The shape of the trade-off function between reproduction and future performance in *Plantago major* and *Plantago rugelii*

Edward G. Reekie, Sonya Budge, and Jennifer L. Baltzer

Abstract: There is a paucity of data describing the nature of the trade-off function between reproduction and future performance. Most studies implicitly assume it is a linear function such that allocation of resources to reproduction results in a proportional decline in future survival and reproduction. We reanalyse data from a field experiment with half-sib families of *Plantago major* L. that suggests this relationship is in fact curvilinear. Low levels of reproductive investment had relatively little impact on future performance and higher levels of investment had a larger impact. To explain this curvilinear pattern, we conducted an experiment to examine the effect of incremental increases in reproductive investment on rates of resource uptake in *P. major* and *Plantago rugelii* Decne. Results suggest that, because of differences in the resource requirements of vegetative versus reproductive tissues, reproduction will have little effect on growth, providing that the limiting resources are required in greater quantities for vegetative as compared with reproductive tissues. These results are in accord with a curvilinear trade-off function between reproduction and future performance and provide an explanation for the maintenance of sexual reproduction in species where seed production may contribute minimally to fitness in the short term.

Key words: reproductive cost, resource allocation, life-history theory, nitrogen uptake, reproductive photosynthesis, *Plantago major*, *Plantago rugelii*.

Résumé : Il y a peu de données décrivant la fonction d'échange entre la reproduction et la performance future. La plupart des études assument implicitement qu'il s'agit d'une fonction linéaire faisant en sortes que l'allocation des ressources à la reproduction résulte en un déclin proportionnel de la survie et de la reproduction futures. Les auteurs ont réexaminé les données d'une expérience sur le terrain impliquant des familles de demi-frères du *Plantago major* L., suggérant que cette relation est en fait curvilinéaire. De faibles niveaux d'investissement reproducteur ont relativement peu d'impact sur la performance future, et des niveaux plus élevés d'investissement ont des impacts plus marqués. Pour expliquer ce patron curvilinéaire, les auteurs ont conduit une expérience afin d'examiner l'effet d'augmentations graduelles de l'investissement reproducteur sur les taux d'accumulation des ressources chez le *P. major* et le *Plantago rugelii* Decne. Les résultats suggèrent que, compte tenu des différences de besoins en ressources des tissus végétatifs versus les tissus reproducteurs, le reproduction aurait peu d'effet sur la croissance, pourvu que les ressources limitantes soient nécessaires en quantités plus élevées pour les tissus végétatifs que pour les tissus reproducteurs. Ces résultats concordent avec la fonction d'échange curvilinéaire entre la reproduction et la performance future et fournit une explication pour le maintien de la reproduction sexuelle chez les espèces où la production de graines peut contribuer minimalement à l'adaptation à court terme.

Mots clés : coût de la reproduction, allocation des ressources, théorie du cycle vital, absorption d'azote, photosynthèse reproductive, *Plantago major*, *Plantago rugelii*.

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Introduction

Reproduction in higher plants is extremely variable in terms of its timing and extent. Since reproductive output (RO) is presumably an important component of fitness and should be subject to strong selection, this variation has generated a great deal of interest and has been the subject of much theo-

rizing (see reviews by Lovett Doust 1989; Willson 1983). A fundamental assumption of these life-history theories is the idea that there is a cost associated with current reproduction such that individual survival and future reproduction are decreased (Williams 1966; Stearns 1989; Willson 1983). These costs result from changes in resource allocation patterns during reproduction with reproductive structures acting as sinks drawing resources away from the vegetative structures reducing growth and, consequently, survival and future reproduction (Bazzaz et al. 2000).

It has been argued that knowledge of the shape of the trade-off function between reproduction and future performance is crucial if we are to understand life-history variation (Calvo and Horvitz 1990; Schmid 1990). Most studies of reproductive cost, however, implicitly assume that this trade-off function is linear (i.e., a unit increase in RO al-

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Fig. 1. Two hypothetical trade-off functions between reproduction and subsequent performance. The upper panel shows the situation wherein resources invested in reproduction result in a linear decline in subsequent performance. The lower panel shows the situation wherein the resources invested in reproduction are supplied in part by increases in the rates of resource uptake resulting in a curvilinear relationship.
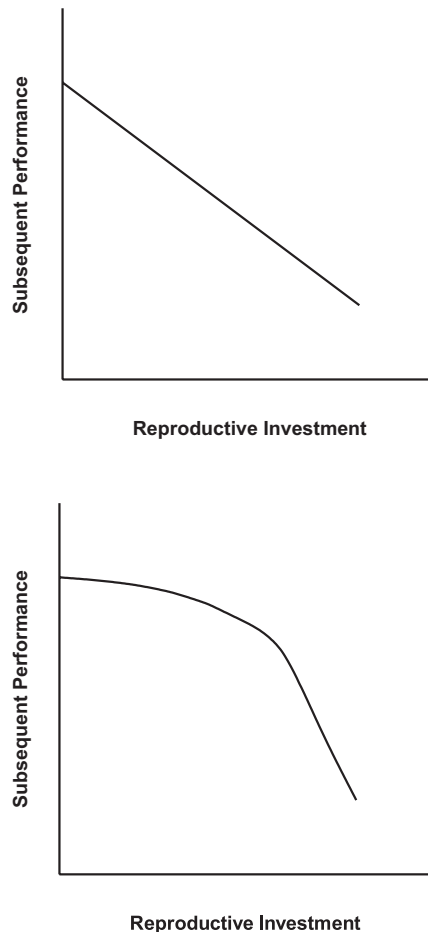
ways results in the same cost regardless of the level of RO; Fig. 1, upper panel). Two basic approaches have been used to examine the relationship between reproduction and future performance (Reznick 1985; Stearns 1989; Bailey 1992). The first experimentally controls reproduction by various means (e.g., removal of flower buds, photoperiod manipulations, control of pollination) and then compares the subsequent performance of the treatments. Most studies of this nature choose to induce only two (rarely three) levels of RO. Obviously, with only two different levels it is impossible to determine whether the relationship between RO and vegetative performance is linear or curvilinear. The second approach to examining the cost of reproduction uses correlation analysis to compare the subsequent performance of plants that differ naturally in the level of RO. This approach is problematic when the primary basis for variation in RO is phenotypic plasticity in response to the environment in that RO is automatically confounded with environmental variation. However, when the variation in RO has a genetic basis, this approach provides a measure of the cost of reproduction that is directly relevant to evo-

lutionary questions (Reznick 1985; Stearns 1989). One might assume that, in a natural population, there would be genotypes with a range of allocation patterns allowing one to examine how cost might vary as RO increases. In reality, if allocation patterns are subject to strong selection, there is likely to be little variation in reproductive allocation within a given population making it difficult to detect any cost associated with reproduction (Bailey 1992), let alone construct an entire cost function.

