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Original article

Nectar and flower production in *Vicia faba* L (field bean) at ambient and elevated carbon dioxide

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Summary — Atmospheric CO_2 has been predicted to double by the year 2100. Elevated CO_2 causes an increase in photosynthetic rate and extra assimilate is allocated to plant growth, seed and fruit production. Increased investment in flowers may have implications for pollination in entomophilous plants. Floral nectar standing crop, flower production and longevity were examined in *Vicia faba*, field bean, at ambient and elevated CO_2. Nectar standing crop did not differ significantly between treatments but plants grown at elevated CO_2 produced approximately 25% more flowers per plant and these lived 17% longer than those grown at ambient CO_2. A plant grown at elevated CO_2 may thus produce more nectar in total and, together with its increased floral display, may be more attractive to pollinators, but pollen flow will not necessarily be improved.

***Vicia faba* / carbon dioxide / climate change / nectar / flower longevity**

INTRODUCTION

The concentration of CO_2 in the atmosphere has been predicted to approximately double from the current 350 $\mu L \cdot L^{-1}$ to 700 $\mu L \cdot L^{-1}$ by 2100 (Pearman, 1988). Elevated CO_2 affects the metabolism and growth of plants (Cure and Acock, 1986; Bazzaz, 1990) and could have profound effects on crop production (Parry, 1992).

Photosynthetic rate of plants grown at elevated CO_2 (700 $\mu L \cdot L^{-1}$) can increase by up to 40% relative to those grown at ambient CO_2 (350 $\mu L \cdot L^{-1}$), leading to increased carbon fixation in most C_3 plant species (Cure and Acock, 1986). The extra carbon

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fixed is allocated to vegetative growth (Bazzaz, 1990; Pitelka, 1994) and to reproduction (Kimball, 1986; Pitelka, 1994). Beneficial effects of extra CO_2 on the seed and/or fruit yields of glasshouse crops have been under investigation for at least 100 years (Wittwer and Robb, 1964) and elevated CO_2 has been used in glasshouses since the 1960s to improve yields of crops such as tomato, lettuce and cucumber (Wittwer and Robb, 1964) and production of flower crops (Goldsberry, 1986). Kimball (1986) reviews the effects of CO_2 on the yields of field crops such as wheat, cotton and soybean.

Though increased fruit and seed yields have been widely demonstrated, there have been fewer studies on how elevated CO_2 might affect the floral biology of a plant species, for example flower production, flower longevity and the rewards available to visiting insects. For insect-pollinated species, these factors may affect reproductive success of the plant by altering insect visitation rates and consequently pollen flow and the effectiveness of pollination. The possibility that climate change could affect plants' reproductive success is of economic importance.

How is elevated CO_2 likely to affect floral characters of a plant? Flower initiation (production) and maintenance (flower longevity and reward production) are costly to a plant (reviewed by Ashman and Schoen, 1996) and may be limited by resources. In such cases, increased resource availability, for example extra carbon fixed at elevated CO_2, would allow added investment in either the initiation of flowers or the maintenance of flowers or both, leading to more longer-lived flowers with extra rewards such as nectar. No studies were found examining the effects of elevated CO_2 on nectar production in any species.

Floral display (the number of flowers open at any one time) is determined by flower number, floral longevity and the period for which the plant is flowering and in this respect plant species vary in their response to elevated CO_2 (Goldsberry, 1986). In general, elevated CO_2 leads to increased initiation and retention of flowers (Acock and Pasternak, 1986; Kimball, 1986) and earlier initiation of flowering (Garbutt and Bazzazz, 1984); these effects have been reported in carnations, roses and several other flower crops (Goldsberry, 1986; Kimball, 1986), and in tomato plants (Wittwer and Robb, 1964; Hicklenton and Jolliffe, 1978). In wheat, rice and pea, tillering is increased (Acock and Pasternak, 1986). Garbutt and Bazzazz (1984) found that populations of a wild plant species, *Phlox drummondii* Hooker, generally flowered earlier and produced twice as many, longer-lived flowers at elevated CO_2 than at ambient CO_2.

This study considers the effect of elevated CO_2 on nectar production (volume, concentration and sugar weight), flower production, longevity and bloom period (phenology) in *Vicia faba*, the field bean, which benefits from bee pollination (Stoddard and Bond, 1987).

MATERIALS AND METHODS

Sixteen *V faba* (cv Sutton) plants were grown from seed in each of two bee-free rooms in the Envirocon® facility at Rothamsted (Lawlor et al, 1993). One room had a CO_2 concentration of 350 $\mu L \cdot L^{-1}$ and the other 700 $\mu L \cdot L^{-1}$. All other conditions were similar: plants were grown in individual 1 L pots in Terra-Green® (Oil-Dri, Colorado) and each was given 1.6 g slow release fertiliser (Osmacote mini®, Sierra, UK). Seeds were grown at 18 °C and exposed to a light regime of 16 h light (02 00–18 00 hours) and 8 h dark. Every 7 days the plants and the CO_2 conditions were swapped between rooms to minimise any external effects owing to rooms or positions within rooms. Flowering began when plants were 4–5 weeks old and flowering stages (table I) were recorded. All recordings were made between 15 30 and 18 00 hours GMT, after any new flowers had opened for that day.

