Oecologia (Berlin) (1983) 57:311–315

Oecologia

Photosynthesis by flowers in *Encelia farinosa* and *Encelia californica* (Asteraceae)

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Summary. Photosynthetic rates by flowers of the shrubs *Encelia farinosa* and *E. californica* were studied during three phenological stages of flower development. Both gross photosynthesis and dark respiration rates in the flowers were of similar magnitude and decreased with floral development. Floral photosynthetic rates were saturated by an irradiance equivalent to one half full noon sunlight. Net photosynthesis of flowers was rarely positive and decreased substantially with increased flower temperature. Gas exchange by the flower was unaffected by the water vapor pressure gradient. These results are analyzed in terms of the microclimate experienced by the flowers and the relative contribution of floral photosynthesis to the economy of the flower.

Introduction

The process of flowering is generally considered to be an energetic cost to a plant and is often quantified by comparison with the energy tied up in the entire plant. Thus, reproductive effort is often described as the ratio of reproductive to total plant biomass. Recently, Bazzaz and Carlson (1979) and Bazzaz et al. (1979) have pointed out that there is an error in this estimate since it ignores any photosynthetic contribution of the reproductive structures themselves. The phototsynthetic CO_2 exchange of reproductive structures has been investigated in a variety of species: annual crops (Flinn et al. 1977, Laval-Martin et al. 1977, Tieszen and Imbamba 1978, Oliker et al. 1978, Constable and Rawson 1980), tree crops (Bean et al. 1963), annuals (Bazzaz and Carlson 1979), and deciduous trees (Bazzaz et al. 1979). The consensus from these studies is that net photosynthetic exchange of flowers and fruits is close to zero. That is, the gross photosynthetic rate of the flower almost exactly offsets the respiration rate. This is quite interesting since during development the respiration rate may vary substantially.

Most of the previous studies on floral and fruit photosynthesis have been conducted under essentially constant environmental conditions (high irradiance, moderate temperature), and, thus, it is difficult to separate the actual from the potential carbon contributions of the reproductive structure to its development. In the study by Bazzaz et al. (1979), however, photosynthesis was measured at the air temperature equal to the mean maximum daily temperature for that period of the growing season. These data allow one to determine seasonal trends, but do not reveal any patterns that may appear on a diurnal basis.

With this in mind, the photosynthetic gas exchange characteristics by reproductive structures of two allopatric shrub species, *Encelia farinosa* and *E. californica* were studied. These species were chosen because they are known to occur in contrasting thermal environments with different diurnal air temperature and relative humidity amplitudes (Ehleringer 1977; Ehleringer and Björkman 1978; Ehleringer and Mooney 1978). *Encelia farinosa* occurs throughout the hot, dry Sonoran Desert in an environment which is characterized by large diurnal temperature fluctuations, whereas *E. californica* occurs in the cooler, wetter region of coastal California, where diurnal temperature fluctuations are moderated by a maritime influence. Both species exhibit copious flowering following vegetative growth.

Methods

Seeds of *E. farinosa* and *E. californica* used for this study were germinated and grown in a glasshouse. Gas exchange (CO_2 and water vapor) of the flowers was measured using an open gas exchange system similar to that described by Ehleringer and Björkman (1977). Gas exchange cuvettes were designed to allow insertion of a flower while maintaining its natural orientation. Measurements were made during three distinct phases of flowering: 1) Bud stage – before any petals appear; 2) Mid-flowering – pollen release period; 3) Post-flowering – after pollen production had ceased and petals had wilted. The ambient CO_2 concentration was maintained at about 330 $\mu l\, l^{-1}$ throughout all photosynthetic measurements. Because of the difficulties in determining surface areas of flowers, CO_2 exchange is expressed in units of nmol CO_2 per gram dry weight per second.

The response of flowers to changes in irradiance was measured on flowers from 3–4 shrubs of each species during each flowering phase. These experiments involved initial exposure of flowers to an irradiance of about 1.8 mmol $m^{-2}\, s^{-1}$ (400–700 nm) until a constant photosynthetic rate was obtained. The light was then decreased in steps to total darkness allowing the photosynthetic rate to equilibrate at each point. Photosynthesis-light response measurements were also collected on the peduncle alone and with the peduncle coated with silicon grease to isolate differences between these parts.

