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REPRODUCTIVE EFFORT IN PLANTS.
2. DOES CARBON REFLECT THE ALLOCATION
OF OTHER RESOURCES?

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Studies that have compared the allocation patterns of biomass and mineral nutrients have found that the proportion of a resource allocated to reproductive structures differs significantly between resources (van Andel and Vera 1977; Lovett Doust 1980; Abrahamson and Caswell 1982). From the point of view of life history analysis, however, the absolute magnitude of reproductive effort (RE) as measured in units of a particular resource is not as important as relative differences among populations or environments. If the relative order of different populations remains the same, it does not matter which resource is used to calculate RE. Abrahamson and Caswell (1982) found that the qualitative ranking of three populations of *Verbascum thapsus* remained more or less the same whether RE was calculated in terms of biomass or various macro-nutrients such as nitrogen, phosphorus, and potassium. The patterns were less concordant when the allocation of some of the micro-nutrients was compared with that of biomass. Furthermore, Abrahamson and Caswell (1982) presented evidence that the rank correlations between the different measures are not as strong when different species or populations spanning a wider range of habitats are considered.

For the concept of allocation to be useful, the supply of some necessary resource must be limited, and the allocation of this resource to one structure or activity must result in a decrease to another structure or activity (Harper 1977). It can be argued, therefore, that RE should be measured in terms of the particular resource whose (relative) scarcity limits plant growth.

Unfortunately, serious practical difficulties arise in applying this approach. First, it may be difficult to determine the limiting resource in a particular environment. Moreover, even in extreme environments, it is unlikely that there is only one limiting resource (Harper 1977). Second, and perhaps more serious, it is unlikely that the same resources are limiting growth in different environments, which makes it impossible to compare the RE of plants from different environments in terms of the same limiting resource.

Thompson and Stewart (1981) have suggested that RE should always be evaluated in terms of mineral resources rather than in terms of carbon. They argued

that since reproductive structures are capable of supplying a portion of their own carbon requirements, the concept of carbon allocation is not relevant. This suggestion certainly avoids the difficulties involved in assessing reproductive photosynthesis. Unfortunately, if carbon is a major limiting resource, ignoring the allocation of carbon would be valid only if the photosynthetic rates of the vegetative and the reproductive parts were identical. If the photosynthetic rate of the reproductive structures is lower than that of the vegetative structures (i.e., the most likely situation), allocation of carbon to reproduction would still result in a decrease in vegetative growth (Reekie and Bazzaz 1987b). Furthermore, this approach does not deal with situations in which the allocation patterns of the various mineral resources differ.

It can be argued that carbon, because of its important structural and energetic role in plants, will tend to reflect the allocation patterns of other resources. Plants store the energy captured in photosynthesis in reduced carbon compounds until the energy is released through respiration. This energy is used to drive all biological processes, including the capture and subsequent utilization of other resources. It should be possible, therefore, to assess the cost of these activities in terms of carbon. To use an economic analogy (Bloom et al. 1985), carbon can be compared to money, whose circulation reveals the allocation patterns of goods and services in human society.

For carbon to be useful as a common currency for evaluating resource-allocation patterns, not only must it be demonstrated that an energetic (i.e., respiratory) cost is associated with other resources, it must also be shown that the carbon cost per unit of a resource increases as that resource becomes more limiting. This is equivalent to the increase in the price of a good or service as it becomes scarcer (the law of supply and demand). If the carbon cost increases as the resource becomes more limiting, then the carbon-allocation pattern becomes biased toward the particular resource(s) limiting growth. Because the concept of resource allocation is meaningful to life history analysis only if the resources are limiting, this is the preferred result.

One way of testing if carbon can be used as a common currency is to compare the allocation of carbon with the allocation of various resources at different levels of these resources. The allocation of carbon would not necessarily reflect the allocation of any particular resource in environments in which a number of resources were limiting growth; however, it could be predicted that the allocation pattern would tend to approach that of the limiting resource. This prediction is based on the assumption that the carbon cost of obtaining this particular resource would become so large that it would overshadow the costs for other, less-limiting resources.

We tested the above prediction using *Agropyron repens* by comparing RE calculated in terms of total carbon with RE calculated in terms of nitrogen and phosphorus along gradients of these two mineral resources.

