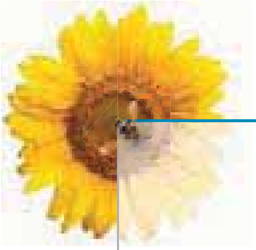


CLIMATE CHANGE AND CROP POLLINATION

Pollination is a crucial stage in the reproduction of most flowering plants, and pollinating animals are essential for transferring genes within and among populations of wild plant species (Kearns *et al.* 1998). Although the scientific literature has mainly focused on pollination limitations in wild plants, in recent years there has been an increasing recognition of the importance of animal pollination in food production. Klein *et al.* (2007) found that fruit, vegetable or seed production from 87 of the world's leading food crops depend upon animal pollination, representing 35 percent of global food production. Roubik (1995) provided a detailed list for 1 330 tropical plant species, showing that for approximately 70 percent of tropical crops, at least one variety is improved by animal pollination. Losey and Vaughan (2006) also emphasized that flower-visiting insects provide an important ecosystem function to global crop production through their pollination services.

The total economic value of crop pollination worldwide has been estimated at €153 billion annually (Gallai *et al.* 2009). The leading pollinator-dependent crops are vegetables and fruits, representing about €50 billion each, followed by edible oil crops, stimulants (coffee, cocoa, etc.), nuts and spices (Table 1). The area covered by pollinator-dependent crops has increased by more than 300 percent during the past 50 years (Aizen *et al.* 2008; Aizen and Harder 2009) (Figure 1.1). A rapidly increasing human population will reduce the amount of natural habitats through an increasing demand for food-producing areas, urbanization and other land-use practices, putting pressure on the ecosystem service delivered by wild pollinators. At the same time, the demand for pollination in agricultural production will increase in order to sustain food production.

Table 1

ECONOMIC IMPACTS OF INSECT POLLINATION OF THE WORLD AGRICULTURAL PRODUCTION USED DIRECTLY FOR HUMAN FOOD AND LISTED BY THE MAIN CATEGORIES RANKED BY THEIR RATE OF VULNERABILITY TO POLLINATOR LOSS

CROP CATEGORY	AVERAGE VALUE OF A PRODUCTION UNIT	TOTAL PRODUCTION ECONOMIC VALUE (EV)	INSECT POLLINATION ECONOMIC VALUE (IPEV)	RATE OF VULNERABILITY (IPEV/EV)
	€ PER METRIC TONNE	10^9€	10^9€	%
Stimulant crops	1 225	19	7.0	39.0
Nuts	1 269	13	4.2	31.0
Fruits	452	219	50.6	23.1
Edible oil crops	385	240	39.0	16.3
Vegetables	468	418	50.9	12.2
Pulse	515	24	1.0	4.3
Spices	1 003	7	0.2	2.7
Cereals	139	312	0.0	0.0
Sugar crops	177	268	0.0	0.0
Roots and tubers	137	98	0.0	0.0
All categories		1 618	152.9	9.5

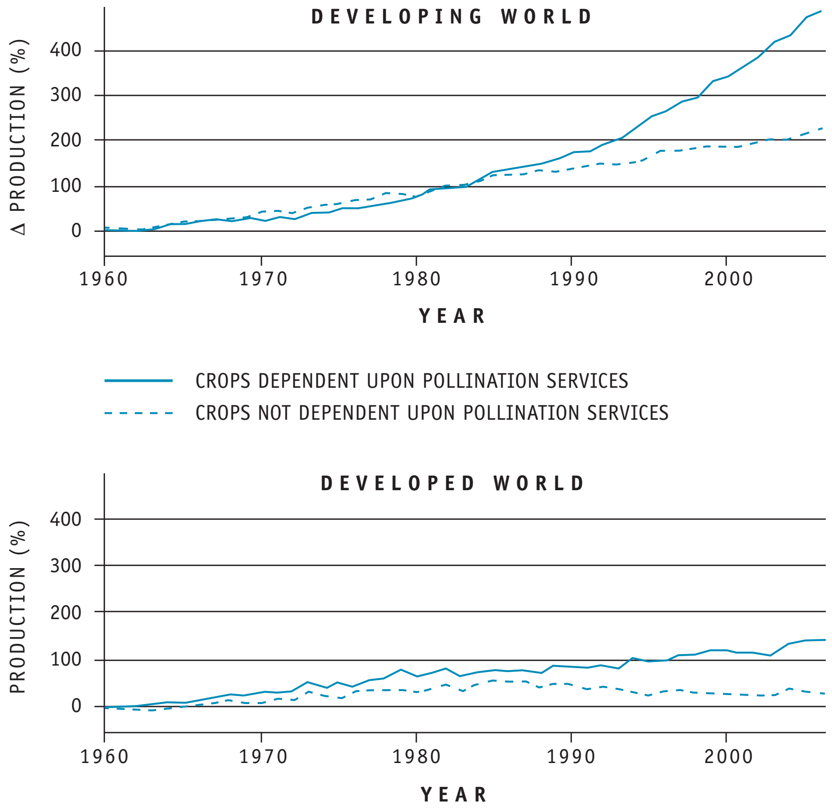
Source: Gallai *et al*. 2009.

