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REPRODUCTIVE EFFORT IN PLANTS. 1. CARBON ALLOCATION TO REPRODUCTION

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The measurement of the allocation of resources to reproduction in contrasting species and in different environments has been the focus of many recent studies (Bazzaz et al. 1987). These studies were intended to test theoretical predictions of how plants divide their resources between vegetative and reproductive activities. Life history models that consider the effects of juvenile versus adult mortality, for example, predict that in environments in which adult mortality is high relative to juvenile mortality, plants should have a high reproductive effort (RE), whereas in environments where juvenile mortality is relatively high, RE should be lower (for reviews, see Bell 1980; Stearns 1980; Willson 1983).

Although studies have compared the RE of a variety of plants in different environments (see, e.g., Pitelka 1977; Abrahamson 1979; Primack and Antonovics 1982), it is still unclear whether the theoretical predictions are borne out. Some studies have confirmed the predictions, whereas others have produced conflicting results (see discussions in Soule and Werner 1981; Willson 1983). We believe that one of the major reasons for this conflict is the difficulty of assessing RE in plants (Bazzaz and Reekie 1985). Three questions are involved in measuring RE: (1) what structures and activities should be considered part of reproduction; (2) what resource, or combination of resources, should be used as the currency of allocation; and (3) whether resource allocation to reproduction necessarily reflects the cost to the plant in terms of lost growth. In this paper, we address the first question, using carbon as the currency of allocation and with specific reference to *Agropyron repens*. In the second and third papers of this series, we address the other questions.

Reproductive effort is often defined as the proportion of total biomass allocated to seeds and other "obvious" reproductive structures and interpreted as representing the carbon or energy allocation of a plant to reproduction. It is questionable whether biomass allocation to reproductive structures truly represents the total carbon cost of reproduction. Reproduction involves not only the production of flowers and fruits but also the production of various ancillary or support structures, the loss of carbon via respiration, and, in some cases, carbon gain through reproductive photosynthesis (i.e., carbon dioxide fixation by reproduc-

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tive organs together with any enhancement of photosynthesis in vegetative parts caused by the act of reproduction; Bazzaz and Reekie 1985).

Unfortunately, it is not always clear which of the plant's structures and activities should be designated as reproductive. In one sense, all structures and activities are reproductive since the ultimate objective of all plant growth is to produce offspring (see discussion in Thompson and Stewart 1981). But plants differ in the manner in which this ultimate objective is achieved. From the point of view of understanding these differences, the objective of vegetative growth can be described as the accumulation of resources (i.e., the means by which future reproduction is increased), and the objective of reproductive growth as an increase in present reproduction.

From a practical standpoint, it is simpler to determine the structures and activities involved in vegetative growth than the structures and activities necessary for reproduction. Many plants go through a prolonged vegetative state before reproducing; therefore, the structures and activities required for vegetative growth can be determined directly. Since the objective of vegetative growth is the accumulation of resources, vegetative growth can be defined as those parts directly involved in the capture of resources plus all necessary support structures and activities. If we use carbon as the currency of allocation, vegetative growth would include the leaves (as the primary organs involved in the capture of carbon) and that portion of the root and stem material required to support the leaves and any respiration resulting from the production and maintenance of these structures.

The structures and activities necessary to support leaf growth can be determined empirically by examining the rate of respiration in vegetative plants and the allometric relationships between leaves and other plant parts. Extrapolation of the allometric relationships to the leaves of reproductive plants would provide an estimate of the vegetative structures in these plants. The respiration of these structures could be estimated using the respiration rates of vegetative plants. The difference between the total carbon use of the plants and the carbon used in vegetative growth and respiration would provide an indirect measure of the carbon used in reproduction. The ability of the plants to compensate for the cost of reproduction through reproductive photosynthesis could be estimated in a similar fashion by comparing whole-plant photosynthesis with an estimate of vegetative photosynthesis calculated using the leaf area of the reproductive plants and the photosynthetic rates of the vegetative plants.

MATERIALS AND METHODS

The Species

Agropyron repens (L.) Beauv. is a wide-ranging, rhizomatous, perennial grass of Eurasian origin. It exhibits much genotypic and phenotypic variation (Westra and Wyse 1981), and populations subject to different disturbance regimens allocate different proportions of their aboveground biomass to fruiting structures (Werner and Rioux 1977). Vegetative and reproductive plants can be grown in similar environments by appropriate manipulations of the photoperiod. Flowering

TABLE 1

SUMMARY OF TREATMENTS IN EXPERIMENTS I AND II

	EXPERIMENT I		EXPERIMENT II	
FACTOR	Level	Designation	Level	Designation
Photoperiod	14 h	V	14 h	V
	18 h	R	18 h	R
Genotype		*H*		*G*
		M		*K*
		S		*T*
Nutrients	1/10-strength N	LN	1/10-strength N	LN
	1/2-strength N	HN	1/5-strength N	MN
			1/2-strength N	HN
			1/10-strength P	LP
			1/5-strength P	MP
			1/2-strength P	HP
			Full-strength N and P	F
Light	480 $\mu mol\,m^{-2}s^{-1}$	LL		
	1200 $\mu mol\,m^{-2}s^{-1}$	HL		

NOTE.—All factors in each experiment were completely crossed in a factorial-treatment design. The nutrient levels in the table refer to the concentration in an Evan's modified Shive solution (5.0 mM $Ca(NO_3)_2$ and 0.5 mM KH_2PO_4). In experiment I, plants were watered with nutrient solution every third day; in experiment II, they were watered every second day.

requires long days, with a critical photoperiod of about 16 h. Large numbers of plants of the same genotype can be propagated from rhizome cuttings, allowing comparisons of vegetative and reproductive plants of the same genotype.

Experimental Design

We conducted two experiments, each of which involved growing three genotypes at two different photoperiods and various levels of resources (table 1).

In the first experiment, there were two levels of irradiance crossed with two levels of nitrogen. In the second experiment, there were seven resource treatments, four levels of nitrogen, and four levels of phosphorus. The different resource states used in the two experiments were chosen to provide a range of reproductive efforts.

The genotypes used in experiment I were collected in Illinois: *H* from a mowed lawn, *S* from a fencerow bordering a cultivated field in Champaign County, and *M* from a cultivated field in Grundy County. The genotypes used in experiment II were collected in Saskatchewan, Canada: *K* from a cultivated field, *G* from a 6-yr-old hayfield, and *T* from a 30-yr-old pasture. The different genotypes were chosen to provide variation in reproductive effort. There was no intention of using these genotypes to make inferences regarding the populations from which they were drawn (i.e., they were treated as fixed factors in the analysis).

