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Effect of reproduction on nitrogen allocation and carbon gain in *Oenothera biennis*

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Summary

1 Reproduction in *Oenothera biennis* has been shown to decrease growth in young plants, whereas reproduction in older plants temporarily increases growth and has no negative effect on growth in the long term. The causes of these variable effects were investigated by examining the effect of reproduction upon photosynthetic rate, leaf area production, chlorophyll content and nitrogen allocation in young versus old plants grown at low versus high nutrient availability.

2 Reproduction was controlled experimentally by gibberellic acid applications, and measurements were made at three developmental stages: bolting, flowering, and capsule maturation. At each stage, measurements were also made on corresponding vegetative plants of the same age.

3 Reproduction decreased nitrogen allocation to roots and increased allocation to shoots. The decrease in root allocation was greater at low nutrient availability. Reproduction increased leaf area and, at bolting, the magnitude of this increase was greater in plants grown at high nutrient availability. Reproduction generally decreased photosynthetic rates, chlorophyll content and nitrogen content of leaves. The magnitude of the decreases was usually less for plants grown at high nutrient availability. Photosynthetic rate increased with reproduction for older plants grown at high nutrient availability in the latter part of the experiment.

4 We suggest that differences among *Oenothera biennis* individuals in the effect of reproduction on carbon gain are related to differences in extent of nutrient reserves. Older plants and plants grown at high nutrient availability have greater nutrient reserves upon which to draw when reproduction is initiated. Reproduction in younger plants grown at lower nutrient availability will rapidly deplete nutrient reserves and nutrients which are part of the photosynthetic apparatus (e.g. the nitrogen within the chlorophyll molecule) will have to be mobilized to supply reproductive structures. Reproduction in this latter case will therefore have more of a detrimental effect on photosynthetic rate and leaf area production.

Keywords: cost of reproduction, life history theory, resource allocation, reproductive effort, size dependent reproduction, time of reproduction

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Introduction

Timing of reproduction in monocarpic perennials is determined to a large extent by plant size: reproduction is postponed until a minimum critical size is reached. Presumably, this critical size is determined by the relationship between plant size and reproductive output, by the demographic cost of postponing the time when offspring themselves will reproduce, and by the risk of not surviving to a future time period (Schaffer 1974; Stearns 1977; Young 1981; Silby & Calow 1986; Lacey 1986). This approach assumes that plant size at reproduction is a good predictor of the resources available for reproduction. Plant size at reproductive maturity is closely correlated with reproductive output in a variety of different species (Samson & Werk 1986; Weiner 1988; Thompson, Weiner & Warwick 1991; Shipley & Dion 1992). There are also correlations between plant size at the time reproduction is initiated and reproductive output in monocarpic perennials (Gross 1981; Reinhartz 1984). However, in spite of these correlations, there is still

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substantial variation in the minimum critical size required for reproduction even within a given population. This has led to attempts to include other factors in addition to size in predicting time of reproduction (Lacey 1986).

One factor that has not yet received the attention it deserves is the extent to which vegetative growth continues after reproduction is initiated in monocarpic plants. Since much of the vegetative growth of some monocarpic plants is actually concurrent with reproduction (see King & Roughgarden 1982a,b; Chiariello & Roughgarden 1984), plant size at the time reproduction is initiated is not necessarily a good predictor of the resources available for reproduction. Indeed, since reproduction involves substantial changes in allocation patterns and physiological processes, the rate of growth before reproduction may bear little relation to the rate after reproduction has been initiated. Studies with iterocarpic perennials suggest that reproduction generally decreases the rate of vegetative growth, but these effects are highly variable depending upon environmental conditions, species, and plant genotype (Antonovics 1980; Jurik 1985; Reekie & Bazzaz 1987a,b; Karlsson *et al.* 1990; Reekie 1991; Reekie & Bazzaz 1992). This variation in the effect of reproduction on growth may be one of the factors responsible for the wide variation in size required for reproduction in monocarpic species. Assuming a given level of reproductive output must be achieved and that reproductive output is proportional to the resources captured in vegetative growth, reproduction should occur at a smaller size when reproduction has less of a negative effect upon growth. Therefore, to understand the factors controlling time of reproduction, it is necessary to understand why reproduction has variable effects upon growth.

