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Descamps, Charlotte ; Quinet, Muriel ; Jacquemart, Anne-Laure

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The effects of drought on plant–pollinator interactions: What to expect?

Charlotte Descamps*, Muriel Quinet, Anne-Laure Jacquemart

Earth and Life Institute–Agronomy, UCLouvain, Croix du Sud 2, box L7.05.14, 1348, Louvain-la-Neuve, Belgium

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Current predictions suggest that in temperate zones climate change will increase the frequency of extreme events such as summer droughts, leading to deficit in water availability for ecosystems. Plants will more often experience water stress during the spring and summer. The effects of drought on plants in these systems have predominantly been studied in wind-pollinated crop species, focusing on vegetative growth or yield. Although a majority of flowering plants (87 % of all angiosperms) is insect-pollinated, the effects of drought on plant–pollinator interactions are not well studied. However, plant pollination and reproduction phases are highly sensitive to this abiotic stress. At plant individual scale, we hypothesize that drought will alter plant–pollinator interactions via (i) signals or cues for insect visitors (floral display, plant height, number of flowers per plant, flower color, shape and size, olfactory compound quantity and composition) and (ii) floral rewards (nectar volume, total sugar concentration, sugar composition, pollen quantity and chemical composition). In this review, we synthesize evidence related to the effects of drought on floral signals and rewards, and discuss how they may disrupt plant–pollinator relationships.

1. Introduction

Under climate change, extreme climatic events such as droughts are projected to increase in frequency, duration and severity (Dai, 2013; IPCC, 2014; EEA, 2017). In temperate regions, the consequences of water deficit during the peak growing months are particularly unclear, since temperate ecosystems are adapted to regular rainfall throughout the year (Spinoni et al., 2018). In these regions, drought in the spring and summer may be harmful for plant–pollinator systems, since these are crucial periods for the growth and reproduction of both flowering plants and their pollinators (Settele et al., 2016). Drought-induced reductions in productivity during these months are thus a major threat to plant–pollinator interactions (Potts et al., 2010; Brown et al., 2016; Nicholson and Egan, 2020). In this review, we discuss how changes in floral signals and rewards due to drought may affect plant and pollinator reproductive success.

The effects of drought on plant physiology are relatively well studied in cropping systems, due to the importance of crop yields for global food security (Pinheiro and Chaves, 2011; Osakabe et al., 2014; Fahad et al., 2017). Water deficit reduces photosynthetic rate (Pinheiro and Chaves, 2011), leading to a reduction in resources available for investment in reproduction (Lemoine et al., 2013). However, the effects of drought on plant–pollinator interactions are not as well understood. Approximately

75 % of all crop species used for human consumption worldwide require insect pollination (Klein et al., 2007), and the proportion of total agricultural area occupied by insect pollinator-dependent crops has regularly increased from 1961 to 2016 (Aizen et al., 2019). Understanding the impacts of drought on insect-pollinated species and plant–pollinator interactions is an economically important, but drastically overlooked issue. If pollinator decline is a hazard for agricultural productivity, it is not less dangerous for wild plants. This ecosystem service is crucial for biodiversity conservation; pollinators maintain plant communities, through producing fruit and seeds which support a large part of biodiversity and endangered species (Perring and Farrell, 1977; IPBES, 2016). About 78 % of plant species are pollinated by animals in temperate regions (Ollerton et al., 2011), and these animals are largely dominated by insects, especially bees (IPBES, 2016).

Mismatches between plants and their pollinators can occur due to climate change and particularly due to extreme events such as drought (Fig. 1). They are observed in terms of distribution and phenology, causing potential spatial and temporal mismatches (Bartomeus et al., 2011; Pyke et al., 2016; Cohen et al., 2018; reviewed in Forrest, 2015). Changes are also observed in terms of morphology and/or attractiveness between plants and pollinators, causing potential morphological and recognition mismatches, (Miller-Struttman et al., 2015; Descamps et al., 2020; Gérard et al., 2020). At individual level, floral signals such

* Corresponding author.

E-mail address: charlotte.descamps@uclouvain.be (C. Descamps).

as color, shape and scent influence flower attractiveness and can signal the reward status of the flower to a pollinator (Gómez et al., 2008; Knauer and Schiestl, 2015; Delle-Vedove et al., 2017). Rewards consist of nectar, the main sugar source, and pollen, the main source of amino acids, proteins and lipids (Nicolson, 2007; Cane, 2016). All of these floral traits related to attracting and provisioning pollinators can be altered by drought (Byers, 2017). For instance, it has been suggested that indirect effects of climatic changes, such as the modifications of floral signals and rewards due to drought, may be more severe than direct effects on pollinators (Ogilvie et al., 2017; Ropars et al., 2020). Because of the dependency of plants and their pollinators, drought can potentially be harmful for both partners of the interactions, reducing plant and pollinator reproductive success (Fig. 2). In this opinion, we will review the impact of drought on floral traits and rewards and the consequence on plant-pollinators interactions.

2. Methods

Our synthesis focuses exclusively on the reported impacts of drought on floral signals and rewards for insect-pollinated species at plant individual level (Fig. 1). Drought is usually defined by climatology publications as “an abnormal water deficit” (Slette et al., 2019) and an ecological definition of drought is given by Crausbay et al. (2017) as “an episodic deficit in water availability that drives ecosystems beyond thresholds of vulnerability, impacts ecosystem services, and triggers feedbacks in natural and/or human systems”. In our review, we considered drought as a reduction of water availability, which can negatively affect plants and pollinators, causing potentially water stress for both of them. We included in our selection studies which concern variation in water availability (artificially or naturally generated) in order to extract information about the consequences on floral traits and rewards, even if these studies did not refer strictly to drought situations by their episodic character. To select papers which concern “drought” impact, we searched on Scopus (November 2019–April 2020) with these keywords: “drought”, “dry environment”, “soil moisture”, “water availability/reduction/decrease”, “water stress” linking with floral traits and rewards (“floral display”, “flower number”, “flower height”, “flower size/shape/color/scent”, “olfactory compounds”, “VOCs”, “nectar concentration”, “nectar quantity”, “pollen quantity”, “pollen viability”). For consistent comparisons among vegetation types, we limited the analysis

to non-tree species and to insect-pollinated species. We selected papers based on the abstract reading, papers that concern only vegetative parameters or only yield impact were not considered. Our analysis is drawn from 55 papers (Table S1) including drought effects on 99 insect-pollinated species from 26 plant families (Table 1). We discuss the current state of knowledge about drought effects on plant cues, and propose perspectives for future research. A conceptual pathway diagram (Fig. 2) synthesizes the direct and indirect links between drought and reproductive success for both partners, i.e. plants and pollinators.