In both experiments, the different genotypes and the two photoperiods were completely crossed with each other and with the various resource treatments, allowing comparison of vegetative and reproductive plants of the same genotype

within each resource treatment. There were eight harvests in the first experiment, with one replication per treatment for the first seven harvests and five replicates for the final harvest. Harvests were spaced at approximately weekly intervals. There were five harvests in the second experiment, with two replicates per treatment at each harvest. The first three harvests were spaced at 2-wk intervals and the fourth and fifth harvests at 3- and 5-wk intervals, respectively.

Plant-Culture Conditions

Plants were propagated from single-node rhizome cuttings 3 cm long. The rhizome material was grown before each experiment from single-node cuttings collected from genotypes in the field and grown in a common greenhouse environment for a period of 6 mo. Plants were grown in plastic pots 12 cm in diameter (1000 cm^3) filled with Turface®. Turface is an inorganic medium (fritted clay) that is porous enough to allow good gas exchange with the atmosphere, making it highly suitable for studies in which the gas exchange of belowground plant parts is to be measured (see, e.g., McCree and Silsbury 1978). The pots were placed in one of two controlled-environment chambers programmed to provide a constant air temperature of 25°C and a relative humidity of 75%. The plants were watered with tap water as required. Nutrients were supplied by watering with Evan's modified Shive solution (Salisbury and Ross 1978) at either 3-day (experiment I) or 2-day (experiment II) intervals.

Both growth chambers were programmed to provide 14 h of high-intensity light (see table 1). The long-photoperiod treatment was produced by providing an additional 4 h of low-intensity light (20 $\mu mol\, m^{-2} s^{-1}$) in one of the chambers. The total quanta of light received during the period of low-light extension was less than 1% of the total light received during the basic photoperiod. To avoid confounding possible chamber effects with photoperiod effects, plants and photoperiod treatments were rotated between chambers at weekly intervals.

The high light level in the first experiment was 1200 $\mu mol\, m^{-2} s^{-1}$. The low light level (480 $\mu mol\, m^{-2} s^{-1}$) was achieved by constructing shade-cloth canopies within the growth chambers. Photon-flux density in the second experiment was 1000 $\mu mol\, m^{-2} s^{-1}$. Constant irradiances at the level of the leaf canopy were maintained over the course of the experiment and between the photoperiod treatments by adjusting the height of the light fixtures above the canopy.

Levels of nitrogen and phosphorus availability were manipulated by changing the concentration of either $Ca(NO_3)_2$ or KH_2PO_4 in the nutrient solution. The levels of calcium and potassium were maintained at the level in a full-strength Evan's solution by appropriate additions of either $CaCl_2$ or KCl. This resulted in some change in the concentration of chlorine anions, but this is unlikely to have had any effect on the plants (see, e.g., Bernstein and Hayward 1958). The four levels of nitrogen availability used in these experiments were 5.0 (F), 2.5 (HN), 1.0 (MN), and 0.5 (LN) mM $Ca(NO_3)_2$, and the four levels of phosphorus were 0.50 (F), 0.25 (HP), 0.10 (MP), and 0.05 (LP) mM KH_2PO_4. The highest-strength solutions of both nitrogen and phosphorus represent the concentrations in a full-strength Evan's solution.

Measurements

Whole-plant dark respiration including that of the roots was measured four times over the course of each experiment using an open infrared gas-analysis (IRGA) system (see Carlson 1983). Each measurement was conducted immediately before one of the harvests, and measurements were made on each harvested plant. The respiration of each plant was monitored for 1–2 h after the plant had reached equilibrium in the chamber. Measurements were made over the course of a 24-h period, and the plants at each measurement interval were selected at random from the various treatments and replications. All measurements were made in the dark (photosynthetic photon-flux density < 1 $\mu mol\, m^{-2} s^{-1}$) and at a temperature of 25°C. Respiration rates in the light were assumed to be the same as those in the dark (Hesketh et al. 1980).

In addition to the whole-plant gas-exchange measurements, net photosynthesis of leaves, stems, and inflorescences was measured separately for each plant part using a semi-closed IRGA system (Bazzaz and Boyer 1972). The net photosynthesis of the leaves in both experiments was measured just before inflorescence emergence. Measurements were confined to recently emerged leaves, and in the case of the reproductive plants, the flag leaf was avoided (the flag leaf in *A. repens* constitutes less than 2% of total leaf area). Net photosynthesis of the inflorescences in experiment I was measured at four stages of development: early anthesis, late anthesis, seed fill, and senescence. In experiment II, gas-exchange measurements of the inflorescences were limited to one measurement of net photosynthesis at early anthesis, the time of maximum photosynthesis. Net photosynthesis of the stems of reproductive plants was measured on day 52 in experiment I and on days 40–43 in experiment II. Photosynthesis was measured at the light levels the plants were grown in, with the various plant parts oriented perpendicular to the light source to obtain comparable measures. Photosynthetic rates were expressed per unit of area in the case of the leaves and per unit of weight for the other plant parts. All gas-exchange measurements were made at a temperature of 25°C.

At every harvest, except the last one in experiment I, the leaf area of each plant was measured using a Licor™ leaf-area meter. The plants were separated into leaves, stems, inflorescences, rhizomes, and roots and oven dried at 65°C for over 48 h before weighing.

Data Analysis

Quadratic growth curves were fit to the logarithmically transformed data of dry weight, leaf area, and respiration versus time data using the techniques of Hunt (1978). Curves were also fit to the dry weight–time data for three different measures of vegetative weight: aboveground biomass excluding inflorescences; total biomass excluding inflorescences; and leaf biomass plus that portion of the stem and root biomass required to support the leaves. The biomass of the leaf-support structures was estimated from the allometric relationships between leaves and roots, between leaves and rhizomes, and between leaves and stems in the vegetative plants. These relationships between leaves and the other plant parts

were estimated by fitting straight-line relationships to the logarithmically transformed data (Hunt 1978). Each of these relationships was fitted to the data as a whole using the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS) with treatments as categorical factors in the analysis. Separate parameter estimates were obtained for each treatment combination.