Animal pollination of both wild and cultivated plant species is under threat as a result of multiple environmental pressures acting in concert (Schweiger *et al*. 2010). Invasive species (Memmott and Waser 2002; Bjerknes *et al*. 2007), pesticide use (Kearns *et al*. 1998; Kremen *et al*. 2002), land-use changes such as habitat fragmentation (Steffan-Dewenter and Tscharntke 1999; Mustajarvi *et al*. 2001; Aguilar *et al*. 2006) and agricultural intensification (Tscharntke *et al*. 2005; Ricketts *et al*. 2008) have all been shown to negatively affect plant-pollinator interactions.

Climate change may be a further threat to pollination services (Memmott *et al*. 2007; Schweiger *et al*. 2010; Hegland *et al*. 2009). Indeed, several authors (van der Putten *et al*. 2004; Sutherst *et al*. 2007) have argued that including species interactions when analysing the ecological effects of climate change is of utmost importance. Empirical studies explicitly focusing on the effects of climate change on wild plant-pollinator interactions are scarce and those on crop pollination practically non-existent. Our approach has therefore been to indirectly assess the potential effects of climate change

Figure 1.1

TEMPORAL TRENDS IN TOTAL CROP PRODUCTION FROM 1961 TO 2006



Source: Aizen *et al*. 2008.

on crop pollination through studies on related topics. We have focused on the effects of climate change on crop plants and their wild and managed pollinators, and studies on wild plant-pollinator systems that may have relevance.

The Fourth Assessment Report (AR4) developed by the Intergovernmental Panel on Climate Change (IPCC) lists many observed changes of the global climate. Most notably, the IPCC has documented increased global temperatures, a decrease in snow and ice cover, and changed frequency and intensity of precipitation (IPCC 2007). The most plausible and, in our opinion with respect to plant-pollinator interactions, the most important effect of climate change is an increase in temperatures. Therefore, we focus on the impacts increased temperatures might have on pollinator interactions. The fact that 11 years - out of the 12 year period from 1995 to 2006 - rank among the 12 warmest years in the instrumental record of global surface temperature (since 1850) (IPCC 2007) provides high confidence of recent warming, which is strongly affecting terrestrial ecosystems. This includes changes such as earlier timing of spring events and poleward and upward shifts in distributional ranges of plant and animal species (IPCC 2007; Feehan *et al.* 2009).

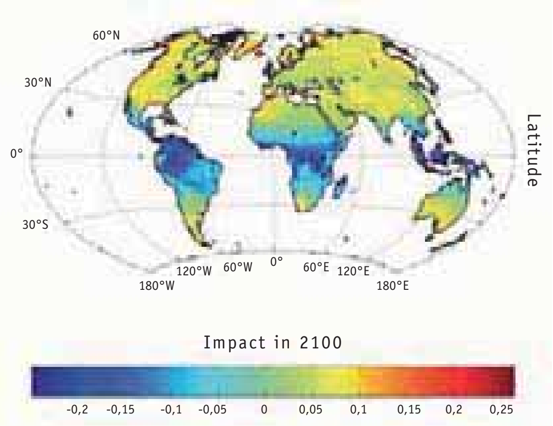
> *The most plausible and important effect of climate change on plant-pollinator interactions can be expected to result from an increase in temperatures.*