3. Results

3.1. Results depend on the methods used

We observed a variety of different protocols for measuring the effects of drought in the literature. Most studies quantified drought by measuring soil water content (42 %, Fig. 3A), and most studies were also performed in greenhouses under controlled conditions (64 %, Fig. 3B). Experimental drought varied also in the stress imposition method from, for example, no watering during 5 weeks to moderate watering once a week. Stress intensity may have been too low in cases, which could explain the absence of measurable effects (see Phillips et al., 2018). The intensity of stress is also qualified differently depending on the studies and the studied species. For example, “severe drought” conditions were considered as 30 % soil water content for *Arabidopsis thaliana* (Ma et al., 2014) while soil water content was below 15 % in water stressed plants for *Borago officinalis* (Descamps et al., 2018). Due to the large number of variables involved in experimental drought studies, comparisons across experiments are difficult.

We found that the precise timing of stress application was not systematically specified in studies. Even if all stages of reproductive phase are sensitive to abiotic stress (Prasad et al., 2008), the early stage, bolting and anthesis, are highly sensitive (El Balla et al., 2013). We thus recommend experimental conditions be clearly explained, including the precise timing, phase and duration of stress application. This challenge has been highlighted recently by Slette et al. (2019) and we strongly suggest following its recommendations regarding the information to be mentioned when studying drought effects.

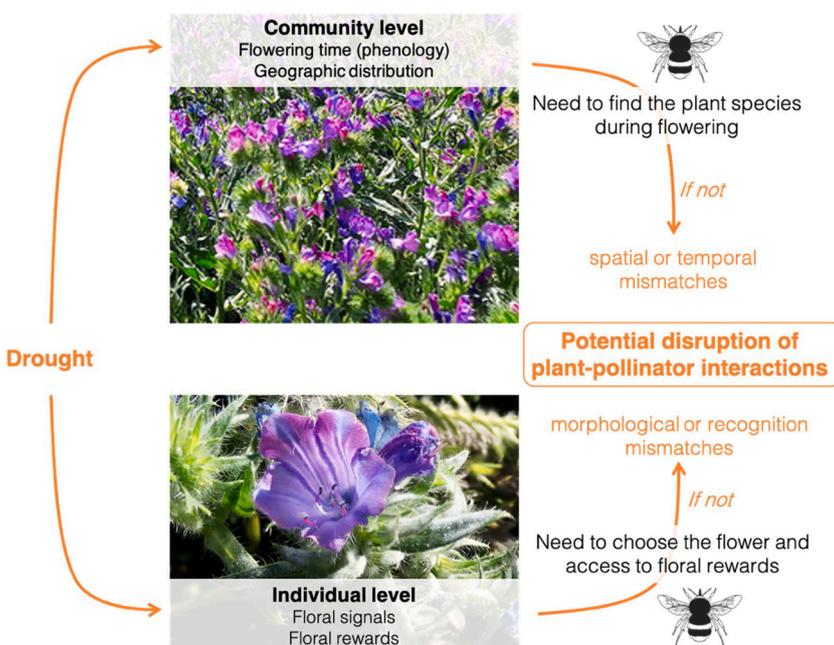


Fig. 1. Potential impacts of drought on plant-pollinator interactions at community level and at plant individual level. At community level, drought may influence flowering time and/or geographic distribution of plant species, which may create temporal and/or spatial mismatches between plant species and insect pollinators if they don't find the plant species in their environment when they emerge in spring or summer. At individual level, drought may influence floral signals and/or rewards, which may create morphological and/or recognition mismatches between plant species and insect pollinators if they change their foraging behavior or if their morphology do not allow them to forage on drought-modified flowers.