Table I. Flower stages of *Vicia faba* from bud to withering (after CS Williams, unpublished).

Flower stage	*Bud/flower*	*Standard petal*	*Wing petals*	*Anthers and pollen*
0	Closed bud	Turning white, still tightly furled	Tightly furled	Anthers undehisced
1	Unfurling bud	Separating along lower flower edge	Becoming exposed	Anthers starting to dehisce
2	Unfurling bud	Separated, not yet horizontal or reflexed	Separating along lower flower edge	Anthers dehisce, pollen in keel pocket
3	Opening bud	Horizontal, becoming erect	Perpendicular to standard	Pollen in keel pocket
4	Open flower	Stiff and reflexed	Perpendicular to standard	
5	Open flower	Stiff and reflexed	Beginning to splay outwards and upwards	
6	Open flower	Reflexed with edges meeting behind petal	Becoming flaccid	
7	Crumpled flower	Wilting and becoming horizontal	Flaccid and becoming necrotic	
8	Withered flower	Collapsed and shrivelled	Collapsed and shrivelled	

Nectar standing crop

Although nectar secretion rate might have been the most appropriate measure of nectar production (emptying a flower of nectar, leaving the flower to accumulate nectar again and then resampling after a set period of time), destructive sampling of flowers was necessary for accurate measurement of nectar content so flowers could not be sampled twice. The measurement taken was nectar standing crop, but the flowers were not visited by bees so this approximates to nectar secretion over the flower's life, minus any nectar that is reabsorbed by the flower.

Nectar standing crop of flowers in different CO_2 conditions was determined by sampling flowers from the first eight nodes on the primary stems of six of the plants in each treatment room once a day between 15 30 and 17 30 hours. The sampling period lasted 28 days. The nodes (1–8) and the position of the first eight flowers on the raceme at each node formed the rows and columns of an 8×8 Latin Square. The following procedure was used to investigate differences in nectar standing crop with respect to flower age and position on the plant. When a flower reached at least stage 1 (unfurling bud; table I), it was assigned a sampling day (to obtain a given age at sampling) according to a randomised Latin Square and the actual stage at this time was recorded. A different Latin Square was used for each plant. The corolla was marked with a pen so that on the following day it was easy to distinguish which flowers were newly opened. Eight different flower ages, from 1 to 8 days, were obtained in this way on each node; in the field, flowers can remain receptive for up to 6 days after anthesis (Stoddard, 1986). Some nodes produced fewer than eight flowers and some flowers aborted, so many missing values resulted, but despite this a large number of flowers (441) were sampled.

The flower to be sampled for nectar was removed from the plant and its developmental stage was noted (table I). The standard petal was removed according to the technique of Davis and Gunning (1993) and the nectar from around the nectaries withdrawn into a 0.5 μL, 1 μL or 5 μL disposable microcapillary tube (depending on the volume present). *Vicia faba* nectaries are described by Davis et al (1988) and illustrated in Davis and Gunning (1992). The length of the nectar column in the tube was measured and the volume of nectar (μL per flower) calculated. The concentration (% = g sucrose per 100 g solution)

was estimated using a pocket refractometer (Bellingham and Stanley Ltd, Tunbridge Wells) and sugar weight (mg sugar per flower) calculated from the volume and concentration (Prŷs-Jones and Corbet, 1991). Although the refractometer was modified to take low volumes, nectar concentration, and hence sugar weight, could not be determined if the volume was less than 0.05 μL.

Flower longevity and production

Bees are most likely to visit fully open flowers in stages 4–6 as they are the easiest to manipulate and probably the most attractive and rewarding, but all flowers (stages 1–7) may help to attract bees from a distance. The longevity of every flower on alternate nodes of the remaining ten plants in each CO_2 treatment was determined. When flowering began (23 January), the plants were labelled and, on each afternoon, the buds in stage 0 or stage 1 were marked on the sepals. The developmental stage reached by each marked flower was recorded daily (at some time between 16 00 and 18 00 hours) until the flower had withered (stage 8). For odd-numbered plants, flowers on nodes 1, 3, 5, etc, were observed and for the even-numbered plants, flowers on nodes 2, 4, 6, etc, were observed. Flowers were followed until 25 February (not the end of flowering, but plants were not watered on 24 February and drought is known to induce flower shed; Gates et al, 1983).

The total number of flowers produced by each plant was recorded until 5 March when all the plants had finally finished flowering.

