Evolution, 47(1), 1993, pp. 61–74

PLASTIC RELATIONSHIPS BETWEEN REPRODUCTIVE AND VEGETATIVE MASS IN *SOLIDAGO ALTISSIMA*

BERNHARD SCHMID AND JACOB WEINER[1]
Botanisches Institut der Universität Basel, Schönbeinstrasse 6, CH-4056 Basel, SWITZERLAND

Abstract.—To test several predictions of a model of linear, size-dependent reproductive output in plants, we analyzed the relationship between shoot vegetative (v) and reproductive (r) mass in five experiments on *Solidago altissima* from an invading population in Switzerland. There was large environmentally-induced and genetic variation in r and v. A large amount of variation in r could be explained by variation in v, using the simple linear model. There was a minimum size for sexual reproduction, and above this size, shoots devoted a relatively constant proportion (about one third) of their biomass to reproductive structures. We detected significant genetic variation for both the minimum size and the slope of the r–v relationship, but there was no evidence for an hypothesized trade-off between minimum size and slope. There was significant genotype-environment interaction for the slope of the r–v relationship. There were also developmental effects on the r–v relationship: plants grown from seeds behaved differently than those of the same genotype grown from rhizomes.

Key words—Genetic variation, genotype-environment interaction, plasticity, reproductive effort, size variability, *Solidago*.

Received September 12, 1990. Accepted June 9, 1992.

The way a plant's biomass is apportioned among different structures is a fundamental aspect of its biology. Life-history theory has put special emphasis on the allocation of resources to sexual reproduction (e.g., Harper, 1967; Gadgil and Bossert, 1970; Abrahamson and Gadgil, 1973). It predicts a trade-off between reproductive allocation and other activities that affect fitness, because resources invested in offspring are not available for future survivorship, growth, and reproduction (Stearns and Koella, 1986; Sackville Hamilton et al., 1987).

Reproductive allocation has traditionally been thought of as the proportion of a plant's total biomass that is in reproductive tissues (e.g., Bazzaz and Reekie, 1985). However, reproductive allocation may change with plant size (Samson and Werk, 1986). To explain changes in reproductive allocation in response to competition, Weiner (1988) proposed a model in which there is a positive minimum size for reproduction above which the relationship between reproductive output and size is linear. In this model, reproductive allocation increases with size (Samson and Werk, 1986). Evidence in support of this model has been found in four species of clonal composites (Hartnett, 1990) and several species of agricultural weeds (Thompson et al., 1991). Size-dependent reproductive allocation could also result from a curvelinear relationship between reproductive output and size, such as a classical "allometric" relationship (Reiss, 1989; Klinkhamer et al., 1990).

To understand how size-dependent reproductive allocation may play a role in natural selection, one must know how the relationship between reproductive output and plant size is influenced by genotype and environment. There are three possibilities: i) a plastic relationship between reproductive output and size i.e., environmentally induced changes in reproductive output are correlated with environmentally induced changes in size; ii) a genetic relationship between reproductive output and size i.e., genetically determined variation in reproductive output is correlated with genetically determined variation in size; and iii) genetic variation in the plastic relationship i.e., different genotypes show different environmentally induced changes in reproductive output associated with environmentally induced changes in size.

We know of no study that has attempted to look at these components of the relationship between reproductive output and size.

Weiner's (1988) model is based on an analogy between a biological plant that pro-

[1] Present address: Department of Biology, Swarthmore College, 500 College Avenue, Swarthmore, PA 19081-1397 USA.

duces seeds and an industrial plant (factory) that produces manufactured goods. His model makes several predictions about size-dependent reproductive output in plants: 1) Significant capital investment is required before there can be any production. Therefore, there is a minimum size for sexual reproduction; 2) After the necessary initial capital investment has been made, costs of production per unit produced may be relatively fixed. Therefore, above the minimum size for reproduction, the relationship between reproductive output and size is linear; 3) Different factory designs will differ in initial capital investment and in fixed costs of production. Therefore, genetic variation may occur in (a) the minimum size for reproduction and in (b) the slope of the relationship between reproductive output and size; 4) Increased capital investment can reduce production costs. Therefore a trade-off may exist between minimum size for reproduction and the slope of the relationship between reproductive output and size.

In the present study we test these predictions using existing data from a series of experiments on single-shoot plants of *Solidago altissima.*

Materials and Methods

Source of Data

The tall goldenrod, *Solidago altissima* L., is a clonal perennial that was introduced from North America (Maryland/Virginia) to Europe in the seventeenth century (Leit-Ross, 1984; Reveal et al., 1987). In both its native and introduced range it typically colonizes old-field sites and often becomes a dominant during secondary succession (Bazzaz, 1968; Bornkamm, 1984). Initial densities of shoots and clones depend on seed input and can reach more than 100/m^2 (B. Schmid, pers. obs.). Following establishment, the number of clones decreases and the number of shoots per clone increases (Hartnett and Bazzaz, 1985). Shoot densities within patches formed by one or several clones depend on rhizome length, which ranges from circa 5 to 20 cm in this species (Schmid et al., 1988; Maddox et al., 1989). The plants in the study population had 2n = 18 chromosomes. This finding contrasts with results from North America, where the species usually is hexaploid (2n = 54; Melville and Morton, 1982; Semple, 1992; we know of no chromosome counts from the Maryland/Virginia region). Further information on the biology of *S. altissima* can be found in Werner et al. (1980), Hartnett (1983), Voser (1983), Schmid et al. (1988), and Meyer (1992).