Using various combinations of the curves described above, a series of derived curves was obtained: relative growth rate (RGR), leaf-area ratio (LAR), net assimilation rate (NAR), whole-plant specific respiration rate (SRR), photosynthetic rate, vegetative respiration, and vegetative photosynthesis. The first three of these curves were derived using the standard formulas (Hunt 1978). Briefly, RGR is growth per unit of time per unit of plant biomass ($g g^{-1} day^{-1}$), LAR is the ratio between leaf area and the total biomass of the plant ($cm^2 g^{-1}$), and NAR is growth per unit of time per unit of leaf area ($g cm^{-2} day^{-1}$). The SRR was defined as the amount of carbon dioxide respired per unit of biomass per unit of time ($g g^{-1} day^{-1}$). The photosynthetic-rate curve was derived by summing whole-plant growth and respiration and expressing the result on a leaf-area basis (i.e., it is a measure of gross photosynthesis expressed in units of $g cm^{-2} day^{-1}$). The vegetative-respiration curve ($g day^{-1}$) is the product of the biomass of the leaves and support structure of the reproductive plants and the SRR of the corresponding vegetative plants. The vegetative-photosynthesis curve ($g day^{-1}$) is the product of the leaf area of the reproductive plants and the photosynthetic rate of the corresponding vegetative plants. To express respiration and growth in the same units, equivalence between dry weight and carbohydrate was assumed and respiration was converted into carbohydrate units using a conversion factor of 1.63, which is the molecular weight of six CO_2 molecules (264) divided by the molecular weight of one carbohydrate unit (162) (Bazzaz and Carlson 1979). Where necessary, confidence limits for the derived values were calculated using approximate methods (Causton and Venus 1981).

Carbon allocation to reproduction was calculated using the above curves. To minimize the propagation of errors involved in lengthy calculations, interactions between main effects not significant at the 0.50 level were removed from the models before the calculations. Biomass carbon allocated to inflorescences was calculated as the difference between total biomass and total biomass excluding inflorescences. Biomass carbon allocated to all reproductive structures was calculated as the difference between total biomass and that of the leaf and leaf-support structures. Cumulative total and vegetative carbon respired over the experimental period was found by integrating the appropriate respiration-time curve. Cumulative reproductive respiration was calculated as the difference between total and vegetative respiration. Reproductive photosynthesis was calculated in the same manner as reproductive respiration, total photosynthesis was calculated as the sum of growth and cumulative total respiration, and vegetative photosynthesis was the integral of the vegetative photosynthesis curve.

The above data were used to calculate five different measures of reproductive effort (RE), as outlined in table 2. The first two represent the most commonly used measures of RE and are based on biomass allocation to "obvious" reproductive structures, using either aboveground biomass (RE1) or total biomass (RE2) to

TABLE 2

SUMMARY OF THE VARIOUS MEASURES OF REPRODUCTIVE EFFORT USED IN THIS STUDY

Measure	Description
RE1	Inflorescence biomass/total aboveground biomass
RE2	Inflorescence biomass/total-plant biomass
RE3	(Inflorescence biomass + reproductive support-structure biomass)/total-plant biomass
RE4	(Inflorescence biomass + reproductive support-structure biomass + reproductive respiration)/(total-plant biomass + total respiration)
RE5	(Inflorescence biomass + reproductive support-structure biomass + reproductive respiration − reproductive photosynthesis)/(total-plant biomass + total respiration − reproductive photosynthesis)

NOTE.—Respiration and biomass carbon were expressed in the same terms by converting respiration values to carbohydrate units and by assuming equivalence between dry weight and carbohydrate.

assess the total resources available to the plant. Reproductive effort 3 (RE3) is similar to RE2, but includes allocation to reproductive support structures as well. The fourth measure, RE4, is perhaps the best measure of the total carbon allocated to reproduction because it takes into account both the biomass and the respiration associated with reproduction. The last measure, RE5, in addition, takes into account reproductive photosynthesis, expressing RE as the net carbon cost of reproduction in relation to the total photosynthesis of the vegetative parts of the plant. It is, therefore, a measure of the carbon cost to the vegetative parts of the plant. Correspondence between these various measures of RE was examined by calculating the rank correlation between pairs of measurements across the various treatments.

Differences between treatments in the gas-exchange rates of separate plant parts were examined by factorial analysis of variance. In the first experiment, there was only one replication for each treatment combination, and the highest-order interaction was therefore used as the error term (Neter and Wasserman 1974). Any interactions between main effects not significant at the 0.50 level were combined with the error term (Carmer et al. 1969).

Unless otherwise stated, the 0.05 level was used to test the significance of effects in all the analyses.

RESULTS

To simplify the presentation of the results, we discuss only those effects involving photoperiod (i.e., reproduction). Many of the effects involving light, nutrients, and genotypes were significant, but they are not directly relevant to our discussion unless they interacted with photoperiod.

Allometric Relationships

Reproduction increased the amount of stem material per unit of leaf weight over all treatments and in both experiments (fig. 1). The magnitude of the increase varied among genotypes in both experiments and among light and nitrogen levels