Although there is a paucity of data on the nature of the relationship between RO and cost, there is physiological evidence that suggests this relationship may not be linear. Numerous studies have shown that reproduction can, to a limited extent, increase rates of resource uptake. The reproductive structures of many plants have the capacity to photosynthesize (e.g., Bazzaz et al. 1979; Reekie and Bazzaz 1987; Galen et al. 1993). Reproductive structures also act as a strong sink altering leaf physiology and increasing leaf photosynthetic rate in many species (Reekie and Bazzaz 1987*a*; Laporte and Delph 1996). The changes in canopy structure and allocation patterns associated with reproduction can also enhance carbon uptake (Reekie and Reekie 1991; Reekie and Bazzaz 1992). More recently, reproduction has also been shown to enhance mineral resource uptake levels above those in vegetative plants (Karlsson et al. 1994; Thoren et al. 1996). Any increase in resource uptake resulting from reproduction will reduce the extent to which reproduction deprives vegetative growth of these resources and will lessen its impact on vegetative growth. Schmid (1990) argued that the capacity of a plant to increase rates of resource uptake in response to reproduction is likely to be limited and predicted that the impact of reproduction on growth will be minimal or perhaps even positive at low levels of reproduction, to increasingly negative as the level of reproduction increases further and starts to deprive vegetative structures of resources. Assuming vegetative growth is correlated with future success (i.e., survival and future reproductive output), this pattern will be reflected in a curvilinear trade-off function between reproduction and future performance similar to that depicted in the lower panel of Fig. 1.

Our objective in the present study was to test the above hypothesis by examining how resource uptake and vegetative growth vary in response to incremental increases in reproductive investment. The species chosen for this study were *Plantago major* L. and *Plantago rugelii* Decne. These morphologically similar species differ markedly in the extent of reproductive investment (Hawthorn and Cavers 1976) allowing us to examine a broad range in RO. We experimentally induced different levels of reproductive investment in these two species by varying the number of weeks plants received an inductive photoperiod. Both species are long-day plants with a critical photoperiod of 14 h light : 10 h dark (Hawthorn 1974). We assessed the effect of these incremental differences in reproductive investment on vegetative performance by examining effects on biomass accumulation, photosynthetic capacity, and nitrogen uptake. To determine if the relationship between reproduction and resource uptake revealed in this experiment was also reflected in the effects of reproduction on future performance we reanalysed data from a previous field experiment with half-sib families of *P. major* (Reekie 1998*b*). The fam-

ilies chosen for this particular experiment were a subset of a larger set of families isolated from a wide range of different habitats and grown in a common environment. The particular families chosen were selected to represent the full range of reproductive investment present in this species. Given the wide range in reproductive investment among these families, we hoped to avoid the problem inherent in most previous studies, i.e., lack of sufficient variation in reproductive investment to adequately characterize the relationship between reproductive investment and future performance.

Materials and methods

Effect of reproduction on resource uptake and allocation

Seeds of *P. major* and *P. rugelii* were collected in eastern Massachusetts and germinated in vermiculite. After 2 weeks of growth, 144 seedlings of each species were transplanted into 400-mL plastic pots filled with Turface, an inert dried-clay medium. Plants were watered on a daily basis and fertilized monthly by watering with a soluble fertilizer (10:52:10, N:P:K; Plant Products Co. Ltd., Brampton, Ont.) solution (5 mL·L^{-1}).

Sixteen plants of each species were randomly assigned to each of nine treatments that provided from 0 to 8 weeks of a 14 h light : 10 h dark (i.e., inductive) photoperiod. The plants were grown in two Conviron E15 chambers. Half of the seedlings of each species were placed in each chamber. Initially the light and temperature regime consisted of a 12 h light : 12 h dark photoperiod with a photosynthetic photon flux density of 230 µmol·m^{-2}·s^{-1} and a day:night temperature of 23:18°C. After 2 weeks, light was increased to 600 µmol·m^{-2}·s^{-1} and the day:night temperature increased to 25:20°C. The photoperiod treatments were initiated 2 weeks later (i.e., 4 weeks after transplanting). The inductive photoperiod consisted of an additional 2 h of low-intensity light (15 µmol·m^{-2}·s^{-1}), 1 h before and 1 h after the regular 12 h light period. To achieve the nine different levels of exposure to the inductive photoperiod, plants were switched between the two growth chambers, one of which provided the regular 12 h light : 12 h dark photoperiod, while the other provided the extended 14 h light : 10 h dark photoperiod. For example, plants in the 0-week treatment remained in the 12 h light : 12 h dark chamber for the duration of the experimental period, while plants in the 8-week treatment were placed in the 14 h light : 10 h dark chamber for the entire 8-week experimental period. As the effect of a given level of reproductive investment may vary depending upon the size or age of the plant (Reekie and Reekie 1991), plants receiving between 1 and 7 weeks of an inductive photoperiod were evenly divided between an early and a late treatment. The early treatment plants were placed in the 14 h light : 10 h dark chamber at the start of the experimental period for 1–7 weeks and then moved to the other chamber for the remainder of the 8-week period. Plants receiving the late treatment were initially placed in the 12 h light : 12 h dark chamber and then transferred to the 14 h light : 10 h dark chamber for 1–7 weeks during the latter part of the 8-week period. After the 8 weeks of photoperiod treatments, both chambers were programmed to provide a 12 h light : 12 h

dark photoperiod for the remainder of the experiment. Plants with their respective photoperiod treatments were rotated between chambers weekly to avoid confounding treatments with possible chamber effects.