In autumn of 1987 we collected seeds and rhizomes from separate clones in a dense population near Basel, Switzerland, to start a series of garden experiments (Table 1) in a nearby area that would be invaded by *S. altissima* if it were not weeded. The aim of the experiments was to investigate effects of plasticity and genetic variation on the potential of this species for invasion of new areas (Weber and Schmid, 1989; Dolt, 1991; Schmid and Weber, unpubl. data). The studied population consisted of three-year-old clones that had colonized a nutrient-poor site abandoned from cultivation in 1983. The sampled clones had three to nine shoots. Electrophoretic analyses of their seed progeny (N = 181) showed no significant deviations from Hardy-Weinberg equilibrium at two loci with two alleles each ($P >$ 0.1).

For the "clones 88" and "half sibs 88" experiments (see Table 1) 24 rhizome families and 24 seed families were propagated in the glasshouse of the Botanisches Institut, University of Basel, and transplanted to the experimental garden when they had reached the rosette stage. Each rhizome family was cloned from a single genetic individual and referred to as a "clone." Each seed family was taken from a single shoot and considered to approximately represent a maternal "half-sib family" for the following reasons. *S. altissima* is self-incompatible (Voser, 1983; Dolt, 1991). Because each shoot has a large inflorescence and is visited by many pollinators, the seeds of a single maternal plant in a dense population of young and small clones probably have many paternal parents. Therefore, if a small random sample of seeds (here 16) is taken from a single maternal plant, only a few of them would be expected to be full sibs. Nineteen clones and half-sib families had identical (maternal) parents. In these first two experiments we grew the plants in 4 × 6 grids at 16 cm spacing in plots containing either pure sand

TABLE 1. Summary of experimental designs. Rhizomes and seeds were collected in an invading, even-aged field population of *Solidago altissima* from three-year old parent clones.

Experiment	Origin of plant material	Families	Plots (=repl.)	Shoots per fam. per plot	Substrate	Density (m^{-2})	Year
Clones 88	Rhizomes from field 1987	24	16	1	sand, soil	40	1988
Clones 89	Rhizomes from "clones 88"	24	8	1	sand, soil	40	1989
Half sibs 88	Seed from field 1987	24	16	1	sand, soil	40	1988
Half sibs 89	Rhizomes from "half sibs 88"	6	8	4	sand, soil	40	1989
Full sibs 89	Seed from crossing "clones 88"	30[1]	4	c. 4	soil	100	1989

[1] In one family all plants were lost and in one of the remaining families there were no flowering plants.

or enriched garden soil. In each plot either every half-sib family or clone was represented by a single-shoot individual. Eight plots (replicates) were used for the "clones 88" and 16 plots for the "half sibs 88" experiment.

After the 1988 experiments were completed, rhizome cuttings were made from the harvested plants. These cuttings were again grown to the rosette stage in the glasshouse and transplanted to the experimental garden in the following year. The 16 plots (eight with sand and eight with soil) that had been used for the "half sibs 88" experiment were now used to grow the progeny from the "clones 88" experiment. Each of the 24 clones was represented by one shoot in each plot ("clones 89" experiment; see Table 1). The remaining eight plots from the "clones 88" experiment were used for the "half-sibs 89" experiment. Here, progeny from only six half-sib families—chosen to represent a wide range of phenotypes—were planted, such that each family was represented by four shoots in each plot. The experimental procedures for these experiments were the same as for those of the previous year.

For the "full sibs 89" experiment 15 clones of the "clones 88" experiment were crossed in three 5 × 5 diallels (without self crosses) yielding 30 full-sib families (see Table 1). Seedlings were raised to the rosette stage in the glasshouse and then transplanted into four plots containing normal garden soil. In this experiment a closer spacing, i.e., an 8 × 18 grid with 10 cm distance between rows and columns, was chosen to test the influence of density stress on the expression of phenotypic variation. The number of replicates varied among families.

In each experiment the plants were harvested at the end of the growing season and separated into stems, leaves, and inflorescences, which were dried and weighed. In addition, the height and phenological stage (vegetative, with buds and/or flowers, and with fruits) of all plants were also recorded. Only plants with fruits were considered to be reproducing. The root and rhizome biomasses were not determined because we knew from previous studies that this would have taken approximately 1 hr per plant (Schmid and Bazzaz, 1992). As an approximation to rhizome biomass we determined the number and maximum length of rhizomes produced in the 1988 experiments.

Analyses

First, we analyzed how the probability of reproduction depended on vegetative mass v (stem + leaves). We chose vegetative mass instead of total (vegetative + reproductive) mass as an independent variable because above-ground vegetative mass reflects photosynthetic machinery and pool of stored assimilates and nitrogen in *S. altissima* (Egli and Schmid, 1991). This was also consistent with the subsequent analysis of the relationship between reproductive and vegetative mass, where the use of total mass as an independent variable would have created statistical problems (Samson and Werk, 1986; LaBarbera, 1989).