Estimates from the IPCC indicate that average global surface temperatures will further increase by between 1.1˚C (low emission scenario) and 6.4 °C (high emission scenario) during the 21st century, and that the increases in temperature will be greatest at higher latitudes (IPCC 2007). The biological impacts of rising temperatures depend upon the physiological sensitivity of organisms to temperature change. Deutsch *et al.* (2008) found that an expected future temperature increase in the tropics, although relatively small in magnitude, is likely to have more deleterious consequences than changes at higher latitudes (Figure 1.2). The reason for this is that tropical insects are relatively sensitive to temperature changes (with a narrow span of suitable temperature) and that they are currently living in an environment very close to their optimal temperature. Deutsch *et al.* (2008) point out that in contrast, insect species at higher latitudes – where the temperature increase is expected to be higher – have broader thermal tolerance and are living in cooler climates than their physiological optima. Warming may actually enhance the performance of insects living at these latitudes. It is therefore likely that tropical agroecosystems will suffer from greater population decrease and extinction of native pollinators than agroecosystems at higher latitudes.

> *Future temperature increase in the tropics, although relatively small in magnitude, is likely to have more deleterious consequences than changes at higher latitudes.*

Figure 1.2

PREDICTED IMPACT OF WARMING ON THERMAL PERFORMANCE OF INSECTS IN 2100



On the basis of patterns in warming tolerance, climate change is predicted to be most deleterious for insects in tropical zones.

Source: Deutsch *et al*. 2008.

Coope (1995) gives three possible scenarios for species' responses to large-scale climatic changes:

- Adaptation to the new environment
- Emigration to another suitable area
- Extinction

The first response is unlikely, since the expected climate change will occur too rapidly for populations to adapt by genetic change (evolution). As temperatures increase and exceed species' thermal tolerance levels, the species' distributions are expected to shift towards the poles and higher altitudes (Deutsch *et al.* 2008; Hegland *et al.* 2009). Many studies have already found poleward expansions of plants (Lenoir *et al.* 2008), birds (Thomas and Lennon 1999; Brommer 2004; Zuckerberg *et al.* 2009) and butterflies (Parmesan *et al.* 1999; Konvicka *et al.* 2003) as a result of climate change. Crop species and managed pollinators may easily be transported and grown in more suitable areas. However, moving food production to new areas may have serious socio-economic consequences. In addition, wild pollinators might not be able to follow the movement of crops.

Insect pollinators are valuable and limited resources (Delaplane and Mayer 2000). Currently, farmers manage only 11 of the 20 000 to 30 000 bee species worldwide (Parker *et al.* 1987), with the European honey bee (*Apis mellifera)* being by far the most important species. Depending on only a few pollinator species belonging to the *Apis* genus has been shown to be risky. *Apis*-specific parasites and pathogens have lead to massive declines in honey bee numbers. Biotic stress accompanied with climate change may cause further population declines and lead farmers and researchers to look for alternative pollinators. Well-known pollinators to replace honey bees might include the alfalfa leaf-cutter bee (*Megachile rotundata*) and alkali bee (*Nomia melanderi*) in alfalfa pollination (Cane 2002), mason bees (*Osmia* spp.) for pollination of orchards (Bosch and Kemp 2002; Maccagnani *et al.* 2003) and bumblebees (*Bombus* spp.) for pollination of crops requiring buzz pollination (Velthuis and van Doorn 2006). Stingless bees are particularly important pollinators of tropical plants, visiting approximately 90 crop species (Heard 1999). Some habits of stingless bees resemble those of honey bees, including their preference for a wide range of crop species, making them attractive for commercial management.

Pollinator limitation (lack of or reduced availability of pollinators) and pollen limitation (insufficient number or quality of conspecific pollen grains to fertilize all available ovules) both reduce seed and fruit production in plants. Some crop plants are more vulnerable to reductions in pollinator availability than others. Ghazoul (2005) defined vulnerable plant species as:

- having a self-incompatible breeding system, which makes them dependent on pollinator visitation for seed production;
- being pollinator-limited rather than resource-limited plants, as is the case for most intensively grown crop plants, which are fertilized; and
- being dependent on one or a few pollinator species, which makes them particularly sensitive to decreases in the abundance of these pollinators.

Food production in industrialized countries worldwide consists mainly of large-scale monocultures. Intensified farm management has expanded at the cost of semi-natural non-crop habitats (Tilman *et al.* 2001). Semi-natural habitats provide important resources for wild pollinators such as alternative sources of nectar and pollen, and nesting and breeding sites. Especially in the United States, many of these intensively cultivated agricultural areas are completely dependent on imported colonies of managed honey bees to sustain their pollination. The status of managed honey bees is easier to monitor than that of wild pollinators. For example, bee numbers and diurnal activity patterns can be easily assessed by visually inspecting the hives. Although not commonly used by farmers, scale hives can yield important information on hive conditions and activity, the timing of nectar flow and the interaction between bees and the environment (http://honeybeenet.gsfc.nasa.gov).

