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REPRODUCTIVE EFFORT IN PLANTS.
3. EFFECT OF REPRODUCTION ON VEGETATIVE ACTIVITY

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The amounts of carbon and other resources invested in structures and activities associated with reproduction constitute the direct costs of reproduction. The indirect costs are the consequences of this investment or the extent to which vegetative activity is reduced by reproduction. The various theories proposed to explain resource-allocation patterns assume that vegetative and reproductive processes compete for a common pool of resources and that an increase in one activity necessarily results in a proportional decrease in the other activity.

For a number of reasons, the correlation between direct and indirect costs of reproduction may not be as close as has been assumed (Bazzaz and Reekie 1985). In a plant that forgoes reproduction in favor of vegetative growth, any increase in vegetative growth would not simply be proportional to the resources diverted from reproduction; the new vegetative structures would in turn acquire more resources and grow further (i.e., in a manner analogous to compound interest). Therefore, the increase in vegetative growth would vary depending on the environment and the plant's innate ability to capture resources. A similar situation develops when allocation is viewed from the opposite perspective. In a plant that allocates resources to reproduction, the decrease in vegetative activity would depend not only on the quantity of resources diverted to reproduction but also on the ability of the plant to compensate for this diversion through photosynthesis by the reproductive parts (see, e.g., Bazzaz et al. 1979) and through increased photosynthesis by the vegetative parts because of reproduction (Reekie and Bazzaz 1987a). The correlation between direct and indirect costs might also break down if vegetative and reproductive growth were limited by different resources (Willson 1983). Competition between vegetative and reproductive growth may also be constrained by a localization of translocation (Alpert et al. 1985). Watson (1984) has suggested that reproduction may not be resource-limited at all. If so, there would not necessarily be any correlation between the direct and indirect costs of reproduction.

In this paper, we examine the relationship between the direct and indirect costs of reproduction in *Agropyron repens*. We define several alternative measures of

the indirect costs and compare them with measures of the direct costs of reproduction described in previous papers (Reekie and Bazzaz 1987*a,b*).

The indirect costs of reproduction can be quantified demographically by comparing the growth and survival of individuals that do or do not reproduce (e.g., Law 1979; Piñero et al. 1982). But this approach, being correlative, has limitations; reproduction may be correlated with a number of other factors, making it difficult to attribute differences between reproductive and vegetative plants entirely to reproduction. Antonovics (1980) has suggested the use of various experimental manipulations, such as photoperiod control or removing reproductive buds, to produce reproductive and vegetative plants under comparable growing conditions. Although such manipulations provide an experimental means of assessing the indirect costs of reproduction, indirect measures of costs are still subject to the same problems as the direct measures. From the point of view of life history analysis, the indirect cost of reproduction should be measured in terms of lost vegetative growth; but determining the degree of reduction in vegetative growth requires that we be able to distinguish between vegetative and reproductive structures and activities. The indirect costs may also vary depending on the currency used to measure them. For example, two plants may incur the same costs of reproduction in terms of lost vegetative biomass, but the degree to which the nitrogen content of the vegetative biomass is reduced by allocation to reproductive structures may vary.

The procedures described previously (Reekie and Bazzaz 1987*a,b*) for the calculation of the direct costs of reproduction can also be used to assess the indirect costs of reproduction. The allometric relationships between leaves and other plant parts in vegetative plants can be used to estimate the vegetative biomass of reproductive plants. Similarly, the respiration rates of the vegetative plants can be used to estimate vegetative respiration in the reproductive plants. Furthermore, if carbon allocation does reflect the allocation of other resources (Reekie and Bazzaz 1987*b*), carbon can be used as the currency to assess the indirect costs of reproduction.