We fit logistic regression models for the proportion, p, of plants that were fruiting at harvest as a function of vegetative mass:

$$p/(1 - p) = \exp(a + b \cdot v') + \epsilon,$$

where v' is the vegetative biomass transformed into a discrete variable with between 15 to 20 equally-sized intervals of which all upper categories with $p = 1$ are pooled, a and b are parameters, and ϵ is the error term. The theory of these models can be found in Finney (1971); they were im-

plemented with the generalized linear approach (McCullagh and Nelder, 1989) using the GENSTAT computer program (Payne et al., 1987). This allowed the inclusion of family effects, family-by-v' interaction terms, and deviations from linearity on the logistic scale (using an indicator variable for each level of v'). Since the models are nested, it is possible to construct an accumulated analysis of deviance table (Payne et al., 1987) in exactly the same way as an analysis of variance table in an ordinary general linear test (see below). The deviance change caused by adding a term to the current model can be used as approximate χ^2 statistic. Expressing the deviance change as a percentage indicates by how much the explained variation of the dependent variable is increased by adding a term during sequential model fitting. To obtain estimates of the minimum size for reproduction we calculated the value of v at which 50% of the plants flowered from models in which the deviations from linearity had not been fitted, and with v' replaced by v. Confidence limits for these estimates were obtained using Fieller's Theorem (Finney, 1971; Payne et al., 1991).

Next, we analyzed phenotypic variance and covariance in reproductive mass r (inflorescences) and vegetative mass v in each experiment. For consistency with the subsequent analysis of the relation between r and v, and to satisfy distributional assumptions, plants that did not reproduce at harvest were excluded. Because of this, among- and within-family variance and covariance components were calculated with a method for unbalanced data (Gower, 1962; Snedecor and Cochran, 1980, p. 346; Payne et al., 1991). A restricted maximum-likelihood method (BMDP program 3V; Dixon, 1988) gave very similar estimates. The estimates were used to calculate heritabilities and genetic environmental correlations, according to the well-known formulae given by Falconer (1981), in four experiments: "clones 88," "clones 89," "half sibs 88," and "full sibs 89." However, these heritability estimates only give a crude indication of the amount of additive genetic variance in the population because maternal effects and (except for the half-sib families) dominance effects are not excluded. The values estimated for half-sib families might also have been inflated by the inclusion of an unknown number of full sibs (see previous section). Further, by analyzing the diallels as 30 full-sib families (instead of 15 "lines") the heritabilities may be underestimated in the "full sibs 89" experiment. This method of analysis was chosen for simplicity and because of imbalance caused by variable crossing success. Randomization tests (Mitchell-Olds, 1986) for the significance of heritability estimates with this most unbalanced data set yielded P-values similar to the parametric method used. The heritabilities and genetic correlations were deliberately pooled across any environmental variation that could have been eliminated (offspring and maternal soil environments; block, plot, and within-plot margin versus center effects). Here and in the other analyses in this paper we consider all environmental variation as means to create the wide range of sizes necessary to investigate size-dependent reproduction.

In the main part of this study we analyzed the relationship between reproductive mass r and vegetative mass v for each of the five experiments, and for the combined data from the "clones 88" and "clones 89" experiments. All calculations were done twice, once including and once excluding plants that were not fruiting at harvest. Both methods gave similar results but, with one exception, we did not use those of the latter for statistical reasons: the reproductive mass of plants which were not fruiting was always zero, giving the impression of a discontinuous relationship and violating the assumption of homoscedasticity. [We are developing an alternative method for analysis of such data which replaces zeros with negative values (Schmid et al., unpubl. data)]. All plants, however, were included to estimate regression parameters for families; these parameters were not individually evaluated for statistical significance but were used as new data values in subsequent analyses (see last paragraph of this section).

The minimal statistical model for each experiment was

$$r = a + b \cdot v + \epsilon = b(v - i) + \epsilon,$$

where a is the intercept on the y-axis, b the

slope parameter, $i = -a/b$ the intercept on the x-axis, and ϵ is the error term. This model was used for the analyses reported in Figure 1. However, because errors may occur in both r and v, and the relative sizes of these errors are not known, we also calculated the reverse regressions. Direct and reverse regression give the extreme parameter estimates for the structural relationship

$$r = a + b(v - \delta) + \epsilon = b[(v - \delta) - i] + \epsilon,$$

where var (ϵ)/var $(\delta) = \lambda = \infty$ for the direct and $\lambda = 0$ for the reverse regression (Kendall and Stuart, 1973).

For the full multiple regression models, v was again first transformed into a discrete variable v' with between 15 to 20 equally-sized intervals. Family effects, family-by-v' interaction terms, and deviations from linearity (using an indicator variable for each level of v') were then added sequentially (general linear test; Neter and Wassermann, 1974). The sequence of v' and family was also inverted to assess how much variation in r would have been explained by variation in v' after adjusting for family differences. Significance tests were constructed from the accumulated analysis of variance table calculated with GENSTAT. The x-intercept and slope for each family in an experiment were then estimated from the model that included all significant ($P < 0.05$) terms but not the deviations from linearity, and with v' replaced by v. Significant family effects (after fitting v') indicate different positions, and significant family-by-v' interaction terms indicate different slopes of r–v regression lines, i.e., genetic variation in the plastic r–v relationship. If this interaction term is not significant and small, it can be concluded that there is also genetic variation in the x-intercept (minimum size for reproduction). Otherwise, the heterogeneity of slopes implies that differences among families in r are not the same at all values of v. We therefore tested if families differed in r at the experiment-wide x-intercept by subtracting this intercept from v to obtain a new variable v_i and calculating family sum of squares adjusted for v_i and family-by-v_i interaction with ordinary analysis of covariance (Hendrix et al., 1982). We concluded that there was genetic variation in the x-intercept for families if the adjusted family term in this analysis was still significant.

Estimates of family intercepts and slopes were compared among three experiments by rank correlation: "clones 88" versus "half sibs 88" (for 19 families "clones 88" could be considered as parents of "half sibs 88"; see "Source of data") and "clones 88" versus "clones 89." To test whether a trade-off existed between minimum size and slope, half of the members of each family were randomly selected to estimate the intercept and the remaining half to estimate the slope for each family separately. The correlation between these estimates was calculated within experiments ("genetic" correlation in the sense of Via, 1984).