The additional light received in the long-photoperiod treatments amounted to less than 0.5% of the light received by plants in the short-photoperiod treatment. Therefore, differences among treatments are most likely related to the effects of photoperiod on development (i.e., the induction of flowering) rather than any direct effect of the additional light on photosynthesis.

To help assess the impact of reproductive investment on carbon uptake, photosynthetic capacity and chlorophyll content of the youngest fully emerged leaf were measured 1 week after the completion of the photoperiod treatments. Photosynthetic capacity of a 9 cm^2 leaf disc was determined using a Hansatech leaf disc oxygen electrode (Delieu and Walker 1983) at saturating light (2400 µmol·m^{-2}·s^{-1}). The same disc was then ground with an Ultra Turrax 800 homogenizer, extracted with 80% acetone, and centrifuged at 2000 × *g*. The chlorophyll absorption measurements were made using a Novaspec spectrophotometer, and the chlorophyll content was calculated as described by Coombs et al. (1985).

Plants were harvested 3 weeks after completion of the photoperiod treatments. Root, stem, live leaf, dead leaf, and reproductive (spikes with the associated capsules and enclosed seeds) biomass were determined after drying at 50°C for greater than 48 h. To assess the impact of reproductive investment on nitrogen uptake, nitrogen concentration of each part (excluding dead leaves) was determined using a LECO CHN-1000 analyser. Nitrogen content was calculated as the product of the nitrogen concentration and the dry mass measurements for individual plant parts and summed to determine total nitrogen uptake of the plant over the course of the experiment.

All statistical analyses were conducted using the general linear models (GLM) procedure of SAS (SAS Institute Inc., 1987). The overall significance of differences among treatments was examined by analysis of variance (ANOVA). The dependent variables included photosynthetic capacity; chlorophyll content; and the dry mass of roots, stems, live leaves, and dead leaves as well as the summed biomass and nitrogen content of vegetative and reproductive structures. All dependent variables were checked for normality prior to analysis. The independent variables included species, treatment, and the interaction between species and treatment. There was a total of 16 treatments that differed in length of exposure to the inductive photoperiod and timing of that exposure (0, 8, and 1–7 weeks applied either either early or late in the experiment).

Effect of reproduction on future performance

To describe the trade-off function between reproduction and future performance we reanalysed data from a previous study (Reekie 1998*b*). The experimental procedures are described in detail in the original publication but are repeated here in summarized form.

Nine plants from each of 15 maternal half-sib families were grown in a uniform 3 × 10 m grass sward in a completely random experimental design. The grass sward was heavily dominated by *Poa pratensis* L. and was established

from commercially available sod. The grass was not mown over the course of the experiment. The 15 families were a subset of a larger sample of 42 families selected from a wide range of habitats including closely mown lawns, coarse turf, forest margins, and hay fields (see Reekie 1998*a* for a description of the sites). The 15 families were selected to represent the full range of reproductive investment observed in the larger sample of 42 families. Plants were grown for a period of 23 months from July 1990 to May 1992. Reproductive output was measured each year by collecting all capsules from individual plants as they matured on a weekly basis. Shoots were harvested on May 19, 1992, to assess plant size at the end of the experiment.

The original study (Reekie 1998*b*) examined the phenotypic and genetic correlations between reproduction and future performance but implicitly assumed a linear relationship between these two parameters. In the present study we test this assumption by fitting both linear and quadratic regressions to the relationship between reproductive output and future performance. Family means were used in the regressions to provide an estimate of the genetic trade-off between reproduction and future performance. The resulting estimates do include a component of environmental effects, but this bias is relatively small (Thomas and Bazzaz 1993; Geber 1990).

Results

Effect of reproduction on resource uptake and allocation

None of the plants that received only a 12 h light : 12 h dark photoperiod flowered, while all plants that were exposed to 8 weeks of the 14 h light : 10 h dark photoperiod flowered. Exposing plants to less than 8 weeks of the inductive photoperiod also induced reproduction, but reproductive biomass increased as the number of inductive weeks increased in both species (Fig. 2). However, there were marked differences between species in the extent and timing of reproduction. Reproductive plants of *P. major* had greater reproductive biomass than *P. rugelii*. *Plantago major* required only one inductive week to flower regardless of whether the inductive photoperiod was received early or late in development, whereas *P. rugelii* required four inductive weeks early in development and only two at a later stage. Late induction resulted in higher reproductive biomass than early induction in *P. rugelii*, a difference that was not apparent in *P. major*. All plants that flowered had set seed by the time the experiment was terminated.

In the vegetative state (week 0), root biomass did not differ between *P. major* and *P. rugelii*, but in the reproductive state (week 8), *P. major* had a much lower root biomass (Fig. 3). Root biomass decreased as the number of inductive weeks increased beyond 2 in *P. major*. In *P. rugelii*, the number of inductive weeks had little effect aside from a slight increase in root biomass compared with the vegetative control in weeks 1–3 for plants induced to flower late.

In general, stem biomass was higher in *P. major* than *P. rugelii* (Fig. 3). Stem biomass in both species increased slightly as the number of inductive weeks initially increased, but further increase in number of inductive weeks decreased stem biomass to levels similar to those in the vegetative controls.

Live leaf biomass was higher in *P. major* than *P. rugelii* in the vegetative state (week 0; Fig. 3). Both species showed an initial increase in live leaf biomass with low exposure to the inductive photoperiod, but as the number of inductive weeks increased, leaf biomass decreased in *P. major*, while in *P. rugelii* it remained more or less constant. As a result, leaf biomass was much greater in *P. rugelii* than *P. major* in the 8-week treatment. In both species, plants induced late tended to have a higher leaf biomass than those induced early, but this difference was greater in *P. rugelii*.

Plantago major had a much higher dead leaf biomass than *P. rugelii* (Fig. 3). There was a slight tendency for the amount of dead leaf biomass to increase with number of inductive weeks in *P. rugelii* but not in *P. major*. There was also some indication that time of induction (early vs. late) had an impact on amount of dead leaf biomass; however, these differences were small, and there was no consistent pattern.