MATERIALS AND METHODS

Plant growth conditions, experimental design, and the calculation of the direct measures of reproductive effort (RE) were as described earlier (Reekie and Bazzaz 1987*a*). Briefly, the plants were grown from single-node rhizome cuttings in controlled-environment chambers. There were two experiments, both of which involved growing three genotypes at two different photoperiods and at various levels of resources in a complete factorial treatment design. There were four resource states in experiment I (two levels of light crossed with two levels of nitrogen) and seven resource states in experiment II (four levels of nitrogen and four levels of phosphorus; the highest nitrogen and phosphorus levels were the same treatment). Both experiments involved sequential harvests: eight harvests in experiment I with one replication per treatment for the first seven harvests and five replicates for the final harvest, and five harvests in experiment II with two replicates at each harvest. The different genotypes used in each experiment were selected for their substantially different allocation patterns and were chosen to

increase the scope of inference for the study. The two photoperiods (14 h and 18 h) allowed both vegetative and reproductive plants to be grown under similar conditions (the total amount of light received was approximately the same in both photoperiods). Whole-plant respiration was measured immediately before each harvest, and respiration over the entire experimental period was estimated from curves fit to the respiration-time data. These data, together with information on the growth of the plants and the allometric relationships between plant parts, were used to construct complete carbon budgets for both vegetative and reproductive growth.

The total nitrogen and phosphorus contents of the plants at final harvest in experiment II were determined separately for individual plant parts. Nitrogen and phosphorus allocation to reproduction was then calculated from the nutrient contents of the various plant parts and the respective weights of the vegetative and reproductive plant parts. Further details concerning these calculations and the measurement of nitrogen and phosphorus concentrations can be found elsewhere (Reekie and Bazzaz 1987b).

The differences in total biomass between treatments at the final harvest were examined by an analysis of variance. The effect of reproduction on total biomass was also examined correlatively by analyzing the relationship between biomass and RE among the replicates in the long-photoperiod treatments of experiment I. The proportion of total biomass allocated to flowers, fruits, and reproductive support structures (RE3, table 1) was chosen as a convenient measure of RE for this analysis. The degree to which the plants were reproducing was perhaps best described by the proportion of total carbon allocated to reproduction (RE4), but because of the manner in which RE4 was calculated, it was not possible to obtain separate estimates for each of the replicates within a treatment. Since RE3 was closely correlated to RE4 in these plants (Reekie and Bazzaz 1987a), it is probably an adequate measure of reproduction for our purposes. Regression analysis was performed using the separate-slopes model of the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS) with genotype, nitrogen, and light as categorical factors in the analysis.

The various direct and indirect measures of RE used in this paper are defined in table 1. Reproductive efforts 3, 4, and 5 were previously defined (Reekie and Bazzaz 1987a). Reproductive effort 4 is perhaps the best measure of the total carbon allocated to reproduction and was included for that reason. Reproductive effort 5 takes into account reproductive photosynthesis, which, as discussed above, may be an important consideration in determining the effect of resource allocation to reproduction on vegetative activity. Reproductive effort 3 was included for purposes of comparison to the corresponding indirect measure of reproductive effort (RE6). The direct measures calculated in terms of nitrogen (RE3_N) and phosphorus (RE3_P) are the same as those used before (Reekie and Bazzaz 1987b) and represent the net allocation of these nutrients to reproductive structures at the time of harvest. Reproductive efforts 6_N and 6_P are the corresponding indirect measures of RE3_N and RE3_P. Reproductive effort 7, which is the indirect equivalent of RE4, is perhaps the best measure of the loss in vegetative activity measured in terms of carbon since it takes both structural and energetic carbon into consideration. Reproductive effort 6 is a simplification of RE7 that