Results

Probability of Reproduction

In all experiments except "clones 88," several plants had not reproduced at harvest. The probability of reproduction on the logistic scale increased more or less linearly with increasing vegetative mass. The size at which the probability reached 50% ranged from 5.53 to 10.51 g among experiments (Fig. 1, see Table 5). Including the deviations from linearity on the logistic scale as an explanatory term resulted in small but nevertheless sometimes significant improvements in the model's fit (Table 2).

Differences among families in probability of reproduction were significant in the "clones 89" and "half sibs 88" experiments (both without or with prior adjustment for the effect of v', see lines 1 and 4 in Table 2) but not in the "half sibs 89" experiment. Since the family-by-v' interactions were not significant in these three experiments, the relationship between probability of reproduction and size was similar for the different families (i.e., similar slope of regression lines on logistic scale). The estimated probability of reproduction at 12 g is lower for the "half sibs 88" (offspring), which were raised from seeds, than for the "clones 89" (parents, although grown a year later), which were raised from rhizome cuttings. Also, the corresponding half-sib families and clones did not rank in the same order in the two experiments (Fig. 2). In the "full sibs 89" experiment, regression lines on the logistic

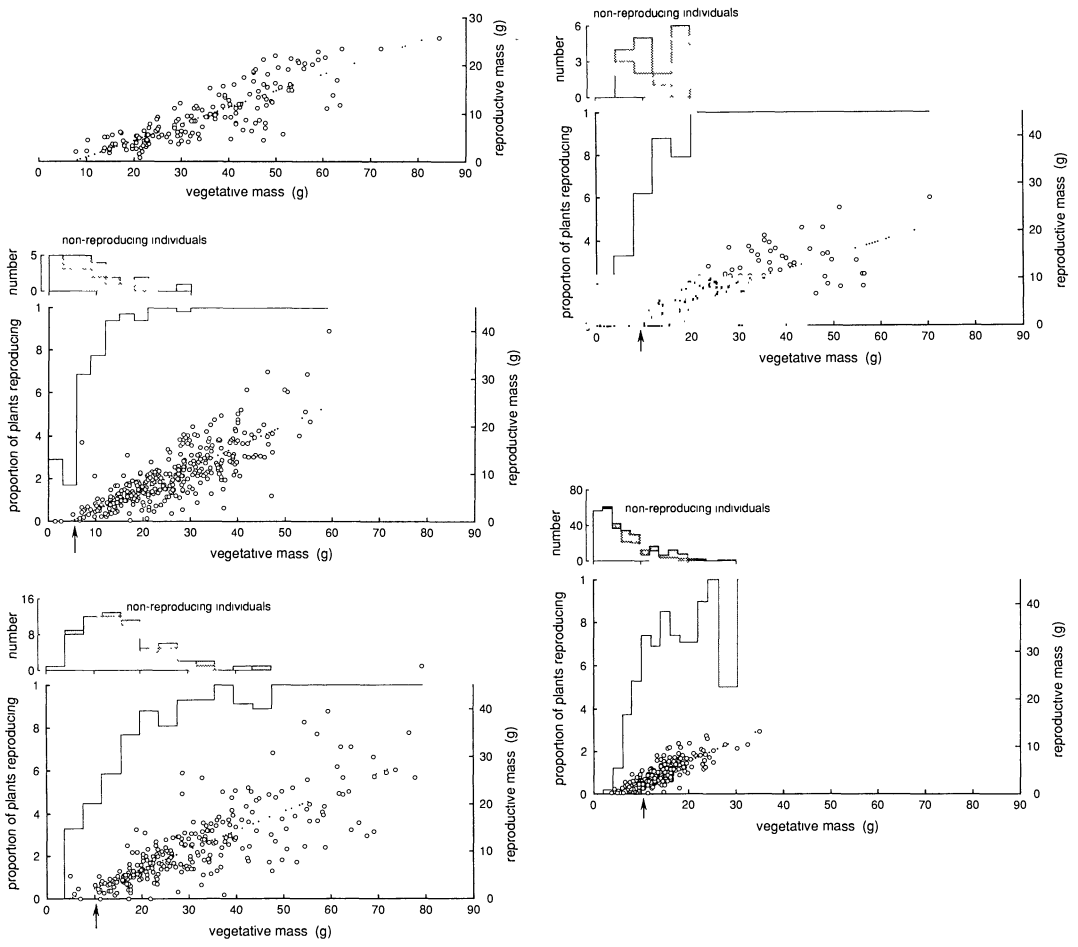

FIG. 1. The relationship between the proportion of plants reproducing and vegetative mass (steps), and reproductive mass and vegetative mass (scatter and regression line), and the size distributions of plants which did not reproduce (excluded from scatter) in (a) "clones 88," (b) "clones 89," (c) "half sibs 88," (d) "half sibs 89," (e) "full sibs 89" experiments. Parameters for all regressions are given in Table 5; the direct regression line is shown. The x-axis for all graphs within a plot is the same. The shaded area in the histograms represents plants with buds or flowers; unshaded area plants without buds or flowers. The arrow points to the vegetative mass at which the probability of reproduction reaches 50% in the logistic regression model. (There is no histogram for "clones 88" because all plants were fruiting at harvest.)

scale differed both in position and slope among families, i.e., there was genetic variation in both the probability of reproduction and in the relationship between probability of reproduction and size (see lines 4 to 5 in Table 2).