Vegetative biomass did not differ between species in nonreproductive plants (Fig. 2). In both species, increasing the number of inductive weeks from 0 to 2 either had no effect on vegetative biomass or marginally increased vegetative biomass; however, as the number of inductive weeks increased further, vegetative biomass decreased in *P. major*, while it remained more or less constant in *P. rugelii*. As a result, in fully induced plants (week 8), vegetative biomass was much smaller in *P. major* than in *P. rugelii*. Plants induced to flower late tended to have a higher vegetative biomass than those induced early in *P. rugelii*.

Total biomass displayed essentially the same pattern as that described above for vegetative biomass (Fig. 2).

Total nitrogen invested in reproductive structures was much greater in *P. major* than *P. rugelii* (Fig. 4). The nitrogen invested in reproduction increased with increasing number of inductive weeks for both species, but it increased at a greater rate in *P. major* than in *P. rugelii*. Plants induced to flower late tended to have a higher reproductive investment than those induced early.

Averaged across all treatments, the nitrogen invested in vegetative structures was greater in *P. rugelii* than in *P. major* (Fig. 4). The nitrogen invested in vegetative structures decreased as the number of inductive weeks increased from 2 to 8, but this decline was much more extreme in *P. major*. There was some indication that late reproduction resulted in less of a decline than early reproduction in *P. rugelii*.

Nitrogen content of the plant as whole (i.e., total nitrogen uptake) increased with reproduction in both species (Fig. 4). In general, plants that were induced late in the experimental period tended to have a higher nitrogen content than plants induced early.

Both species decreased in photosynthetic capacity as the number of inductive weeks increased (Fig. 5). This pattern mirrored the response of chlorophyll content (Fig. 5). In *P. major*, plants receiving the inductive photoperiods late tended to have a higher chlorophyll content than those receiving it early, while the opposite was true for *P. rugelii*. A similar (nonsignificant) trend was seen in the photosynthetic data.

Effect of reproduction on future performance

Reproductive output among the 15 families ranged from 0.23 to 0.75 g in the first year of the study. In spite of this wide range in reproductive output, there was little evidence

Fig. 2. Reproductive, vegetative, and total biomass as affected by the degree to which reproduction was induced. Induction was controlled by varying the number of weeks plants were exposed to an inductive photoperiod. Plants that were partially induced (1–7 weeks) were exposed to the inductive photoperiod either early (circles) or late (squares) in the experimental period. Error bars are SEs. The *F* value with the associated degrees of freedom in parentheses is given for differences among species (spp), treatments (trt), and the interaction between species and treatment (sxt) on each graph. Asterisks indicate significance at the 0.05 level.
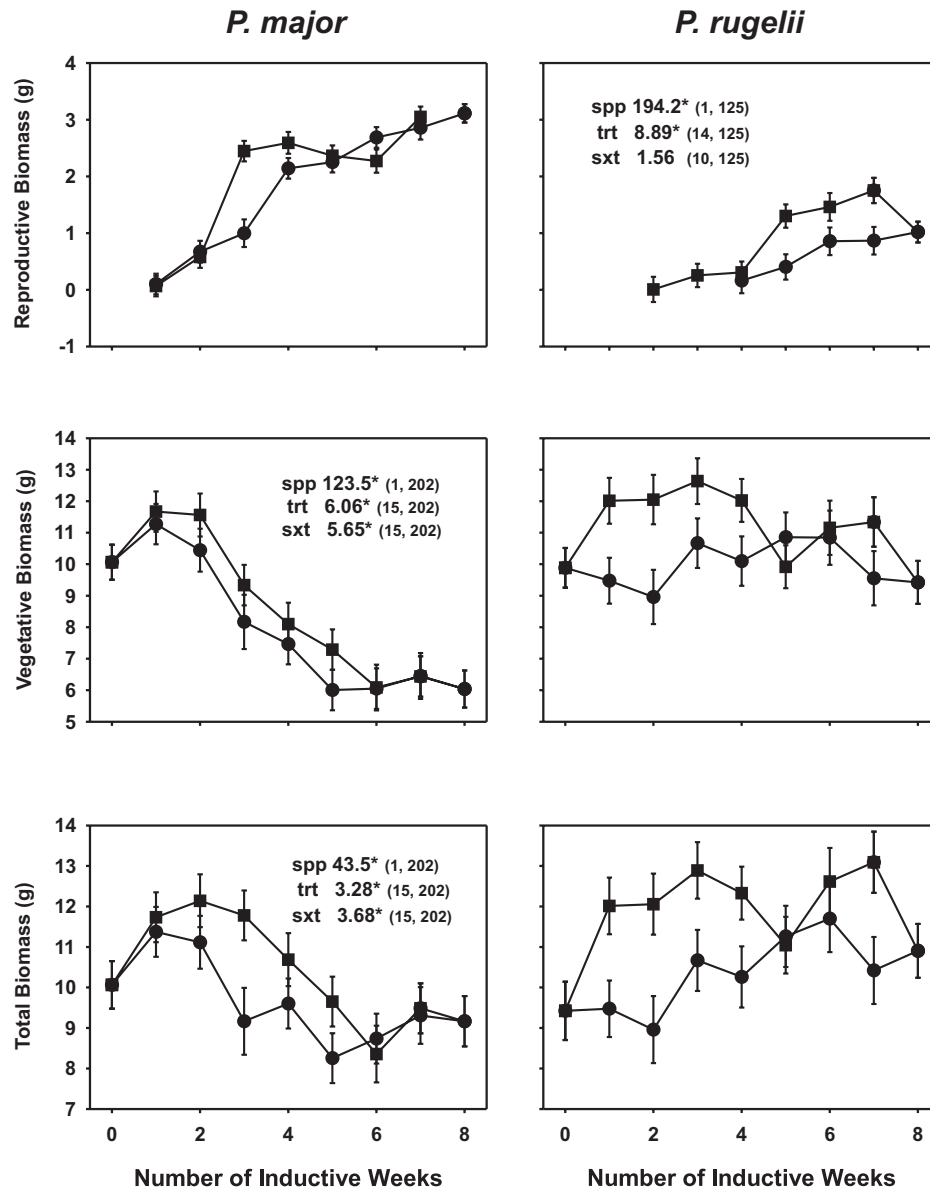
for a cost associated with reproduction. Although there was an indication that families with the highest level of reproductive output were smaller than average the following year (Fig. 6), overall, the linear relationship between size and reproductive output was not significant ($p = 0.1445$). However, when a quadratic term was fitted in addition to the linear term to generate a curvilinear regression, the model became significant ($p = 0.0492$). The curve generated by the curvilinear regression (Fig. 6) was similar to the hypothetical curve presented in the lower panel of Fig. 1 in that low levels of reproduction had little effect on subsequent growth and only at higher levels was there a measurable cost. There was no significant relationship between reproductive output

in year 1 and reproductive output in year 2 regardless of whether a linear or curvilinear model was fitted to the data (data not shown).