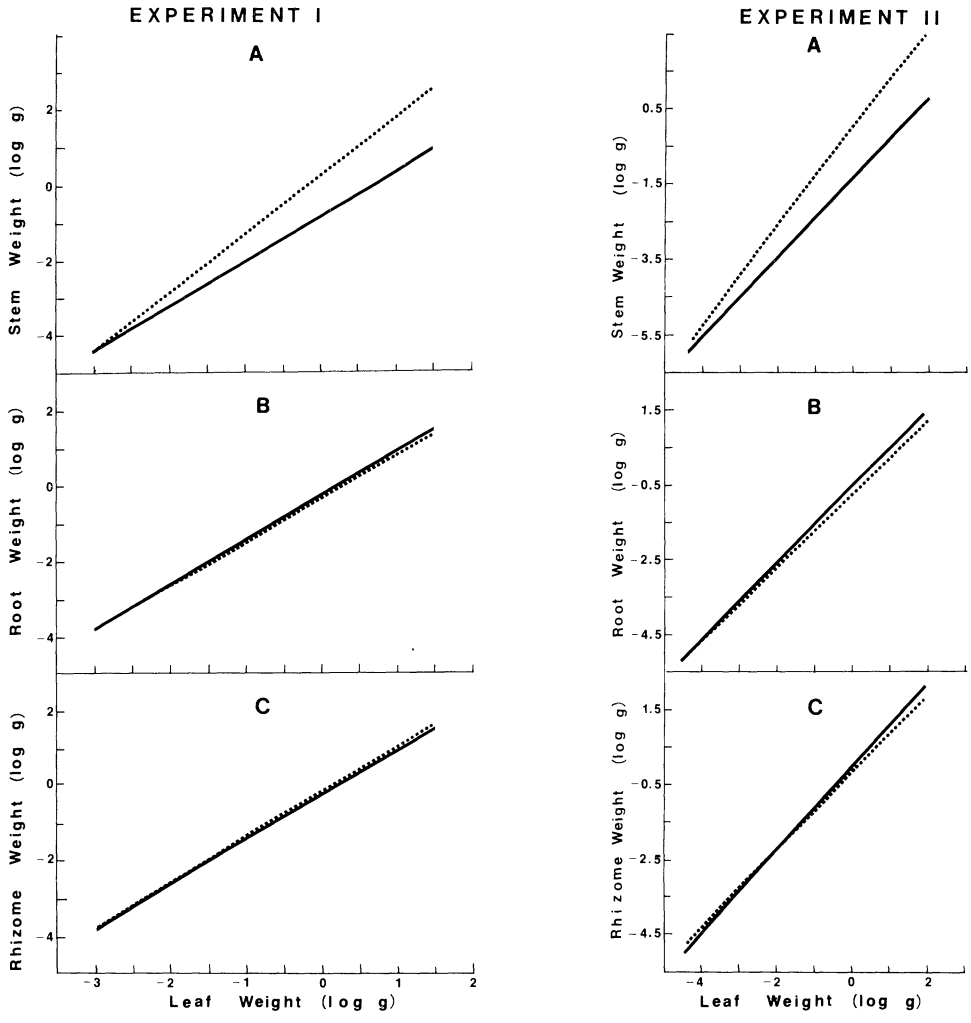


FIG. 1.—Allometric relationships, for plants in experiments I and II, between leaves and other plant parts: *A*, stems; *B*, roots; *C*, rhizomes. The relationships are presented for the main effect of photoperiod: *solid lines*, vegetative plants; *dashed lines*, reproductive plants. The level of significance for differences between the slopes of vegetative and reproductive plants in experiment I were 0.0001, 0.249, and 0.8514 for stems, roots, and rhizomes, respectively. The level of significance for differences between the intercepts were 0.0001, 0.0070, and 0.7574. The level of significance for differences between the slopes of vegetative and reproductive plants in experiment II were 0.0001, 0.0280, and 0.0690 for stems, roots, and rhizomes, respectively. The level of significance for differences between the intercepts were 0.0001, 0.0001, and 0.0670.

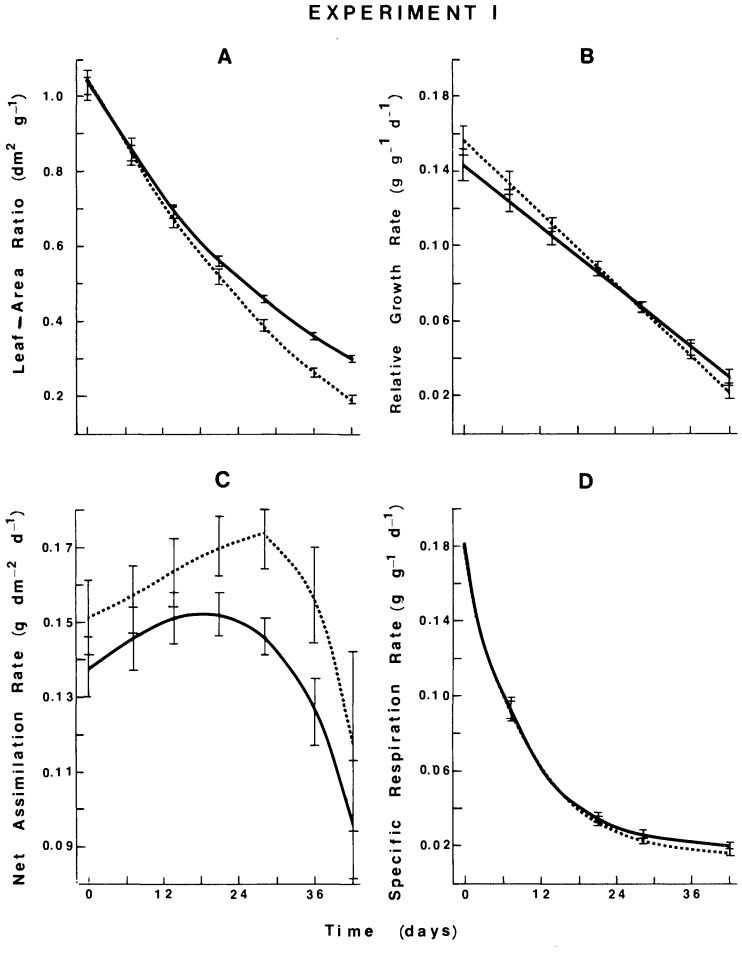
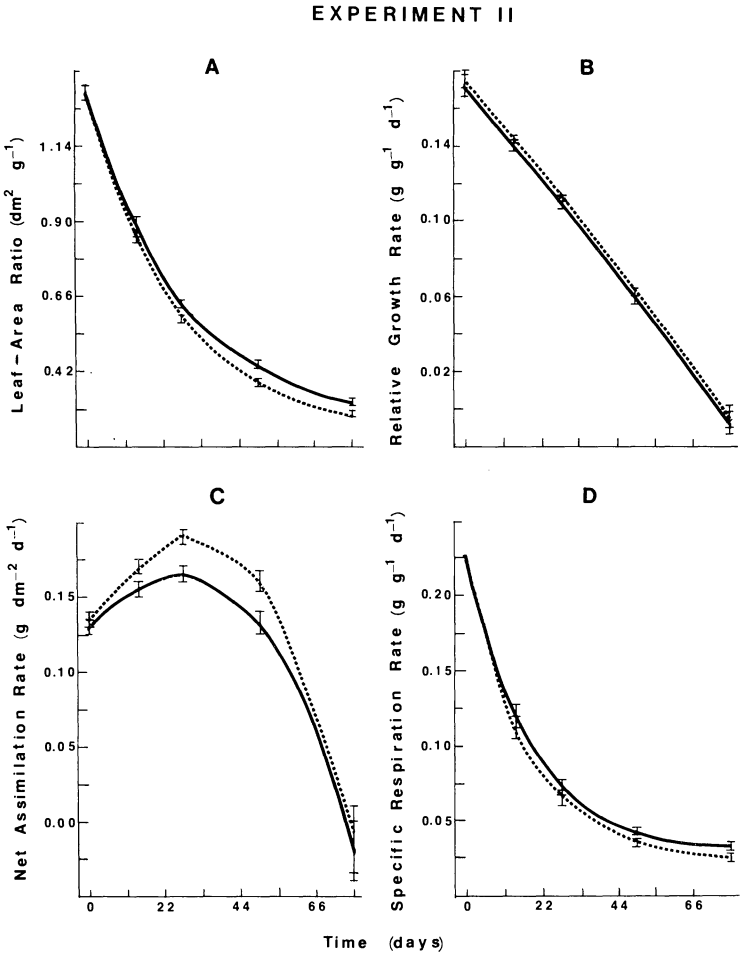


FIG. 2.—Growth-analysis parameters for whole plants in experiments I and II: *A*, leaf-area ratio; *B*, relative growth rate; *C*, net assimilation rate; *D*, specific respiration rate. Values are

in experiment I (Reekie 1985). Reproduction resulted in a slight decrease in the amount of root material per unit of leaf area. There were no significant interactions between photoperiod and any of the other effects. Reproduction did not affect the relationship between rhizomes and leaves.