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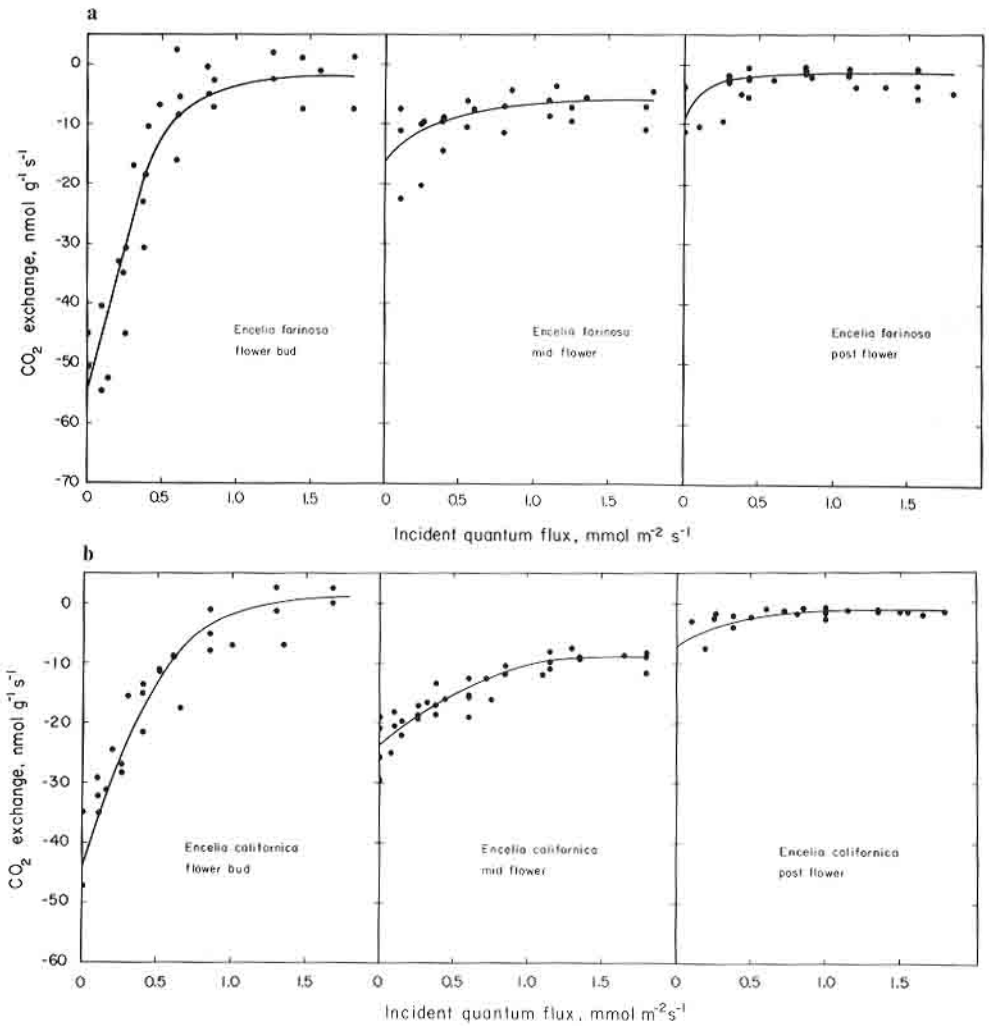

Fig. 1 a, b. Light response of net photosynthesis in the three phenological phases of flower development for **a** *Encelia farinosa* and **b** *Encelia californica*. Measurements were made at a flower temperature of 25° C, 330 $\mu l\, l^{-1}$ CO_2, and 21% O_2. Quantum flux represents that incident on a horizontal surface at flower height. Measurements were made on 3–5 flowers of each phenological phase. Curves were fitted by eye

The response of flowers to changes in temperature was measured on flowers from 3–5 shrubs of each species during each flowering phase. Temperature responses were measured at saturating irradiances and in the dark to compare the effect of temperature on net photosynthesis to its effect on dark respiration. The flowers were initially exposed to low temperatures until a constant photosynthetic rate was obtained. The temperature was then increased in steps until about 45° C, allowing the photosynthetic rate to equilibrate at each step.

