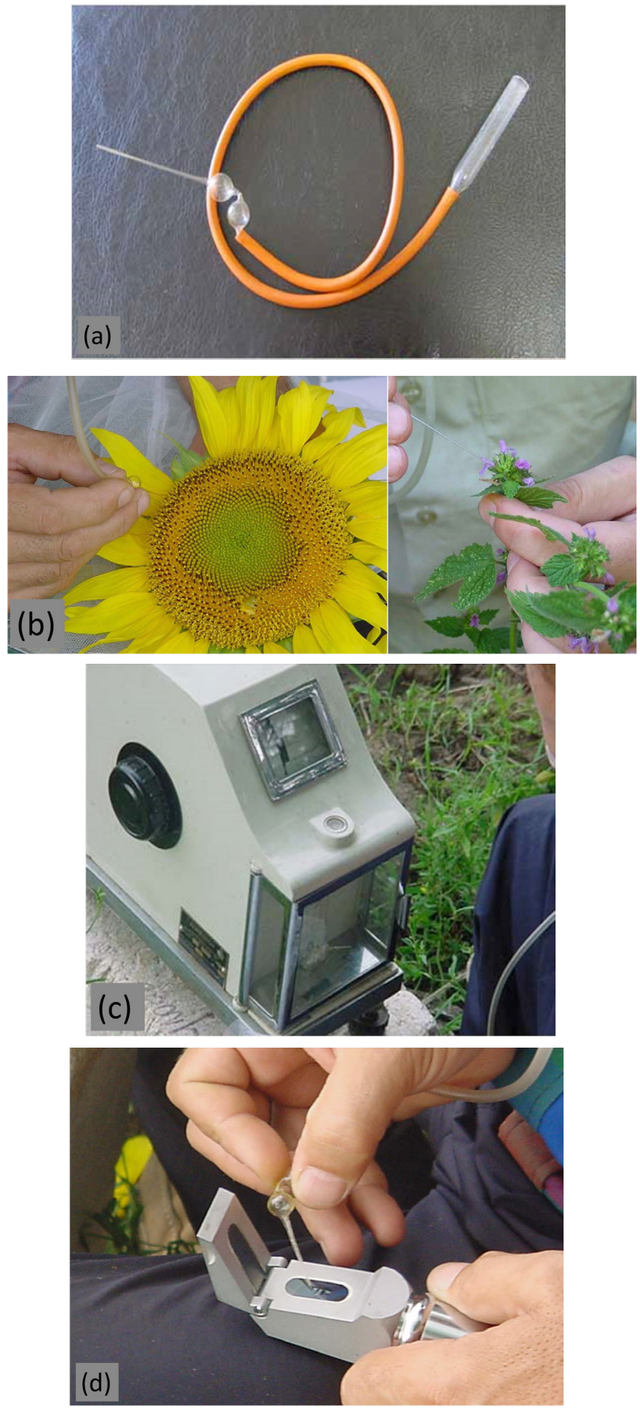

Fig. 2. Illustration of the nectar collection with the capillary pipet of the ICDA: general view of the device (a), nectar aspiration on *Helianthus annuus* and *Lamium purpureum* (b), field balance (c), refractometer (d)

Surveys were not carried out in cultivated stands of cropped plants such as flowerbeds or field strips, but in large populations growing freely, so that the sampled flowers included at the same time all stages of flowers at anthesis available in a given location and on a given date. All flowers (open flowers) were previously bagged for 24 hours prior to nectar sampling to avoid insect foraging (see also Jabłoński & Szklanowska, 1979). Thus, for a given plant species, we did not look at the nectar secretion dynamics of individual flowers over their full period of anthesis by bagging flowers over various length extending to the full duration of this period as done by Jabłoński (2002, Tab. 1). Instead, the protocol used in the studies we selected aimed at assessing the average nectar secretion rate of a given population of flowers, that were sampled based on their relative abundance at the time of sampling in the study site. Thus our approach is more representative of a landscape study at the bee radius level. Indeed, the nectar secretion rate per flower was based on at least ten nectar samples per day which were considered as pseudo-replicates, over a minimum of two days per week, and for as long as permitted by the original area of land with the species under study was flowering. Before nectar sampling, the duration of anthesis was determined. In order to do this, a few buds (n=2-3) were tagged and bagged on different individual plants (n=15 per species). Anthesis duration was measured from bud opening to the first signs of senescence on these tagged flowers (range from 1 to 8 days, as reported in Tab. 1 of Jabłoński (2002).