TABLE 1

SUMMARY OF THE VARIOUS DIRECT AND INDIRECT MEASURES OF REPRODUCTIVE EFFORT
USED IN THIS PAPER

Direct Measure		Indirect Measure	
RE3	(Reproductive biomass)/(total biomass of reproductive plant)	RE6	(Total biomass of vegetative plant – vegetative biomass of reproductive plant)/(total biomass of vegetative plant)
RE3 _N	(Nitrogen in reproductive biomass)/(nitrogen in total biomass of reproductive plant)	RE6 _N	(Nitrogen in total biomass of vegetative plant – nitrogen in vegetative biomass of reproductive plant)/(nitrogen in total biomass of vegetative plant)
RE3 _P	(Phosphorus in reproductive biomass)/(phosphorus in total biomass of reproductive plant)	RE6 _P	(Phosphorus in total biomass of vegetative plant – phosphorus in vegetative biomass of reproductive plant)/(phosphorus in total biomass of vegetative plant)
RE4	(Reproductive biomass + reproductive respiration)/(total biomass and respiration of reproductive plant)	RE7	(Total biomass and respiration of vegetative plant – vegetative biomass and respiration of reproductive plant)/(total biomass and respiration of vegetative plant)
RE5	(Reproductive biomass + reproductive respiration – reproductive photosynthesis)/(total biomass and respiration of reproductive plant – 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. The various direct measures of RE are the same as previously defined (Reekie and Bazzaz 1987a).

may be an adequate approximation. The relationships between the various costs and measures of RE were examined by calculating Spearman's rank correlations between pairs of measures across all treatment combinations.

The various measures of indirect costs described above were calculated at the end of the experiment in this study. These measurements could also be made in terms of growth in subsequent growing seasons. Providing that the indirect costs are calculated in terms of the resources limiting growth (or in terms of a resource reflecting the allocation of the limiting resources), the timing of the calculation should be irrelevant.

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 were not directly relevant to our study unless they interacted with photoperiod.

Reproduction increased the total weight of the plants slightly in both experiment I ($P < 0.0245$) and experiment II ($P < 0.0004$) (fig. 1). In experiment I, there