Floral display

On each day from 24 January to 25 February, the total number of flowers in stages 1–7 (inclusive) and stages 4–6 (inclusive) on each plant were counted.

Methods of analysis

Nectar standing crop

For nectar volume per flower, data for the 441 successfully sampled flowers were analysed. For flowers containing less than 0.05 μL (103 at

Table II. Nectar standing crop means and flower longevity means for each treatment and summary of analyses of variance to examine (i) the effect of CO_2 and flower age on nectar standing crop and (ii) the effect of CO_2 on flower longevity.

Variable	*Untransformed means* (n)		*Treatment effects*					
			CO_2		*Flower age*		*CO_2 × age*	
	Elevated CO_2	*Ambient CO_2*	*F (df)*	*Prob*	*F (df)*	*Prob*	*F (df)*	*Prob*
(i) Nectar standing crop								
*Sugar weight per flower (mg)	0.189 (107)	0.140 (110)	0.916 (1,10)	> 0.05	14.73 (7,73)	< 0.001	2.15 (7,73)	0.05
*Volume per flower (μL)	0.269 (214)	0.228 (227)	0.021 (1,10)	> 0.05	32.86 (7,265)	< 0.001	2.24 (7,265)	0.03
Concentration (%)	27.94 (107)	23.81 (110)	2.031 (1,10)	> 0.05	15.00 (7,73)	< 0.001	0.75 (7,73)	> 0.05
(ii) Flower longevity								
No days spent in stages 1–7	6.9 (536)	5.8 (432)	11.24 (1,18)	< 0.01	—	—	—	—
No days spent in stages 4–6	4.4 (523)	3.1 (412)	34.70 (1,18)	< 0.01	—	—	—	—

$P < 0.05$ is considered significant. * Transformed to natural logarithms after adding an offset of 0.005.

ambient CO_2 and 100 at elevated CO_2), concentration and sugar weight per flower could not be measured so these flowers were omitted from the analyses of these variables ($n = 217$ for each analysis). Data were transformed if necessary (table II), analyses of variance tables were constructed using regression techniques, and treatment differences were tested with F–tests (table II).

Flower longevity and production

Analyses of variance (table II) were computed, using regression techniques, to assess the effect of CO_2 on (i) the number of days that each flower spent in stages 1–7 (inclusive) and (ii) the number of days that each flower spent in stages 4–6 (inclusive). Residual plots suggested transformation of the data was unnecessary. Some flowers were missed during examination but their stage could often be inferred from the records on the previous and following day.

The total numbers of flowers per plant were transformed to natural logarithms, and treatment means were compared using a two–sample t–test.

Floral display

The counts of flowers in stages 1–7 and 4–6 form sets of repeated measurements, one set for each of the 20 plants. Data of this kind can be considered as analogous to those arising from a split-plot design with plants equivalent to whole plots and time periods equivalent to subplots. However, adjacent time periods may be more highly correlated than those further apart. To allow for this the degrees of freedom in the subplot stratum of the resulting analysis of variance tables were adjusted by multiplying them by ε (Greenhouse and Geisser, 1959), a measure of the correlation between successive time periods, before testing treatment differences with F–tests. Before analysis, missing values were estimated given the observed level of ante-dependence in the data.

RESULTS

Nectar standing crop

Flowers contained 0–3.44 μL nectar per flower at concentrations of 6–50% (equiv-

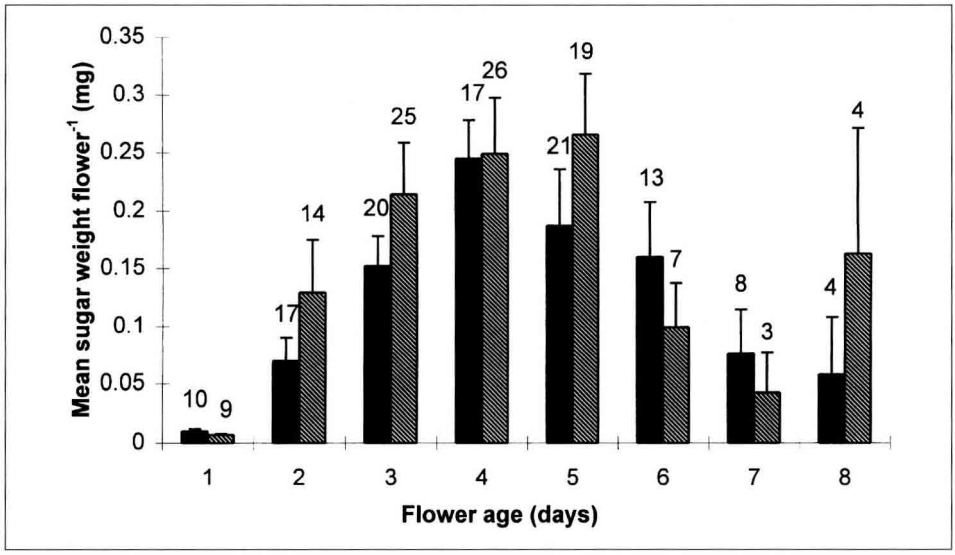

Fig 1. Mean sugar weight per flower (± standard error) for flowers of different ages measured in days after opening. Means presented are of the untransformed raw data though analysis of variance was performed on transformed data (table II). Numbers above columns indicate sample sizes ($n = 217$). ■ flowers grown at ambient CO_2; ▨ flowers grown at elevated CO_2.