MATERIALS AND METHODS

Experimental design, plant growth conditions, and the calculation of carbon allocation to reproduction were as described earlier (Reekie and Bazzaz 1987a) for

experiment II. Briefly, the plants were grown from single-node rhizome cuttings in controlled-environment chambers. There were 42 treatments: seven resource treatments crossed with three genotypes and two photoperiods in a complete factorial design. Each treatment was replicated 10 times allowing five harvests of two replicates each over the course of the experiment. The resource treatments consisted of two separate gradients: four levels of nitrogen and four levels of phosphorus (the highest levels of nitrogen and phosphorus were the same treatment). The different genotypes were selected on the basis of preliminary experiments that indicated they differed substantially in their allocation patterns and were chosen to increase the scope of inference of the experiment. 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.

In determining the carbon cost of mineral allocation to reproduction, it is irrelevant whether the carbon came from vegetative or reproductive photosynthesis. Therefore, RE4 ([inflorescence biomass + reproductive support-structure biomass + reproductive respiration]/[total biomass + total respiration]; Reekie and Bazzaz 1987a) was used to measure the carbon allocated to reproduction in this study.

Total nitrogen and phosphorus contents of the plants at final harvest were determined separately for green leaves, dead leaves, stems, inflorescences, roots, and rhizomes. Nitrogen analyses were confined to the nitrogen treatments, and phosphorus analyses to the phosphorus treatments. Total nitrogen was determined by an ammonia-distillation process using a semi-micro-Kjeldahl steam-distillation unit (Bremner 1965) following an aluminum-block digestion technique (Gallaher et al. 1976). Material was ashed and dissolved in 1.0 N nitric acid before the determination of phosphorus by a single-solution technique (Murphy and Riley 1962). Nitrogen and phosphorus allocation to reproduction was calculated from the nutrient contents of the various plant parts and the respective weights of the vegetative and reproductive plant parts. Reproductive and vegetative biomasses were determined using the allometric relationships between plant parts in the totally vegetative plants as previously described (Reekie and Bazzaz 1987a).

Net mineral allocation at maturity may not represent the true division of mineral resources between vegetative and reproductive growth because it does not take into account the reallocation of mineral nutrients from one plant part to another. It can be argued, however, that once nutrients are permanently allocated to reproduction (i.e., nutrient allocation at maturity), any time that might have been spent as part of a vegetative structure is trivial compared with the infinite amount of time now spent as part of reproductive structures. At any rate, lacking a more satisfactory procedure, we adopted the present procedure as the best approximation of mineral allocation available. It is also the procedure followed in all previous studies of mineral allocation to reproduction.