The present study is a continuation of a earlier study of the effect of reproduction on growth in *Oenothera biennis* (Reekie & Reekie 1991). This species is a short lived monocarpic perennial commonly found in recently disturbed or low nutrient habitats with an open canopy (Hall *et al.* 1988). It exists as an acaulescant rosette in the vegetative state, and forms elongate stems bearing leaves, flowers and capsules in the reproductive state. As vernalization is required, it does not normally reproduce in its first year. Reproduction also requires the plant to reach a minimum critical size. Thus, depending upon growth rates, reproduction may take place in the second, third, or subsequent years of growth. Reproduction can also be induced artificially in unvernalized plants by applying gibberellic acid (GA). Gibberellic acid is a naturally occurring plant growth regulator that induces many rosette-forming plants to undergo stem elongation and to flower (Salisbury & Ross 1978).

Reekie & Reekie (1991) examined the effects of reproduction upon growth in *Oenothera biennis* by inducing reproduction experimentally in vegetative rosettes through gibberellic acid applications. It was found that early reproduction decreases growth compared to vegetative controls, while late reproduction increases growth temporarily, and has no negative effect upon growth in the long term. It was postulated that these contrasting effects are a function of differences in level of mineral reserves among plants of different ages. The present study tests this hypothesis by examining the effect of reproduction upon leaf area, photosynthesis, and nitrogen allocation in young versus old plants grown at either low or high nutrient availability.

Materials and methods

Seeds were collected from a 2-year-old successional field located in Kings County, Nova Scotia (45°06′N, 64°24′W). Seeds were collected in the spring from seed stalks formed the previous year. Plastic flats filled with a commercial potting soil (ASB-Greenworld Ltd. Point Sapin, New Brunswick) were used for seed germination. Flats were placed in a growth chamber that provided a 25/15 °C day/night temperature, a photosynthetic photon flux density of 100 μmol m^{-2} s^{-1}, and a 14-h photoperiod. A second batch of seeds was germinated 15 days after the first, following the same procedures, to produce two cohorts of seedlings.

At the cotyledon stage, 72 plants from each cohort were transplanted into plug trays (4 cm^3 $seedling^{-1}$) using the same soil as used in germination flats. Plants were placed in a glasshouse, which provided natural light levels (maximum irradiance 1800 μmol m^{-2} s^{-1}) and temperatures ranging from 15 to 30 °C. The experiment was conducted over the period from 1 May to 5 September. When the first true leaves were fully emerged the plugs were transplanted into 1.35-L azalea pots containing one part sand to one part turface (Aimcor, Deerfield, IL). Turface is an inorganic growing medium consisting of compressed clay particles and has a minimal nutrient content. Nutrients were supplied by watering with a soluble fertilizer (Plant-Products, Brampton, Ontario) at a concentration of 200 p.p.m. Initially a 15:30:15 N:P:K formulation was used, but on day 27 the fertilizer was changed to a 20:20:20 formulation. Both formulations were complete fertilizers supplying both macro- and micro-nutrients. Nutrients were applied twice a week until day 44 of the experiment, after which the low nutrient treatment plants received applications once every two weeks. The high nutrient treatment continued to receive applications twice a week until the end of the experiment. Starting on day 57, a 1000 p.p.m. solution of gibberellic acid (GA_3) was sprayed on half of the plants in each treatment to induce flowering. The GA was applied daily until bolting occurred. All GA-treated plants flowered and produced seed, while plants that did not receive GA remained vegetative. Pots were rotated among pos-

itions within the glasshouse twice a week to minimize possible position effects.