The density of flowers at anthesis was calculated by multiplying the average number of plants per unit area by the average number of fresh-looking flowers (i.e. at anthesis) per plant. The quadrat method (1m x 1m, evenly spaced along a straight transect) was performed on the whole area in homogeneous habitats, while it was carried out by stratified sampling in heterogeneous habitats. The number of targeted plants was recorded as well as their land cover in % and the number of flowers at anthesis per plant. The output of these calculations gave us the number of flowers at anthesis per ha. Such measurements required almost one day per sampled field.

Statistical analyses

All statistical analyses were performed using R (R-Development-Core-Team 2016). The coefficient of variation (SD = standard deviation / mean) of the melliferous potential was calculated within each botanical family based upon the average value of available honey yields. The trends of MP values were tested using generalized linear models (GLM). F statistics were obtained by ANOVA for groups' homogeneity effects. Families were treated as a random factor using linear mixed-effects models (LME-library nlme) when analysing the effects of ecological and botanical features. Factors were reordered for the corolla colour effect based on 'white' level as an intercept.

From the 417 MP values reported in the corpus of the data we used, we reported both maximum and minimum values, in addition to the mean value that we calculated from the MP figures reported by each author and a range of variation within each family.

RESULTS

Melliferous potential vs. botanical features

The complete list of results for the 153 species is presented in S1-Table1 (on line) and ranged from 10 to 1000 kg honey/ha. We found that the family explained 29.8% of the MP variation ($F=18.93$, $p>0.05$), while the family*species interaction explained 70.7% of this variation ($F=9.70$, $p<0.01$). The distribution of the MP values for the 153 species was skewed and largely dominated by low melliferous potentials (Fig. 3).

Some botanical families were extensively investigated (e.g. Lamiaceae, Fabaceae and Asteraceae), while others were not (e.g., Ranunculaceae, Iridaceae, Geraniaceae). Only one third of the families contain more than one species with numbers ranging from 2 to 40 species per family (Tab. 1). According to the median value, the most nectariferous species belonged to Apocynaceae, Lythraceae and Rutaceae, but these families were represented by only one studied species. The MP had a high SD (90-115%) among species for Brassicaceae, Asteraceae, Apiaceae, Boraginaceae and Malvaceae, while the SD of species of Fabaceae, Cucurbitaceae, Lamiaceae, Polygonaceae and Ranunculaceae was lower (50-86%). Families that contain such top melliferous plants (MP≥300 kg/ha) as Boraginaceae,