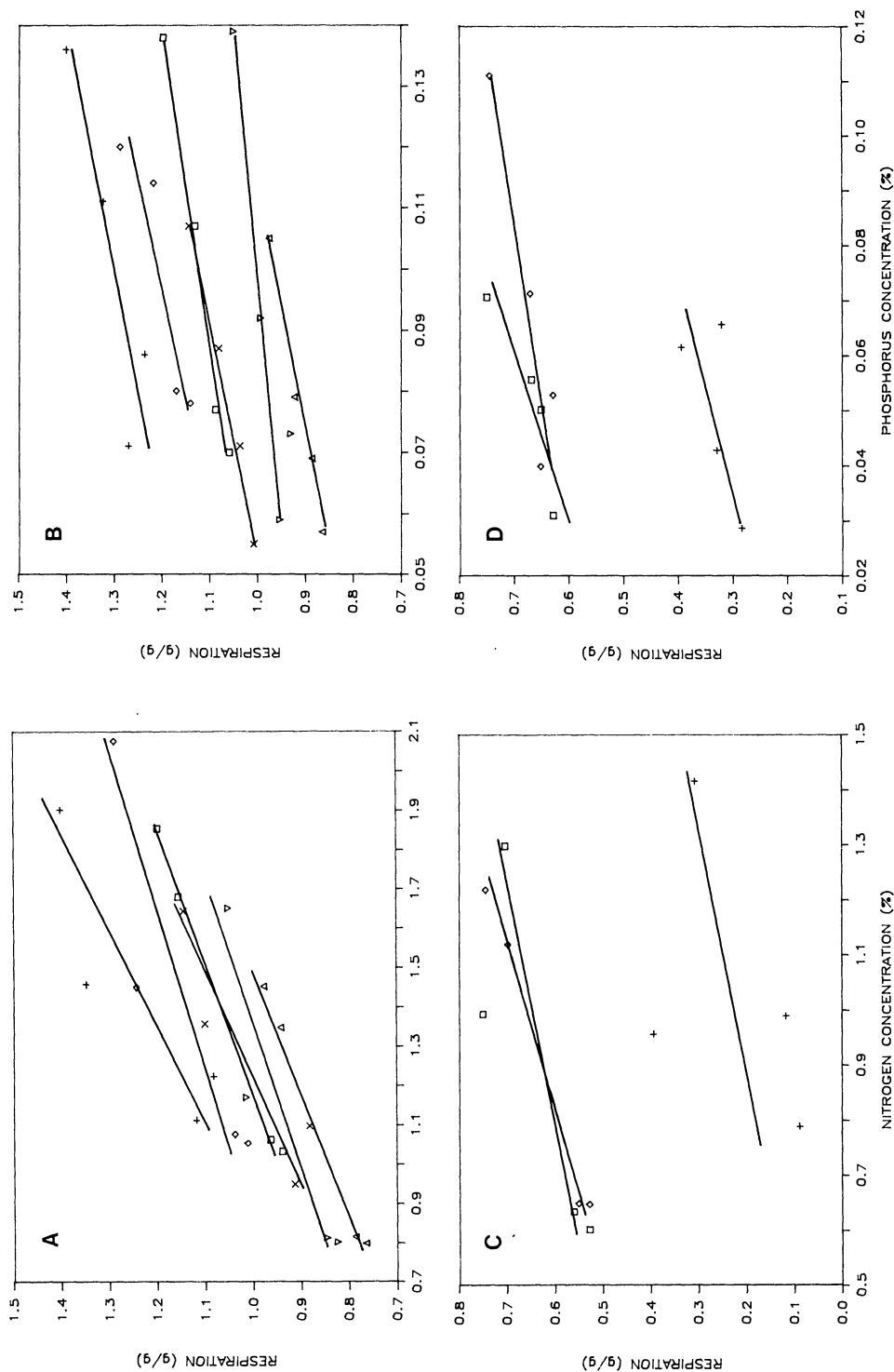


FIG. 1.—Relationship in the tissue of whole plants (A, B) and in reproductive tissue alone (C, D) between respiration per unit of tissue and concentration of either nitrogen (A, C) or phosphorus (B, D). A, B, the symbols represent either vegetative plants (□, +, ◇) or reproductive plants (Δ, ×, ∇) of genotypes G, K, and T, respectively. C, D, the symbols (□, +, ◇) represent genotypes G, K, and T, respectively. The lines are the fitted relationships for each of the various treatment combinations.

The relationships between respiration and levels of applied nitrogen and phosphorus and between respiration and the concentration of these minerals in the tissues were examined by linear regression. Separate analyses were done for whole-plant growth (both vegetative and reproductive plants) and for reproductive growth alone. The heterogeneity-of-slopes model of the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS) was used to fit relationships for each of the genotype-by-photoperiod treatments and to determine the overall significance of the relationship between respiration and nutrient level or concentration.

The correspondences between RE's calculated in terms of total carbon and in terms of nitrogen or phosphorus were examined by calculating Spearman's rank correlations for pairs of measures across genotypes and nutrient treatments.

RESULTS AND DISCUSSION

Relationship between Respiration and Nutrient Levels

To establish that total carbon allocation reflects the allocation of nitrogen and phosphorus, it must be shown (1) that the carbon cost per unit of tissue increases as the concentration of these nutrients in the tissue increases and (2) that the carbon cost of nitrogen and phosphorus uptake and allocation increases as these resources become more limiting. The first question was addressed by examining the relationship between the respiration requirement per unit of growth and the concentration of nitrogen and phosphorus in the tissues. The second question was addressed by expressing the respiration requirement for growth in terms of respiration per unit of nitrogen or phosphorus within the tissues and by examining the relationship between these values and the level of nutrients in the growth medium. Because RE is expressed as a ratio between reproductive and total growth, these two questions were addressed both at the level of whole plants and for reproductive tissue alone.

The respiration requirement per unit of growth increased with the concentration of nitrogen and phosphorus within the tissues (fig. 1). This relationship was true for whole-plant growth ($P < 0.001$ for nitrogen concentration and $P < 0.0001$ for phosphorus concentration) as well as for reproductive growth alone ($P < 0.0395$ for nitrogen concentration and $P < 0.0085$ for phosphorus concentration).