In most developing countries, crops are produced mainly by small-scale farmers. Here, farmers rely more on unmanaged, wild insects for crop pollination (Kasina *et al.* 2009). To identify the most important pollinators for local agriculture, data on visitation rate alone does not necessarily suffice. Crop species may be visited by several species of insects, but several studies have shown that only a few visiting species may be efficient pollinators. An effective pollinator is good at collecting, transporting and delivering pollen within the same plant species.

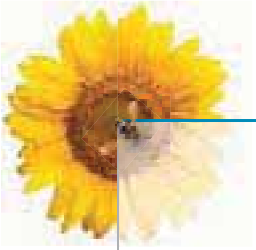
In a recent review, Hegland *et al.* (2009) discussed the consequences of temperature-induced changes in plant-pollinator interactions. They found that timing of both plant flowering and pollinator activity seems to be strongly affected by temperature. Insects and plants may react differently to changed temperatures, creating temporal (phenological) and spatial (distributional) mismatches – with severe demographic consequences for the species involved. Mismatches may affect plants by reduced insect visitation and pollen deposition, while pollinators experience reduced food availability.

We have found three studies investigating how increased temperatures might create temporal mismatches between wild plants and their pollinators. Gordo and Sanz (2005) examined the nature of phenological responses of both plants and pollinators to increasing temperatures on the Iberian Peninsula, finding that variations in the slopes of the responses indicate a potential mismatch between the mutualistic partners. Both *Apis mellifera* and *Pieris rapae* advanced their activity period more than their preferred forage species, resulting in a temporal mismatch with some of their main plant resources (Hegland *et al.* 2009). However, Kudo *et al.* (2004) found that early-flowering plants in Japan advanced their flowering during a warm spring whereas bumble bee queen emergence appeared unaffected by spring temperatures. Thus, direct temperature responses and the occurrence of mismatches in pollination interactions may vary among species and regions (Hegland *et al.* 2009).

Memmot *et al.* (2007) simulated the effects of increasing temperatures on a highly resolved plant-pollinator network. They found that shifts in phenology reduced the floral resources available for 17 to 50 percent of the pollinator species. A temporal mismatch can be detrimental to both plants and pollinators. However, the negative effects of this changed timing can be buffered by novel pollination interactions. Intensively managed monocultures usually provide floral resources for a limited time period. The survival rate and population size of the main pollinators may decrease if the foraging activity period is initiated earlier than the flowering period of the crop species. A loss of important pollinators early in the season will reduce crop pollination services later in the season. In such cases, introducing alternative food sources might be an option for farmers. In more heterogeneous agroecosystems, which are characterized by a higher diversity of crops and semi-natural habitats, pollinators may more readily survive on other crops and wild plants while waiting for their main food crop to flower.

We find the empirical support for temporal mismatches to be weak because of the limited number of studies available in the literature. Spatial mismatches between plants and their pollinators resulting from non-overlapping geographical ranges have not yet been observed. Despite the possibility of moving crop species to areas of suitable climate, we still believe that spatial and temporal mismatches between important crop species and their pollinators are highly probable in the future. Temporal mismatches and lack of synchronicity in plant and animal phenologies are likely because crop plant phenologies probably respond to climate variables in comparable ways to wild plants. Spatial mismatches may also be likely because of the socio-economic costs and consequences of moving food production to new areas, particularly in impoverished countries with high population density and a high degree of pollinator dependence for food production(Ashworth *et al.* 2009). Therefore, it is of the utmost importance for global food production and human well being that we understand the effects of climate change on animal-pollinated crops in order to counteract any negative effects.

> *Temporal mismatches are likely because crop plant phenologies probably respond to climate variables in comparable ways to wild plants. Spatial mismatches may also be likely because of the socio-economic costs of moving food production to new areas, particularly in impoverished countries.*



TEMPERATURE SENSITIVITY OF CROP POLLINATORS AND ENTOMOPHILOUS CROPS

POLLINATORS' SENSITIVITY TO ELEVATED TEMPERATURES

Bees are the most important pollinators worldwide (Kearns *et al.* 1998) and like other insects, they are ectothermic, requiring elevated body temperatures for flying. The thermal properties of their environments determine the extent of their activity (Willmer and Stone 2004). The high surface-to-volume ratio of small bees leads to rapid absorption of heat at high ambient temperatures and rapid cooling at low ambient temperatures. All bees above a body mass of between 35 and 50 mg are capable of endothermic heating, i.e. internal heat generation (Stone and Willmer 1989; Stone 1993; Bishop and Armbruster 1999). Examples of bee pollinators with a body weight above 35 mg are found in the genera *Apis, Bombus, Xylocopa and Megachile*. Examples of small bee pollinators are found in the family Halictidae, including the genus *Lasioglossum*. All of these groups are important in crop pollination.