alent to 0–1.01 mg sugar per flower). There was no significant effect of CO_2 on weight of sugar per flower (table II); and the interaction between CO_2 and flower age was only weakly significant. However, there was a significant effect of flower age on sugar weight per flower. New flowers and old flowers contained less sugar per flower than 3–5-day old flowers (fig 1). Flowers in stages 1–7 contained some nectar, though there was little in newly opening flowers and most in fully open flowers (stages 4–6) (fig 2).

Carbon dioxide had no significant effect on nectar concentration or volume whilst the interaction between CO_2 and age was not significant for concentration and was only weakly significant for nectar volume (table II). Flower age, however, had a highly significant effect on both nectar concentration and volume. The trends for nectar concentration and volume per flower with age were similar to those for sugar weight per flower (fig 1).

Flower longevity and production

There was a significant difference in flower longevity (days spent in stages 1–7) between CO_2 treatments, and also in the number of days each flower remained fully open (stages 4–6) (table II). Flowers lived longer and remained fully open longer at elevated CO_2 (table II).

Plants grown at elevated CO_2 produced significantly more flowers [156.8 (± 9.2) flowers per plant] than those grown at ambient CO_2 [124.8 (± 13.1) flowers per plant]. These means may be underestimates as the plants were water-stressed towards the end of flowering.

Floral display and bloom period

Strong correlation existed between time periods (stages 1–7, $\varepsilon = 0.102$; stages 4–6, $\varepsilon = 0.138$). There was no interaction between CO_2 and time period for number

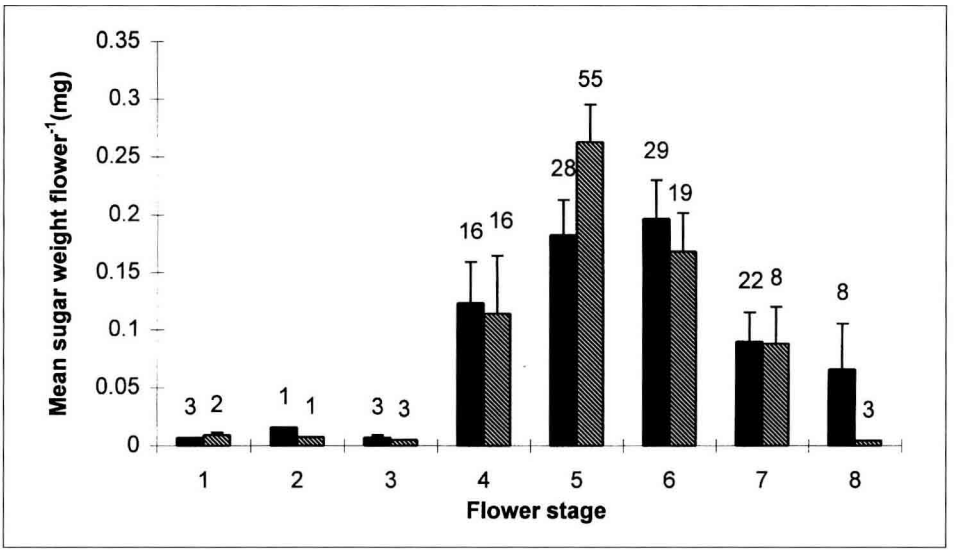

Fig 2. Mean sugar weight per flower (± standard error) for flowers sampled at different stages (table I). Numbers above columns indicate sample size ($n = 217$).

■ flowers grown at ambient CO_2; ▨ flowers grown at elevated CO_2.

of flowers in stages 1–7 per plant per day or for those in stages 4–6 per plant per day ($P > 0.05$). Over the whole flowering period, there were always more flowers on plants at elevated CO_2 than on plants at ambient CO_2 (fig 3a; $F_{1,18} = 13.47$; $P < 0.05$). There were also more fully open flowers (stages 4–6) per plant per day (fig 3b; $F_{1,18} = 24.32$; $P < 0.01$). Time period also had a marked effect on number