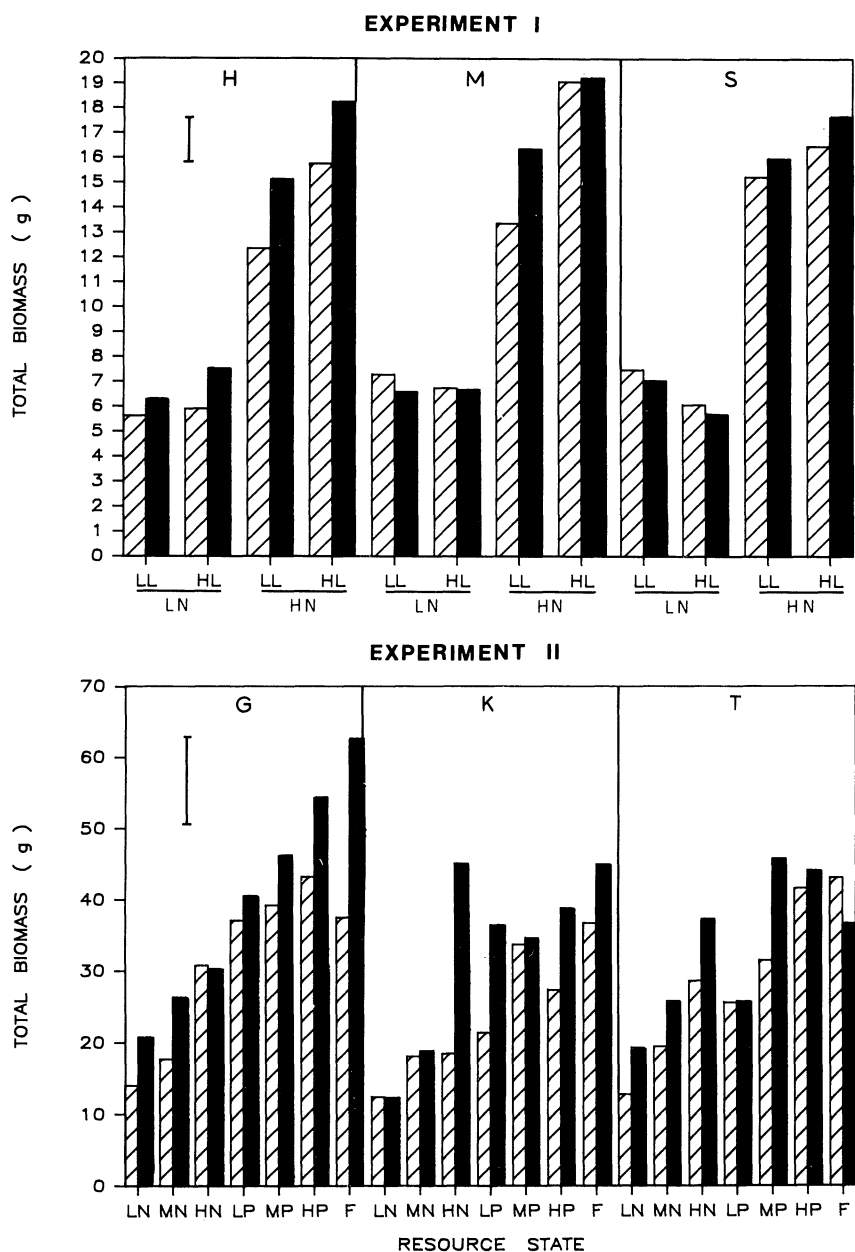


FIG. 1.—Total biomass in experiments I and II at final harvest. *Hatched bars*, vegetative plants; *solid bars*, reproductive plants. Error bars represent one-half of the 95% confidence interval for a single treatment mean. The treatment designations represent various combinations of light, nitrogen, and phosphorus availability: irradiance, $480 \mu\text{mol m}^{-2}\text{s}^{-1}$ (LL) or $1200 \mu\text{mol m}^{-2}\text{s}^{-1}$ (HL); nitrogen, 0.5 (LN), 1.0 (MN), 2.5 (HN), or 5.0 (F) mM $\text{Ca}(\text{NO}_3)_2$; and phosphorus, 0.05 (LP), 0.10 (MP), 0.25 (HP), or 0.50 (F) mM KH_2PO_4 . The level of light in experiment II was held constant at $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$. The level of those mineral nutrients not being manipulated was maintained at the level found in a full-strength Evan's modified Shive solution. Nutrients were supplied every third day in experiment I and every second day in experiment II.