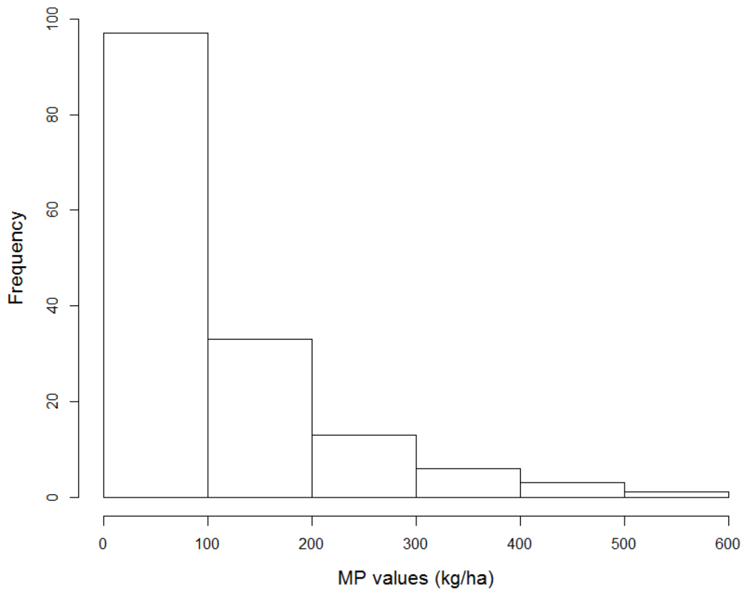

Fig. 3. Distribution of the melliferous potential (MP) for 153 melliferous species

Apiaceae, Fabaceae and Apocynaceae had only one top species, except for Lamiaceae. Indeed, there was no clear link between MP values and particular families, except perhaps for Lamiaceae.

Within the Lamiaceae, Fabaceae and Asteraceae families (18 to 40 studied species per family), several important nectar-producing genera contained many good melliferous species, and some of these have also been intensively surveyed for a long time. For example, *Phacelia tanacetifolia* (Boraginaceae) is a particular case since many data were available from 1949 to 2012 from seven authors, who reported MP ranging from 150 to 1000 kg/ha (S1-Table1). The top-ten plant species were *Phacelia tanacetifolia* (566 kg/ha), *Lavandula angustifolia* (460 kg/ha), *Asclepias syriaca* (430 kg/ha), *Echinops sphaerocephalus* (417 kg/ha), *Salvia officinalis* (380 kg/ha), *Salvia verticillata* (375 kg/ha), *Melilotus albus* (syn. *Trigonella alba*) (333 kg/ha), and *Coriandrum sativum* (324 kg/ha). Large variations in melliferous potentials were detected within botanical families, and sometimes within genera, in particular in the Lamiaceae. From these results, we conclude that the melliferous potential is an intrinsic characteristic of a species with little incidence of the genus or family.

Melliferous potential vs. ecological features

The melliferous potential of ruderal plants was significantly higher than that of crops and segetal weeds ($F=4.211$; $Df_1=2$, $Df_2=149$; $p<0.05$; Fig. 4a), while the number of melliferous species

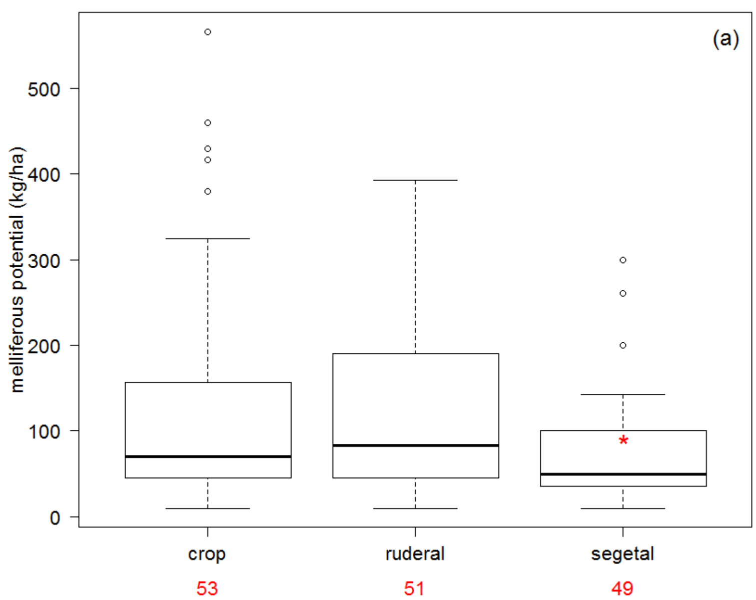

Fig. 4a. Habitat and melliferous potential (MP). Medians are represented by the black thick lines. Numbers in red indicate the number of values for each category. The potential of segetals is significantly lower than that of the two other groups.