In addition to endothermy, many bees are also able to control the temperatures in their flight muscles before, during and after flight by physiological and behavioural means (Willmer and Stone 1997). Examples of behavioural strategies for thermal regulation include long periods of basking in the sun to warm up and shade seeking or nest returning to cool down (Willmer and Stone 2004). With respect to the potential effects of future global warming, pollinator behavioural responses to avoid extreme temperatures have the potential to significantly reduce pollination services (Corbet *et al.* 1993).

Endothermic abilities and thermal requirements show a wide variation among different groups of bees. Most bee species have upper critical body temperatures (UCT) of 45-50°C (Willmer and Stone 2004). Although desert and tropical bees face both high solar radiation and high air temperature, there seems to be no major difference in UCT between bees in different biogeographical regions (Pereboom and Biesmeijer 2003). However, because of bees' contrasting abilities to generate heat when active, the maximum ambient temperature at which they can maintain activity may be somewhat below their UCT (Willmer and Stone 1997). The activity patterns of bees during the day also depend on the bees' coloration and body size (Willmer and Stone 1997; Bishop and Armbruster 1999). For example, Willmer and Corbet (1981) found that small, light-coloured *Trigona* bees in Costa Rica foraged on the flowers of *Justicia aurea* in full sunlight, while large, dark-coloured bees foraged in the morning and evening to avoid overheating.

The European honey bee (*Apis mellifera*) is the most widely distributed bee species worldwide and has evolved into several ecotypes adapted to different climatic regions (Figure 2.1). Two of the ecotypes are especially valued by beekeepers: The Carnolian honey bee (*Apis mellifera carnica*) and the Italian honey bee (*Apis mellifera ligustica*).

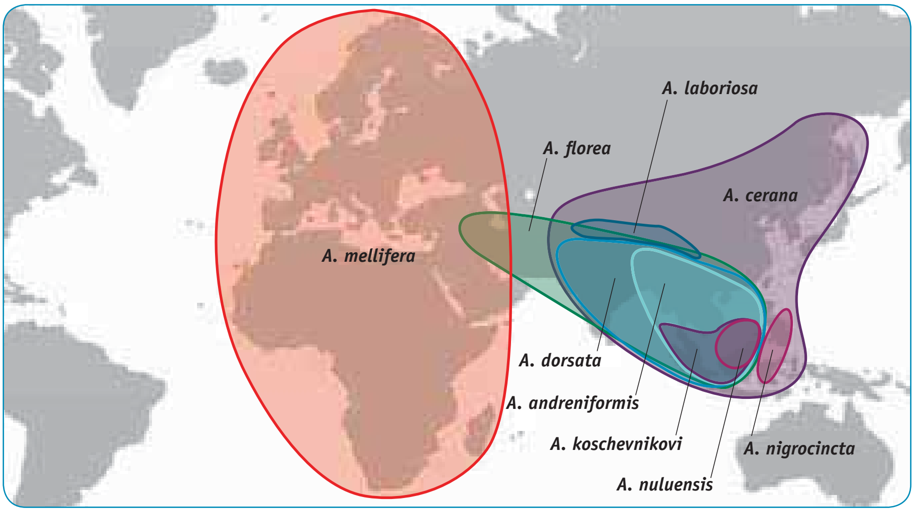
The native distribution of *A. mellifera* extends from the southern tip of Africa to Scandinavia and Russia in the north and from the Caspian Sea and beyond theEastern Ural Mountains in the east to Ireland in the west (Figure 2.1: red patch). *Apis mellifera* includes 25 subspecies or ecotypes (Figure 2.2). Each ecotype has evolved to the climatic and environmental conditions in its region, and therefore possesses a unique genetic variability.