Heritabilities and Correlations

In the environments tested, vegetative and reproductive mass, as well as their sum, total above-ground mass, showed substantial genetic variation among families within the study population (Table 3). The heritability estimates calculated for clones were very consistent between years but higher than those from half-sib families. Under the assumption that the variation among families from the "half sibs 88" experiment (V_{fh}) represented 25% additive genetic variance, and the difference of the within-family variations from the "half sibs 88" and "clones 88" experiments ($V_{eh} - V_{ec}$) 75% additive and 100% dominance variance (see Falconer, 1981), the following calculations yielded estimates for the two types of variation in the population: 1) additive genetic variance $= 4 \cdot V_{fh} = 52.8$ for vegetative and 10.7 for reproductive mass; 2) dominance variance

TABLE 2. Analysis of deviance for logistic regression model of proportion of plants reproducing at harvest (all plants fruited in the "clones 88" experiment); for the first two terms two possible fitting sequences are shown. *df*: degrees of freedom, %*DV*: change in deviance due to the addition of the term to the model (=approximate χ^2) expressed in increments in multiple "R^2" in % (see e.g., SAS, 1989), approximate significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Experiment							
	Clones 89		Half sibs 88		Half sibs 89		Full sibs 89	
Source of variation	*df*	%*DV*	*df*	%*DV*	*df*	%*DV*	*df*	%*DV*
Genetic family	23	34.3***	23	20.5**	5	6.2	28	7.8
Linear regression on v' (on logistic scale)	1	36.9***	1	28.0***	1	58.9***	1	45.1***
Linear regression on v' (on logistic scale)	1	46.4***	1	28.4***	1	54.7***	1	43.5***
Genetic family	23	24.7*	23	20.2**	5	10.3	28	9.5*
Family-by-v' interaction	23	7.3	23	11.0	5	10.5	28	12.7***
Deviation from linearity (on logistic scale)	6	6.6	11	6.9	3	16.3*	10	7.1***
Residual	47	14.9	123	33.6	11	8.2	152	27.2
Total change in deviance (100%)		155		233		60		472

$= V_{eh} - V_{ec} - V_{ec} - 3 \cdot V_{fh} = 70.3$ for vegetative and 30.9 for reproductive mass. These estimates indicate that at least half of the genetic variation in the study population was probably due to dominance effects. The heritability estimates from the "full sibs 89" experiment are intermediate between those from the clones experiments and the "half sibs 88" experiment which is consistent with the intermediate amount of dominance variance among full sibs (Falconer, 1981). The among-family (i.e., genetic) correlations between r and v were very high and higher than the within-family (i.e., environmental) correlations (Table 3).

Relationship between Reproductive and Vegetative Mass

The simple linear model (without deviations from linearity) with a positive minimum size for reproduction was generally consistent with the pattern of data obtained in the five experiments (Table 4). If estimated by direct regression, minimum size for reproduction was not significantly greater than zero only in the "half sibs 89" experiment and ranged from 4.38 to 7.39 g in the other experiments (Table 5). If estimated by reverse regression minimum size was greater than zero in all experiments, ranging from 7.26 to 15.32 g (Table 5). Above the minimum size, plants allocated about one third of their additional biomass to reproductive structures and two thirds to vegetative mass. The stronger competition in the "full sibs 89" experiment reduced plant size more than twofold compared with the other experiments, but had little effect on minimum size for reproduction or on the proportion of biomass allocated to sexual reproduction above he minimum size.

If the vegetative mass was fitted first, the regression on it accounted for 47.8 to 72.1% of the variation in reproductive mass in the

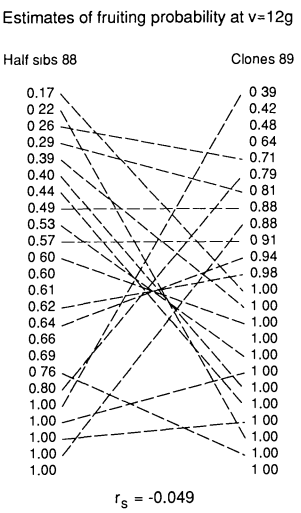

FIG. 2. Estimates of the probability of reproduction for different families of *Solidago altissima* at a vegetative size of 12 g (from logistic regression) in two experiments; families derived from the same parent plant are connected by a line. The rank correlation given below the bundle of lines is not significant ($P > 0.1$).

TABLE 3. Heritabilities of reproductive mass (r) and vegetative mass (v), and correlations between r and v (overall, among, and within families), calculated from variance and covariance components excluding plants that were not reproducing. Within-family variation was pooled over two soil types in the first four experiments; heritabilities were not calculated for "half sibs 89" because they were selected from extreme parents. N: number of families; Rep: coefficient of family-variance component.

Experiment	N	Rep	Heritabilities (± SE)			Correlation between r and v		
			v	r	$v + r$	Overall	Among	Within
Clones 88	24	7.1	0.418 ± 0.093	0.420 ± 0.093	0.424 ± 0.093	0.845	0.866	0.821
Clones 89	24	13.4	0.409 ± 0.082	0.396 ± 0.082	0.425 ± 0.083	0.792	0.860	0.729
Half sibs 88	24	11.0	0.219 ± 0.164	0.175 ± 0.155	0.218 ± 0.164	0.797	0.933	0.791
Half sibs 89	6	26.4	—	—	—	0.705	0.912	0.700
Full sibs 89	28	8.7	0.245 ± 0.112	0.360 ± 0.132	0.294 ± 0.121	0.829	0.896	0.809