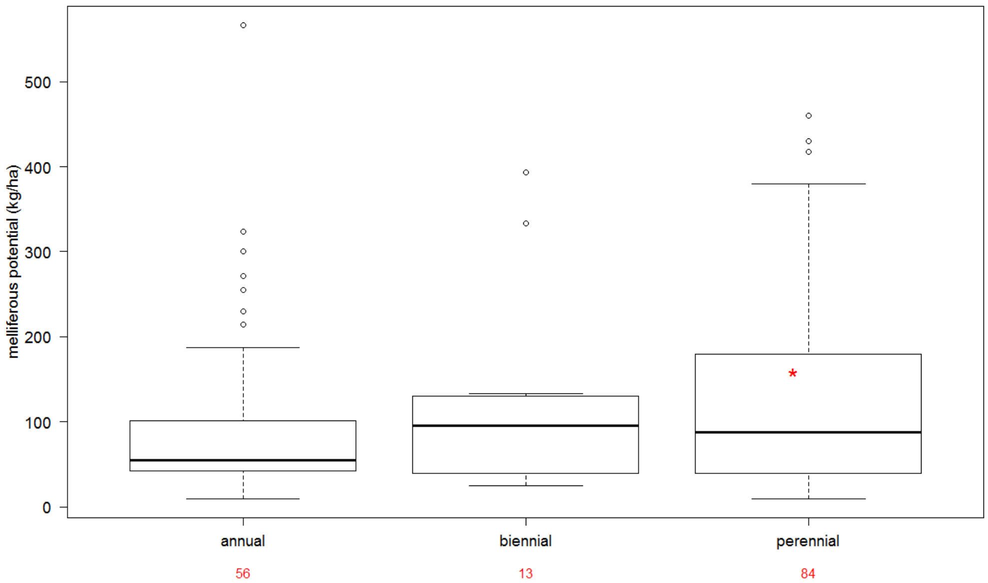

Fig. 4b. Life cycle and melliferous potential (MP). Medians are represented by the thick black lines. Numbers in red indicate the number of values for each category. The potential of perennials is significantly higher than that of the other two groups.

was fairly evenly distributed among all habitats sampled (less so in segetals weed group). High honey output was an important feature for ruderal vegetation, especially for perennial and ruderal. In this group, the most frequent and abundant therophytes were *Salvia pratense*, *Salvia verticillata and Trifolium repens*. With regard to dominant species, the geophytes *Cirsium* sp. is the most common melliferous weed in cultivated areas. More generally in our results, the most melliferous species were represented among the vegetable gardens and crops but had limited potential compared to those from ruderal areas and meadow habitats. There were significant differences in the melliferous potentials between annual and perennial plant species. Indeed, the MP of perennials was significantly higher than that of biennials and annuals ($F=2.306$; $Df_1=2$, $Df_2=149$; $p<0.05$; Fig. 4b). Perennials (55% of the studied species) are widely present in weed communities.

The median MP for the main biological types was as follows (in kg/ha): chamaephyte 237.0, hemitherophyte 120.0, hemicryptophyte 75.5, cryptophyte 63.0, therophyte 53.0. But hemicryptophytes had the highest contribution for the number of studied species (n=76, 47%), followed by therophyte (n=54, 35%). The chamaephyte trait was associated with a significant positive effect of MP while there was a negative effect for therophytes based on LME (153 observations, $p<0.01$). Prominent examples of chamaephytes are generally numerous in Mediterranean dry ecosystems (e.g. *Thymus vulgaris* or *Lavandula angustifolia*).

Melliferous potential vs. flower features

Corolla colours were classified into the blue, pink, violet, white (including a few green ones) and yellow groups. Plant species with pink flower corolla had significantly higher MPs ($p<0.05$). The melliferous potential was also significantly higher for species blooming in the summer than in the spring ($p<0.01$).