The response of flowers to changes in vapor pressure deficit was measured on flowers from 3 shrubs of *E. californica* during the mid-flowering stage. These studies involved exposing the flowers to saturating irradiances and different vapor pressure deficits while maintaining the flowers at 20° C. The flowers were initially exposed to very low VPDs. The VPD was then increased in steps allowing the photosynthetic rate to equilibrate at each point. Unfortunately, a lack of flowering *E. farinosa* plants prevented the measurement of *E. farinosa* flowers' response to vapor pressure deficits.

Chlorophyll content was measured on petals, disk flowers, involucral bracts and peduncles during each stage in order to delineate the centers of active photosynthesis in the flowers. Chlorphyll content was determined in 80% acetone as described by Arnon (1949).

Statistical comparisons of the data were made using the Students t-test.

Results and discussion

Photosynthesis-light responses for flowers from *E. farinosa* and *E. californica* were very similar. Flowers of both species displayed low net gas exchange rates and were saturated at moderate light levels (0.8–1.2 mmol $m^{-2}s^{-1}$ quantum flux), strongly implying that the flowers would be light saturated throughout almost the entire day. As the flowers developed, both dark respiration and gross photosynthesis decreased, resulting in response curves saturating at progressively lower irradiances (Fig. 1). Dark respiration decreases significantly between flower bud and mid-flower stages for both *E. farinosa* ($P<0.01$) and *E. californica* ($P<0.05$) and between mid-flower and post-flower for *E. californica* ($P<0.01$) (Fig. 2). Although dark respiration decreased substantially during development, net photosynthesis never became more than slightly positive. This is because gross photosynthesis decreased significantly between the flower bud and mid-flower stages in *E. farinosa* ($P<0.001$) and between all three stages in *E. californica* ($P<0.05$). There were no significant differences between CO_2 exchange rates of corresponding stages of the two species. The pattern of decreasing respiration and gross photosyn-

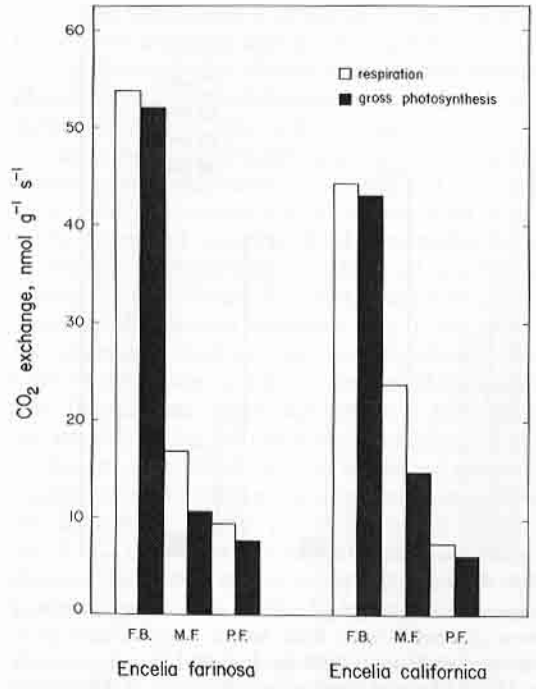

Fig. 2. Dark respiration and gross photosynthesis rates of *Encelia farinosa* and *E. californica* flowers during different phenological stages. Gross photosynthesis was measured at saturating quantum flux. *F.B* flower bud, *M.F.* mid-flower, *P.F.* post-flower

thesis by the flowers of both *E. farinosa* and *E. californica* as they mature is consistent with the results of Bazzaz et al. (1979). However, absolute CO_2 exchange rates in *Encelia* ranged from -35 to -60 nmol CO_2 g^{-1} s^{-1} for bud respiration. These were greater than the maximum values of about -30 nmol CO_2 g^{-1} s^{-1} reported by Bazzaz et al. (1979). These greater rates may be related to either the higher, overall leaf photosynthetic and growth rates observed in *Encelia* species or to the shorter time period of fruit development (Ehleringer and Björkman 1978).