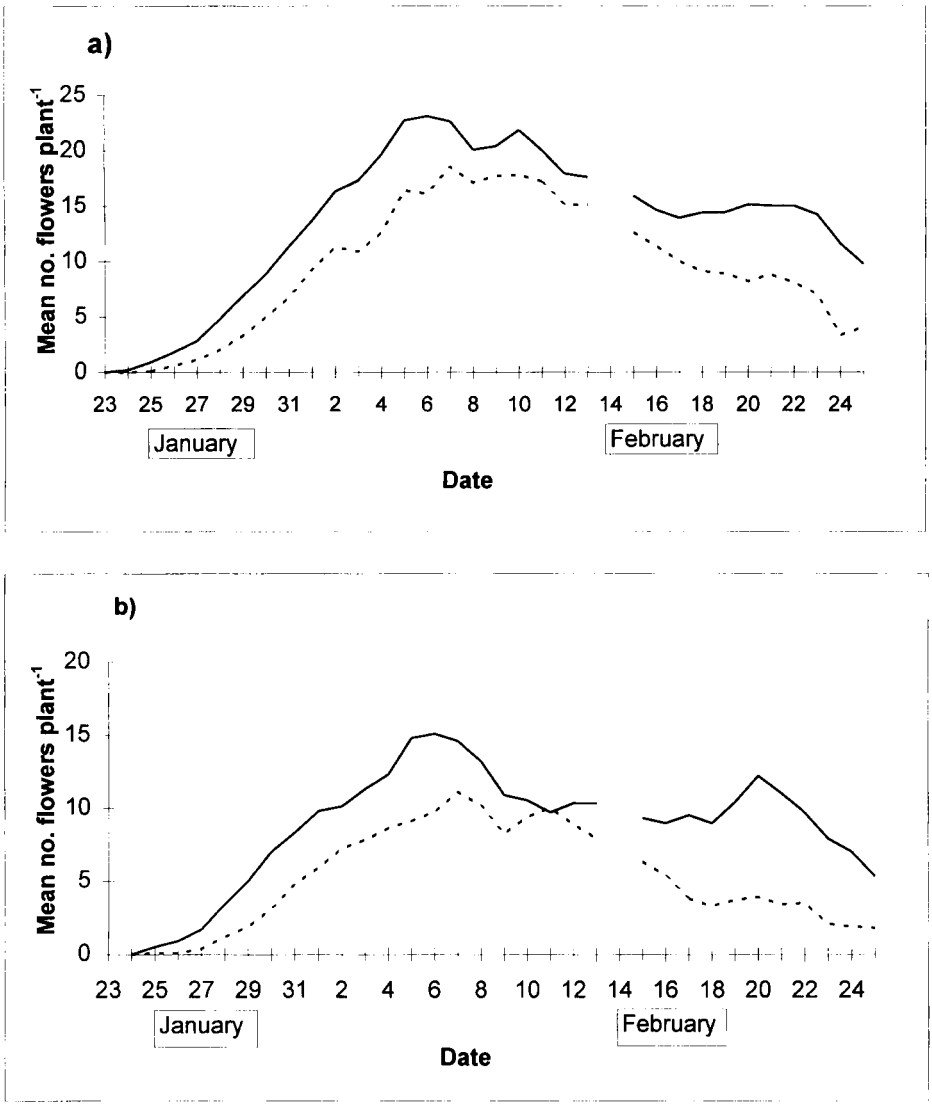

Fig 3. Mean number of a) flowers in stages 1–7 per plant and b) flowers in stages 4–6 per plant for each day after the start of flowering. No data were collected on 14 February. ---- plants grown at ambient CO_2; —— plants grown at elevated CO_2.

of flowers per plant per day ($F_{3,57} = 39.94$; $P < 0.01$) and on the number of fully open flowers per plant per day ($F_{4,74} = 28.73$; $P < 0.01$). Plants at elevated CO_2 started flowering earlier (by 2 or 3 days) and many finished later than those at ambient CO_2.

DISCUSSION

Nectar standing crop per flower was highly variable, with many flowers containing no extractable nectar; volumes recorded were similar to those obtained by others (Stoddard and Bond, 1987; Davis et al, 1988; Free, 1993). Fully open flowers contained the most nectar and there was a strong relationship with flower age. The accumulated nectar approximates to the nectar secreted by the flower and since the flowers were not visited by insects, the decrease in sugar content with flower age suggests reabsorption is taking place (Búrquez and Corbet, 1991). Surprisingly, elevated CO_2 had no significant effect on mean nectar standing crop per flower.

Individual flowers grown at elevated CO_2 lasted for about 1 day longer than those at ambient CO_2 (7 days instead of 6). In both treatments, the flowers took approximately 1 day to open, but they remained fully open for 4 days at elevated CO_2 and 3 days at ambient CO_2, making each flower at elevated CO_2 potentially available for bees' visits for 15–25% longer than flowers grown at ambient CO_2. In both treatments, the flowers took about 2 days to wither fully. The measurements for floral longevity in this experiment are comparable with those of Bond et al (1980) who note that, in the field, the standard petal of a *V faba* flower collapses (stage 7) 3–5 days after opening.

