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Experimental ecology of *Dryas octopetala* ecotypes. V. Field photosynthesis of reciprocal transplants

J. B. McGraw

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The response of photosynthesis to reciprocal transplanting was measured in 1980, 1981, and 1986 in two genetically-distinct populations of *Dryas octopetala*, a circumpolar dwarf shrub. Contrary to expectation, photosynthetic rates were lowest in “home” environments and highest in “foreign” sites. Also, “native” plants had lower photosynthetic rates than “alien” plants. A “rapid-transplant” experiment showed that the observed pattern was not caused by environmental differences between sites at the time of measurement, but rather by the long-term response of transplants to the environment. These results, in combination with the results of an analysis of the fitness response to transplanting (published elsewhere), caution against assuming that a positive relationship always exists between photosynthetic rate and fitness. Integrated measures of carbon gain may be more appropriate as measures of plant performance.

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1. Introduction

Of the physiological traits that vary among plant populations, primary ecological importance is often attributed to photosynthesis (Hiesey and Milner 1965). This assumption seems justified by the central role of photosynthesis in the carbon economy of plants (Mooney 1972). If plant growth rate is defined as net dry weight gain per unit time, net photosynthesis (on a whole-plant basis) for the same time period is proportional to plant growth rate (Osmond et al. 1980). Moreover, growth rate is often positively correlated with fitness, at least in theory (McGraw and Wulff 1983).

Numerous studies have demonstrated the existence of variability among populations in photosynthetic properties. Populations vary with respect to effects of temperature (Fryer and Ledig 1972, Machler and Nosberger 1977, Teramura and Strain 1979), light (Holmgren 1968, Gauhl 1976, Teramura and Strain 1979), and drought (Al-Ani et al. 1972) on leaf photosynthetic rates. Fewer published studies have sought such vari-

ation and failed to find it (but see McNaughton et al. 1974, Kemp et al. 1977, and Clough et al. 1979).

The majority of studies demonstrating population-level variation in photosynthesis have been carried out in “common environments” (usually greenhouse or growth chambers). The more powerful reciprocal transplant design (Clausen et al. 1940) allows determination of components of phenotypic variance among populations. Mooney and Billings (1961) simulated such a reciprocal transplant design in a growth chamber study with arctic and alpine populations of *Oxyria digyna*. Although a formal analysis of variance was not presented, both genetic and environmental effects on net photosynthetic rate were evident. A simulated reciprocal transplant was also carried out in growth chambers with bog and alpine populations of *Ledum groenlandicum* (Riebesell 1981), with similar results. However, photosynthetic responses of plants grown under controlled conditions do not necessarily correspond to their responses in field-grown plants, as has been clearly demonstrated with C₃ and C₄ tidal marsh species (DeJong et

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al. 1982). It is therefore surprising that photosynthetic measurements have not been reported for field reciprocal transplants, where native and alien plants are exposed to normal seasonal changes in the environment and multifactorial differences between sites.

In the present study, I determined the photosynthetic response of ecotypes to a field reciprocal transplant experiment with the arctic shrub, *Dryas octopetala* L. (Rosaceae). A concurrent study showed that survival, growth and potential seed production (i.e., collectively approximating fitness) over eight growing seasons was highest for ecotypes transplanted to home sites (McGraw 1982, McGraw and Antonovics 1983a, 1983b, McGraw, in press). My null hypothesis was that maximum photosynthetic rates at peak season would parallel the observed fitness response to transplanting, i.e., maximum photosynthetic rates would be highest for plants grown in home sites. Maximum photosynthetic rate was chosen as an index of the photosynthetic response since it sets the theoretical limit of photosynthetic yield (Avery 1977).

2. Methods

2.1. Study site and plant materials

Reciprocal transplants and photosynthetic measurements were conducted near Eagle Summit at mile 106 on the Steese Highway in an unnamed mountain range of interior Alaska (65°25'N 145°30'W; elevation 1050 m). The 6 ha study site encompassed a snow-free ridgetop (fellfield) and an adjacent area of late-lying snow (snowbed) (see McGraw and Antonovics 1983a or Miller 1982, for detailed description). *Dryas octopetala*, a circumpolar, dwarf shrub species, is found throughout the snowbank study site. However, two distinct ecotypes reach greatest abundance in snowbed and fellfield zones, with very little overlap in distribution (McGraw and Antonovics 1983a). In a narrow strip between the fellfield and snowbed, intermediate forms may be found which are genetically different from either extreme form (McGraw and Antonovics 1983a). Fellfield plants have small (5–15 mm) deciduous leaves and a compact mat-forming growth habit. Snowbed plants have larger leaves (15–50 mm) that often persist and function photosynthetically for two growing seasons. The growth habit of snowbed plants tends to be more clonal than that of the fellfield ecotype, with lower shoot densities and extensive adventitious rooting from the woody stems. The snowbed ecotype is found primarily in Alaska and probably evolved from the fellfield form during the Pleistocene (Hultén 1959).