The response of net photosynthesis in *Encelia* flowers is clearly dominated by the temperature dependence of dark respiration. During each flowering stage, net photosynthesis exhibited a strong negative relationship to temperature (Fig. 3). Dark respiration displayed a negative linear response to flower temperature. The slopes of the temperature dependence of photosynthesis and respiration approached zero as flowering progressed, reflecting the pattern of decreasing dark respiration and gross photosynthesis with flower maturity. Net photosynthesis became positive only at lowest temperatures (below 10° C), where the rate of dark respiration was lowest. During the late spring when *Encelia* are in flower, the flower temperatures are not normally that low. Ehleringer (1977) reported that at the time when each species was in flower that air temperatures during the daylight hours fluctuated between 12–25° C at the *E. californica* site and between 16–32° C at the *E. farinosa* site. If we assume that floral temperature was equal to air

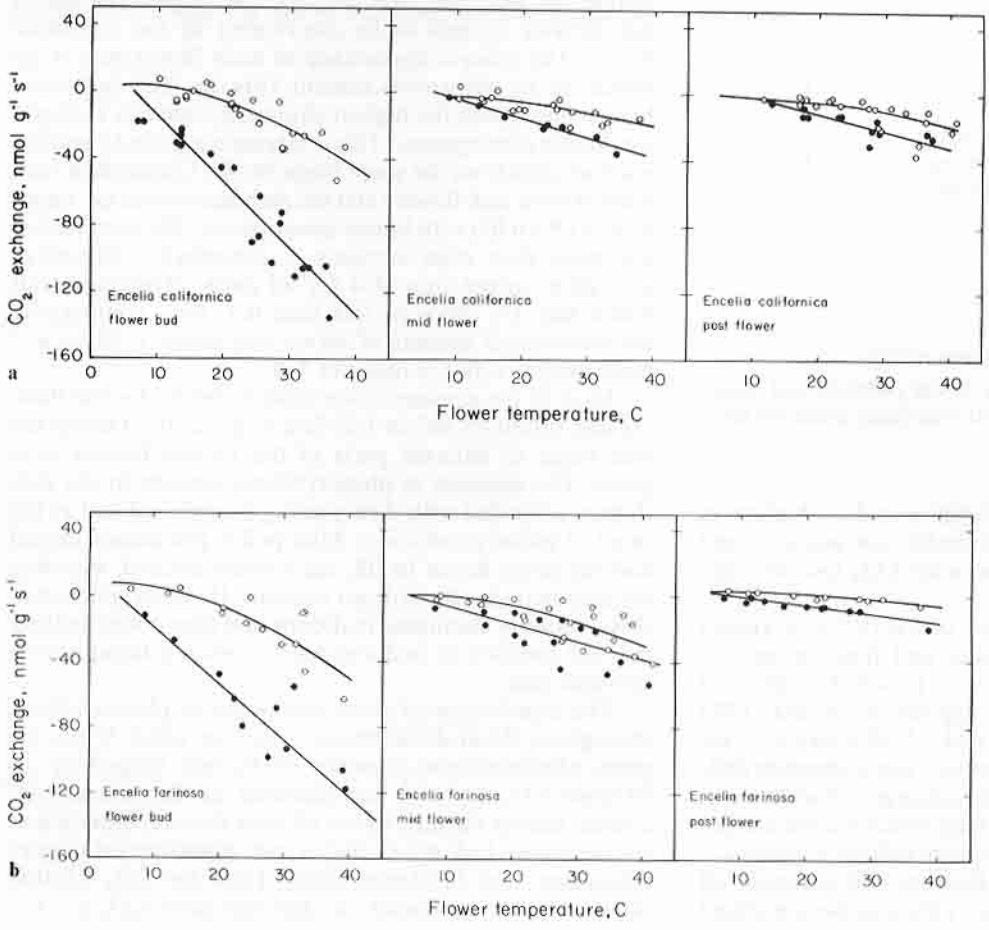

Fig. 3a, b. Temperature response of net photosynthesis (open circles) and dark respiration (closed circles) of **a** *Encelia farinosa* and **b** *Encelia californica* flowers. Regressions for the net photosynthesis responses are: *E. farinosa* flower bud, $y=8.97-0.0379\ T^2$ with $r^2=0.67$; mid flower, $y=0.71-0.019\ T^2$ with $r^2=0.54$; post flower, $y=3.97-0.006\ T^2$ with $r^2=0.90$; *E. californica* flower bud, $y=6.11-0.0\ 3\ T^2$ with $r^2=0.73$; mid flower, $y=-1.19-0.012\ T^2$ with $r^2=0.45$; post flower, $y=-0.07-0.011\ T^2$, with $r^2=0.56$. Regressions for the dark respiration responses are: *E. farinosa* flower bud, $y=13.66-3.42\ T^2$ with $r^2=0.66$; mid flower, $y=3.8-1.07\ T$ with $r^2=0.48$, post flower, $y=5.17-0.553\ T$ with $r^2=0.88$; *E. californica* flower bud, $y=21.7-3.89\ T$ with $r^2=0.89$; mid flower, $y=8.48-1.17\ T$ with $r^2=0.94$; post flower, $y=9.08-1.05\ T$ with $r^2=0.74$. All gas exchange measurements were done at saturating light intensities and with 330 $\mu l\ l^{-1}$ CO_2. Measurements were made on 3–5 flowers of each phenological phase. All regressions are significant ($P<0.01$)

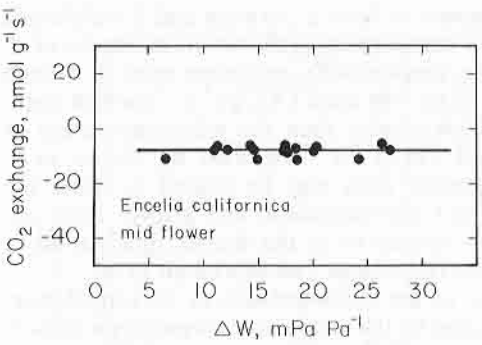

Fig. 4. Vapor pressure deficit response of net photosynthesis of *Encelia californica* flower during the mid-flower stage. All measurements were made at saturating light intensities, 330 µl l^{-1} CO_2, 21% O_2, and flower temperatures of 20° C. Measurements were made on 3 flowers

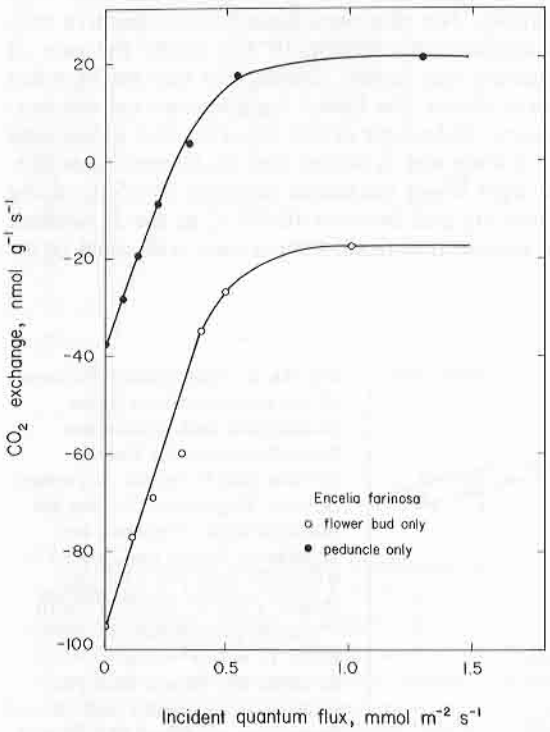

Fig. 5. Photosynthetic light response in the peduncle and flower bud of *Encelia farinosa*. Measurements were made under the same conditions as Fig. 1

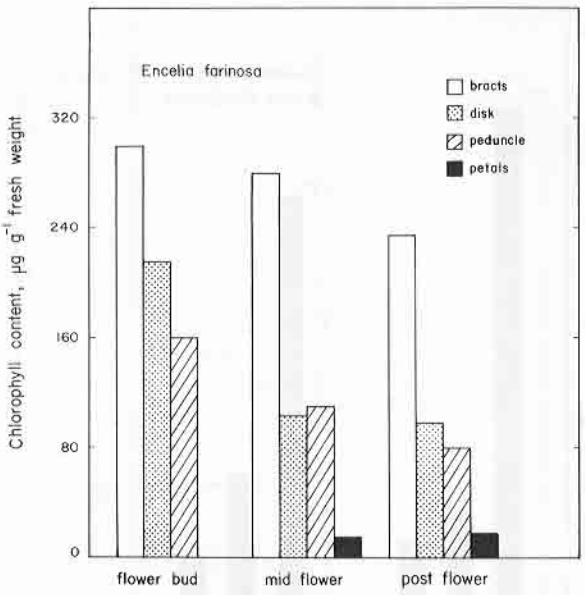

Fig. 6. Development of chlorophyll content in floral structures of *Encelia farinosa* expressed on a fresh weight basis. Chlorophyll content decreased significantly between bud and flower stages in disk flowers ($P<0.01$) and peduncles ($P<0.01$). Chlorophyll content of leaves is about 1,700 µg g^{-1} fresh weight. Chlorophyll content of the petals is not significantly different from 0 ($P>0.2$)