Growth Analysis

In general, the leaf-area ratio (LAR) declined with reproduction (fig. 2). Reproduction had no significant effect on relative growth rates, however, because the net assimilation rate of the reproductive plants was generally greater than that of the vegetative plants. Reproduction had relatively little effect on the specific respiration rate (SRR). The effect of reproduction on both LAR and the net



presented for the main effect of photoperiod: *solid lines*, vegetative plants; *dashed lines*, reproductive plants. Error bars depict 95% confidence intervals.

assimilation rate (NAR) varied with both genotype and resource level (for details, see Reekie 1985).

CO_2-Exchange Rates of Plant Parts

In experiment I, there was no difference between vegetative and reproductive plants in leaf net photosynthesis as tested by the main effect of photoperiod (fig. 3). However, there were significant interactions of photoperiod with genotype and with light. Photosynthesis increased with reproduction in genotype *H* and decreased in both *M* and *S*. Reproduction increased rates more at low light than at high light.

In experiment II, there was again no significant main effect of photoperiod on

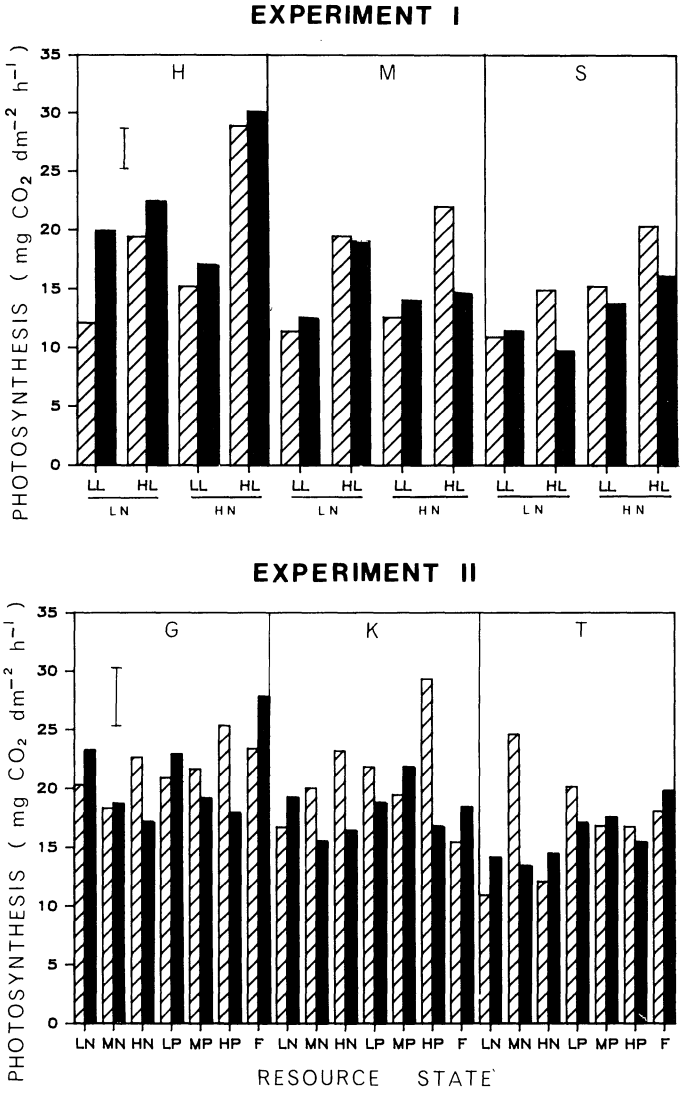


FIG. 3.—Leaf net photosynthesis at time of inflorescence emergence in experiments I and II. See table 1 for key to treatment designations. The error bar represents one-half of 95% confidence interval for a single treatment mean. *Hatched bars*, vegetative plants; *solid bars*, reproductive plants.

leaf net photosynthesis, but there was a significant photoperiod-by-nutrient interaction (fig. 3). Reproduction consistently increased photosynthesis in both the low-nitrogen and full-strength nutrient treatments. Reproduction appeared to lower photosynthesis in the high-phosphorus treatment.

Limited measurements of inflorescence and culm photosynthesis indicate that both the inflorescences and culms were capable of substantial photosynthesis.

The photosynthetic rate of the inflorescences declined markedly with age, but at its maximum (early anthesis), it was about 5.0 mg $CO_2 g^{-1} h^{-1}$. Similar rates were found for the culms (6.2 mg $CO_2 g^{-1} h^{-1}$). Maximum photosynthetic rates for leaves, expressed on a dry-weight basis, were around 30 mg $CO_2 g^{-1} h^{-1}$.

Carbon Allocation to Reproduction

Reproductive effort, measured as the proportion of aboveground biomass allocated to inflorescences (RE1), was relatively small, ranging between 0% and 14% (fig. 4). There were apparent differences between both genotypes and resource treatments. The RE1 of the genotypes in experiment I ranked $H < M < S$, and that in experiment II $K < T < G$. Reproductive effort 1 increased with both light and nitrogen in experiment I and with nitrogen in experiment II. The RE1 of the phosphorus treatments was higher than that of the low-nitrogen treatments but did not increase with the level of phosphorus.

Allocation patterns similar to those of RE1 resulted when RE was calculated as the proportion of total biomass allocated to inflorescences (RE2). The absolute magnitude of the values decreased, but the differences between treatments remained more or less the same (fig. 4). The rank correlation between RE1 and RE2 was 0.99 ($P < 0.0001$) in experiment I and 1.00 ($P < 0.0001$) in experiment II (tables 3, 4).

Including reproductive stem material in the estimate of RE (RE3) substantially increased RE (fig. 4). Values of RE3 ranged between 12% and 45%. Even plants in those treatments in which no inflorescences were produced by the end of the experiment had some reproductive stem material. Dissections of several stem apexes from the nonflowering, long-photoperiod plants in both experiments revealed that these plants were in the process of flowering, but had not yet had time to produce seed. Both experiments were terminated when the majority of the plants had flowered and set seed but before the seed had shattered and dispersed. The rank correlation between RE3 and RE2 was 0.89 ($P < 0.0001$) in experiment I and 0.38 ($P < 0.0826$) in experiment II (tables 3, 4). The correlations between RE3 and RE1 were slightly lower. These weaker correlations were not simply a function of the facts that some plants exposed to the long-photoperiod treatments did not flower and that plants in all treatments showed at least some enhanced stem production. Omission of the nonflowering plants from the analysis did not affect the correlations in experiment I (plants flowered in every treatment except one) and completely removed any correlation between RE3 and either RE1 or RE2 in experiment II (tables 3, 4).