Reproductive plants were harvested at three stages: bolting (day 93), flowering (day 117) and capsule maturation (day 128). Capsule maturation in this instance refers to the stage at which capsules were rapidly expanding in size and is the point at which the resource drain upon vegetative structures is likely to be at its maximum. At each harvest, vegetative plants of the same age and nutrient treatment were also harvested for comparison. There were six replicates of each of the eight treatments (2 cohorts × 2 nutrient levels × 2 reproductive states) at each harvest. Net photosynthesis, leaf area, leaf chlorophyll content, and dry weight of component parts were determined at each of the three harvests. Nitrogen content of individual plant parts was determined for plants in the final harvest.

Net photosynthesis of the most recent fully emerged leaf was measured with a gas exchange system (LI-6250, LI-COR, Lincoln, NB). Plants were placed in a growth chamber providing a photosynthetic photon flux density of 700 μmol m^{-2} s^{-1}, and a 20 °C temperature one hour prior to measurements to allow acclimatization. Air from outside the building was pumped into the growth chamber to maintain ambient CO_2 levels. The analyser was calibrated daily with a 400 μL CO_2 L^{-1} gas stream. The gas exchange system was placed in the open mode to allow the leaf to equilibrate with chamber conditions and to adjust flow through the desiccant column to maintain ambient vapour pressure. The system was then placed in the closed mode for measurements. All measurements were completed within an 8-h period and finished before 18.00 hours on the day of the harvest.

Leaf area (leaf blade and petiole) was determined with a leaf area meter (LI-3100, LI-COR, Lincoln, NB). The most recent fully emerged leaf was ground up with a homogenizer (IKA Labortechnich, Staufen, Germany), added to an 80% acetone solution for four minutes and centrifuged in a cuvette. A spectrophotometer (4049-011, Novaspec, LKB Biochrom Ltd, Cambridge, UK) was used to measure absorption of the resulting solution at 652 nm. Conversion to mg of chlorophyll per leaf was done as described by Ross (1974). Plant material was dried for at least two days at 50 °C, then weighed separately as roots, stem, vegetative and reproductive leaves (i.e. leaves produced before versus after bolting), and reproductive parts (i.e. buds, flowers, and capsules). Plant material was ground to pass through a 1-mm-mesh screen using a grinding mill (CYCLOTEC 1093, Tecator, Hoganas, Sweden) and a 150–200-mg subsample was used for nitrogen determination using an elemental analyser (CHN-1000, LECO, St. Joseph, MI).

From the raw data, mg of chlorophyll cm^{-2} leaf, mg nitrogen cm^{-2} leaf and proportion of nitrogen allocated to various plant parts were calculated. Data were analysed by analysis of variance using the general linear models procedure of SAS (Statistical Analysis System, Cary, NC). It was a completely random experimental design and a factorial treatment design. Separate analyses were conducted for each harvest. Unless otherwise stated, the 0.05 level of probability was used for all tests of significance.

Results

Reproduction resulted in a marked decrease in the nitrogen allocated to roots ($P < 0.0001$), and a marked increase in stem allocation ($P < 0.0001$) (Fig. 1). On average, there was also a slight decrease in N allocation to leaves with reproduction ($P < 0.0001$). The decrease in root allocation with reproduction was greater at the lower level of applied nutrients ($P < 0.0320$ for the interaction). The increase in stem allocation with reproduction was greater for cohort two than cohort one ($P < 0.0010$ for the interaction). Increasing the level of applied nutrients increased N allocation to leaves in cohort one, but not in the younger cohort ($P < 0.0181$ for the interaction). In reproductive plants, allocation to reproductive structures (i.e. flowers and fruits) was approximately 22% of total plant nitrogen averaged across treatments. Reproductive allocation was greater in plants grown at low nitrogen ($P < 0.0250$ for the interaction).