DISCUSSION

Our values of melliferous potentials were obtained in southern Romania under natural conditions but vary depending on the environmental and meteorological context. The quantity of sugar produced in the flowers is totally a plant trait that is expressed by the nectar quantity (amount per flower) and quality (sugar concentration). The MP of a plant species in an area at a given time thus depends on edaphic (soil) and weather factors which determine the flower density and the nectar flow. Many of our values are globally similar to those recorded in the literature, but can differ slightly for specific values. We undertook a comparative study with MP values from sixty-five common species obtained in Poland by Kołtowski (2006). His method was close to ours except for the sampling method of the flowers, as he recorded the nectar secretion dynamics of flowers over their whole period of anthesis.

We concluded that our melliferous potentials were lower in our survey by a mean value of -34 kg/ha (paired student t.test, df=64, p-value = 0.06). This difference can be explained by both the environmental conditions and the sampling method. Climatic conditions in southern Romania are warmer than those in Poland. The average of annual temperatures and rains for Bucuresti (44° 25′ N, 26° 06′ E) and Calarasi (44° 12′ N, 27° 20′ E) in Romania are 10.8°C / 598 mm and 11.5°C / 499 mm, respectively, while those in Lublin in Poland (51° 25′ N, 21° 58′ E) are 7.6°C / 540 mm (*https://fr.climate-data.org).* The difference in the sampling method for individual flowers was explained above. Unfortunately, we found few information about the sampling method of the flowers used in the fields in other studies, but we know that the recent ones aimed to get a representative distribution of the flowering stages in a given field just in the studies we used (Ion, 2007; Baude, 2016).

Melliferous potential vs. botanical features

While only few species are significant for honey production, honey plant distribution must be studied for establishing apiaries as well as for a sustainable management in diversified farming habitats. Plants with a melliferous potential over 300 kg honey/ha should be called 'honey plants' because they are particularly suited for honey production, and these include *Phacelia tanacetifolia*, *Lavandula angustifolia*, *Asclepias syriaca*, *Salvia officinalis, Melilotus albus* (syn. *Trigonella alba*), and *Coriandrum sativum*. Conversely, others show a low potential (20 to 50 kg/ha) but can still be important for beekeeping because plants such as *Brassica napus* or *Sinapis* spp are sometimes abundant and have a long blooming period. Among the species under study, those in the Lamiaceae, Boraginaceae and Fabaceae were ranked at a highest level, those in the Apiaceae, Asteraceae and Cucurbitaceae at an intermediate level, and those in such important families as Brassicaceae at the lowest level.

Coriander is the most outstanding melliferous species in the Apiaceae, while others are considered of occasional value, e.g., *Foeniculum vulgare* or *Angelica archangelica*. Some taxa have been investigated for secretion biology, e.g. *Angelica sylvestris,* for which the floral nectar production rates can differ between sexual phases (Stpiczyńska, Nepi, & Zych, 2015). Therefore, the lack of studies on the melliferous potential of other species in the Apiaceae is probably linked with their uniformity in their floral appearance, and their 'weak' melliferous potential probably hides a very large variability (10 to 500 kg/ha).

The family Brassicaceae illustrates a particularity as it shows a low potential in all genera studied except for a single species in one genera: A high value of 325 kg/ha was reported for oilseed rape, while the melliferous potential of other *Brassica* species reached only around 50 kg/ha. The crop varieties from past decades gave rise to new genotypes of oilseed rape and confirm the strong influence of genetic factor on the melliferous potential.

Our results classify species in the Lamiaceae family as having a high melliferous potential, reinforced by a medium coefficient of variation and could set this group among the best candidates for honey crops. Among forty-three studied species of Lamiaceae, *Salvia*, *Mentha* and *Stachys* represent the largest genera. *Salvia* is the genus with the highest honey potential (over 600 kg/ha), while *Mentha* and *Stachys* have medium values (around 200 kg/ha), and other genera have low values (under 100 kg/ha). This family includes 'honey species' with very different biological types from xerophytes (e.g. *Salvia pratensis*, *Lavandula sp*., *Thymus vulgaris*), to hygrophytes (e.g. *Mentha aquatica, Mentha pulegium, Stachys palustris*). Such a large infra-generic variation was not found in other families.