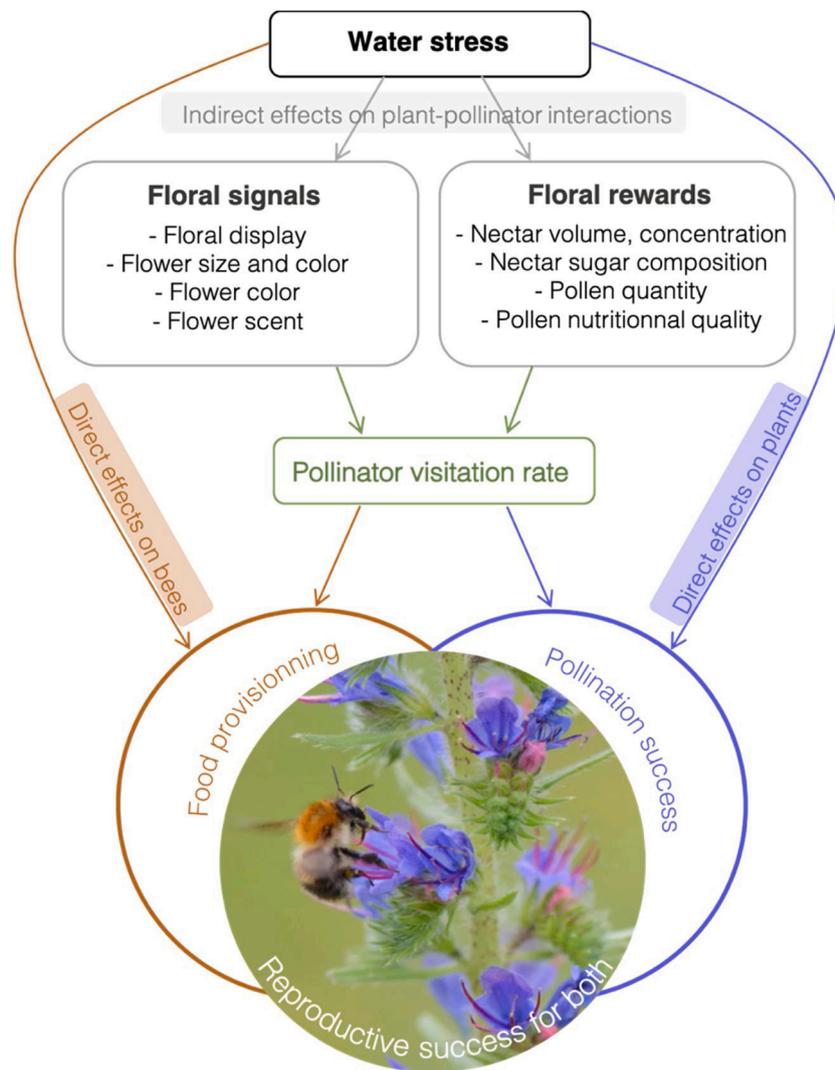


Fig. 2. Path diagram showing direct and indirect links among water stress and reproductive success for both plants and pollinators. Water stress could affect bees and plants both directly (brown and blue arrows) and indirectly through their effects on floral rewards and signals (grey arrows) which has consequences for pollinator visitation rate (green arrows) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

3.2. Changes in floral signals decrease plant attractiveness

3.2.1. Smaller plants with fewer flowers

Floral stem height contributes to floral attractiveness since higher flowers are more visible and accessible than lower flowers (Ouvrard et al., 2018). Plant height is reduced under water stress, in most cases by 10–20 % (Mal and Lovett-Doust, 2005; Kahl et al., 2019), but 2 studies indicate reductions of up to 50 % (Al-Ghazawi et al., 2009; Qaderi et al., 2012, see Table 2). In 4 out of 16 studies, water stress had no effect on plant height (Table 2). However, stress was applied in these cases at the time of flower initiation, after vegetative development was complete. When stress was applied earlier, plant height decreased in both controlled and field conditions. Thus, the effects of drought on stem height depend on the stage of development in which water stress occurs.

Plant height differed between natural populations along a rainfall gradient (Lázaro-Nogal et al., 2015; Lambrecht et al., 2017). For example, flowering stems of *Senna candolleana* (Fabaceae) were 150 cm high in dry sites (approx. 100 mm rainfall per year) and 250 cm in mesic sites (approx. 400 mm rainfall, Lázaro-Nogal et al., 2015). This size decrease along a rainfall gradient can be due to phenotypic plasticity and/or to genetic adaptation resulting from natural selection (Lambrecht et al., 2017). Such reductions in height under drought could be explained by changes in resource allocation. Reductions in shoot/root

ratios can lead to an overall reduction in growth of aerial vegetative and reproductive tissues (Poorter et al., 2012; Eziz et al., 2017). Mechanistically, water stress may also be associated with reduced cell elongation, which explains some of the reduced stem height (Prasad et al., 2008; Gray and Brady, 2016).

In addition to being smaller, plants under drought usually produce fewer flowers. Flower number and density is considered as signal for pollinator attractiveness (Schiestl and Johnson, 2013; Fowler et al., 2016). Drought-related reductions in flowers ranged from 30 to 50% in the studies we reviewed (Table 2). In *Arabidopsis thaliana*, when the water stress was applied over several weeks, an initial slowdown or stop in the rate of new flower formation could be observed, followed by a partial recovery in flower production (Ma et al., 2014). For almost 75 % of the studied species, the total number of flowers produced under drought remained lower than under well-watered conditions (but see Gray and Brady, 2016). Depending on the species, drought also led to high percentages (up to 50 %) of flower abortion (Fang et al., 2010; Guo et al., 2013; Descamps et al., 2018).

Abortion of flower buds or of flowers reduces the maintenance costs and water loss associated with flowers (Galen et al., 1999; Lambrecht and Dawson, 2007). In *Onobrychis viciifolia*, reducing the number of flowers per plant allowed plants to maintain similar per-flower nectar production under drought than under control condition (Phillips et al.,

Table 1

List of family and species covered by the 55 selected studies ; crop species are indicated by an asterisk.

Family	Species
Alliaceae	<i>Allium cepa</i> *
Asclepiadaceae	<i>Asclepias syriaca</i> , <i>A. exaltata</i>
Asteraceae	<i>Achillea millefolium</i> , <i>Chrysanthemum leucanthemum</i> , <i>Dorycnium pentaphyllum</i> , <i>Heterotheca villosa</i> , <i>Hypochoeris radicata</i> , <i>Madia sativa</i>
Balsaminaceae	<i>Impatiens capensis</i> , <i>I. parviflora</i>
Boraginaceae	<i>Borago officinalis</i> , <i>Echium plantagineum</i> , <i>E. vulgare</i> , <i>Mertensia ciliata</i> , <i>Phacelia hastata</i>
Brassicaceae	<i>Arabidopsis thaliana</i> , <i>Brassica napus</i> *, <i>B. rapa</i>
Campanulaceae	<i>Campanula rotundifolia</i>
Calochortaceae	<i>Calochortus subalpinus</i>
Caryophyllaceae	<i>Silene littorea</i> , <i>S. vulgaris</i>
Cistaceae	Many species (N = 37), <i>Helianthemum syriacum</i>
Ericaceae	<i>Calluna vulgaris</i> , <i>Erica multiflora</i>
Euphorbiaceae	<i>Dalechampia scandens</i>
Fabaceae	<i>Chamaecrista fasciculata</i> , <i>Cicer arietinum</i> *, <i>Lathyrus pratensis</i> , <i>Lens culinaris</i> *, <i>Onobrychis vicifolia</i> , <i>Phaseolus vulgaris</i> *, <i>Pisum sativum</i> *, <i>Prunella vulgaris</i> , <i>Senna candollena</i> , <i>Trifolium pratense</i> , <i>T. repens</i> , <i>Trigonella moabitica</i>
Geraniaceae	<i>Pelargonium hortorum</i>
Lamiaceae	<i>Rosmarinus officinalis</i>
Lobeliaceae	<i>Lobelia siphilitica</i>
Lythraceae	<i>Lythrum salicaria</i>
Myrtaceae	<i>Leptospermum scoparium</i>
Onagraceae	<i>Clarkia breweri</i> , <i>C. concinna</i> , <i>Epilobium angustifolium</i>
Phrymaceae	<i>Mimulus guttatus</i> , <i>M. nasutus</i>
Plantaginaceae	<i>Collinsia heterophylla</i> , <i>Globularia alypum</i>
Polemoniaceae	<i>Ipomopsis aggregata</i> , <i>I. longiflora</i> , <i>Leptosiphon androsaceus</i> , <i>Phlox drummondii</i> , <i>Polemonium viscosum</i>
Ranunculaceae	<i>Aquilegia coerulea</i>
Rosaceae	<i>Fragaria virginiana</i> , <i>Potentilla recta</i>
Scrophulariaceae	<i>Scrophularia californica</i>
Solanaceae	<i>Nicotiana quadrivalis</i> *, <i>Solanum lycopersicon</i> *