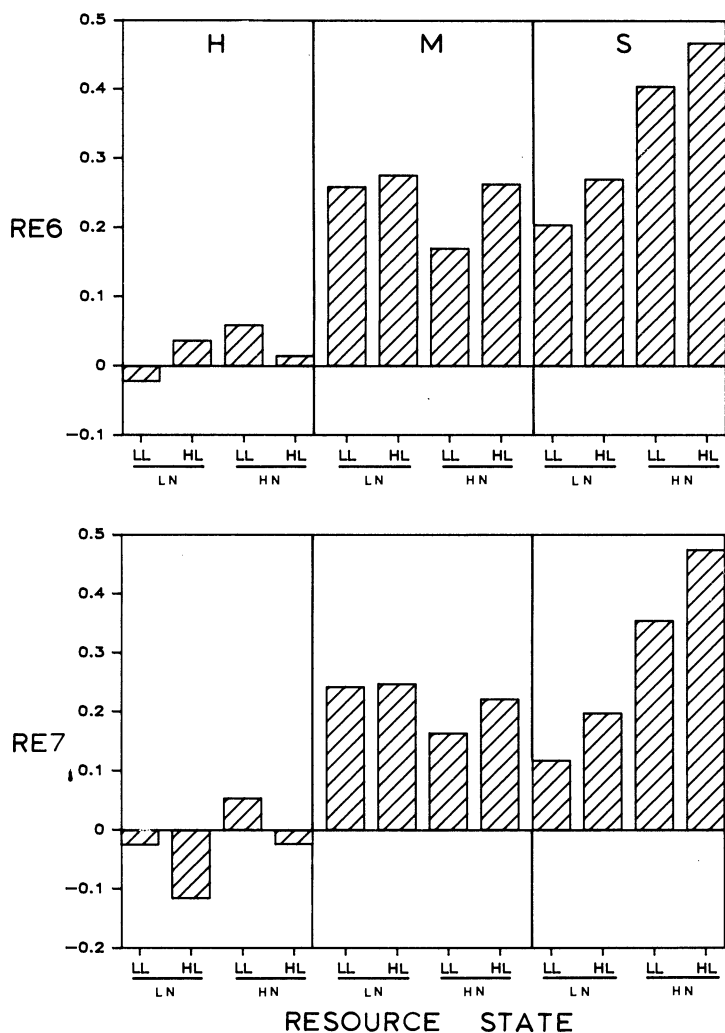


FIG. 2.—Reproductive effort calculated in terms of indirect costs in experiment I. See table 1 for definitions of the various measures of reproductive effort and figure 1 for the key to treatment designations.

was also a nitrogen-by-photoperiod interaction ($P < 0.0482$); the increase in total weight with reproduction was confined to the high-nitrogen treatments. At low nitrogen, there was either no increase or a slight decrease. There was no nutrient-by-photoperiod interaction in experiment II.

Regression of total biomass on RE3 for the reproductive plants in experiment I confirmed that reproduction had little detrimental effect on total biomass. There was no overall effect of RE3 on total weight ($P < 0.4120$), nor were any of the individual relationships fit to the separate treatments significant.

Reproductive effort calculated in terms of the decrease in vegetative biomass

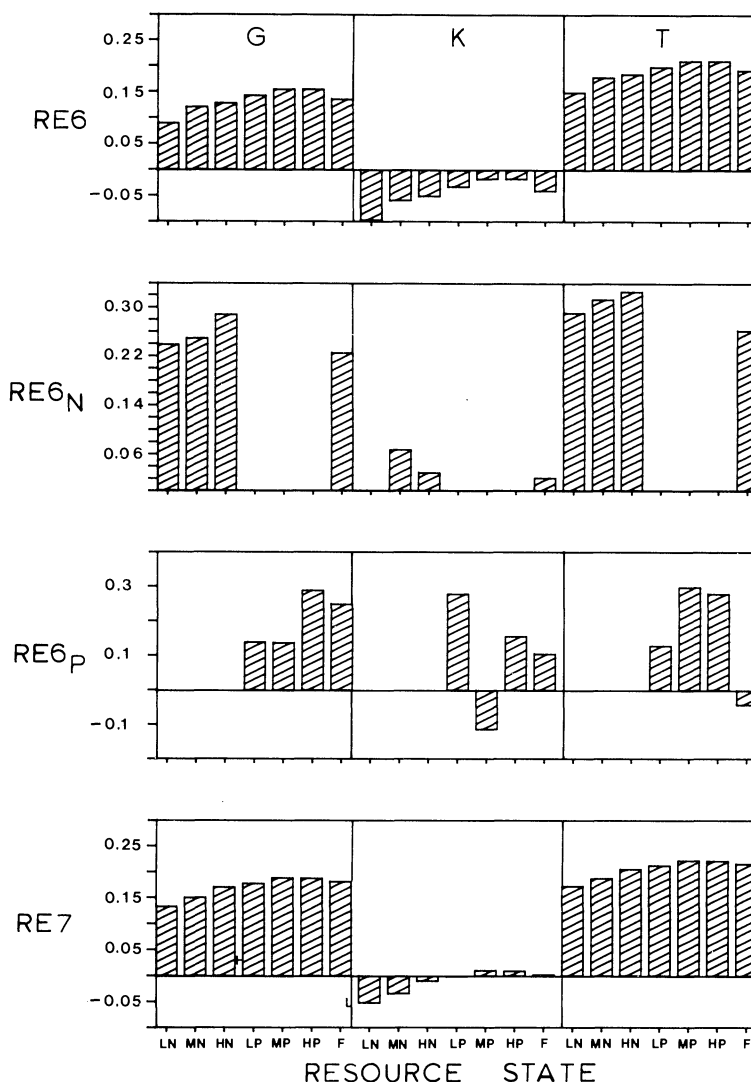


FIG. 3.—Reproductive effort calculated in terms of indirect costs in experiment II. See table 1 for definitions of the various measures of reproductive effort and figure 1 for the key to treatment designations.