The Asteraceae species in our corpus generally did not present a high MP value, except for *Echinops, Taraxacum,* and *Cirsium* spp. However, this group must be considered in any agro-environmental scheme due to its large diversity of taxa and its status as the most important source of honey in the world (Crane, 1975). With a melliferous potential low and similar to that of other Heliantheae representatives, sunflower confirms that its honey potential results mainly from the extent of its surface rather than by an especially high level of nectar secretion.
The Fabaceae family includes a large number of melliferous species used in bee-friendly farming and their relationships with pollinators are traditionally well-known by farmers and beekeepers. Two of them, *Melilotus alba* (syn. *Trigonella alba*) and *Trifolium repens* belong to our ten best honey plants, having a potential assessed at up to 500 kg/ha. While not having a very high potential (27 to 100 kg/ha), crops of the Cucurbitaceae have to be considered in an agronomic system as a diversified source of nectar for bees communities over the summer months.

Melliferous potential vs. ecological features

Two major results of our study are the higher melliferous potential of perennial species on one hand, and of ruderal species on the other. Many plants belong to both and this effect was also recently concluded in urban area for perennials by Hicks et al. (2016), who suggested that they may have a better capacity to use some water resources to produce elaborated sap. We did not find any other relationships between melliferous potential and ecological features, perhaps because of discontinuous characterisation. The extended growing season and a long duration of flowering seem to be major attributes of perennial and ruderal species in contrast to annual and segetal species, adapted to grow in crop habitats. Many ruderals are opportunistic and will bloom whenever it is warm and wet enough, from April through September, and even sometimes in the middle of autumn. Ruderal species have been duly documented by Denisow & Wrzesień (2015) to be able to flower for a long period and to have a great adaptability to difficult environments unfit for other species. The high melliferous potential of ruderals can be of particular interest to gain honey yields, and they could be used as elements of natural landscapes to maintain the diversity of honey bee diet in agricultural landscapes. Among them, species such as *Echium vulgare* or *Salvia* sp. could be useful over important areas to increase plant biodiversity in arable land, especially in regions with dry and fragile conditions.
A lower melliferous potential of segetal species was found within all botanical families analysed in our study. Most of them are annual and grow spontaneously in crops, with a life cycle adapted to that of the crop. They bloom at the same time as crops and periodically are suppressed by agricultural practices. Interactions are known between segetals and crops for available resources, and weed abundance can reduce crop yields and induce conflict with farmers (Bretagnolle & Gaba, 2015). In addition, these species have evolved under the constraint of human activity. Some segetals show a moderate potential (100 to 200 kg honey/ha), e.g. *Anchusa officinalis*, *Cynoglossum officinale, Digitalis lanata, Linaria vulgaris, Prunella vulgaris, Symphytum officinale, Trifolium hybridum.* Some species like *Sinapis arvensis* (46 kg/ha) and *Stachys annua* (132 kg /ha) also have short vegetation cycle or early flowering induction and can therefore be good candidates for intercropping.
Differences between annual and perennial species in term of melliferous potential were confirmed for species of the same genera, for example *Lamium*. The yield of annual species (*Lamium amplexicaule* and *Lamium purpureum*: 60 kg /ha for both) is lower than that of the perennial one (*Lamium album:* 132 kg/ha) and their benefit as a valuable resource for bees was confirmed by Denisow & Wrzesień (2015). Annual plants are more sensitive than perennials to temperature conditions at the soil surface, while perennials are probably better able to use resources in deep soil and also have strong roots which accumulate nutritional reserves that enable them to develop a higher floral potential (Grimau et al., 2014; Hicks et al., 2016). In addition, they exhibit such favourable

phenotypic traits as extended growing season and a long duration of flowering. According to Wratten et al. (2012) who discussed the enhancement of the long-term pollinators' fitness, setting melliferous perennial and ruderal species can improve resources for honey bees and the ecosystem services that this enhanced biodiversity can provide.