The fact that the respiration requirement for growth increased as nutrient concentration increased means that total carbon allocation (i.e., biomass plus respiratory carbon) tends to reflect the allocation of these nutrients. For example, two plants may allocate the same biomass to seeds, but the first plant may produce seeds with a high nitrogen content relative to the second plant and to the vegetative tissues of the same plant. Therefore, RE calculated in terms of nitrogen reveals that the first plant has a higher RE than the second plant, even though they have the same biomass allocation to reproduction. If RE is calculated in terms of total carbon, however, the first plant has a higher RE because of increased respiratory costs.

Respiration per unit of nitrogen (fig. 2) decreased as the level of applied nitrogen

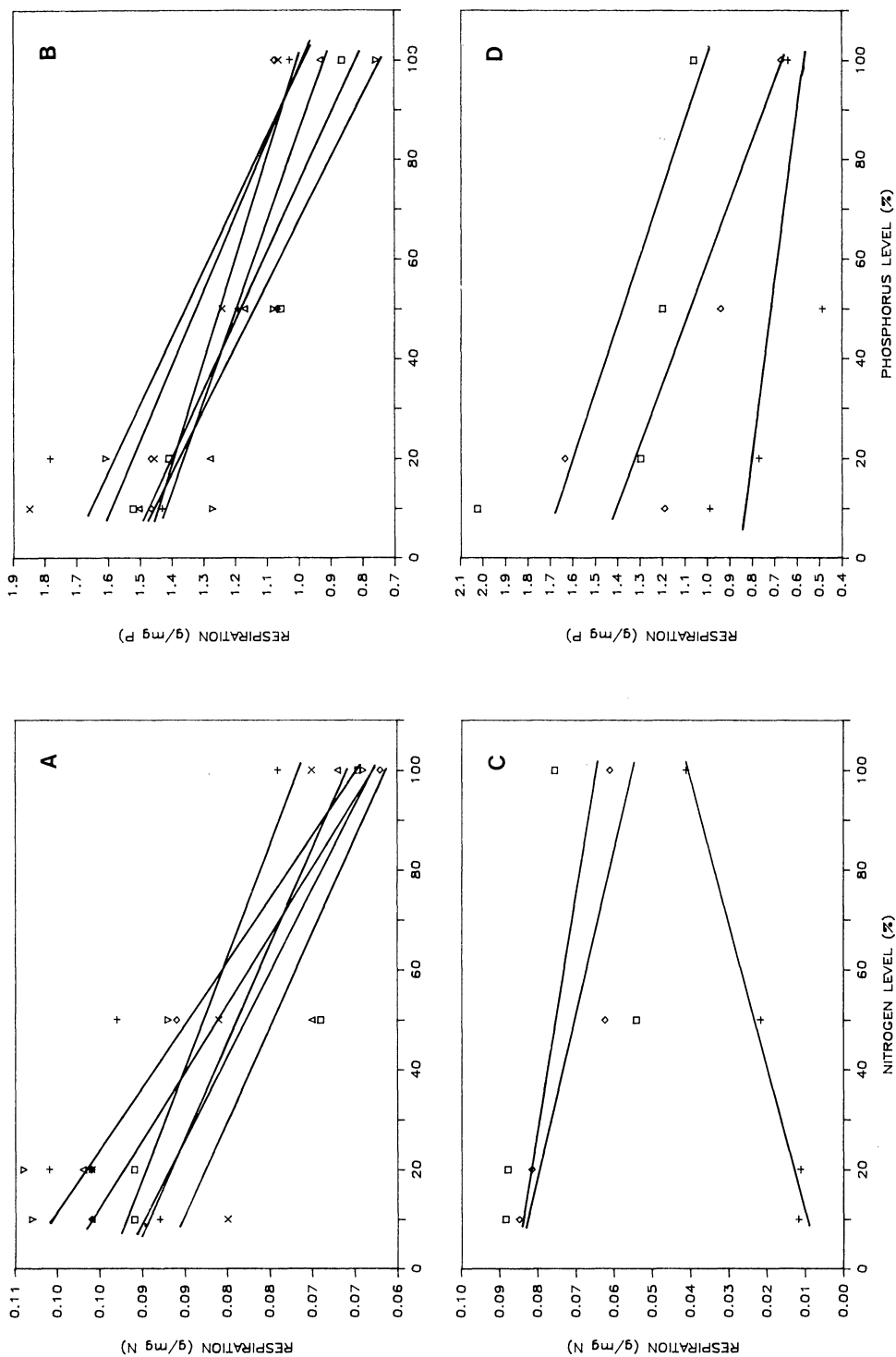


FIG. 2.—Relationship for whole plants (A, B) and for reproductive tissue alone (C, D) between respiration per unit of either nitrogen (A, C) or phosphorus (B, D) and the level of these nutrients in the growth medium expressed as a percentage of that in a full-strength nutrient solution. A, B, the symbols represent either vegetative plants (\square , $+$, \diamond) or reproductive plants (Δ , \times , ∇) of genotypes G, K, and T, respectively. B, D, the symbols (\square , $+$, \diamond) represent genotypes G, K, and T, respectively. The lines are the fitted relationships for each of the various treatment combinations.