The natural distribution of the European dark bee *(Apis mellifera mellifera)* is found in a region where average July temperatures range from 15-20°C (Figure 2.3), which may represent their thermal tolerance. The Eastern honey bee *(Apis cerana)* is native to parts of Asia (Figure 2.1: violet patch). The giant honey bee *(Apis dorsata)* lives only at tropical and adjacent latitudes in Asia (Figure 2.1: blue patch) and occurs less widely than the Eastern honey bee *(Apis cerana)*, but can live at higher altitudes. The dwarf honey bee *(Apis florea)* is more restricted than that of the larger *A. dorsata* and *A. cerana*. It is also mainly found in Asia (Figure 2.1: green patch).

The effect of climate change on pollinators depends upon their thermal tolerance and plasticity to temperature changes. Our goal was to obtain thermal tolerance data for the most important pollinators worldwide. However, a literature review indicates that this information is missing for most species.

Figure 2.1

GLOBAL DISTRIBUTION OF THE *APIS* GENUS.



Source: Franck *et al*. 2000; Le Conte and Navajas 2008. Figure printed with permission from P. Franck (Franck 1999).

Figure 2.2

MAIN GEOGRAPHIC RACES OF *APIS MELLIFERA*.

A, M, C and O are the four evolutionary branches.

Source: Ruttner 1988; Franck et al. 2000; Le Conte and Navajas 2008). Figure printed with permission from P. Franck (Franck 1999).

Figure 2.3

THE NATURAL RANGE OF *APIS MELLIFERA*.

The natural range of *Apis mellifera mellifera* coincides with the 15-20° zone (July average temperatures).

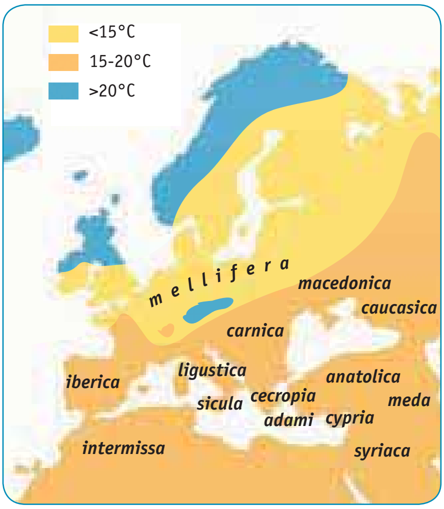


Figure printed with permission from D. Pritchard (Pritchard 2006).

that this information is missing for most species. There is an urgent need to investigate the thermal tolerance of important crop pollinators and differences in thermal tolerance among *Apis* species and sub-species. Some of these are better adapted to warmer climates and may therefore move into new areas where they can function as crop pollinators under future climate conditions.

ENTOMOPHILOUS CROPS' SENSITIVITY TO ELEVATED TEMPERATURES AND DROUGHT

Plant development is mainly determined by mean temperature and photoperiod (Nigam *et al.* 1998). As global temperatures increase, crops will be grown in warmer environments that have longer growing seasons (Rosenzweig *et al.* 2007). An increased temperature of 1-2°C may have a negative impact on crop growth and yield at low latitudes, and a small positive impact at higher latitudes (Challinor *et al.* 2008). Extreme temperatures and drought are short-term events that will likely affect crops, particularly during anthesis (Wheeler *et al.* 1999).

While it is clear that drought and water stress will negatively affect crop growth and yield, their impacts on pollination functions are less well understood. Most of the work carried out on the impacts of drought on crop yield is from research on non-pollinator-dependent crops such as grain crops or wild plants. We do however believe that similar effects may occur with pollinator-dependent crops. Akhalkatsi and Lösch (2005) found reductions in inflorescence and flower numbers in the annual garden spice legume *Trigonella coerulea* when subjected to controlled drought conditions. Flowers with fewer attractants are less attractive to pollinators (Galloway *et al.* 2002; Pacini *et al.* 2003; Mitchell *et al.* 2004; Hegland and Totland 2005) and will experience reductions in pollination levels, with decreased seed quality and quantity (Philipp and Hansen 2000; Kudo and Harder 2005). Crop species experiencing drought stress may also produce lower seed weight and seed number, resulting in reduced yield (Akhalkatsi and Lösch 2005). Yield reduction under drought may also result from a decrease in pollen viability along with an increase in seed abortion rates, which have been identified as the most important factors affecting seed set (Melser and Klinkhamer 2001; Boyer and Westgate 2003).

> *Drought may impact floral attractants, making flowers less visited by pollinators.*