Discussion

Effect of reproduction on resource uptake and allocation

Regardless of whether one compares the two species, which differ markedly in the extent of reproduction, or whether one examines the impact of increasing the number of inductive weeks within *P. major*, the results suggest that limited reproduction has no negative effects on growth. Taken together, reproductive biomass of the two species

Fig. 3. Root, stem, live leaf, and dead leaf biomass as affected by the degree to which reproduction was induced. Induction was controlled by varying the number of weeks plants were exposed to an inductive photoperiod. Plants that were partially induced (1–7 weeks) were exposed to the inductive photoperiod either early (circles) or late (squares) in the experimental period. Error bars are SEs. The *F* value with the associated degrees of freedom in parentheses is given for differences among species (spp), treatments (trt), and the interaction between species and treatment (sxt) on each graph. Asterisks indicate significance at the 0.05 level.
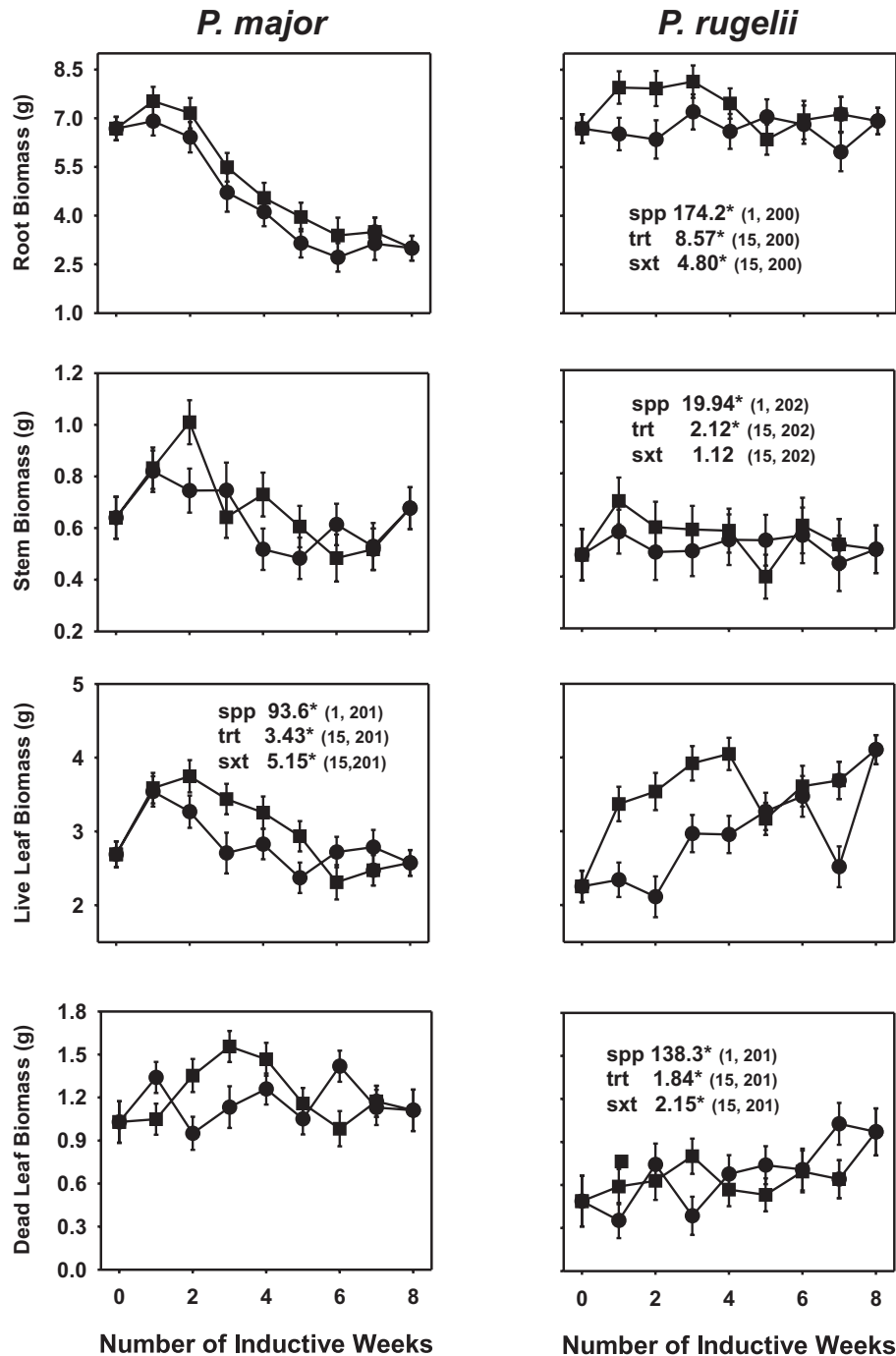
ranged between 0 and 3 g across the various treatments. Regardless of species, at low levels of investment (<1.5 g reproductive biomass) there were no negative effects of reproduction on vegetative biomass, and in the case of plants induced to flower at a later age, reproduction increased vegetative biomass. Only in *P. major*, where reproductive biomass exceeded 1.5 g, did reproduction depress vegetative

growth. A similar pattern was observed in the case of nitrogen uptake. Low levels of reproductive investment did not deprive vegetative organs of nitrogen and carbon; rather, reproduction stimulated both carbon and nitrogen uptake above the levels observed in vegetative plants. This is reflected in the effect of reproduction on total biomass and total nitrogen. Regardless of the level of reproductive