increased in the case of whole plants ($P < 0.0001$) but showed no clear relationship with the level of applied nitrogen for reproductive tissue alone ($P < 0.7076$). It is unclear why these different patterns were found. Respiration per unit of phosphorus (fig. 2) decreased as the availability of phosphorus increased, both for whole plants ($P < 0.0001$) and for reproductive tissue ($P < 0.0320$).

Despite the lack of any significant effect of nitrogen availability on respiration per unit of nitrogen in reproductive structures, the majority of the evidence indicated that respiration per unit of nutrient increases as nitrogen and phosphorus become more limiting. The present study does not provide information regarding the mechanistic basis for this increase, but it may be related to the cost of producing and maintaining the "machinery" (e.g., root biomass, enzyme systems) necessary for resource uptake and utilization, even though this machinery may not be fully utilized when resource levels are low. The increase in the carbon cost per unit of nutrient as nutrients became more scarce suggests that total carbon allocation tends to be biased toward the resource or resources most limiting to plant growth.

Correspondence between Mineral and Total Carbon Measures of Reproductive Effort

At low levels of applied nitrogen, there was a close correspondence between RE measured in terms of total carbon and RE measured in terms of nitrogen; both measures of RE increased as the level of nitrogen increased from 10% to 50% (fig. 3). The two measures tended to converge at the lowest level of applied nitrogen. At the highest level, RE measured in terms of nitrogen decreased sharply, whereas RE measured in terms of carbon continued to increase. Differences between genotypes generally remained the same regardless of currency. The overall rank correlation between RE calculated using carbon and RE calculated in terms of nitrogen across all nitrogen treatments and genotypes was 0.804 ($P < 0.0016$). The correlation between the two measures at the two lowest levels of nitrogen availability was 1.00; at the two highest levels of nitrogen availability, it was 0.086.

Differences among the phosphorus treatments in carbon allocation to reproduction were small, but all three genotypes exhibited similar responses; RE increased as phosphorus increased from 10% to 20% and then gradually declined as the level of phosphorus was increased further (fig. 3). Reproductive effort measured in terms of phosphorus, although generally lower than that calculated using carbon, showed more or less the same pattern. There was no tendency for the two measures of RE to converge as phosphorus became more limiting. Genotype differences remained unchanged. The overall rank correlation between measures was 0.930 ($P < 0.0001$). The correlation between measures at the two lowest levels of applied phosphorus was 0.971, compared with 1.000 at the two highest levels.

The convergence at low levels of applied nitrogen between RE calculated in terms of carbon and RE calculated in terms of nitrogen supports the idea that carbon can be used as a currency to evaluate nitrogen-allocation patterns. At high levels of nitrogen, carbon allocation apparently reflects not only the allocation of