Reproductive effort calculated as the proportion of total carbon allocated to reproduction (RE4) exhibited more or less the same pattern as RE3 and was of a similar magnitude (fig. 4; tables 3, 4). The strong correlation between RE3 and RE4 did not result from a low respiratory requirement; as much as 46% of reproductive biomass in experiment I and 75% in experiment II was used in reproductive respiration.

The magnitude of reproductive photosynthesis varied greatly among genotypes and resource treatments. Genotype *H*, for example, had very high rates of reproductive photosynthesis; reproductive photosynthesis more than compensated for

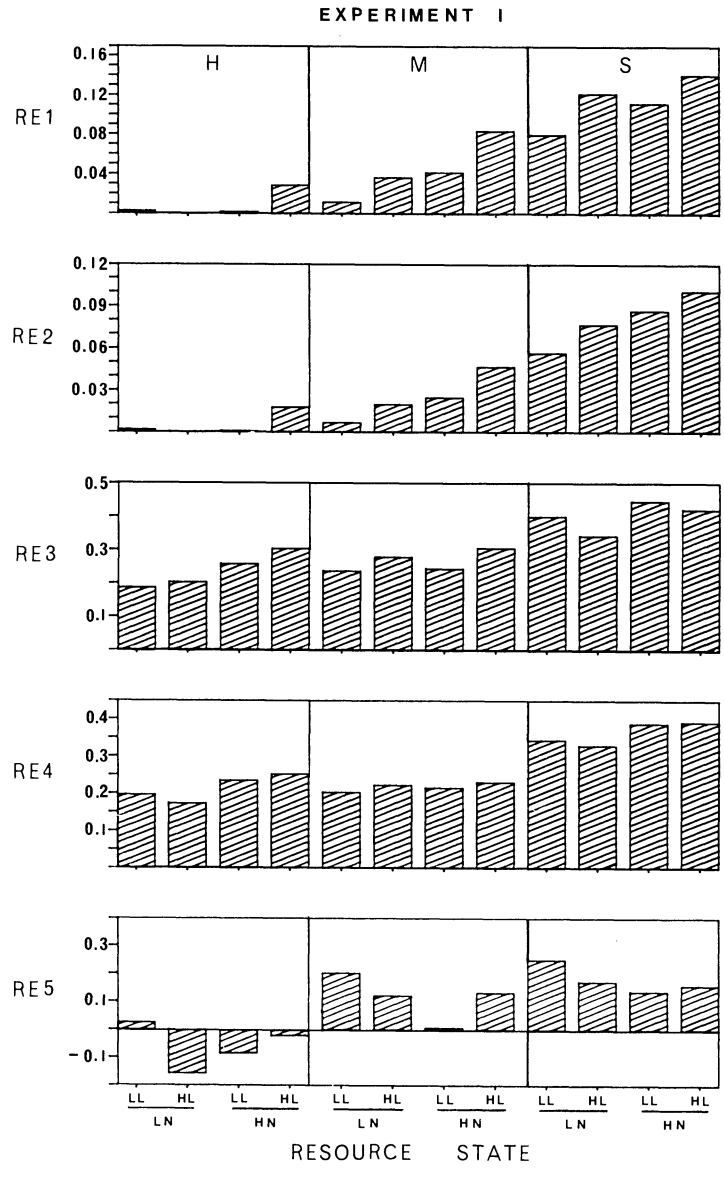


FIG. 4.—Reproductive effort in experiments I and II (*facing page*) as measured by various means. See table 1 for description of treatment designations and table 2 for definitions of the various measures of RE. Reproductive effort is expressed as a proportion.

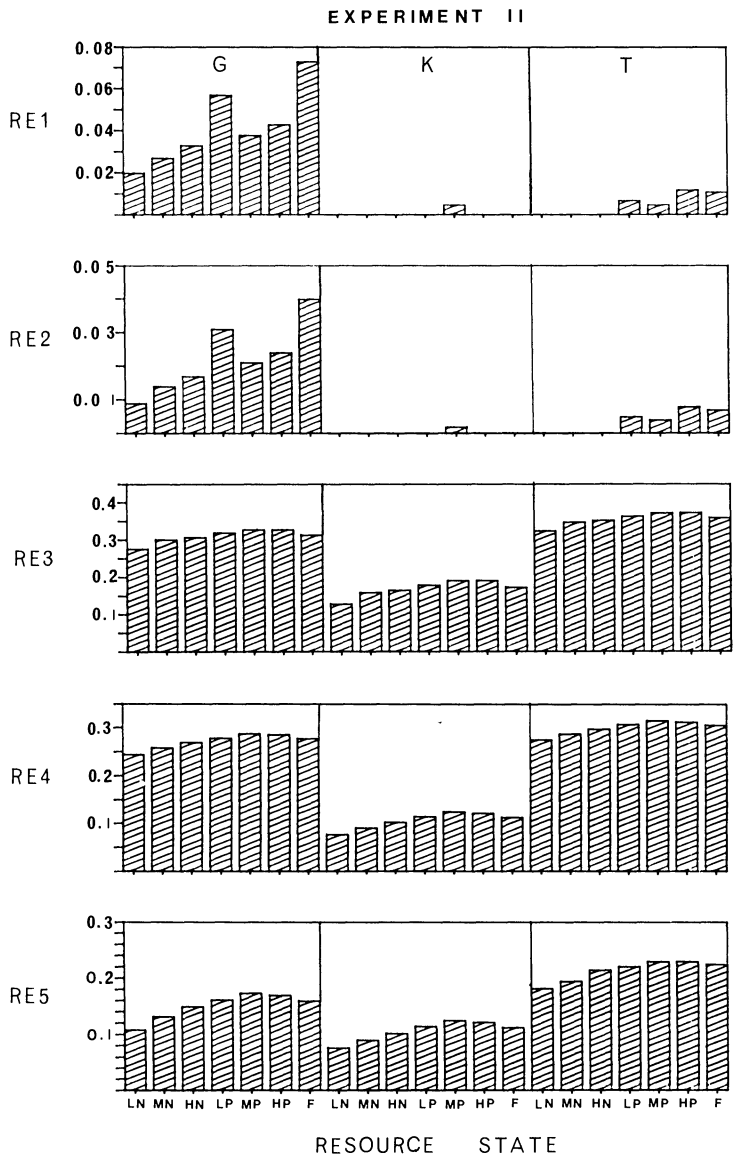

EXPERIMENT II
G
K
T
RE1
RE2
RE3
RE4
RE5
0.08
0.06
0.04
0.02
0.05
0.03
0.0
0.4
0.3
0.2
0.1
LN MN HN LP MP HP F LN MN HN LP MP HP F LN MN HN LP MP HP F
RESOURCE STATE