Fig. 4. Nitrogen content of reproductive, vegetative, and total biomass as affected by the degree to which reproduction was induced. Induction was controlled by varying the number of weeks plants were exposed to an inductive photoperiod. Plants that were partially induced (1–7 weeks) were exposed to the inductive photoperiod either early (circles) or late (squares) in the experimental period. Error bars are SEs. The *F* value with the associated degrees of freedom in parentheses is given for differences among species (spp), treatments (trt), and the interaction between species and treatment (sxt) on each graph. Asterisks indicate significance at the 0.05 level.
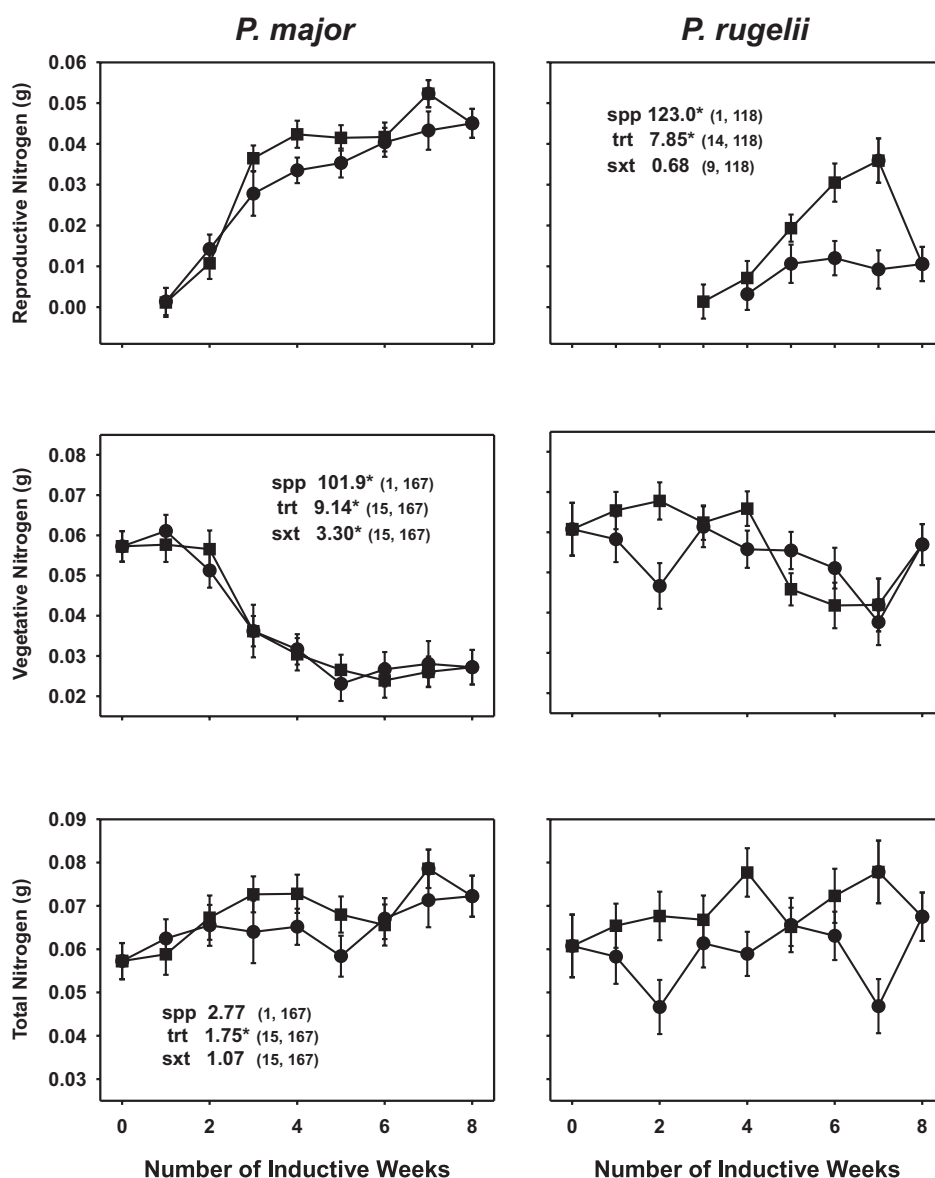

investment, reproduction increased total nitrogen in both species and increased total biomass in *P. rugelii*. It also increased total biomass in *P. major* at low levels of reproductive investment. It is clear that these species have mechanisms to compensate for both the carbon (i.e., biomass) and nitrogen invested in reproduction providing the level of reproductive investment is relatively low.

The fact that late reproduction generally had less negative, or in some cases, more positive effects on resource uptake, suggests that it is not the absolute level of reproductive investment that is most critical. Rather, it is the level of reproductive investment relative to the resources already accumulated by the plant that will determine the effect of reproduction on growth. Plants that reproduce late are larger than plants that

reproduce early and, consequently, have a larger store of resources to draw upon (see also Reekie and Reekie 1991).

The ability of a variety of plants to compensate for the carbon cost of reproduction has been well documented (Bazzaz et al. 2000). As described earlier, this compensation may involve direct photosynthesis by the reproductive structures as well as reproductive enhancement of leaf photosynthesis by various mechanisms. Both species in our study produce reproductive structures that are green throughout their development, and it seems likely that direct photosynthesis by these structures was involved in reducing the carbon cost of reproduction. It is also clear that limited reproduction stimulated leaf allocation increasing the leaf area available for photosynthesis. There is no evidence that