(RE6) showed more or less the same pattern as RE calculated in terms of the loss in vegetative growth and respiration (RE7) (figs. 2, 3). The correlation between these two measures was 0.965 in experiment I (table 2) and 0.984 in experiment II (table 3). In experiment I, both indirect measures of RE decreased slightly with increased light in genotype *H* but increased in genotypes *M* and *S*. Increased nitrogen increased RE in genotypes *H* and *S* but had little effect in genotype *M*. Reproductive effort increased in the order $H < M < S$. In experiment II, RE

TABLE 2
RANK CORRELATIONS BETWEEN MEASURES OF REPRODUCTIVE EFFORT BASED ON
DIRECT AND INDIRECT COSTS IN EXPERIMENT I

	RE4	RE5	RE6	RE7
RE4	1.000			
RE5	0.427 (0.1667)			
RE6	0.664 (0.0185)	0.636 (0.0261)		
RE7	0.538 (0.0709)	0.594 (0.0415)	0.965 (0.0001)	1.000

NOTE.—See table 1 for definitions of the various measures of reproductive effort. Values in parentheses are levels of significance for the correlation.

increased with nitrogen in all three genotypes, but phosphorus had little effect. Reproductive effort increased in the order $K < G < T$.

Calculating RE in terms of nitrogen lost to vegetative growth (RE_{6N}) resulted in patterns similar to those found by calculating the indirect measures in terms of carbon at low levels of applied nitrogen. At the highest level of nitrogen (F), however, RE_{6N} decreased sharply, whereas RE6 and RE7 continued to increase. The overall correlation between RE_{6N} and the carbon-based measures of RE remained high, and the relative ranks of the three genotypes remained unaltered.

There were no consistent trends among the phosphorus treatments when RE was calculated in terms of the phosphorus lost to vegetative growth (fig. 3). Even the substantial differences observed between genotypes when RE was calculated in terms of other currencies disappeared.

In experiment I, neither RE4 nor RE5 was a particularly good reflection of the indirect measures of RE, even though the direct and indirect measures were positively correlated (table 2). In experiment II, RE4, RE_{3P}, RE5, and, to a lesser extent, RE_{3N} were all highly correlated with the indirect measures based on carbon and nitrogen (table 3). Reproductive effort based on the loss of vegetative phosphorus was not correlated with any other measure of RE.

DISCUSSION

Reproduction did not reduce the overall growth of *Agropyron repens* in this study. Surprisingly, reproduction enhanced total growth in the more favorable resource states. This was reflected both in the comparisons between the final biomass of vegetative and reproductive plants (fig. 1) and in their relative growth rates over the course of the growth period (Reekie and Bazzaz 1987a). This result was not an artifact of comparisons between photoperiod treatments (i.e., a photoperiod effect per se rather than a reproductive effect). Regressions of final biomass on RE among the long-photoperiod plants in experiment I support these conclusions. Both direct photosynthesis by the reproductive structures and repro-

TABLE 3
RANK CORRELATIONS BETWEEN MEASURES OF REPRODUCTIVE EFFORT BASED ON DIRECT AND INDIRECT COSTS IN EXPERIMENT II

	RE4	RE3 _N	RE3 _P	RE5	RE6	RE6 _N	RE6 _P	RE7
RE4	1.000							
RE3 _N	0.804 (0.0016)							
RE3 _P	0.930 (0.0001)	1.000 (0.0000)						
RE5	0.937 (0.0001)	0.790 (0.0022)	0.937 (0.0001)					
RE6	0.992 (0.0001)	0.825 (0.0010)	0.951 (0.0001)	0.978 (0.0001)				
RE6 _N	0.818 (0.0011)	0.951 (0.0001)	1.000 (0.0000)	0.825 (0.0010)	0.853 (0.0004)			
RE6 _P	0.308 (0.3306)	-0.500 (0.6667)	0.168 (0.6021)	0.294 (0.3540)	0.378 (0.2262)	-0.500 (0.6667)		
RE7	0.992 (0.0001)	0.804 (0.0016)	0.951 (0.0001)	0.965 (0.0001)	0.984 (0.0001)	0.818 (0.0011)	0.266 (0.4038)	1.000