Regardless of harvest time, leaf area increased with

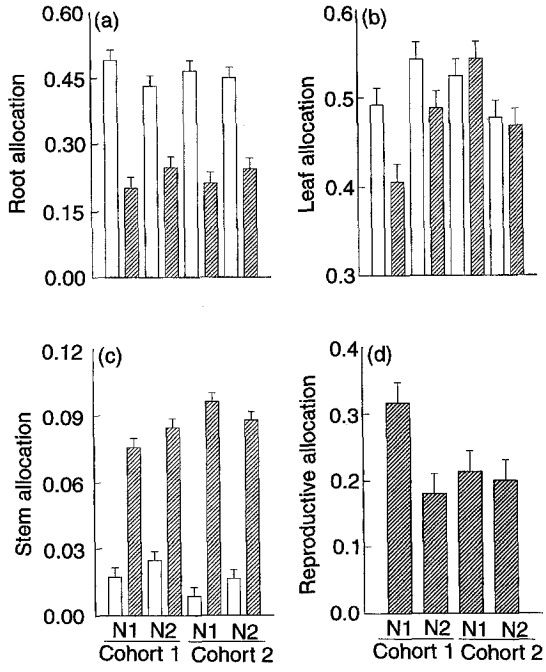

Fig. 1 Proportion of total plant nitrogen allocated to: (a) roots, (b) leaves, (c) stems and (d) reproductive parts in vegetative (open bars) versus reproductive (hatched bars) plants at capsule maturation. There were two cohorts, grown at either low (N1) or high (N2) nutrient availability. Error bars depict one standard error of a single treatment mean.

level of applied nutrients and was greater in the first cohort than the second ($P < 0.05$) (Fig. 2). The nutrient effect was greater for plants in the second cohort at bolting ($P < 0.0016$ for the interaction) and greater for plants in the first cohort at capsule maturation ($P < 0.0155$). Leaf area generally increased with reproduction ($P < 0.05$), but at bolting, this increase was small or absent for plants grown at the low level of applied nutrients ($P < 0.0476$ for the interaction). There was also a marginally significant three way interaction among age, level of applied nutrients and reproductive state at flowering; the increase in leaf area with reproduction was greatest in the case of the older plants grown at high nutrients ($P < 0.0593$).

In leaves produced after bolting, nitrogen content per unit area increased with nutrient availability ($P < 0.0001$) and age of cohort ($P < 0.0034$), and decreased with reproduction ($P < 0.0001$) (Fig. 3). Reproduction ($P < 0.0001$) and nutrients ($P < 0.0001$) also had similar effects in the case of leaves produced before bolting. However, the decrease with reproduction was more pronounced at low nutrient availability ($P < 0.0292$ for the interaction).

Chlorophyll content increased with level of applied nutrients at flowering ($P < 0.0001$) and at capsule maturation ($P < 0.0001$) (Fig. 4). This increase was greater in the younger cohort at flowering ($P < 0.0027$). Reproduction generally decreased chlorophyll content at flowering ($P < 0.0034$) and at capsule maturation ($P < 0.0437$). The magnitude of this decrease was less, or was entirely absent in the case of plants grown at the high level of applied nutrient in the last harvest ($P < 0.0317$ for the interaction).

Photosynthetic rates increased with level of applied nutrients in the latter two harvests ($P < 0.0001$) (Fig. 5). The younger cohort had higher photosynthetic rates at bolting ($P < 0.0206$), but was not significantly different from the older cohort in the latter two harvests. Reproduction generally decreased photosynthesis at bolting ($P < 0.0105$), flowering ($P < 0.0001$) and capsule maturation ($P < 0.0087$).

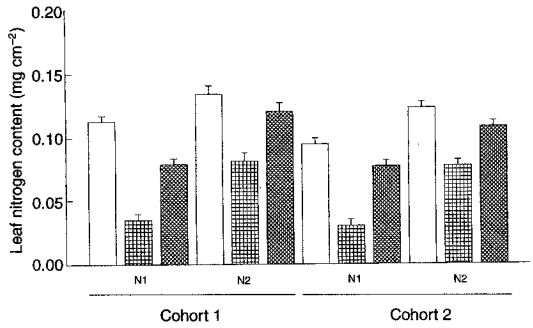

Fig. 3 Nitrogen content of leaves in vegetative (open bars) versus reproductive plants at time of capsule maturation. Leaves on reproductive plants were divided into two categories: those produced before bolting (cross hatched bars) and those produced after bolting (diagonal cross hatched bars). There were two cohorts, grown at either low (N1) or high (N2) nutrient availability. Error bars depict one standard error of a single treatment mean.