Fig. 5. Photosynthetic capacity and total chlorophyll content of the most recent fully emerged leaf as affected by the degree to which reproduction was induced. Induction was controlled by varying the number of weeks plants were exposed to an inductive photoperiod. Plants that were partially induced (1–7 weeks) were exposed to the inductive photoperiod either early (circles) or late (squares) in the experimental period. All measurements were made at the end of the 8-week experimental period. Error bars are SEs. The F value with the associated degrees of freedom in parentheses is given for differences among species (spp), treatments (trt), and the interaction between species and treatment (sxt) on each graph. Asterisks indicate significance at the 0.05 level.
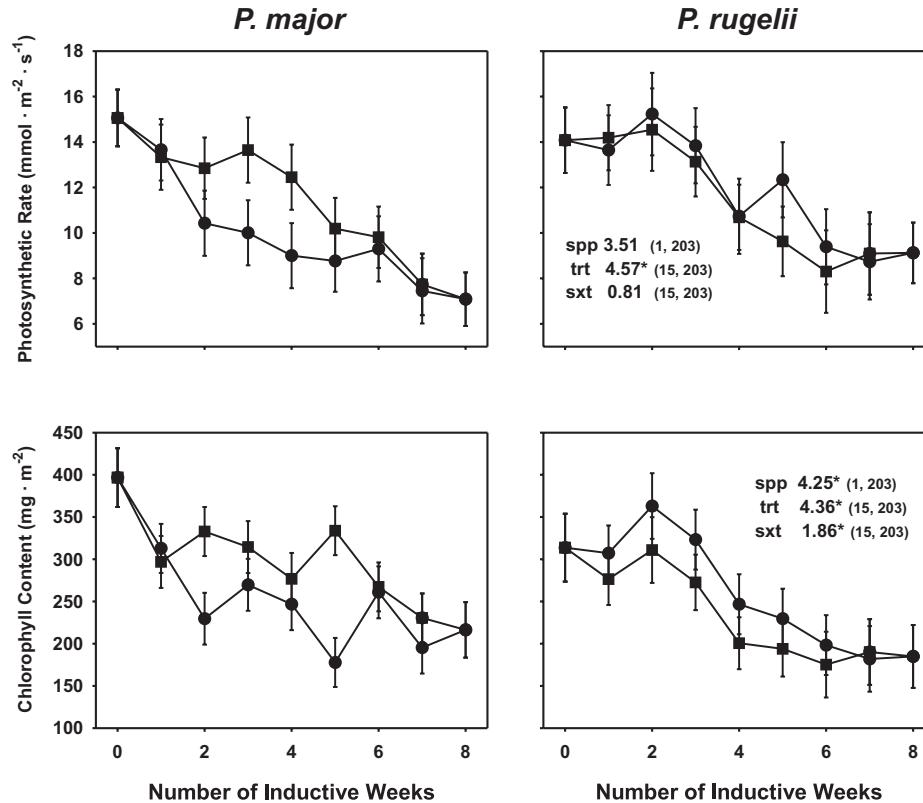

reproduction enhanced photosynthetic rate per unit leaf area through increases in sink strength. Indeed, the available data suggests that reproduction decreased photosynthetic rate. Given that reproduction decreased leaf nitrogen concentration (data not shown), this decline is not surprising. Nitrogen is required for chlorophyll and the various proteins present in the photosynthetic apparatus, such as ribulose 1,5-bisphosphate carboxylase–oxygenase (Rubisco). However, these data do not preclude the possibility that reproduction enhanced leaf photosynthesis through sink effects. We measured photosynthesis under conditions of saturating light and carbon dioxide. This provides a measure of how reproduction affects the capacity of the photosynthetic apparatus, but this measure does not necessarily reflect how reproduction affects photosynthetic rates under actual growth conditions. Aside from the production of the inflorescence, neither *P. major* nor *P. rugelii* display marked changes in morphology with reproduction; therefore, it is unlikely that morphological changes and their effect on self-shading (Reekie and Reekie 1991) are involved in explaining their ability to compensate for the carbon cost of reproduction.

Although the capacity of plants to compensate for the carbon cost of reproduction has been reasonably well documented, the extent to which plants are able to compensate for the nitrogen cost has not been studied extensively. In par-

ticular, the mechanisms responsible for this compensation are unclear. Obviously, reproductive structures are unlikely to be directly involved in nutrient uptake as they are in the case of carbon uptake. Therefore, reproduction must increase nitrogen content by (*ii*) increasing the absorptive area of the root system, (*ii*) enhancing uptake per unit root area, or (*iii*) decreasing nitrogen losses through senescence of plant parts. In the present study, limited reproduction either had no effect on root biomass or, in the case of plants induced to reproduce at a later age, increased root biomass. Only at high levels of reproduction (i.e., >2 g spike biomass in *P. major*) did reproduction decrease root biomass. This indicates increases in the absorptive area of the root system may explain some of the increased nitrogen uptake but cannot explain all of the increased uptake as reproduction increased total nitrogen content of the plants at all levels of reproduction in both species. It is unlikely that decreases in nitrogen losses can explain this increase in nitrogen content as reproduction either had no effect on leaf senescence or slightly increased senescence. Therefore, increases in the both root absorptive area and in the rate of nutrient absorption per unit area appear to be involved in compensating for the nitrogen cost of reproduction in these species.

Given that reproduction was able to induce increases in both carbon and nitrogen uptake by vegetative organs, this

Fig. 6. Effect of reproduction on subsequent performance in *P. major* growing in a grass sward. Capsule mass in 1990 was used as the measure of reproductive investment and shoot biomass in May of 1992 was used as the measure of subsequent performance. Individual points represent a mean of 9 individuals for each of 15 half-sibling families. The 15 families were chosen on the basis of a preliminary experiment with a larger sample of families to represent the full range of genetic variation in reproductive investment present in this species. The line was fitted by means of least squares regression with both a linear and quadratic term in the model. The line represents the genetic trade-off between reproduction and future performance.
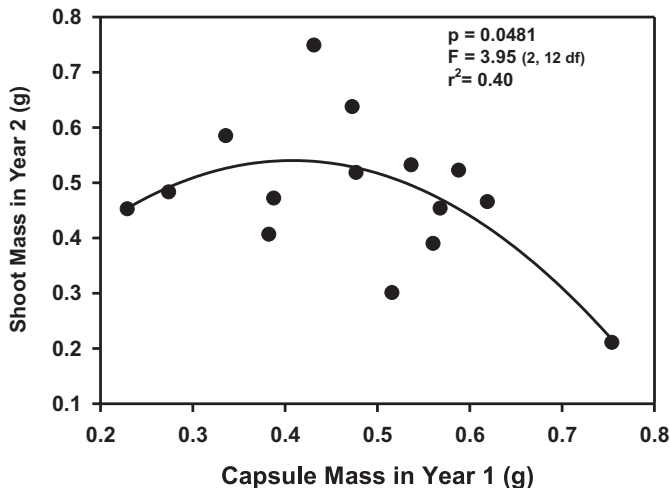
raises the question as to why vegetative plants apparently maintain suboptimal rates of nutrient uptake. Plant size is closely related to fitness in a wide variety of species (e.g., Farris and Lechowicz 1990; Mitchell-Olds and Bergelson 1990; Schwaegerle and Levin 1990). Consequently, one would expect selection to maximize resource uptake to increase plant size. One possible answer to this question lies in the different resource requirements of vegetative versus reproductive tissues. Because of differences in function, vegetative and reproductive structures will invariably differ in nutrient composition and resource requirements to some degree. For example, the nitrogen concentration in the reproductive structures of *Plantago* is substantially higher than that in any of the vegetative organs (data not shown). Differences are also likely to be found in the concentrations of other mineral nutrients (Abrahamson and Caswell 1982), the respiratory (i.e., carbon) cost of tissue construction (Goldman and Willson 1986; Reekie and Bazzaz 1987), and the water required for transpiration (Galen et al. 1999). As a result, vegetative growth may be limited by a particular resource or combination of resources, while reproductive growth will be limited by a different set of resources. This difference in limiting factors means that, to some extent, reproductive growth may occur at little or no cost to vegetative growth. To use a hypothetical example, assume reproductive growth in *Plantago* is limited by nitrogen, while vegetative growth is limited by water availability. The reproductive structures would presumably have a much lower water requirement for transpiration than the leaves because of their lower surface area to weight ratio