Melliferous potential vs. flowering features

Our study showed a seasonal effect on the melliferous potential, it being significantly higher for species blooming in the summer than those flowering in the spring. We found that the concentrated period of blooming in the summer is spread especially over the first half of the summer and the majority of plant species that are flowering in this period are excellent melliferous species, such as *Salvia verticillata, Salvia pratensis, Stachys germanica, Stachys palustris, Lavandula angustifolia, Trigonella alba, Melilotus* spp or *Coriandrum sativum*. This result is interesting as the quantity of bee foragers is normally higher in the summer and so the nectar available may therefore be better collected. We can conclude that setting up some summer plants in the cropping landscape may be important to improve nectar resources for bees.

The flower colour also seems to be associated with the melliferous potential level, as the species with white and yellow corollas appear to have a lower melliferous potential than the blue, violet and pink ones (e.g. *Salvia*, *Lavandula*, *Phacelia, Stachys* and most of Boraginaceae). In addition, based on our corpus of data, the melliferous species with certain flower colours bloom at particular times of the year. Arnold et al. (2009) also reported an association between the months of flowering and the colour of flowers when flowers were considered according to human colour, but the succession of flowering colours has been a controversial topic. For example, Robertson (1924) stated that greenish-yellow flower species tend to bloom earlier in the year than those with other colours, while McCann (1986) claimed that spring flowers were most frequently white and late summer flowers more likely to be yellow. Warren & Billington (2005) concluded that there is a significant interaction between the flower colour and the month of flowering, and that yellow, white, and pink/purple flowers are most abundant in early summer, while blue flowers are more or less constant in abundance throughout the flowering season (Arnold et al., 2009). Our data also confirm that plants with pink coloured corollas (found as better nectar producers) appear later in the season than the white and yellow ones, and consequently better honey producers. On the other hand, some authors did not consider that the bees had a preference for the coloured flowers, as Harborne (1982) who wrote that the bees preferred yellow and blue flowers. We also observed the colour distribution within the habitat feature classes, showing more white plants in ruderals and yellow plants in segetals, but these trends were not significant.

We conclude that our results showed some great possible choices in melliferous cropping to improve the diet diversity for honey bees, which is necessary for colony sustainability. The most productive are non-native plants such as *Asclepias* or *Phacelia*. The invasive potential of these plants is related to the good functioning or not of the ecosystem services of the considered territory in addition to farming practices (e.g. with or without crop rotation). It will therefore be prudent not to advise the implementation of such taxa under any environmental conditions.

In addition, our study also shows the limits of use of the melliferous potential assessments. In particular, such crop plants as sunflowers succeed in providing some large honey yields to beekeepers thanks to their widespread availability rather than because of their superior MP. Odoux et al. (2012) and Requier et al. (2015) have focussed on the spatio-temporal variations for the resources available to honey bee colonies in a cereal system, and our results provide data on a wide range of plants available to install in this context. However, according to our results unless they are set up in large areas, annual and segetal species appear here as secondary candidates for bee-friendly cropping systems. Also, it is useful to remember that

the interest of flower planting is not limited to nectar since pollen supply is also essential for bee sustainability. Indeed, Alaux et al. (2017) provided evidence that pollen diet diversity benefits honey bee health through late summer flowering intercrops.
This paper based on 153 herbaceous plants highlights some general trends carried out in the same zone in Europe in spite of a certain long-term review from many various works. High melliferous potential was clearly detected for some botanical species, but the major results are shown for the ruderals and perennials which confirm their best sugar producer position. The colourful corolla flowers stand out as later and higher producers. Many of the top melliferous species are common and good candidates to be cropped in agricultural fields as associated crop, intercrop or fallow. A long-term survey on all these melliferous data was an opportunity allowed by a very large homogeneous dataset that had rarely ben synthetized to our knowledge. This work thus provides or reinforces knowledge on the melliferous potential of many plant species. It is hoped that our results provide some solutions for agronomic innovation, crop diversification, and honey production.

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ANNEX 1 (SEE SM ON LINE)

Corpus of references for building the data set.

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