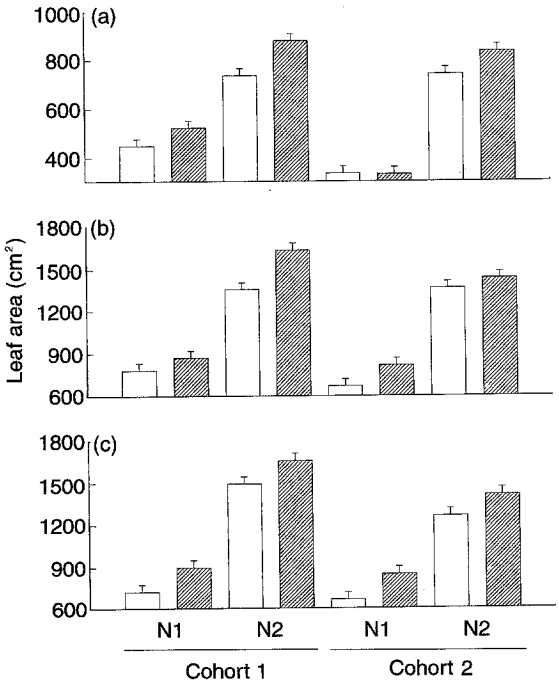

Fig. 2 Leaf area of vegetative (open bars) versus reproductive (hatched bars) plants at three reproductive stages: (a) bolting, (b) flowering, and (c) capsule maturation. There were two cohorts, grown at either low (N1) or high (N2) nutrient availability. Error bars depict one standard error of a single treatment mean.

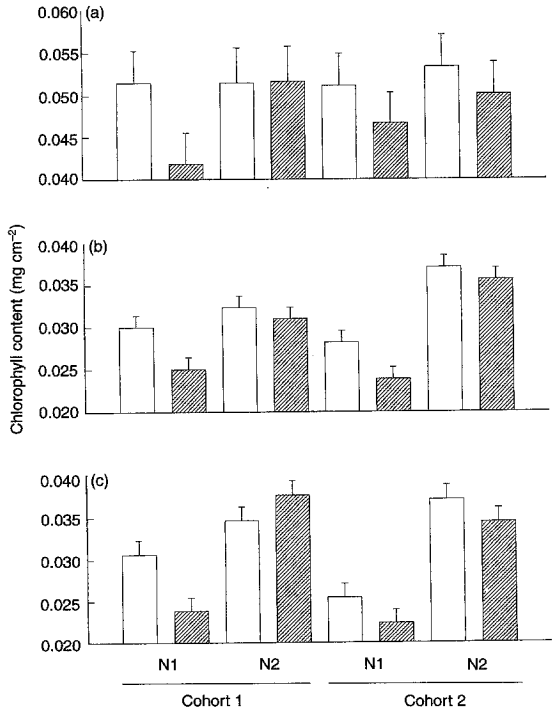

Fig. 4 Chlorophyll content of vegetative (open bars) versus reproductive (hatched bars) plants at three reproductive stages: (a) bolting, (b) flowering, and (c) capsule maturation. There were two cohorts, grown at either low (N1) or high (N2) nutrient availability. Error bars depict one standard error of a single treatment mean.