TABLE 3

RANK CORRELATIONS BETWEEN VARIOUS MEASURES OF REPRODUCTIVE EFFORT IN EXPERIMENT I

	RE1	RE2	RE3	RE4	RE5
RE1		0.982 (0.0001)	0.827 (0.0017)	0.709 (0.0146)	0.518 (0.103)
RE2	0.986 (0.0001)		0.873 (0.0005)	0.764 (0.0062)	0.545 (0.0827)
RE3	0.853 (0.0004)	0.888 (0.0001)		0.945 (0.0001)	0.418 (0.2006)
RE4	0.776 (0.0030)	0.818 (0.0011)	0.951 (0.0001)		0.318 (0.3403)
RE5	0.601 (0.0386)	0.622 (0.0307)	0.489 (0.1063)	0.427 (0.1667)	

NOTE.—Values above the diagonal were calculated using only those treatments in which inflorescences were produced. Values below the diagonal were calculated using all reproductive treatments. The figures given in parentheses are levels of significance for the correlation.

TABLE 4

RANK CORRELATIONS BETWEEN VARIOUS MEASURES OF REPRODUCTIVE EFFORT IN EXPERIMENT II

	RE1	RE2	RE3	RE4	RE5
RE1		1.000 (0.0000)	−0.168 (0.6021)	−0.196 (0.5419)	−0.224 (0.4845)
RE2	1.000 (0.0000)		−0.168 (0.6021)	−0.196 (0.5419)	−0.224 (0.4845)
RE3	0.375 (0.0943)	0.375 (0.0943)		0.986 (0.0001)	0.972 (0.0001)
RE4	0.418 (0.0594)	0.418 (0.0594)	0.992 (0.0001)		0.986 (0.0001)
RE5	0.293 (0.1966)	0.293 (0.1966)	0.978 (0.0001)	0.973 (0.0001)	

NOTE.—Values above the diagonal were calculated using only those treatments in which inflorescences were produced. Values below the diagonal were calculated using all reproductive treatments. The figures given in parentheses are levels of significance for the correlation.

the cost of reproduction, resulting in a net carbon gain to the plant (fig. 4). Genotype *K*, on the other hand, had no reproductive photosynthesis; in fact, vegetative photosynthesis was decreased by reproduction. In general, however, the cost of reproduction was reduced substantially by reproductive photosynthesis. This was particularly true in the case of the combined low-light and low-nitrogen treatment in experiment I. Values of RE5 ranged between −16% and 25%. The rank correlations between RE5 and RE4 were 0.43 ($P < 0.1667$) and 0.97 ($P < 0.0001$) for experiments I and II, respectively (tables 3, 4).

DISCUSSION

Biomass Allocation to Obvious Reproductive Structures

In calculating RE using aboveground structures alone, it is assumed (incorrectly in some cases) that the proportion of biomass aboveground is relatively constant over the comparisons being made among genotypes and in different environments. In the present study, the close correlation between RE1 and RE2 (tables 3, 4) means that for *Agropyron repens*, RE calculated on the basis of aboveground biomass is a good indicator of allocation on a total-plant basis across a wide range of environments.

Total Biomass Allocation to Reproduction

The increase in the amount of stem material per unit of leaf mass indicates that a large proportion of the stem material in the reproductive plants can be attributed to reproduction (fig. 1). That stems make up such a large proportion of total reproductive costs can perhaps be explained by the fact that *A. repens* is both self-incompatible and wind-pollinated. Stem elongation would enhance both pollen exchange with conspecifics and seed dispersal.

The lack of any increase in either the amount of roots or rhizome mass per unit of leaf mass in the reproductive plants means that there is no reproductive requirement for these structures. This does not imply that reproductive growth is independent of these structures since reproduction is clearly dependent on activities that take place in these structures (e.g., nutrient uptake in roots). It means only that no new roots or rhizomes were produced over and above those required for vegetative growth. The carbon cost of the reproductive activities that take place in the roots or rhizomes would be reflected in the respiratory requirement for reproductive growth (e.g., increases in the rate of mineral uptake in already existing roots and the reallocation of minerals from vegetative structures require an expenditure of energy).

The poor correlation between total biomass allocation to reproduction and measures of RE based on biomass allocation to "obvious" reproductive structures in experiment II (table 4) indicates that the simpler measures of RE (RE1 and RE2) used in some previous studies cannot be used as substitutes for the more exact measure (RE3). The correlations break down primarily because of differences among genotypes in the amount of reproductive stem material per inflorescence. The better correlations among these measures of RE in experiment I reflect the different sets of genotypes used in each experiment. Given that the variation in the importance of plant height in either the dispersal of seeds or the exchange of pollen is likely to depend on the surrounding canopy, the differences among genotypes in the amount of reproductive stem material per inflorescence are not surprising. Jurik (1985) has similarly found substantial differences among *Fragaria* populations in the amount of ancillary and support structures produced per seed.

Total Carbon Allocation to Reproduction

The lack of any major effect of reproduction on specific respiration rates of whole plants (fig. 2) means that the respiratory requirements for vegetative and reproductive growth were similar. The close correspondence between whole-plant respiration and reproductive respiration was probably responsible to a large degree for the good correlation between RE3 and RE4 (tables 3, 4). Plants with a high respiratory requirement for reproductive growth, for example, also had a high respiratory requirement for total growth, and, as a net result, RE was not affected by inclusion of respiratory costs in the analysis.

The present study represents one of the first attempts to include respiratory costs in an analysis of RE in plants. Bazzaz and his coworkers (Bazzaz and Carlson 1979; Bazzaz et al. 1979), as well as others (e.g., Evans and Rawson 1970; Abernethy and Wright 1975; Werk and Ehleringer 1983; Williams et al. 1985), measured the respiration of reproductive structures. However, they did not measure whole-plant respiration, nor did they relate the reproductive cost to the total carbon captured by the plant. These studies also differ from the present one in that the respiratory costs of reproduction were estimated using direct measurements of respiration in the reproductive structures. We determined reproductive respiration indirectly, as the difference between the measured total respiration and the predicted respiration of the vegetative plant parts. This method has an advantage over direct measurements in that the respiration associated with reproduction may not be entirely confined to the reproductive structures (e.g., the respiration associated with the uptake and translocation of nutrients to reproductive structures). Direct measures of the respiration of reproductive structures reveal only a portion of total reproductive respiration.