2018). Four studies did not report any changes in the number of flowers associated with drought (Table 2; Prieto et al., 2008; del Cacho et al., 2013; Gallagher and Campbell, 2017; Phillips et al., 2018). These studies were performed under uncontrolled (field) conditions, which may explain the lack of observed effects. For example, species growing in dry calcareous grasslands could be more adapted to drought conditions than species from well-watered habitats such as wet meadows (Phillips et al., 2018). In another field study on the perennial *Mertensia ciliata*, no difference in the number of flowers was observed between water-stressed and control plots (Gallagher and Campbell, 2017). This result was explained as plants can use previously stored resources to restart spring growth even under drought (Gallagher and Campbell, 2017). In this case, the effects of stress would only be visible after several years of drought. Finally, species-specific differences in flowering time and the water use strategies may also explain these divergent results (Prieto et al., 2008). To our knowledge, there are no long-term studies that track

the effects of drought on floral traits. Such studies may be useful to better understand bee-pollinated species strategies facing drought.

3.2.2. Flower size reduction

Most studies reported a reduction in flower size from 5 % to 60 % due to drought (Table 2). Flower size reduction was often assumed to be related to water stress. However, flower size acts as a visual cue for pollinators; decreasing the size has potential consequences on pollinator visitation rates and on the type of pollinators visiting the flower (bees, syrphids, etc. ; Stanton and Preston, 1988; Gómez et al., 2008, 2020). Galen (1999) highlighted that, under drought, corollas had smaller petals with smaller and more densely packed cells, due to a reduction in cell elongation, than unstressed plants. Smaller corollas need less water to maintain turgor in their cells, improving plant water status. Water loss from evaporation and transpiration is also reduced in smaller corollas compared to larger corollas (Galen et al., 1999; Lambrecht and Dawson, 2007; Teixido and Valladares, 2014).

The evolutionary mechanisms underlying reduced flower size in response to water stress are still under debate for many species. Smaller corollas may be the result of selection in dry habitats (Herrera, 2005; Lambrecht and Dawson, 2007; Lambrecht, 2013) or a product of floral phenotypic plasticity (Carroll et al., 2001; Mal and Lovett-Doust, 2005; Caruso, 2006; Edwards et al., 2012). In dry environments, pollinator-mediated selection has been proposed as the driver for adaptive floral size (Miller, 1981). In this case, floral traits are correlated with the flower visitor type. Herrera (2005), for example, observed that both the proportion of large bees and the size of *Rosmarinus* flowers increased from the coast to the mountains in the Iberian Peninsula along a precipitation gradient. Other authors suggest that reduced flower size is an example of adaptive phenotypic plasticity (Carroll et al., 2001; Mal and Lovett-Doust, 2005; Caruso, 2006; Edwards et al., 2012). Selection can of course occur simultaneously from both pollinators and abiotic factors (Caruso et al., 2019).

Stamens and carpels may also be shortened by drought (Mal and Lovett-Doust, 2005; Edwards et al., 2012; Su et al., 2013; Lambrecht et al., 2017). Drought stress can cause flower deformity (e.g., decreasing petal number) and affect flower morphogenesis (Smith and Zhao, 2016). We hypothesize that these modifications to floral organs may have consequences for fertilization and pollination by insects. For example, a reduced distance between anther and stigma favors self-pollination (Mal and Lovett-Doust, 2005).

3.2.3. Flower color preserved

Although flower size was widely investigated, only 3 studies measured the impact of water availability on flower color (Table 2). Pigments in the flowers are visual signals for attraction of pollinators, and are under selective pressure (Glover, 2011; Borghi et al., 2019). No effects of drought were detected for flower pigmentation in any of the studies, either in controlled conditions for *Pelargonium hortorum*

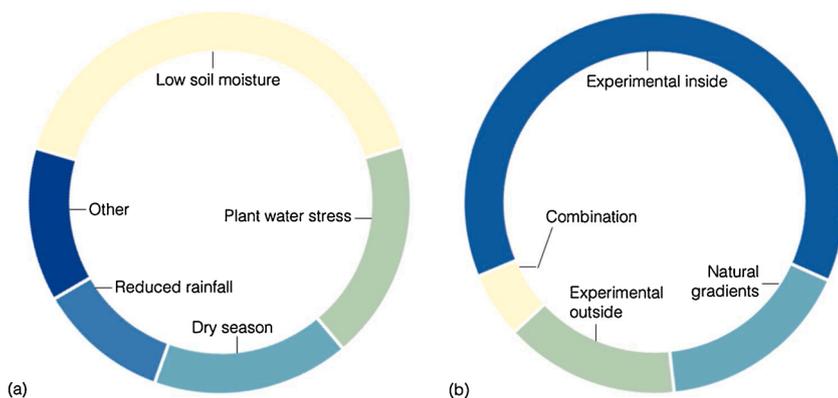


Fig. 3. Diversity of selected water-stress studies (N = 55) in terms of (a) water stress application method according Slette et al. (2019) and (b) experimental setups. (a) Studies quantified water stress mainly by measuring soil water content (low soil moisture, N = 23), to a lesser extent, by analyzing plant water stress, such as measuring the wilting point (N = 10), (3) performing observations in dry seasons with less precipitation (N = 9), reducing rainfall quantity (reduced rainfall, N = 6) or by other method such as calculating index of water stress or for some studies or by describing “dry conditions” without any details (other, N = 7). (b) Studies were performed under controlled conditions in greenhouses (N = 35), or by doing observations along natural gradients, for example, from coastal regions to mountain (N = 9), or by simulating drought events with shelter in natural plant population outside (N = 8), or by combining several setups described above (N = 3).