2.2. Reciprocal transplants

In late July, 1979, adult plants from each of the two *D. octopetala* populations were transplanted to fellfield and

snowbed sites (n=10 for each treatment). Transplants to "home" sites for each ecotype served as controls for transplants to alien sites. Some soil was transferred with each plant to minimize root damage. A zone 2–4 cm wide was cleared of vegetation around each transplanted individual. The surrounding plant community was otherwise undisturbed. Plants were watered once immediately following transplanting and then allowed to become established.

2.3. Photosynthesis measurements

Maximum photosynthetic rate was measured on leaves of *D. octopetala* with a portable apparatus designed to deliver $^{14}\text{CO}_2$ to an intact leaf enclosed in a cuvette (Shimshi 1969, Tieszen et al. 1974). Photosynthetic measurements were made by enclosing a leaf in the cuvette and exposing the leaf to labelled air for 30 s. Leaf discs of known area were then excised from the labelled leaf and immediately placed in a mixture of 0.5 ml methanol and 0.5 ml phenethylamine in scintillation vials (Bigger and Oechel 1982). The methanol-phenethylamine mixture killed the tissue, preventing release of assimilated ^{14}C through respiration, and dissolved ^{14}C -labelled products of photosynthesis. The samples were stored for counting at a later date.

Temperature and light measurements were made in order to ensure that the field exposure technique would give consistent estimates of maximum photosynthetic $^{14}\text{CO}_2$ uptake. All photosynthesis measurements were made on leaves oriented perpendicular to direct incoming irradiance. No measurements were made on leaves exposed to a photosynthetic photon flux density of less than $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Air temperatures varied less than 4°C over the course of any one experiment. Measurements of the time course of leaf temperatures for a leaf enclosed in the leaf cuvette showed that leaf temperature increased only 1.45°C after 30 s. Therefore temperature effects on photosynthetic rates during the measurement interval were presumed to be negligible.

Samples were prepared for counting by the procedure of Bigger and Oechel (1982) and counted with a Beckman LS-250 Liquid Scintillation Counter. Due to quench problems, every sample was spiked with a known radioactivity to determine a counting efficiency for each sample. Photosynthetic rates were then calculated according to Tieszen et al. (1974).

Maximum photosynthetic rate was measured on August 10, 1980 and August 3, 1981 on adult *D. octopetala* plants in each of the populations which were transplanted reciprocally in 1979. The 1980 measures were performed on 5 replicate leaves within each population in each site. In 1981, ten replicate leaves were taken per population in each site. In both years, all measurements were made on one day in order to minimize variability arising from daily variations in environmental factors. In 1981, 5 leaves per treatment were measured in the morning and the remainder were measured in the after-

noon to eliminate possible effects of time of day on photosynthetic rates.

2.4. Rapid transplant experiment

Photosynthetic rate in the reciprocal transplant experiment may be determined by the effect of the environment accumulated over long periods of time (1 or 2 yr), intermediate lengths of time (days or months) or by immediate differences between environments at the time of measurement. To distinguish the effects of immediate environmental differences from longer term effects, one plant each of the snowbed and fellfield ecotypes was placed in a pot and rapidly "transplanted" by physically moving the pot from one site to the other. Plants transplanted in this way were allowed to adjust to each site for 15 minutes before photosynthesis was measured; enough time to allow photosynthetic rate to respond to the slight environmental change. These "rapid transplant" measurements were made on 4 August, 1981, one day after measurements on long-term transplants.

3. Results and discussion

The hypothesis that maximum photosynthetic rates would be highest in the home site for ecotypes in a reciprocal transplant experiment was refuted. Although maximum photosynthetic rates were generally higher in 1981 than in 1980, the overall trends were the same in both years (Fig. 1). Maximum photosynthetic rates were lower in the home site than in a foreign site for both ecotypes. In addition, maximum photosynthetic rates were lower for the native ecotype than for the alien ecotype at both sites. A two-way analysis of variance of the

Tab. 1. Results of two-way analysis of variance on maximum photosynthetic rates in the long-term reciprocal transplant experiment (Type III sums of squares are shown).