and the fact that the reproductive spike in *Plantago* is upright and parallel to the incoming light for most of the day, while the leaves are orientated more or less perpendicular to the incoming light. Allocation of resources to reproduction in this case would initially have little negative effect upon vegetative growth as the water requirement for reproductive growth would be small relative to that required for the leaves, and the nitrogen requirement of the reproductive structures could be met through increased rates of nitrogen uptake. Note, however, that there will be a limit to which resources can be allocated to reproduction with little effect on vegetative growth in that the allocation of nitrogen to reproductive structures will eventually reach the point where it exceeds the capacity of the plant to increase its uptake rate and nitrogen will start to limit vegetative growth as well.

The above scenario is simplistic in that it is likely that, in many cases, there is more than one resource limiting growth (Bloom et al. 1985; Chapin et al. 1987). However, it does serve to illustrate how the differing resource requirements of vegetative versus reproductive growth could account for how plants are able to partially compensate for the resource cost of reproduction through increases in rates of resource uptake. Those resources whose rate of uptake is increased in response to reproduction are simply those that were not limiting vegetative growth but that are required in greater amounts for reproductive growth. A logical prediction that arises from this hypothesis is that the impact of reproduction on vegetative growth will vary depending upon which resources are limiting. If the resource that is limiting vegetative growth is required in equal or greater amounts by reproductive growth then the cost will be high. On the other hand, if the resource that is limiting vegetative growth is required in smaller amounts for reproductive growth, the cost will be low. This may explain why a variety of studies have shown that the cost of reproduction varies depending upon the availability of specific resources or among habitats (Syrjänen and Lehtilä 1993; Ågren and Willson 1994; Primack et al. 1994; Thoren et al. 1996; Reekie 1998*b*).

Effect of reproduction on future performance

In spite of the wide range in reproductive investment observed among the 15 families in this experiment, there was little evidence for reproductive cost until capsule mass exceeded 0.6 g. In *P. major,* capsules make up approximately 50% of the total reproductive mass (data not shown). Therefore, costs were only observed when reproductive mass exceeded 1.2 g. This corresponds well to the value at which reproduction started to deprive vegetative growth of resources in the growth chamber experiment (1.5 g). It is clear the capacity of reproduction to stimulate rates of resource uptake not only reduces its immediate impact on vegetative growth; it reduces its impact on future performance. Given that vegetative growth determines plant size, and size is probably the single best predictor of future success in plants (Farris and Lechowicz 1990; Mitchell-Olds and Bergelson 1990; Schwaegerle and Levin 1990), this conclusion is to be expected.

The trade-off function between reproduction and future performance generated by curvilinear regression (Fig. 6) was similar to the predicted curve presented in the lower panel of Fig. 1. Note that, even though this relationship was significant, there was a great deal of scatter in the data and that, unless one was specifically looking for a curvilinear relationship, this pattern would have been easy to miss. The scatter in the data is to be expected given that differences among families in RO are likely to be confounded with other unrelated genetic differences that would affect plant growth. However, this data set does illustrate that providing there is a large enough range in reproductive output among the genotypes being compared, genetic correlations between reproduction and future performance are not necessarily linear. One caveat to this conclusion is that the relationship depicted in Fig. 6 was highly dependent upon the single family in which capsule mass exceeded 0.6 g. The rarity of families with a very high reproductive output is to be expected. If reproductive cost does increase disproportionately at high levels of reproductive investment, there would be strong selection to reduce the level of reproductive investment to the point where cost is minimal. This may be the reason why many studies have been unable to detect any cost associated with reproduction (see literature reviewed in Bazzaz et al. 2000).

The fact that low levels of reproduction may not entail a significant cost has important consequences for understanding the evolution of plant life histories. It implies that, even though seed production may contribute only minimally or not at all to fitness, selection will favour maintenance of a low level of allocation to sexual reproduction. Although we often assume that reproductive output (i.e., fecundity) is closely related to fitness (indeed, we often assume it is equivalent to fitness), fecundity is only one component of fitness, and its importance varies substantially depending upon the life-span of a species, whether it is monocarpic or iterocarpic, and whether or not clonal propagation is possible (Caswell 1986). In fact, for some plant species its impact on fitness in the short term is minimal. This is the situation in a number of clonal species, where most population growth is accomplished through vegetative propagation and successful establishment from seed is rare (Schmid 1990). The maintenance of flowering and seed production in these species has been explained in terms of its importance for long-distance dispersal (seeds are often dispersed to a greater distance than clonal propagules) and its role in sexual recombination and, therefore, the generation of genetic diversity. Although both of these attributes of seed production are crucial for the evolutionary success of a species in the long term, the lack of any negative impact on vegetative growth makes it much easier to explain the maintenance of a low level of seed production in the short term.

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