Table 2

Effect of water stress on floral signals and floral rewards: ☹ decrease; ○ no effect; ☺ increase; ✳ modification; in brackets, the first number indicated the number of studies, the second number indicated the number of species concerned.

Category	Modification	Water stress effect	Reference	
Floral signals	-Floral display	Plant height	☹ (16; 17) (Boutraa and Sanders, 2001; Mal and Lovett-Doust, 2005; Caruso, 2006; Sánchez-Blanco et al., 2009; Al-Ghzawi et al., 2009; Qaderi et al., 2012; Edwards et al., 2012; Quinet et al., 2015; Lázaro-Nogal et al., 2015; Burkle and Runyon, 2016; González et al., 2016; Lambrecht et al., 2017; Glenny et al., 2018; Kahl et al., 2019; Descamps et al., 2020; Walter, 2020)	
			○ (4;6) (Burkle and Runyon, 2016; Descamps et al., 2018, 2020; Glenny et al., 2018)	
		Flower or inflorescence number	☹ (21;25) (Peñuelas et al., 2004; Caruso, 2006; Prieto et al., 2008; Sánchez-Blanco et al., 2009; Al-Ghzawi et al., 2009; Fang et al., 2010; Su et al., 2013; El Balla et al., 2013; del Cacho et al., 2013; Ma et al., 2014; Thomson, 2016; Burkle and Runyon, 2016; González et al., 2016; Descamps et al., 2018; Glenny et al., 2018; Phillips et al., 2018; Kahl et al., 2019; Brunet and Van Etten, 2019; Descamps et al., 2020; Walter, 2020; Suni et al., 2020) // Flower abortion : (Fang et al., 2010; Guo et al., 2013; Descamps et al., 2018)	
			○ (6;9) (Caruso, 2006; Prieto et al., 2008; del Cacho et al., 2013; Gallagher and Campbell, 2017; Glenny et al., 2018; Phillips et al., 2018)	
		Floral longevity	☹ (2;2) (Arathi et al., 2002; Jorgensen and Arathi, 2013)	
	-Flower parameters	Color		○ (2;2) (Sánchez-Blanco et al., 2009; del Valle et al., 2015)
				✳ (1;1) (Brunet and Van Etten, 2019)
		Size of flower or inflorescence		☺ (21;30) (Villarreal and Freeman, 1990; Frazee and Marquis, 1994; Carroll et al., 2001; Mal and Lovett-Doust, 2005; Herrera, 2005; Caruso, 2006; Lambrecht and Dawson, 2007; Halpern et al., 2010; Edwards et al., 2012; El Balla et al., 2013; Guo et al., 2013; Opedal et al., 2016; Burkle and Runyon, 2016; Burkle and Runyon, 2016; González et al., 2016; Gallagher and Campbell, 2017; Lambrecht et al., 2017; Descamps et al., 2018, 2020; Glenny et al., 2018; Mantel and Schweigart, 2019; Brunet and Van Etten, 2019; Suni et al., 2020)
				○ (3;4) (Caruso, 2006; Kay and Picklum, 2013; Walter, 2020)
		VOCs quantity	☺ (3;3) (Burkle and Runyon, 2016; Glenny et al., 2018; Campbell et al., 2019)	
		○ (2;2) (Burkle and Runyon, 2016; Glenny et al., 2018)		
	VOCs composition	✳ (2;4) (Burkle and Runyon, 2016; Campbell et al., 2019)		
Floral rewards	-Nectar	Nectar volume	☹ (10;11) (Villarreal and Freeman, 1990; Wyatt et al., 1992; Carroll et al., 2001; Halpern et al., 2010; Waser and Price, 2016; Gallagher and Campbell, 2017; Descamps et al., 2018, 2020; Brunet and Van Etten, 2019; Suni et al., 2020) // Nectarless flowers : (Phillips et al., 2018)	
				○ (2;4) (Phillips et al., 2018; Descamps et al., 2020)
				☺ (1;1) (Suni et al., 2020)
		Nectar concentration		○ (8;10) (Villarreal and Freeman, 1990; Carroll et al., 2001; Halpern et al., 2010; Gallagher and Campbell, 2017; Descamps et al., 2018, 2020; Phillips et al., 2018; Brunet and Van Etten, 2019)
				☺ (1,1) (Descamps et al., 2020)
				☺ (1,1) (Suni et al., 2020)
		Nectar sugar content per flower		○ (2;2) (Clearwater et al., 2018; Descamps et al., 2020)
				☹ (4;4) (Waser and Price, 2016; Descamps et al., 2018, 2020; Suni et al., 2020)
				○ (2;2) (Villarreal and Freeman, 1990; Clearwater et al., 2018)
-Pollen	Pollen quantity		☹ (1;1) (Waser and Price, 2016)	
			○ (2;2) (Galen, 2000; Descamps et al., 2018)	
	Pollen viability		☹ (5;5) (Turner, 1993; Al-Ghzawi et al., 2009; Fang et al., 2010; Su et al., 2013; Descamps et al., 2018)	
			○ (1;1) (Guo et al., 2013)	

(Sánchez-Blanco et al., 2009) or in the field for *Silene littorea* (del Valle et al., 2015). Brunet and Van Etten (2019) studied three (chroma, hue and reflectivity) color parameters on *Aquilegia coerulea*, but only the reflectivity (total reflected light between 400 and 700 nm) increased under drought. Although leaves frequently accumulate phenolic compounds that can change their color during stress, the color of the flowers tend to be preserved under stress since flower color depends on other pigments such as anthocyanins or carotenoids (van der Kooi et al., 2019). In addition to pigmentation, all the optical properties of flowers (chromatic and achromatic contrast, saturation and brightness, gloss, fluorescence, polarization and iridescence) are involved in visual floral signaling (van der Kooi et al., 2019) and responses of these properties to abiotic stress remain unexplored until now.