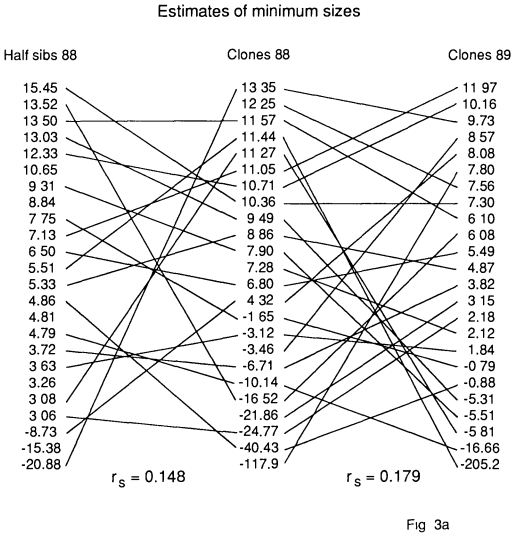

Fig 3a

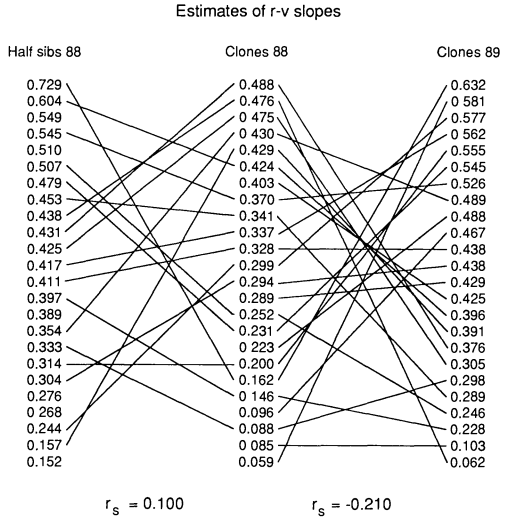

Fig 3b

experiments (line 3 in Table 4). 3.8 to 15.8% of the remaining variation could be attributed to differences among families (including their interaction with vegetative mass; lines 4 and 5 in Table 4). The deviations from linearity were significant in two of the five experiments but relatively small as judged by the improvements in the fit of the model (line 6 in Table 4).

Differences among families in reproductive mass were always significant if this term was fitted first in the regression analyses (line 1 in Table 4). In both half-sibs experiments, however, these differences could be largely accounted for by differences in vegetative mass among families, hence the family term was not significant if fitted after the regression of reproductive mass on vegetative mass (line 4 in Table 4). In the other experiments, families significantly differed among each other in reproductive mass in ways not accounted for by differences in vegetative mass. However, using the test for differences in r at the experiment-wide x-intercept estimated from direct or reverse regression, it was detected that only in the

FIG. 3. X-intercepts (minimum sizes for reproduction) (a) and slopes (b) for the relationship between reproductive and vegetative mass for different families of *Solidago altissima* in three experiments; families derived from the same parent plant are connected by lines. The rank correlations given below the bundles of lines are not significant ($P > 0.1$). Note that negative minimum sizes in (a) could arise if a family regression line was poorly determined, for example because all plants of that family had a similar vegetative mass.

"clones 89" experiment did this significant genetic variation in position of regression lines include significant genetic variation in minimum size ($P \leq 0.01$; see "Materials and methods: Analyses").

The significant family-by-v' interactions in the two clones experiments and the "half sibs 88" experiment (Table 4) indicated that significant genetic variation in the plastic relationship between reproductive and vegetative mass (slope of regression lines) occurred in the study population.

Estimates of family intercepts and slopes could be compared among experiments that used families originally derived from the same plants (Fig. 3). The clones, which were raised from rhizome cuttings, tended to start reproduction at a smaller minimum size and to have lower slopes than the half sibs, which were raised from seeds. High correlations between "half sibs 88" or "clones 89" as offspring and "clones 88" as parents were obtained for separately calculated family means of reproductive and vegetative mass, consistent with the relatively large heritabilities of these characters (see Table 3). However, no such correlations could be detected for the family intercepts (minimum sizes) and slopes among these experiments, as indicated by rank correlation coefficients that were close to zero (Fig. 3). For the slopes this is not consistent with the significant genetic variation observed within experiments. It follows that there must be plasticity in the relationship between reproductive and vegetative mass: environmentally induced changes in reproductive output associated with environmentally induced changes in size varied among families in different ways depending on whether 1) plants were raised from rhizomes or seed ("clones 88" versus "half sibs 88" experiments) or 2) in different years ("clones 88" versus "clones 89" experiments). The hypothesis of genetic variation in this plasticity in the relationship between reproductive and vegetative mass was tested directly for the "clones 88" and "clones 89" experiments by a combined regression analysis (Table 6). This analysis confirmed that the between-year changes in slopes varied significantly among clones (family-by-year-by-v' interaction).