temperature, then net CO_2 exchange would be highest in the early morning hours (but probably not positive) and would then decrease, remaining at a net CO_2 loss throughout the day.

The atmospheric vapor presure deficit (VPD) is known to affect leaf stomatal conductance and thus the gas exchange of leaves. During the flowering period, *E. californica* and *E. farinosa* flowers may be exposed to diurnal VPD fluctuations of 9–15 mPa Pa^{-1} and 15–45 mPa Pa^{-1}, respectively (Ehleringer 1977). However, vapor pressure deficit had no significant effect on gas exchange in *Encelia* flowers (Fig. 4). Net photosynthetic rates remained unchanged over the entire range of vapor pressure deficits measured.

The involucral bracts, disk flowers, and peduncle all displayed photosynthetic activity. This was demonstrated by measuring the light response of photosynthesis in flowers and peduncles separately. A clear dependence of CO_2 exchange on light was seen (Fig. 5). The largest portion of this activity appears to be contributed by the involucral bracts. The relative importance of each flower part is reflected in its chlorphyll content (Fig. 6). The involucral bracts maintained the highest chlorphyll contents throughout flower development. This is interesting in that the flowers nod quickly as the seeds begin to fill. Chlorophyll contents of both disk flowers and the peduncle decreased significantly ($P<0.05$) with flower development. The petals never had more than trace amounts of chlorphyll. Chlorophyll a/b ratios ranged from 3–4 for all parts, excepting petals which had a/b ratios of less than 0.5. As a comparison, the chlorophyll content of leaves was about 1,700 µg g^{-1} fresh weight, with a/b ratios of 3–4.

Most of the photosynthate contributed by *Encelia* flowers was produced before full flowering occurs. During the bud stage, all external parts of the *Encelia* flowers were green. The decrease in photosynthetic activity in the disk flowers coincided with their turning brightly colored at the onset of pollen production. After pollen production ceased and the seeds began to fill, the flowers nodded, exposing the involucral bracts to direct sunlight. However, photosynthetic capacity continued to decline and thus it was unlikely that the function of nodding was to enhance floral photosynthetic rate.

The significance of these low levels of photosynthesis throughout floral development is not yet clear. While the gross photosynthetic capacity of flowers ranged up to 80 nmol CO_2 g^{-1} s^{-1} and declined as temperature increased during the day, leaves of both *Encelia farinosa* and *E. californica* had much higher net photosynthetic rates (Ehleringer and Björkman 1978). These net CO_2 fixation rates were on the order of 200–400 nmol CO_2 g^{-1} s^{-1}

under full irradiance, depending on the amount of leaf pubescence (Ehleringer and Björkman 1978).

To illustrate the relative contribution of flowers to the photosynthate pool of the entire plant, four *Encelia farinosa* shrubs in flower were collected near the Ibex Mountains in California and divided into various components (Ehleringer, unpublished data). The total leaf and flower weights were used in conjunction with measured field photosynthetic rates and assumed light absorption by the canopy to provide a conservative estimate of total photosynthetic uptake for each shrub. The maximum total gross photosynthesis by the flowers averaged only 1.5% (S.E. = 0.585) of the calculated total net leaf photosynthesis. The contributions of the flowers is further decreased by diurnal temperature fluctuations. How significant is this contribution to the overall fitness of the individual plant? Photosynthesis by flowers appears capable of offsetting much of the respiration costs after the initial investment in a floral structure has been made. From previous studies, this can account for 2.3% to 64.5% of the total carbon required by the flowers (Bazzaz et al. 1979), but for *Encelia* species is not known.

Acknowledgments. This work was supported by NSF Grant No. DEB81-13136. Kenneth Werk was also supported by a postgraduate scholarship granted by NSERC.

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Received November 1, 1982