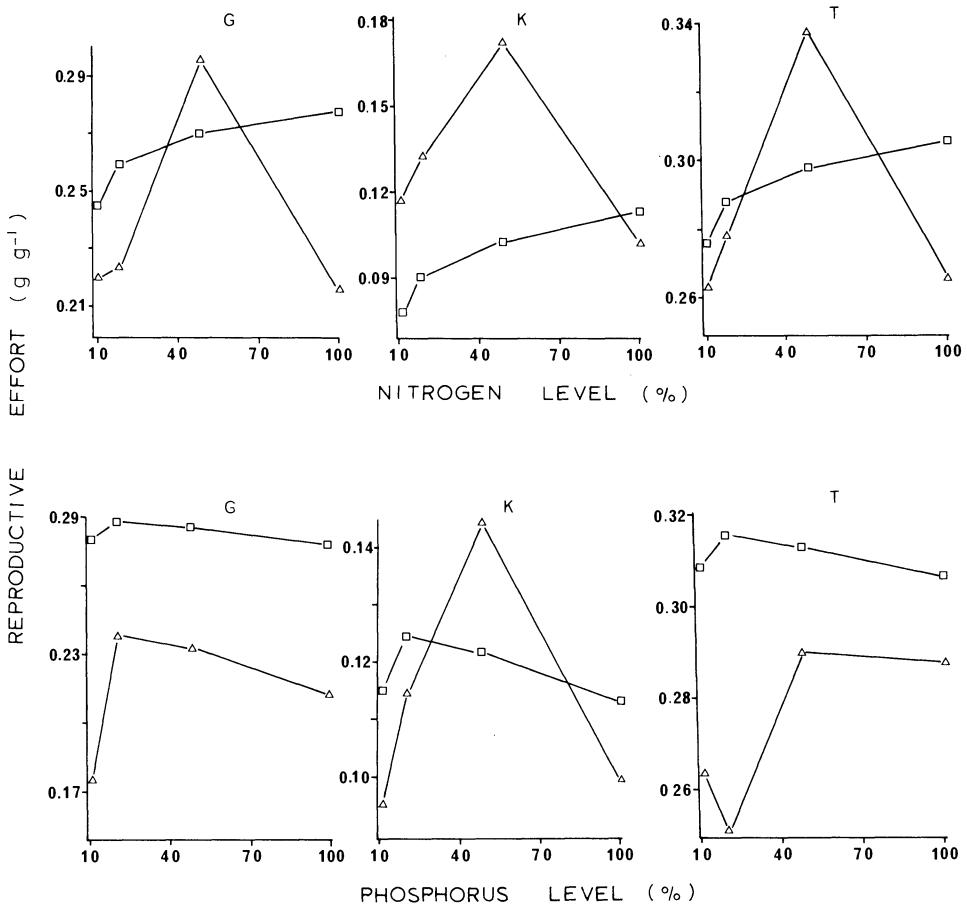


FIG. 3.—Reproductive effort calculated in terms of total carbon (□) and either nitrogen or phosphorus (△) in relation to the level of these nutrients in the growth medium for genotypes G, K, and T. Nutrient level is expressed as a percentage of that in a full-strength nutrient solution.

nitrogen and biomass but also the allocation of other resources that involve respiratory costs. As nitrogen becomes more limiting, however, the respiratory cost per unit of nitrogen increases, and carbon allocation becomes biased toward that of nitrogen. Therefore, from the point of view of life history analysis and the allocation of limiting resources, carbon allocation is a good measure of nitrogen allocation. This does not necessarily mean that carbon limits growth; it simply means that the allocation of a limiting resource (i.e., nitrogen) is reflected in the allocation of carbon.

The lack of convergence between carbon- and phosphorus-based measures of RE as phosphorus becomes less available is difficult to interpret; the levels of phosphorus availability used in this experiment may not have been low enough to result in convergence. Phosphorus availability had little effect on total growth

(Reekie and Bazzaz 1987*b*), and even at the lowest level it may not have been a seriously limiting factor. The respiratory cost per unit of phosphorus increased as the level of phosphorus decreased; it is conceivable that if phosphorus had been more limiting, carbon allocation would have become biased toward phosphorus allocation and the two measures of RE would have eventually converged.

SUMMARY

The assessment of reproductive effort (RE) in plants has been hampered by the uncertainty about which resource should be used as the currency to evaluate resource-allocation patterns. In this paper, we argue that carbon, because of its important energetic role in plants, tends to integrate the allocation patterns of other resources and can therefore be used as a common currency to assess allocation patterns. We show that the respiratory cost of plant growth in *Agropyron repens* increases as the concentration of nitrogen and phosphorus in the tissue increases. Furthermore, the respiratory cost per unit of nutrient generally increases as these nutrients become less available. This means not only that carbon allocation tends to reflect the distribution of other nutrients, but also that the allocation of carbon tends to be biased toward that of the most limiting resources. The second point is particularly important because the concept of resource allocation is relevant in life history studies only if resources are limiting growth. This bias in the allocation of carbon is reflected in the convergence at low levels of applied nitrogen of RE calculated in terms of total carbon (biomass plus respiratory carbon) and that calculated in terms of nitrogen. In our experiments, the overall rank correlation between RE calculated in terms of carbon and nitrogen across various genotypes and resource treatments was 0.804. Convergence was not evident between reproductive efforts calculated in terms of carbon and phosphorus, probably because phosphorus was not a seriously limiting factor in these experiments. However, the overall rank correlation between carbon- and phosphorus-based measures of RE was still high (0.900), suggesting that even when phosphorus is not limiting, carbon is an adequate measure of phosphorus allocation.

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