Jurik (1983) used theoretical calculations to estimate total carbon allocation to flowers and fruits in populations of *Fragaria* and related this cost to the total carbon captured by the plant; in this way he obtained a measure of RE equivalent to RE4 of the present study. Like the present study, Jurik found that differences in RE between populations remained more or less the same whether RE was calculated in terms of biomass or in terms of total carbon.

The good correlation between RE3 and RE4 suggests that it is not necessary to measure respiratory costs to evaluate RE in *A. repens*. Caution must be used in extrapolating from these results, however. The good correlation does not reflect any lack of difference among treatments in respiratory costs, but rather the similarity within a treatment of the respiratory costs of vegetative and reproductive tissues.

Net Carbon Allocation to Reproduction

The increase in net assimilation rate (NAR) in reproductive plants (fig. 2) indicates that reproductive photosynthesis is occurring. The increase in NAR in the latter part of the experimental period can be attributed, at least in part, to direct photosynthesis by the reproductive structures. Direct measures of net photosynthesis in the inflorescences and culms have shown that these structures have significant photosynthetic activity. Often, however, it was found that the

NAR of the reproductive plants increased before inflorescence emergence and elongation of the culms. This is particularly true in the low-light and low-nitrogen treatments and in genotype *H* in experiment I (Reekie 1985). Direct measures of leaf net photosynthesis in experiment I (fig. 3) showed significant reproductive enhancement in genotype *H* and at low light. This suggests that reproductive enhancement of leaf photosynthesis is at least partially responsible for reproductive photosynthesis. The effect of reproduction on leaf photosynthesis can probably be attributed to an increase in sink size (Burt 1964; Neales and Incoll 1968).

Reproductive photosynthesis was important in reducing the cost of reproduction. This is reflected in the substantial decrease in the magnitude of RE that resulted when reproductive photosynthesis was taken into consideration (fig. 4). In experiment II, reproductive photosynthesis accounted for as much as 62% of the total cost of reproduction; in a few cases in experiment I, reproductive photosynthesis actually exceeded the total reproductive cost. The importance of reproductive photosynthesis in reducing the cost of reproduction is also reflected in the growth of the plants. Reproduction had no effect on the relative growth rate (RGR) in any of the various treatments, even though substantial amounts of carbon were allocated to reproduction and the leaf-area ratio (LAR) declined (fig. 2). Reproductive photosynthesis is probably an important factor in determining the cost of reproduction in many other plant species as well. Several investigators have shown that reproductive structures in a number of species are capable of substantial photosynthetic activity (Thorne 1963; Kriedemann 1966; Ong et al. 1978; Bazzaz and Carlson 1979; Bazzaz et al. 1979; Werk and Ehleringer 1983; Williams et al. 1985; Jurik 1985).

The poor correlation between RE4 and RE5 in experiment I means that total carbon allocation to reproduction does not reflect the cost to the vegetative parts of the plant. Differences among treatments in the ability to compensate for the cost of reproduction through reproductive photosynthesis override differences in total allocation. Plants that received both low light and low nitrogen were unable to compensate for the cost of reproduction to the same extent as plants in the more favorable resource states. As a result, the treatments with the lowest carbon allocation to reproduction had the largest net cost.

The high positive correlation between RE4 and RE5 in experiment II (table 4) probably reflected the generally better growing conditions in this experiment; plants received nutrients every other day rather than every third day, and all plants received high light. There were also substantial differences among genotypes in the ability to compensate for the cost of reproduction in both experiments, but these differences either accented already existing differences in RE or were insufficient to change the relative ranks of the genotypes. Genotypic differences in reproductive photosynthesis may well have a much more marked effect on comparisons of RE in cases where either a different combination of genotypes or a wider range of genotypes is compared.

Bazzaz et al. (1979) found substantial differences among tree species in the photosynthetic rates of flowers and fruits and suggested that comparisons of RE based on biomass allocation to reproductive structures could be misleading. The present study has shown that even within the same species there can be differ-

ences in both the photosynthetic rate of floral structures and the degree to which reproduction may enhance leaf photosynthesis. Furthermore, these differences have been shown to result in changes in the relative ranks of different plants in terms of their RE. Intraspecific differences in rates of reproductive photosynthesis, which may well be common, may be a significant factor in determining reproductive success and therefore selective differentials.

Implications for Studies of RE in Plants

The present study has shown that, even among genotypes of the same species, biomass allocation to flowers and fruits may not reflect the carbon cost of reproduction. This conclusion does not invalidate earlier studies that considered only biomass allocation to flowers and fruits but does suggest caution in their interpretation. Biomass allocation to seeds and fruits provides a comparative measure of reproductive output (i.e., how successful a plant is in turning resources into propagules). Reproductive output is a crucial measure of plant fitness; indeed, the desire to explain differences in reproductive output was the impetus for the development of the various life history theories concerning RE. Equating reproductive output with reproductive effort and using differences in reproductive output among various plants to test the predictions of life history theory can, however, be very misleading (see also Thompson and Stewart 1981). To test these predictions, it will be necessary to consider not only reproductive output but also total resource allocation to reproduction and its effect on vegetative growth (Reekie and Bazzaz 1987*b*). In this regard, RE4 provides the best measure of total carbon allocation to reproduction and may also provide some indication of how other resources are allocated (Reekie and Bazzaz 1987*a*). In addition, RE5 provides a measure of the effect of reproduction on vegetative growth when an insufficiency of carbon limits growth.

SUMMARY

Reproductive effort, or the proportion of an organism's resources allocated to reproduction, is a crucial aspect of an organism's life history; the optimal allocation of resources to reproduction in different environments has been the subject of much theorizing. Adequate tests of these theories have been hampered by the difficulties involved in assessing reproductive effort. In this paper, we address the problem of determining which structures and activities should be considered part of reproduction, using *Agropyron repens* as the experimental material.

We approached the problem by first determining the structures and activities necessary for vegetative growth and then determining reproductive structures and activities by subtraction. Using carbon as the currency of allocation, we defined vegetative growth as those structures directly involved in the capture of carbon (i.e., leaves) plus all necessary support structures and activities. The necessary support structures and activities were determined by comparison with vegetative plants grown under similar conditions.

Reproduction in *A. repens* involves not only the production of flowering and fruiting structures, but also the production of a substantial amount of stem

material, the loss of carbon through respiration, and carbon gain through photosynthesis. Reproductive photosynthesis includes both direct photosynthesis by the reproductive structures and reproductive enhancement of leaf photosynthesis. Simple measures of reproductive effort based on biomass allocation to flowering and fruiting structures do not adequately reflect carbon allocation to reproduction since there is both genotypic and environmentally induced variation among plants in the amount of reproductive stem material and in the ability to compensate for the cost of reproduction through reproductive photosynthesis.

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