TABLE 4. General linear tests for regression model of reproductive mass (r), excluding plants that were not reproducing (all plants fruited in the "clones 88 experiment"); for the first two terms two possible fitting sequences are shown. *df*: degrees of freedom, %SS: sum of squares in % = increments in multiple R^2 in %, significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	Experiment									
	Clones 88		Clones 89		Half sibs 88		Half sibs 89		Full sibs 89	
	df	%SS	*df*	%SS	*df*	%SS	*df*	%SS	*df*	%SS
Genetic family	23	48.8***	23	42.6***	23	12.6***	5	5.6**	27	25.5***
Linear regression on v'	1	35.1***	1	30.8***	1	54.3***	1	44.5***	1	48.2***
Linear regression on v'	1	72.1***	1	62.4***	1	63.2***	1	47.8***	1	67.1***
Genetic family	23	11.8***	23	10.9***	23	3.7	5	2.3	27	6.6**
Family-by-v' interaction	23	4.0*	23	4.0***	23	6.8***	5	1.5	27	2.8
Deviation from linearity	16	1.3	17	3.2***	17	2.5	13	8.3*	14	1.3
Residual	107	10.8	267	19.5	197	23.8	134	40.1	181	22.2
Total sum of squares (100%)		5,622		11,942		15,954		3,609		1,714

TABLE 5. Estimates of minimum size to reproduce from logistic regressions, and estimates of minimum size and slope from direct regression (line shown in Fig. 1) and reverse regression; mean and 95% confidence limits are given. (Direct and reverse regressions performed with reproducing plants only; see "Materials and Methods" for explanation of statistical techniques.)

		Direct regression		Reverse regression	
Experiment	Minimum size (g)	Minimum size (g)	Slope	Minimum size (g)	Slope
Clones 88	—[1]	7.39 ± 2.97	0.345 ± 0.033	15.32 ± 2.20	0.483 ± 0.046
Clones 89	5.53 (2.07–7.69)	4.46 ± 1.98	0.448 ± 0.037	12.36 ± 1.31	0.708 ± 0.059
Half sibs 88	10.3 (5.50–13.3)	4.54 ± 2.85	0.405 ± 0.037	14.19 ± 1.92	0.632 ± 0.057
Half sibs 89	9.48 (4.66–11.9)	0.17 ± 4.57	0.296 ± 0.047	13.63 ± 2.44	0.595 ± 0.093
Full sibs 89	10.5 (9.69–11.4)	4.38 ± 0.88	0.436 ± 0.036	7.26 ± 0.64	0.629 ± 0.053

[1] All plants flowered.

The correlations between independent estimates of family intercepts (minimum sizes) and slopes (see "Materials and methods: Analyses") were not significant and close to zero in all experiments.

DISCUSSION

The Minimum Size for Reproduction

These data provide the most detailed evidence to date for a minimum size requirement for reproduction in any plant species. Earlier research on reproduction in facultative biennials (Werner, 1975; Gross, 1981) has shown that small plants may have a low or zero probability of reproduction. More recently, Primack and Hall (1990) used logistic regression to relate probability of reproduction to plant size in an orchid species. Here, we both analyzed the shape of this relationship in more detail and looked for genetic variation in the relationship. *Solidago altissima* does not show a sharp transition from zero to one in the probability of reproduction at a certain size. Rather, there is a relatively slow linear increase in the log-"odds" ratio of reproducing with increasing vegetative size. It then seems reasonable to define the minimum size for reproduction as the size at which the probability of reproduction reaches 50%. Does this minimum size represent an unavoidable developmental constraint, or could natural selection change it? The significant variation among families in those experiments with parallel response lines (non-significant family-by-v' interactions in Table 2), indicate that there is some genetic variation in minimum size. Therefore minimum size for reproduction, as defined above, may not be an absolute constraint, and it could evolve in either direction in this population.

In some species (e.g., facultative biennials) the onset of reproduction may be pri-

TABLE 6. General linear test for regression model of reproductive mass (r), excluding plants that were not reproducing, when the two clone experiments are combined; for the first two terms two possible fitting sequences are shown. *df*: degrees of freedom, %SS: sum of squares in % = increments in multiple R^2 in %, significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Experiment Source of variation	*df*	%SS
Genetic family	23	34.8***
Linear regression on v'	1	29.3***
Linear regression on v'	1	56.1***
Genetic family	23	8.0***
Year	1	6.8***
Family-by-v' interaction	23	3.6***
Year-by-v' interaction	1	0.3*
Family-by-year interaction	23	3.3***
Family-by-year-by-v' interaction	23	2.0*
Deviation from linearity	16	0.7
Year-by-deviation interaction	12	1.0
Residual	379	18.3
Total sum of squares (100%)		17,574

marily determined by size. In other species, such as *S. altissima,* small size may prevent reproduction, but only quite large sizes guarantee that reproduction will commence. This could reflect the influence of several other factors (e.g., photoperiodism) on the timing of reproduction. In *S. altissima,* a plant's reproductive output (if it does reproduce) is more strongly determined by its size than is its probability of reproduction.

The minimum size for reproduction can also be defined as the x-intercept of the relationship between reproductive and vegetative mass. Estimation of the intercept from ordinary linear regression presents a statistical problem because both variables may contain error variance (errors-in-variables problem; see e.g., Kendall and Stuart, 1973; Leamer, 1978). Because we did not know the relative sizes of these variances, we gave the extreme parameter estimates from direct and reverse regressions (Table 5). The true parameters probably lay somewhere in between these estimates. In this case they would be very similar to the minimum sizes estimated from the 50% probability of reproduction (Table 5). There was less evidence for genetic variation among families in minimum size when estimated from linear regression (see above) than when estimated from logistic regression.

Biomass may not be the most important aspect of size in determining whether or not a plant reproduces. In several species (most notably *Pisum sativum*) reproduction by a shoot can only occur after a specific number of leaves has formed (Sachs, 1991). Most of these species still require environmental induction such as photoperiodic and temperature conditions after the required number of leaves develop before they will flower.