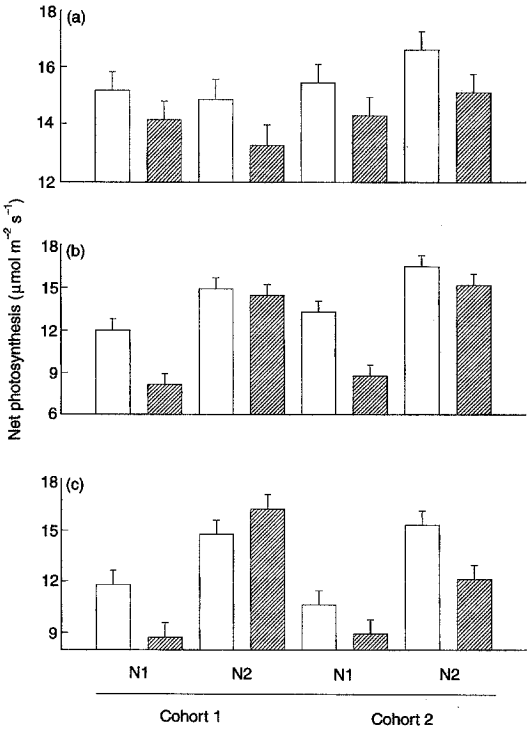

Fig. 5 Net photosynthesis of the most recent fully emerged leaf of vegetative (open bars) versus reproductive (hatched bars) plants at three reproductive stages: (a) bolting, (b) flowering, and (c) capsule maturation. There were two cohorts, grown at either low (N1) or high (N2) nutrient availability. Error bars depict one standard error of a single treatment mean.

However, there was no decline in photosynthesis at the high level of applied nutrients in the older cohort at capsule maturation ($P < 0.0130$ for the interaction). Photosynthesis decreased less with reproduction at the high level of applied nutrients in the second harvest ($P < 0.0053$).

Discussion

A review of the literature suggests that reproduction is unlikely to have a significant negative impact upon carbon gain, for a variety of reasons. Reproductive structures often contain chlorophyll and are active photosynthetically, and thus may supply a significant proportion of their own carbon requirements (Maun 1974; Bazzaz *et al.* 1979; Werk & Ehleringer 1983; Williams *et al.* 1985; Heilmeier & Whale 1987). Reproductive meristems and developing seeds are strong metabolic sinks, and increases in sink size can enhance photosynthetic rate in vegetative structures (Burt 1964; Neales & Incoll 1968). This reproductive enhancement of photosynthesis can compensate, and under some conditions, even over-compensate, for the carbon allocated to reproduction (Reekie & Bazzaz 1987a). Reproduction may also increase resource allocation to leaves (Reekie & Bazzaz 1992) and so increase whole plant photosynthesis.

In the case of *Oenothera biennis*, reproduction has been shown to increase carbon gain through its effects on leaf morphology and canopy structure (Reekie & Reekie 1991). Vegetative rosettes produce elongate leaves with a petiole to prevent self shading. Due to stem elongation, self-shading is less of a problem in reproductive plants. These plants produce short leaves with no petiole. Because of the low area to weight ratio of the petiole, reproductive leaves have a much higher specific leaf area than vegetative leaves. In older plants, the increase in specific leaf area with reproduction is sufficient to compensate for the reduction in leaf allocation associated with reproduction, and total leaf area is maintained or even increased. These effects upon leaf area can compensate for the carbon allocated to reproduction and total growth may actually increase slightly with reproduction.

Given that reproduction tends to enhance the carbon assimilation capacity of the plant, it follows that the detrimental effects of reproduction upon growth are probably associated with its impact upon the uptake of other resources (i.e. water and mineral nutrients). In the present study, water availability was not limiting; plants were grown in large pots (1.35 L) and watered as required. Of the various mineral nutrients, nitrogen is likely to have been the most limiting. Nutrients were supplied by watering with a complete fertilizer solution which had a relatively low nitrogen content (15:30:15 or 20:20:20 N:P:K). Nitrogen availability has a marked impact upon the carbon assimilation capacity of plants. Nitrogen is an integral part of the chlorophyll molecule and is part of the various structural and enzymatic proteins required for photosynthesis. As a result, the rate of photosynthesis is linearly related to nitrogen content of leaves and leaf area production is closely correlated with nitrogen availability (Field 1986; Evans 1989).

Given the relationship between nitrogen and carbon assimilation, the contrasting effects of reproduction in *Oenothera biennis* at low versus high nutrient availability, are easily explained. Reproduction involves the re-allocation of nitrogen from roots and leaves to stems, flowers and fruits (Fig. 1). The depletion of nitrogen reserves within the roots was greater, and a larger proportion of total nitrogen was allocated to reproduction, at low nutrient availability (Fig. 1a,d). This resulted in a greater re-mobilization of metabolically active nitrogen in the leaves as reflected in the greater decrease in leaf nitrogen (Fig. 3) and chlorophyll (Fig. 4b,c) with reproduction at low nutrient availability. As a consequence, photosynthetic rate declined more with reproduction at low, than at high nutrient availability (Fig. 5b,c).