Our estimates of flower production are higher than those previously reported (50–80 flowers per plant; Free, 1993). Most *V faba* cultivars are indeterminate (Gates et al, 1983; though see Stoddard, 1993), and in the absence of insect visitation vegetative growth and flowering continue for longer, but even so, the greater number of flowers on plants grown at elevated CO_2 (25% more) and the prolonged flowering period suggest that at least some extra assimilate is used to increase initiation and maintenance of flowers.

Individual flowers did not contain more nectar when grown in elevated rather than ambient CO_2, but if one assumes that the active nectar secretion period is when the flower is fully open (stages 4–6: fig 2) then, because the flowers at elevated CO_2 were fully open for longer, one would expect them to accumulate more nectar by the time they started to wither, even if secretion rates were similar for both treatments. Mean nectar standing crop in 5-day old flowers was still increasing in elevated CO_2, but had begun to decline for flowers in ambient CO_2 (fig 1). On this day, flowers in elevated CO_2 are still likely to be fully open (stage 6) and secreting nectar, while those at ambient CO_2 are beginning to wither and presumably to reabsorb nectar (fig 2). After the 5th day, flowers at elevated CO_2 also begin to wither. At elevated CO_2 the period of nectar secretion lasts longer but it seems to be balanced by increased reabsorption (when the flowers begin to wither) since the overall standing crop is similar between treatments.

On any one day there is likely to be a larger floral display on a plant grown in elevated rather than ambient CO_2 (fig 3) so that, in a future elevated CO_2 environment, the rewards available to bees from the plants will be greater than in current conditions, though how this will affect flower visitation rate is uncertain.

At elevated CO_2 *V faba* flowers do not secrete more nectar individually: increased nectar may not necessarily improve pollen flow, since increased rewards may lead to longer-lasting insect visits (Kato, 1988). This may enhance pollen removal or deposition on the individual flower but overall foraging rate would be reduced, potentially reduc-

ing pollen flow. Nor would increased nectar levels help in the attraction of pollinators from a distance. *Vicia faba* does, however, invest extra assimilate in initiation and maintenance of flowers at elevated CO_2, increasing the floral display. How might these changes influence insect visitation? Harder and Barrett (1996) suggest that floral display acts antagonistically in the roles of pollinator attraction and pollen dispersal. When floral display is increased, either by an increase in total flower production, an increase in flower longevity, or both, more pollinators are likely to be attracted to the plant. This could reduce the number of pollinators visiting other plant species in the area which do not have the same response to CO_2 (Garbutt and Bazzazz, 1984) and thereby increase *V faba*'s share of pollinators. But in many cases, larger floral displays result in more pollinator visits per plant, but fewer visits per flower (Harder and Barrett, 1996; Snow et al, 1996) and increased levels of self-pollination, particularly geitonogamy (Handel, 1983; Harder and Barrett, 1995, 1996). Pollen flow per flower can sometimes, therefore, be reduced by increasing floral display (Harder and Barrett, 1995). This is likely to have severe consequences in species where inbreeding depression is pronounced. *Vicia faba* can produce viable seeds from geitonogamy although cross-pollination produces better seed.

Thus, over the flowering period, a *V faba* plant growing at elevated CO_2 is likely to produce more nectar in total than one at ambient CO_2 which, combined with its increased floral display, may make it more attractive to pollinators (in relation to other plants which do not respond this way) but may not necessarily enhance pollen flow. The increased floral display will also increase the resources available to the populations of bees and other insects feeding on these flowers.

Carbon dioxide enhancement may also affect the bees directly (Nicolas and Sillans, 1989). Short bursts of pure CO_2, used to anaesthetise honey bees, have been shown to alter subsequent foraging behaviour (Ribbands, 1950; Ebadi et al, 1980) and hormonal activity (Bühler et al, 1983) but it is possible that even small changes in atmospheric CO_2 may alter the bees' behaviour, though to lesser extent. Receptors on honey bees' antennae respond to tiny changes in CO_2 concentration (Lacher, 1967; Stange and Diesendorf, 1973) and when CO_2 concentrations rise in the hive (for example from 1 to 3% CO_2 in atmosphere), bees alter their entrance fanning behaviour to improve hive ventilation (Seeley, 1974). Such small changes in CO_2 may also alter their motivation to forage (Bühler et al, 1983) which may in turn affect pollination. In glasshouses, there is no noticeable effect on bumble bee behaviour or colony development when CO_2 levels are doubled to promote fruit set (van Doorn, personal communication), although there may be effects on colony development when CO_2 levels are 20 or 30 times ambient, near the CO_2 distribution lines. Such effects are currently being investigated (van Doorn, personal communication) and may have implications for pollination levels in a future CO_2-rich environment.

The effects of increased CO_2 concentrations on the floral biology of plants are likely to have important consequences, whether good or bad, on insect-pollinated systems. To investigate these consequences further, studies of plants in the presence of pollinators at elevated CO_2 are required.