3.2.4. Olfactory signal modification

Pollinators may use floral scent constituted by volatile organic compounds (VOCs) emitted by flowers to detect the presence of rewards (Chittka and Raine, 2006; Wright and Schiestl, 2009). More than 1700

VOCs have been detected in flowers (Knudsen et al., 2006). Flower scent may act as long-range attractants compared to visual cues which act as short-range attractants (Raguso, 2008; Hirota et al., 2012; Junker and Parachnowitsch, 2015). The emission of these molecules depends on the rate of their biosynthesis and on their volatility, solubility, and diffusibility (Borghi et al., 2019). Abiotic stress generally increases emission of VOCs (reviewed by Peñuelas and Staudt, 2010, and Farré-Armengol et al., 2013). A small number of studies had investigated changes in floral scent due to abiotic factors. Only three studies, performed on herbaceous plants from North America, explored how soil water content influences VOCs (Table 2). Burkle and Runyon (2016) and Glenny et al. (2018) worked on the same group of species (*Campanula rotundifolia*, *Heterotheca villosa*, *Phacelia hastata*, *Potentilla recta*) and observed that water stress increased the total amount of VOCs produced as well as modified their composition. This was mainly observed for two out of the four tested, *Campanula rotundifolia* and *Potentilla recta*. A shift in the composition of floral volatiles of water-stressed *Ipomopsis aggregata* is observed (Campbell et al., 2019). The floral bouquet of stressed plants

contained more monoterpenes α -pinene and (*E*)- β -ocimene and sesquiterpene (*E,E*)- α -farnesene and less 1,3-octadiene and the benzenoid benzyl alcohol than non-stressed plants. VOCs are produced through different pathways that could respond differentially to drought (Campbell et al., 2019). This study highlighted the non-linear response of floral volatile composition to soil water content (Campbell et al., 2019). Floral VOC composition seems to be more determinant for pollinator attraction than the VOC total quantity (Raguso, 2008; Burkle and Runyon, 2017; Glenny et al., 2018). Studies about the effect of drought on flower scent are still limited.

3.3. Floral rewards are declining, decreasing food supply for pollinators

3.3.1. Nectar volume decreased while nectar concentration and composition were less affected

The two principal components of nectar, water and sugars, are reduced in response to drought (Lemoine et al., 2013; Lamaoui et al., 2018). Drought was generally associated with lower volumes of nectar compared with well-watered plants in the studies we examined (Table 2). Reduced nectar volume could be explained by a shortage in water supply (Wyatt et al., 1992). However, drought did not always result in reduced nectar volume. For example, Phillips et al. (2018) did not observe any reduction of nectar volume per flower for *Lathyrus pratensis*, *Onobrychis viciifolia*, and *Prunella vulgaris* due to drought and attributed this to the plants' conservative growth strategy and overall resistance to drought. Surprisingly, Suni et al. (2020) observed an increase of nectar volume under water stress for some populations of *Phlox drummondii*. They investigated nectar production at several time points in plants across differing precipitation regimes and showed that plants had different nectar production strategies (Suni et al., 2020). Interestingly, plants from drier environments produced more nectar with higher sugar content as a result of water-stressed conditions. By contrast, plants from wetter environments produced less nectar with lower sugar content under water stress (Suni et al., 2020).

The production of nectar under drought may also depend on the reproductive strategy of a species. For example, Phillips et al. (2018) observed nectarless flowers in response to water stress for *L. pratensis* and *P. vulgaris*, which they attributed to these species' capacity for self-pollination. By contrast, *O. viciifolia*, which is an obligate cross-pollinated species that needs to attract pollinators with nectar, did not exhibit nectar reductions. The impact of water stress thus depends on the plant species and may be linked with its breeding system.

The effects of drought on the sugar concentration of nectar and sugar quantity per flower are less obvious than effects on nectar volume. Eight studies reported no significant change in sugar concentration in response to drought (Table 2) although one study found an increase of sugar concentration in nectar of *Echium plantagineum* (Descamps et al., 2020). When considering total nectar sugar quantity per flower (concentration \times volume) there is no consensus in the literature about the impact of water stress. Total sugar quantity in nectar per flower may decrease, increase or remain stable in response to water stress depending on the study (Table 2). Sugar per flower probably depends on photosynthesis, but also plant species, population and experimental design. One study recently examined the effects of drought on nectar sucrose composition and found no effect (Clearwater et al., 2018). However, studies investigating the effect of water stress on sugar composition of nectar are very rare. The associations between nectar quality and abiotic stress are obviously complex and further investigation is required to disentangle drought effects from other factors.

3.3.2. Failures of pollen maturation under water stress

Pollen quantity is determined early in flower development, during microsporogenesis (Goldberg et al., 1993). Drought applied at the beginning of blooming did not seem to affect pollen grain number in the study by Descamps et al. (2018). However, pollen quantity can be reduced if drought is applied earlier. Waser and Price (2016) showed

that pollen production quickly reached an asymptote regarding the availability of water in natural conditions.

Anther and pollen development are the reproductive stages most sensitive to water stress (Smith and Zhao, 2016; Yu et al., 2019). Detailed studies showed that water stress negatively impacts metabolic transport mechanisms of sucrose which reduces the stored starch or lipid in the pollen grain (Borghi et al., 2019). Pollen viability, which may vary from a few minutes to several days according plant species and environmental conditions, may be affected by drought (reviewed by Smith and Zhao, 2016; Pacini and Dolferus, 2019; Bellusci et al., 2010; Borghi et al., 2019). Disruption of pollen development due to drought has been mainly studied in Poaceae species and in *Arabidopsis thaliana* (Koonjul et al., 2005; Li et al., 2015). Studies with other herbaceous species have also found a decrease in pollen viability under drought (Turner, 1993; Al-Ghzawi et al., 2009; Fang et al., 2010; Su et al., 2013; Descamps et al., 2018, Table 2). Only 1 out of the 10 studies we found examining pollen viability did not show effects of drought (Guo et al., 2013). Although the impact of water stress on pollen viability has been extensively investigated, its effect on pollen composition as nutritional resource for pollinators remains largely unknown. Bees forage pollen as a source of polypeptides, amino acids and sterols. Reduction in viability could be linked to lower protein contents (Muth et al., 2016), but this hypothesis needs verification. The effects of drought on chemical composition of pollen also deserve further investigation.