Year	Source of variation	df	SS	F	P
1980	Site	1	2.01	0.21	0.66
	Ecotype	1	1.54	0.16	0.70
	Site × ecotype	1	59.25	6.05	0.02
1981	Site	1	22.36	1.26	0.27
	Ecotype	1	30.35	1.71	0.20
	Site × ecotype	1	165.09	9.32	0.004

data revealed no significant overall differences in photosynthetic rates between sites or ecotypes (Tab. 1). However, the trends noted above were revealed statistically as a significant interaction between site and ecotype in both years ($p < 0.05$). This pattern of photosynthetic response was consistent between years and was exactly opposite to the response of fitness components (growth, survival, and fitness) of the same plants in the same two year period (McGraw and Antonovics 1983a).

The observed response to transplanting was apparently not a response to differences between aerial environments at the time measurements were being made: there was no effect of site in the rapid transplant experiment. This is not surprising since differences in temperature (fellfield; 13.1°C, snowbed; 14.6°C), wind speed (fellfield; 17–50 km h⁻¹, snowbed; 0–25 km h⁻¹), and irradiance (no measureable difference) measured at the time of the experiment were minimal.

In 1986, seven years after the original transplants, net photosynthesis was measured with a Li-Cor LI-6000 infra-red gas analysis system. Due to low sample size ($n=5$ for each treatment) and variable light conditions during measurement, the variability in photosynthetic rate was high. However, there was a trend toward an interaction between ecotype and site with the same pattern as the 1980 and 1981 results (2-way ANOVA, $p < 0.10$); photosynthetic rates were lowest in home sites.

The results of the present study, and those of Riebesell (1981), not only contradict the original hypothesis, but they support the opposite hypothesis that photosynthetic capacity would correlate negatively with fitness. Clearly, in the extreme, this second hypothesis cannot be generally true. If it were, plants with a very low maximum photosynthetic rate would have the highest fitness, which cannot be true in the extreme. At the least, however, the present data caution against assuming that an increase in photosynthetic rate necessarily increases plant fitness, or that photosynthetic optima necessarily correspond with fitness optima. Photosynthetic rate on a leaf area basis is negatively correlated with fitness under some field conditions.

The resolution of the apparent dilemma created by these data may lie in the realization that it is the inte-

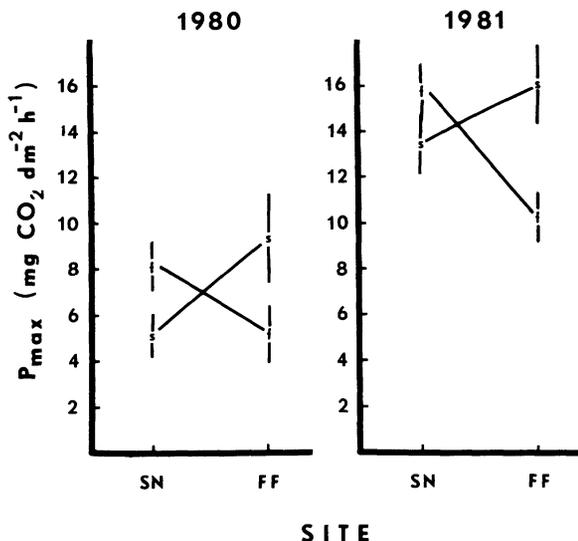


Fig. 1. Maximum photosynthetic rates in the reciprocal transplant experiment. Vertical bars represent 1 standard error. FF and SN refer to fellfield and snowbed sites, respectively. f and s refer to fellfield and snowbed ecotypes, respectively.

grated carbon gain which is relevant to fitness. As suggested by several recent studies, carbon gain integrated over time is more important than instantaneous photosynthetic rates to plant growth and fitness (Chabot and Bunce 1979, Mooney and Gulmon 1979, Bunce et al. 1979, Oechel and Mustafa 1979). In a similar sense, carbon gain integrated over larger parts of the plant than leaves (whole branches, tillers, etc.) may be more relevant to fitness than photosynthesis on a leaf area basis (Garbutt 1986). The present study, in contradicting the original hypothesis, supports the idea that integration of photosynthesis over space and time will be necessary to understand the relationship between photosynthesis and plant performance in natural environment.

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