NOTE.—See table 1 for definitions of the various measures of reproductive effort. Values in parentheses are levels of significance for the correlations.

ductive enhancement of leaf photosynthesis (Reekie and Bazzaz 1987a) contribute to this enhanced growth. Reproduction, however, did affect the pattern of growth in *A. repens*. Although total growth did not decrease, in most treatments vegetative growth was reduced.

Differences among genotypes and among resource treatments in the relationship between indirect and direct costs in experiment I (table 2) suggest that resource allocation to reproduction may not be a reliable indicator of the cost of reproduction to vegetative growth. Part of the reason why total resource allocation to reproduction was not necessarily a good indicator of the indirect costs was the difference among treatments in the extent to which reproductive photosynthesis compensated for carbon cost. The positive correlation between RE5 and the indirect measures in experiment I was significant, even though RE5 did not correlate with RE calculated in terms of total carbon allocation to reproduction (RE4). Differences in reproductive photosynthesis, however, cannot completely account for differences between direct and indirect costs since the correlation between RE5 and the indirect measures in experiment I was weak. Apparently, other factors in addition to carbon were limiting vegetative growth.

The good correlation between direct and indirect costs in experiment II contrasts with the situation in experiment I. This parallels the differences in reproductive photosynthesis between treatments in experiments I and II discussed earlier (Reekie and Bazzaz 1987a). The better growing conditions in experiment II (all plants received high light, $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, and nutrients were applied every second day rather than every third day) may account for the generally damped differences between resource treatments in this experiment.

The high correlation between RE6 and RE7 suggests that it is not necessary to measure respiration to get a good approximation of the total indirect carbon cost of reproduction in *A. repens*. This high correlation parallels that found between RE3 and RE4. Caution must be used in extrapolating from these results. The correlation may break down when plants with vegetative and reproductive tissues that differ more substantially in their respiratory costs are compared (Reekie and Bazzaz 1987a).

The correlations between the indirect measures based on carbon and the indirect measure based on nitrogen were relatively high. In most cases, indirect costs based on carbon would be a good approximation of nitrogen costs. The lack of any correlation between these measures and the costs measured in terms of phosphorus, however, indicates that caution must be exercised in assuming indirect costs are independent of currency. Whether reproductive costs are measured in direct or indirect terms, the question of the appropriate currency must be addressed. In this respect, the suggestion that carbon can be used as a common currency (Reekie and Bazzaz 1987b) deserves further consideration. The lack of a correlation between indirect phosphorus costs and other measures of the cost of reproduction may reflect the fact that phosphorus was not a major limiting factor in this experiment (fig. 1). From the point of view of determining whether carbon can be used as a common currency, it would be useful to know if the same pattern emerged at more-limiting phosphorus concentrations.

The substantial differences in the effect of reproduction on vegetative activity

among resource states in experiment I and among genotypes in both experiments suggest an alternative explanation to traditional life history models for differences among plants in the amount of resources allocated to reproduction. Plants that allocate more of their resources to reproduction may simply be those plants that experience the least unit cost in terms of lost vegetative activity. For example, it is often observed that plants in early-successional habitats allocate a larger proportion of their biomass to reproduction than do plants in late-successional habitats (e.g., Abrahamson 1979). These differences in RE are often explained in terms of the relative survival rates of adults versus juveniles in these environments (Willson 1983). It is possible, however, to explain differences in RE between plants in early- and late-successional habitats in terms of the effect of reproduction on vegetative activity. It is conceivable that plants in early-successional habitats experience less loss of vegetative activity per unit of resources allocated to reproduction than do plants in late-successional habitats. This may occur because of the particular genotypes involved in early- versus late-successional habitats or perhaps because of the generally higher availability of resources in many early-successional habitats (Bazzaz 1983). If so, early-successional plants may allocate more resources to reproduction simply because the cost to the plant is low.