4. Consequences for plants and pollinators under drought

4.1. Complex responses for pollinator visitation rate

As shown in Fig. 2, the rate of pollinator visitation depends on visual and olfactory signals as well as floral rewards (Nicolson, 2011; Schiestl and Johnson, 2013; Fowler et al., 2016; Barragán-Fonseca et al., 2020). Changing these cues and rewards can induce a change in pollinator behavior. For example, pollinator visitation rate is affected by variation in flower size (Gómez et al., 2008) or by a modification of nectar or pollen composition (Somme et al., 2014). Floral display, which depends on floral stem height, on number of flowers and their size, is crucial for attracting pollinators (Schiestl and Johnson, 2013; Barragán-Fonseca et al., 2020). This parameter is clearly negatively affected by drought as stressed plants can be smaller, with fewer flowers, and flowers with a smaller size compared to unstressed plants. Several studies that tested the impact of altered cues on pollinator behavior have found variable results for pollinator visitation rates (Table 3). In each of these studies, a subset of signals have been modified and it is unclear whether a single signal or combination of signals may be driving the response. For example, in the study of Glenny et al. (2018), VOCs increased under water stress but visual signals were greatly altered, suppressing visitation rates. The effect of water stress on pollinator visitation rate is non-linear and complex as shown by Gallagher and Campbell (2017) and Descamps et al. (2018). Further behavioral studies will be required to investigate the relative importance of the different floral signal modifications due to drought for insect attractiveness. In order to link changes in visitation rates due to drought with an effect on plant reproduction, studies should systematically take into account parameters such as the amount of pollen deposited on stigmas and/or fruit and seed set but it is not always the case.

Altered floral signals or rewards may attract different pollinator taxa. For instance, there is a well-known correlation between insect proboscis length and corolla depth. Long-tongued insects are abundant pollinators, sometimes specialized or oligolectic, on deep corolla tube flowers, while short-tongued pollinators remain polylectic on short tube or open corolla flowers (Borrell, 2005; Müller-Struttman et al., 2015; Klumpers et al., 2019; Gérard et al., 2020). Changes in pollinators may in turn affect pollen deposition effectiveness since for example smaller pollinators have a lower single-visit pollen deposition rates compared to larger pollinators (Solís-Montero and Vallejo-Marín, 2017).

Table 3

Effect of water stress on floral signals and/or floral rewards and their consequence on pollinator visitation rate. (⬇️) decrease; (○) no effect; (⬆️) increase; (✳️) modification.

Reference	Modified signals or rewards due to water stress	Pollinators observed	Effect on pollinator visitation rate
(Al-Ghzawi et al., 2009)	Plant height, flower number, pollen viability	Honey bees ; wild bees	(⬇️) Honey bees : on average, 75 % of worker honey bees visited flowers of well-watered plants, whereas 20 % of worker honey bees visited flowers of moderately-watered plants. Drought-stressed flowers had low (5%) honey bee workers visits. Wild bees made 80 % of their visits to flowers of well-watered plants, whereas 15 % and 10 % of the total visits were directed towards flowers of moderately-watered and drought stressed plants, respectively.
(Burkle and Runyon, 2016)	Plant height, flower number, flower size, VOC quantity, VOC composition	88 % bees (Apoidea), 12 % other (flies, butterflies)	(⬇️) For <i>Campanula rotundifolia</i> : pollinator visits per flower and per plant decreased by half; for <i>Potentilla recta</i> : drought drastically reduced per-plant pollinator visitation 22.5-fold. (○) For <i>Heterotheca villosa</i> , no effect. (⬆️) For <i>Phacelia hastata</i> : drought increased per-flower visitation 10-fold.
(Waser and Price, 2016)	Nectar volume, nectar sucrose quantity, pollen quantity	Hummingbird	(⬆️) Visit rate increase (nectar production decrease → visit length decrease and flower visited increase); pollen load per flower decrease (pollen quantity decrease).
(Gallagher and Campbell, 2017)	Flower size, nectar volume	303 pollinators observed, two were flies, eight were solitary bees and the rest were bumblebees	(✳️) We found strong evidence for nonlinear effects of soil moisture on pollinator visitation, largely mediated through changes in corolla

Table 3 (continued)

Reference	Modified signals or rewards due to water stress	Pollinators observed	Effect on pollinator visitation rate
(Glenny et al., 2018)	Flower number, flower size, VOC quantity, VOC composition	95 % bees (36 species), 5 % flies (N = 408 individuals)	(⬇️) size and floral display size. Pollinator visitation rate per plant was 52 % lower to drought-treated plants compared to control plants only for <i>Potentilla recta</i> . (○) For 3 other species (<i>Campanula rotundifolia</i> , <i>Heterotheca villosa</i> , <i>Phacelia hastata</i>), no effect (less signals/rewards modified compared to <i>P. recta</i>).
(Descamps et al., 2018)	Flower number, flower size, nectar volume, nectar sucrose quantity	33 bumblebees (N visits = 1148 flowers)	(✳️) Water stress decreased the number of visited flowers at 21 °C and increased it at 27 °C.