Similarly, the contrasting effects of reproduction on growth in young versus old plants (Reekie & Reekie 1991), can also be explained in terms of nitrogen allocation. In monocarpic perennials, reserves of nitrogen and other mineral nutrients accumulate with plant age. For example, in *Arctium tomentosum*, 20%

of the nitrogen required for reproduction is supplied by reserves accumulated in the roots during the first year of growth (Heilmeier *et al.* 1986). Young plants therefore have fewer reserves which are more likely to be depleted by reproduction and require the mobilization of metabolically active nitrogen. This will deprive the photosynthetic apparatus of needed resources and so reduce carbon assimilation.

In the present study, differences among age classes were small relative to those observed in the previous study (Reekie & Reekie 1991). This is probably a reflection of the smaller range of ages examined in the present study. Nevertheless, there were differences between the two cohorts in their response to reproduction. Younger plants allocated a larger proportion of total nitrogen to stems with reproduction (Fig. 1c). This supports the idea that reproduction depletes N reserves to a greater extent in young plants. Furthermore, both leaf area (Fig. 2a,b) and photosynthetic rate (Fig. 5c) exhibited a more positive response to reproduction in the older cohort, particularly at high nutrient availability.

Although the present study only examines the relationship between reproduction and carbon gain in *Oenothera biennis*, the results have more general implications. We suggest that because of the potentially beneficial effects of reproduction upon photosynthetic surface area and photosynthetic rate that have been documented in a variety of species, the negative effects of reproduction upon growth will generally be less at high nutrient availability. Studies with several other species support this conclusion. Heilmeier and co-workers examined lifetime carbon and nitrogen balance in the monocarpic perennial, *Arctium tomentosum* (Heilmeier *et al.* 1986; Heilmeier & Whale 1987). They suggest the decrease in vegetative biomass they observed during seed filling was a direct consequence of nitrogen re-allocation and the effect this had on carbon gain. Sinclair & De Wit (1975) examined the photosynthate and nitrogen requirements for seed production in a variety of crop species. They found that the nitrogen requirements for seed production often exceed rate of nitrogen uptake and that nitrogen must be re-mobilized from vegetative structures to support reproduction. They predict that this re-mobilization will result in the 'self-destruction' of the plant at low levels of nitrogen availability.

The idea that reproduction has different effects upon growth depending upon level of N reserves has implications for understanding the factors controlling time of reproduction. Attempts to explain variation in reproductive timing have largely focused on the demographic characteristics of the populations involved, i.e. variation in survivorship schedules and how this may select for different life histories (Schaffer 1974; Stearns 1977; Young 1981; Silby & Calow 1986; Lacey 1986). These studies clearly illustrate the importance of survivorship patterns in explaining genetic differentiation in reproductive timing. However, much of the life history variation observed in the field has an environmental, rather than a genetic basis (see literature reviewed in Bazzaz & Ackerly 1992). Traditional life history theory was developed to explain genetic differentiation among populations and does not directly address environmental variation (Bazzaz & Ackerly 1992). It can only be used to explain phenotypic plasticity in life history characteristics if an individual can 'predict' the probability of its continued survival, and the likely success of its offspring in different environments. Although this is possible, i.e. survivorship may be closely correlated with environmental cues such as resource availability, it is more parsimonious to explain phenotypic variation in terms of direct environmental effects. The present study provides one example of such direct effects. Since reproduction has negative effects upon carbon gain at low nutrient availability, a larger minimum critical size will be required to produce a given level of reproductive output, than at high nutrient availability. Therefore, in low nutrient environments, reproduction may be postponed to allow plant size to increase to a larger size than would be the case in high nutrient environments. Simple physiological mechanisms such as these, may help explain the wide phenotypic variation found in the size required for reproduction in many monocarpic plants.

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