SUMMARY

One basic assumption of the various theories proposed to explain differences in resource-allocation patterns among plants is that different structures or activities are alternatives: a gain in one results in a proportional loss in another. We attempted to test this assumption in *Agropyron repens* by determining whether the resources allocated to reproduction reflect the effect of reproduction on vegetative growth. This was done by comparing the growth of reproductive and vegetative plants grown under conditions differing only in photoperiod.

Reproduction in this species was much less costly than the resources allocated to reproduction would indicate. Despite the large proportion of resources allocated to reproduction in most treatments, reproduction had little detrimental effect on total growth; in a few cases, it actually enhanced vegetative growth. There were substantial differences among genotypes and environments in the relationship between the resources allocated to reproduction and its effect on vegetative activity. This suggests that even in comparisons of plants of the same species, resource allocation to reproduction is not necessarily a reliable indicator of the cost of reproduction. Furthermore, since plants can experience different costs per unit of resource allocated to reproduction, it is conceivable that differences among plants in the resources allocated to reproduction may, in part, reflect these differences in cost. A plant with a low cost of reproduction, for example, may be able to allocate a larger proportion of its resources to reproduction. This suggestion represents an alternative to the traditional explanations of life history theory for differences in reproductive effort among plants.

In our experiment, the relative differences among different plants in the effect of reproduction on vegetative activity remained the same whether the effect was measured in terms of lost biomass, lost carbon (biomass plus respiration), or lost

nitrogen. There were differences, however, between these measures of the cost of reproduction and the cost measured in terms of lost vegetative phosphorus, suggesting that it is important to use the appropriate currency to evaluate the cost of reproduction.

EPILOGUE

The overall objective of this series of papers was to determine the best measure of reproductive effort (RE) for testing the predictions of life history theory concerning how plants allocate their resources between vegetative and reproductive activities. Life history theory, for example, suggests that differences among plants in reproductive output can be explained by competition for resources between vegetative and reproductive growth and by differences among environments in the relative survival rates of adults and juveniles. Increases in the proportion of resources allocated to propagules in environments where juvenile survival is high, and decreases where juvenile survival is low, are in accord with this theory. Changes in the proportion of resources allocated to propagules, however, may not be the result of differences in the amount of resources allocated to reproduction, as the theory suggests. As demonstrated by the first paper in this series, a high reproductive output might be the result of a decrease in the resources allocated to ancillary reproductive structures and activities and a consequent increase in the resources allocated to propagules. Furthermore, as suggested in the third paper, differences in reproductive output may be more a function of differences among plants in the degree to which resource allocation to reproduction affects vegetative growth than a function of differences in adult versus juvenile survival.

It follows from the above discussion that no one measure of RE is sufficient to test the predictions of life history theory. If we assume that carbon adequately reflects the allocation of those resources limiting plant growth, at least three different measures are required. It must first be shown that in environments where juvenile survival is high relative to adult survival, the proportion of carbon allocated to propagules is high compared with that in plants in environments where juvenile survival is low. Second, the increase in carbon allocation to propagules in environments where juvenile survival is high must result from an overall increase in the proportion of carbon allocated to reproduction. Finally, not only must these plants allocate a larger proportion of their resources to reproduction, but this allocation must result in a decrease in vegetative growth such that RE calculated in terms of indirect cost is greater than in environments where juvenile survival is relatively low. If any of these tests fails, then the resource-allocation patterns are not in accord with present theory.

Our study has been confined to one species. Some of the conclusions concerning the correspondence between measures of RE may well have been different had a species other than *Agropyron repens* been chosen. Differences between species in the proportions of ancillary reproductive structures, chemical composition, and rates of reproductive photosynthesis are likely to have an effect on how closely the different measures of RE are correlated. The methods and techniques we have

developed for examining these questions, however, can potentially be applied to a wide range of species. Only by answering these questions for a number of species with different growth forms and habits will it be possible to make more-general conclusions.

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