Linear Relationship between Reproductive and Vegetative Mass

Our data also support the hypothesis that the relationship between reproductive and vegetative mass is close to linear. While deviations from linearity were significant in some cases, the contribution of this nonlinearity in accounting for variation was small (Table 4). Weiner (1988) hypothesized that linear size-dependent reproductive output is most likely to occur when size differences are caused by competition rather than other environmental factors, and data on several species of agricultural weeds (Thompson et al., 1991) support this generalization. In our experiments the linear model worked well for size differences that have been generated by a variety of factors. In the one experiment ("full sibs 89") in which competition was clearly an important determinant of size, the model performs as well, but not noticeably better, than in the other experiments where competition was less important.

Weiner (1988) argued that the relationship between reproductive and vegetative mass represents an important aspect of a plant's life-history strategy. If this is the case we might expect this relationship to have experienced strong stabilizing selection, resulting in little or no genetic variation in the relationship within the population. However, our data are consistent with our hypothesis that there is significant genetic variation in this relationship. In fact, there was even a significant genotype–environment (year) interaction for the relationship. If we consider that part of the relationship between reproductive and vegetative mass that is environmentally-induced to be a "plastic" relationship, then we can say that: (i) our results demonstrate plasticity in this plastic relationship, and (ii) they provide evidence for genetic variation in this plasticity in the plastic relationship. Alternatively, one could refer to (ii) as genetic variation for plasticity in the relationship between reproductive and vegetative mass.

There are several possible explanations for the existence of genetic variation in the relationship between reproductive and vegetative mass. We mention two. 1) Assuming that both minimum size and slope are subject to natural selection, persistence of genetic variation in both could result if there were a negative genetic correlation between the two (e.g., Stearns, 1989). However, using the correlations between the independent family estimates as approximate genetic correlations (cf. Via, 1984), we did not find evidence for the hypothesis of a trade-off between the minimum size and slope. Although we could not test for a trade-off between reproductive mass and below-ground rhizome biomass, we found no or weakly-

positive phenotypic, genetic, and environmental correlations between reproductive mass and rhizome number or maximum rhizome length in the 1988 experiments. If vegetative mass was held constant (i.e., partialled out), phenotypic and environmental correlations were still close to zero but genetic partial correlations between reproductive mass and rhizome number, became significantly negative. This does suggest a genetic trade-off: selection for higher reproductive output would only be possible at the expense of reduced clonal growth. In another study with *S. altissima,* Weis et al. (1987) found no evidence of a negative relationship between reproduction and clonal growth. 2) Genetic variation in the relationship between reproductive and vegetative mass could also occur because of genotype–environment interactions that determine the relationship in a particular situation. If different genotypes respond in different ways to different environments, such that the rankings (and presumably selective advantages) of genotypes change among environments or from year to year (Fig. 3), genetic variation could be maintained. In fact, genotypes were ranked differently in 1988 and 1989 according to their minimum sizes for reproduction and also according to the slope of the relationship between reproductive and vegetative mass (experiments with clones). The significant genetic variation for plasticity in the relationship is evidence for the existence of complex genotype–environment interactions in the study population (Schlichting, 1989; Bell, 1991).

Differences between Plants from Seeds versus Rhizomes

While our data present evidence that there was genetic variation in both the minimum size for reproduction and the slope of the relationship between reproductive and vegetative mass within the study population, the expression of this genetic variation seemed to differ not only between years ("clones 88" versus "clones 89," Table 6) but also between plants propagated from seeds versus those propogated from rhizomes ("half sibs 88" versus "clones 88," Fig. 3). The differences between seed- and rhizome-derived plants might reflect a larger initial amount of resources stored in the below-ground organs of the rhizome-derived plants. However, the experiments were started when seed- and rhizome-derived plants had reached the same rosette size. Also, the fact that in 1988, the seed-derived plants had a greater proportional allocation to reproduction (slope) than the rhizome-derived plants (Table 5) suggests that they did not put more resources into storage. Therefore, we conclude that the observed differences between seed- and rhizome-derived plants probably reflect developmental effects. For example, it has been shown for the closely related species *S. canadensis* and *S. gigantea* that plants raised from rhizomes can express more phenotypic variation than plants raised from seeds (Schmid and Bazzaz, 1990). It could be argued that developmental variation represents a third type of variation, in addition to genotypic and environmental, all of which can interact with each other to determine variation in phenotypes in nature.

All our results are for single-shoot plants of *S. altissima.* Shoots, as modules of a clonal plant, have a semi-determinate growth form and, in this respect, are more comparable to non-clonal individuals than would be entire genets of several connected shoots. Relationships between vegetative and reproductive mass may be different for whole genets of connected shoots or for non-clonal plants.

Analysis of the factors that determine reproductive output is an important part of the study of evolution in natural populations. The analysis of the genotypic and environmental influences on reproductive output in plants provides an opportunity to integrate the study of individual size and growth with the study of reproduction, and may ultimately help us to understand the factors that determine fitness in nature. When an activity or structure such as reproductive allocation is allometric in the broad sense i.e., it has a biological relationship to size (Gould, 1966), genetic and phenotypic (e.g., norms of reaction) analysis of the allometric relationships may provide more insights into the biology of the organism than the analysis of simple phenotypic characters or correlations of characters.

Acknowledgments

We thank P. Egli, A. Erhardt, B. Jäggi, H. Müller, H-P. Rusterholz, R. Schweizer, E. Weber, R. Winzeler, and P. Wyss for help with the experimental work, and D. Reznick, D. Matthies, and two anonymous reviewers for comments on the manuscript. Comments by R. Sackville Hamilton and A. Weis were especially helpful. This research was supported by grants no. 3.031-0.87 and 3.441-0.86 from the Swiss National Science Foundation and a grant from the Roche Research Foundation.

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Corresponding Editor: D. Reznick