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Résumé — Production de nectar et de fleurs chez la féverole, *Vicia faba* L, au taux de CO_2 ambiant et à un taux plus élevé. On a prédit le doublement du CO_2 atmosphérique d'ici l'an 2100. Une teneur élevée en CO_2 provoque une augmentation de la photosynthèse chez la plupart des plantes étudiées et une grosse partie du carbone supplémentaire fixé sert à la croissance et à la reproduction de la plante. Les rendements en graines ou en fruits sont souvent accrus en présence d'un taux élevé de CO_2, mais la biologie florale peut être elle aussi affectée, ce qui a des conséquences pour la pollinisation des plantes entomophiles. Chez certaines espèces la production de fleurs et leur longévité sont accrues sous CO_2 élevé, mais nous n'avons trouvé aucune étude portant sur la production de nectar. Nous avons étudié chez la féverole la production de nectar floral (volume, concentration et poids des sucres/fleur), la production de fleurs et leur longévité. Les plantes ont été cultivées dans deux pièces dépourvues d'abeilles, l'une avec un taux de CO_2 ambiant (350 µL/L), l'autre avec un taux plus élevé (700 µL/L). Des fleurs d'âge connu (1–8 jours) ont été prévelées, leur stade de développement noté (tableau I) et leur nectar extrait à l'aide de microcapillaires de 0,5 µL, 1 µL et 5 µL. Le volume de nectar a été obtenu en mesurant la hauteur de la colonne de nectar dans le tube (µL/fleur). La concentration du nectar (%; g saccharose pour 100 g de solution) a été déterminée à l'aide d'un réfractomètre de poche. Le poids des sucres dans le nectar (mg/fleur) a été calculé à partir du volume et de la concentration (Prŷs-Jones et Corbet, 1991). La longévité de chaque fleur sur les noeuds alternés de dix plantes (non échantillonnées pour le nectar) a été notée pour chacune des deux teneurs en CO_2. Chaque après-midi, les boutons floraux au stade 0–1 étaient marqués et leur stade de développement noté chaque jour entre 16.00 et 18.00 h jusqu'au flétrissement (stade 8). Le nombre total de fleurs produites par chacune de ces plantes a été noté jusqu'à ce qu'elles aient toutes fleuri. La production de nectar a varié de 0 à 3,44 µL/fleur avec des concentrations allant de 6 à 50 % (0–1,01 mg de sucre/fleur). Le traitement au CO_2 n'a pas eu d'effet significatif sur le poids de sucre/fleur, mais l'âge de la fleur en a eu un (tableau II): les fleurs pleinement ouvertes âgées de 3 à 5 jours contenaient plus de nectar que les fleurs plus jeunes ou plus vieilles (fig 2). Les plantes cultivées sous CO_2 élevé ont eu en moyenne significativement plus de fleurs/plante que les plantes cultivées sous CO_2 ambiant: respectivement 156,8 (±9,2) et 124,8 (±13,1) fleurs/plante. Elles ont également vécu significativement plus longtemps (7 jours au lieu de 6) et sont restées pleinement ouvertes pendant 4 jours au lieu de 3. En conséquence, une plante cultivée sous CO_2 élevé avait, à n'importe quel jour donné, significativement plus de fleurs ouvertes qu'une plante cultivée sous CO_2 ambiant (fig 3). Donc, sur la période de floraison, elle est susceptible de produire au total plus de nectar ce qui, combiné avec son offre accrue de fleurs, peut la rendre plus attractive pour les pollinisateurs (par rapport à d'autres plantes répondant différemment), mais n'augmente pas nécessairement sa production de pollen. L'offre accrue de fleurs augmente aussi les ressources disponibles pour les populations d'abeilles et d'autres insectes floricoles. Il est probable que les effets de concentrations accrues en CO_2 sur la biologie florale des plantes aura des conséquences importantes, bonnes ou mauvaises, sur les systèmes entomophiles. Les données de la littérature montrent que le comportement des pollinisateurs peut être directement affecté par un léger accroissement du niveau de CO_2. Pour connaître ces conséquences, il est nécessaire d'étudier les plantes en présence des pollinisateurs dans des conditions de CO_2 élevé.