4.2. Plant reproductive success negatively affected

A wide variety of plant structures associated with reproductive success may be affected by water stress, including pollen viability, pollen tube growth, stigma receptivity, ovule number, ovule fertilization and seed development (Turner, 1993; Frazee and Marquis, 1994; Guilioni et al., 2003; Fang et al., 2010; Su et al., 2013; Kay and Picklum, 2013; Sehgal et al., 2019). Drought decreases pollen viability, but can also impair pollen tube growth (Fang et al., 2010). Borrell (2005) observed a 30 % reduction in pollen tubes reaching ovules under water stress resulting in decreased fertilization. Although carpels appear to be generally less sensitive to drought than stamens (Su et al., 2013; Teixido and Valladares, 2019), drought could negatively affect the stigma receptivity or ovule number (Turner, 1993; Frazee and Marquis, 1994; Su et al., 2013; Kay and Picklum, 2013). Several studies have reported the abortion of ovaries under drought stress (Alqudah et al., 2011; Smith and Zhao, 2016). In *Lens culinaris*, even though pollen tubes reached the ovules and fertilization took place, post-fertilization abortion impaired seed development (Sehgal et al., 2019). All these factors may contribute to decreased seed and fruit sets. The reduction of fruit and seed sets under water stress is well established in the literature (Turner, 1993; Galen, 2000; Bourtra and Sanders, 2001; Guilioni et al., 2003; Al-Ghzawi et al., 2009; El Balla et al., 2013; del Cacho et al., 2013; Ma et al., 2014; Sivakumar and Sridvidhya, 2016; Mantel and Sweigart, 2019; Sehgal et al., 2019) and mostly follows linear response to stress (Gallagher and Campbell, 2017).

4.3. Food supply for pollinators, quantity, and probably quality reduced under drought

Declines in flower number and floral rewards due to water stress may reduce the food supply for pollinators and thus affect pollinator populations (Miller-Struttman et al., 2015; Baude et al., 2016). Flower life span may decrease under water stress (Primack, 1985) and the time-window for floral rewards may shorten. Bees, for example, can experience nutritional shortage because of reduced floral reward quantity or quality (Vaudo et al., 2015). Carvell et al. (2017) showed

that the floral resource availability is a major limiting factor for bumblebee survival. Though there are few studies on the nutritional quality of floral rewards resulting from abiotic stress, we hypothesize that quality decreases overall under drought. For example, low-viability pollen and nectar with a low sugar content is likely to have a lower nutritional quality for insects. Decreases in nutritional benefits increase the marginal visiting costs for insects, since they have to visit more flowers to collect a same quantity of nutrients. Lastly, decreasing floral resource quantity could also increase the resource competition between wild and managed bees (Thomson, 2016).

Despite these predictions, there is a need for more data on the effects of drought on pollinator food supply. Among insect pollinators, bees depend exclusively on floral resources (nectar and pollen) for their food. The nutritional quality (e.g., nectar sugar composition, amino acid content, pollen protein content) is crucial for bee survival, as evident in experimental studies where lower quality of floral resources have been associated with decreasing bee longevity or reproductive capacity (Hoover et al., 2012; Vaudo et al., 2015; Ziska et al., 2016). In nectar, the sugar source for pollinators, differences in sugar content under drought have been studied. Investigations about modifications due to drought in pollen composition, the main source of proteins and lipids for pollinators, are still needed.

5. Conclusion: What's next?

This synthesis focused on the effects of drought on floral attractiveness and floral rewards for insect pollinators. We suggest that the modifications in floral signals and rewards in response to drought could lead to negative consequences for both plants and pollinators in terms of reproductive success for plants and food provisioning for insects. We focused our analyses on plant individual scale; however, these modifications have also consequences at the population level. Even if no particular differences were observed at the individual level between wild and crop species, the implications at the population level differ. For crop species, at the field scale, each individual flowers are surrounded by thousands of congeners that can decrease its attractiveness to pollinators (named 'dilution effect') and potentially decrease its reproductive success. However, each individual of crop species may be less influenced by the mean level of attractiveness per individual compared to each individual of wild species which compete locally with other species for pollinators. This can lead to different effects in terms of reproductive success. Furthermore, for wild species, the effects of drought in the field may also differ between populations of the same species, as it was shown by Caruso (2006) on *Lobelia siphilitica* and by Suni et al. (2020) on *Phlox drummondii*. The population effects and implications on reproductive success should not be neglected in further studies on the effect of droughts on crop or wild species.

Drought-induced modifications may generate negative morphological or behavioral mismatches between plants and their pollinators. Such mismatches, recently reviewed by Gérard et al. (2020) in the context of global warming, may also occur due to drought through the same mechanisms, at individual level. These mismatches have the potential to disrupt plant–pollinator interactions and can lead to change the structure and abundance of insect-pollinated species and pollinators (Biesmeijer et al., 2006; Rafferty, 2017; Walter, 2018; Gérard et al., 2020). Moreover, the combined effects of drought and global warming may compound deleterious effects on plant–pollinator interactions.

Future research should seek to understand how drought affects morphological and behavioral mismatches between plants and pollinators. There is a lack of information about the impact of drought on important floral signals such as color and scent, as well as the nutritional qualities of floral rewards, which are crucial for insect health and development. More studies are necessary, particularly, in highly attractive entomophilous species, such as those belonging to the Brassicaceae, Lamiaceae and Rosaceae families, due to the high quantities and high nutritional qualities of their floral resources. Finally, the

majority of the studies discussed in this paper were performed under controlled conditions, which may be unrealistic approximations of field conditions. Following Phillips et al. (2018), it is crucial to observe the effects of stressors on plant–pollinator interaction in a variety of habitats to successfully predict the consequence of drought, which will likely be habitat-dependent. As climate modelling predict in the coming years that the occurrence of spring and summer droughts for temperate regions will increase, it would also be necessary to measure the effect of repeated droughts on wild herbaceous species. Future meta-analyses about drought effects at individual and population levels require a larger set of observations and experiments performed under similar and comparable conditions. Large sets of data will allow us to model and predict future evolution in plant–pollinator interactions in the context of global and climatic changes. Such data will help inform a sustainable future for the plant–pollinator systems crucial for our society.

CRediT authorship contribution statement

Charlotte Descamps: Conceptualization, Data curation, Formal analysis, Methodology, Funding acquisition, Software, Visualization, Writing - original draft, Writing - review & editing. **Muriel Quinet:** Conceptualization, Project administration, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing. **Anne-Laure Jacquemart:** Conceptualization, Investigation, Project administration, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

There is no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2020.104297>.

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