***Vicia faba* / nectar / dioxyde carbone / changement climatique / longévité fleur**

Zusammenfassung — Nektar-und Blütenproduktion bei *Vicia faba* (Pferdebohne) bei normalem und bei erhöhtem Kohlendioxid-Gehalt in der Umgebung. Nach einer Vorhersage könnte sich der Gehalt des atmosphärisches Kohlendioxid bis zum Jahr 2100 verdoppeln. Erhöhte CO_2 Konzentrationen hat bei den meisten untersuchten Pflanzen eine erhöhte Photosyntheserate zur Folge, wobei das zusätzliche CO_2 für das Wachstum und die Vermehrung der Pflanzen genutzt wird. Häufig ist die Ernte von Samen oder Früchten bei erhöhtem CO_2 verbessert, die Blütenbiologie könnte aber ebenfalls beeinflußt werden, was Folgen für die Bestäubung der insektenabhängigen Pflanzen haben könnte. Einige Arten zeigen bei erhöhtem CO_2 eine erhöhte Blütenproduktion und Blühdauer, aber es wurden keine Untersuchungen über die Nektarproduktion gefunden. Bei *Vicia faba* wurden deshalb der florale Nektarertrag (Volumen, Konzentration und Gewicht des Zuckers pro Blüte), die Anzahl der Blüten und die Blühdauer untersucht. Die Pflanzen der Pferdebohne wuchsen in zwei bienenfreien Versuchsräumen: einer bei normalem CO_2-Gehalt der Umgebung (350 $\mu L \cdot L^{-1}$), der andere mit erhöhtem CO_2 -Gehalt (700 $\mu L \cdot L^{-1}$).Altersmarkierte Blüten (1 - 8 Tage) wurden entfernt, ihr Entwicklungsstadium (Tabelle I) notiert und der Nektar mit einer Mikrokapillare (0,5 µL, 1 µL oder 5 µL) extrahiert. Die Länge der Nektarsäule in der Kapillare wurde gemessen, um das Nektarvolumen (µL pro Blüte) zu bestimmen. Die Konzentration des Nektars (%; g Saccharose pro 100 g Lösung) wurde mit einem Taschenrefraktometer bestimmt. Das Zuckergewicht (mg pro Blüte) wurde aus dem Volumen und der Konzentration berechnet (Prŷs-Jones und Corbet, 1991). Die Lebensdauer von allen Blüten auf alternierenden Knoten von 10 Pflanzen (die nicht für Nektaruntersuchungen besammelt waren) wurden bei beiden CO_2 Behandlungen notiert. Jeden Nachmittag wurden die Knospen im Stadium 0-1 markiert und ihre Entwicklungszeit täglich zwischen 16.00 und 18.00 Uhr protokolliert, bis sie verwelkt waren (Stadium 8). Die Gesamtzahl der Blüte pro Pflanze wurde für jede einzelne Pflanze bestimmt, bis alle abgeblüht waren. Der Nektarertrag betrug zwischen 0 und 3,44 µL Nektar pro Blüte mit einer Konzentration von 6 - 50% (0-1,01 mg Zucker pro Blüte). Die CO_2 Behandlung zeigte keinen deutlichen Einfluß auf die Zuckermenge pro Blüte. Das Alter der Blüten hatte dagegen einen signifikante Wirkung auf das Zuckergewicht pro Blüte (Tabelle II): 3-5tägige, vollständig geöffnete Blüten enthielten mehr Nektar als jüngere oder ältere Blüten (Abb 1 und 2). Pflanzen, die unter erhöhtem CO_2 gewachsen sind, hatten im Durchschnitt 156,8 (±9,2) Blüten pro Pflanze. Das sind signifikant mehr als bei normalem CO_2-Gehalt gewachsenen Pflanzen, die 124,8 (±13,1) Blüten hatten. Bei erhöhtem CO_2 Gehalt hielten sich die Blüten signifikant länger (7 statt 6 Tage) und blieben 4 statt 3 Tage in voller Blüte. Entsprechend hatte eine Pflanze, die unter erhöhtem CO_2 gewachsen waren, an jedem beliebigen Tag signifikant mehr offene Blüten als die Normalpflanzen (Abb 3). Demnach ist es wahrscheinlich, daß *V faba* Pflanzen, die unter erhöhtem CO_2 wachsen, insgesamt mehr Nektar produzieren als unter Normalbedingungen. Das würde sie, in Kombination mit erhöhtem Blütenangebot, attraktiver für Bestäuber machen (im Vergleich zu anderen Pflanzen, die nicht in gleicher Weise reagieren). Das bedeutet nicht notwendigerweise eine Erhöhung der Pollenverbreitung. Eine erhöhtes Blütenangebot wird auch die Nahrungsquellen für die Populationen von Bienen und anderen sich von Blüten ernährenden Insekten erhöhen. Die Effekte von erhöhten CO_2-Konzentrationen auf die Blütenbiologie von Pflanzen haben wahrscheinlich wichtige Konsequenzen, gute oder schlechte, auf das System der Bestäubung durch Insekten. In der Literatur gibt es ebenfalls Hinweise, daß das

Bestäuberverhalten von geringfügigen Erhöhungen des CO_2-Gehaltes direkt beeinflußt wird. Um diese Folgen genauer zu erforschen, sind weitere Versuche mit Pflanzen zusammen mit ihren Bestäubern unter erhöhter CO_2 Atmosphäre nötig.

***Vicia faba* / Kohlendioxid / Klimawechsel / Nektar / Blühdauer /**

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