

# Estimating effects of constraints on plant performance with regression quantiles

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Rates of change in final summer densities of two desert annuals, *Eriogonum aberratum* and *Haplopappus gracilis*, as constrained by their initial winter germination densities were estimated with regression quantiles and compared with mechanistic fits based on a self-thinning rule proposed by Guo et al. (1998); *Oikos* 83: 237–245). The allometric relation used was equivalent to  $S = N_f (N_i)^{-1} = c_f (N_i)^{-1}$ , where  $S$  is the ratio of final to initial densities (survivorship),  $c_f$  is a constant that is a final density specific to the species and environment,  $N_i$  is the initial plant density, and  $N_f$  is final plant density. We used regression quantiles to estimate  $c_f$  assuming the exponent of  $-1$  was fixed (model 1,  $N_f (N_i)^{-1} = c_f (N_i)^{-1}$ ) and also obtained estimates by treating the exponent as a parameter to estimate (model 2,  $N_f (N_i)^{-1} = c_f (N_i)^{\lambda}$ ). Regression quantiles allow rates of change to be estimated through any part of a data distribution conditional on some linear function of covariates. We focused on estimates for upper (90–99th) quantiles near the boundary of the summer density distributions where we expected effects of self-thinning to operate as the primary constraint on plant performance. Allometric functions estimated with regression quantiles were similar to functions fit by Guo et al. (1998) when the exponent was constrained to  $-1$ . However, the data were more consistent with estimates for model (2), where exponents were closer to  $-0.4$  than  $-1$ , although model fit was not as good at higher initial plant densities as when the exponent was fixed at  $-1$ . An exponential form (model 3,  $N_f (N_i)^{-1} = c_f (N_i)^{\lambda} e^{\gamma N_i}$ ) that is a generalization of the discrete logistic growth function, where estimates of  $\lambda$  were  $-0.23$  to  $-0.28$  and estimates of  $\gamma$  were  $-0.003$  to  $-0.006$ , provided better fit from low to high initial germination densities. Model 3 predictions were consistent with an interpretation that final summer densities were constrained by initial germination densities when these were low ( $< 40$  per  $0.25 \text{ m}^2$  for *Eriogonum* and  $< 100$  per  $0.25 \text{ m}^2$  for *Haplopappus*) and were constrained by the self-thinning process at higher germination densities. Our exponential model (3) estimated with regression quantiles had similar form to the mechanistic relation of Guo et al. (1998) when plotted as a survivorship function, but avoided the unrealistic assumption that all populations attained a similar final density, and was based on a statistical model that has formal rules for estimation and inference.

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Recently, authors investigating a variety of ecological phenomena have suggested that the effects of fundamental ecological processes may best be viewed as constraints on observed patterns of variation (Brown

and Maurer 1987, Goldberg and Scheiner 1993, Kaiser et al. 1994, Terrell et al. 1996, Thomson et al. 1996, Guo et al. 1998, Cade et al. 1999). In their study of self-thinning in plants, Guo et al. (1998) proposed a

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mechanistic relation to describe the constraints between survival of individual plants and density of conspecifics based on an allometric rule;  $S = c_f (N_i)^{-1}$ , where  $S$  is survival (0–1),  $c_f$  is a final density specific to the species and environment, and  $N_i$  is the initial plant density. These relations were graphically fit to data for two Chihuahuan Desert annuals, *Eriogonum abertianum* Torr. (Polygonaceae) and *Haplopappus gracilis* (Nutt.) A. Gray (Asteraceae), as constraints on the boundary of the survival distributions. Other constraint relations were fit to boundaries of survival distributions of the above species as functions of the density of heterospecific annuals or perennials. The mechanistic relations specified by Guo et al. (1998) may be reasonable models of self-thinning in plants, but the lack of formal rules as to how these relations should be fit to observed data, specifically how  $c_f$  should be determined, is problematic. Furthermore, as we shall show, the data actually provide more support for exponents less than the  $-1$  specified by Guo et al. (1998) when the exponents are estimated with a statistical procedure that is appropriate for models of constraints on statistical variation.

The mechanistic approach to fitting constraint lines proposed by Guo et al. (1998) does not recognize sampling variation as would a statistical procedure, and, thus, there is no formal methodology for evaluating whether or not the data are consistent with the hypothesized relation. However, as noted by Guo et al. (1998), there are many inherent difficulties with statistical approaches currently employed for estimating self-thinning relations. Here we propose the use of a recently developed class of regression estimators, regression quantiles, to estimate functional relations near the boundaries of data distributions (Cade et al. 1999). These boundaries are of inherent interest in observational studies of self-thinning relations because mortality caused by factors other than intraspecific competition, e.g., physical stress, disease, disturbance, herbivory, and interspecific competition, will reduce survival below the hypothesized self-thinning relation (Weller 1987, Lonsdale 1990, Osawa and Allen 1993, Guo and Rundel 1998, Guo et al. 1998). Similar concerns have been voiced for observational studies of interspecific competition in plants (Hutchings and Budd 1981, Goldberg 1987, Pacala and Silander 1990, Goldberg and Scheiner 1993).

Regression quantiles have been used for analyzing effects of ecological limiting factors, where the relevant rates of change estimated were near the extremes of distributions (Terrell et al. 1996, Scharf et al. 1998, Cade et al. 1999). The self-thinning relations developed by Guo et al. (1998) are just variants of the limiting factor theme (Thomson et al. 1996, Cade et al. 1999). Competition for limiting resources from conspecifics and heterospecifics places an upper constraint on survival of these desert plants, and it is the functional rate of change at the boundary of the survival distribution

that is of interest in describing the effects of competition. Regression quantiles estimate rates of change in any conditional quantile of a response distribution as a linear function of covariates (Koenker and Bassett 1978, Koenker and Portnoy 1996). The limiting relation implied by self-thinning in plants focuses our attention on rates of change near the upper boundary of density distributions, e.g., at a quantile such as the 99th where 99% of the density distribution is below the estimated function. Estimating constraints for self-thinning models with regression quantiles does not require subjectively selecting a subset of points to use in estimation as is done with other regression methods (Weller 1987). We examine three alternative models for estimating constraints on thinning relations with regression quantiles for *Eriogonum* and *Haplopappus* density changes between winter and summer and compare these statistical estimates with the mechanistic relations proposed by Guo et al. (1998).

## Methods

*Eriogonum* and *Haplopappus* densities were measured on 384 0.25-m<sup>2</sup> permanent quadrats that were censused at the end of winter (April–May) and end of summer (August–September) in 1992 near Portal, Arizona, USA (Guo et al. 1998). These two common annuals of the Chihuahuan Desert have a biseasonal life history: germination takes place after the winter rains, some growth and flowering occurs during the spring, but greatest growth and reproduction occurs after the summer rains (Guo et al. 1998). Survival during the May–June drought period is influenced by plant size and root development that occurs before the dry season. Water is the limiting resource and depletion of soil moisture during the spring drought is the principal cause of mortality. Survivorship was defined as final summer density divided by initial winter density (Guo et al. 1998). There was some small amount of late winter germination that occurred after the initial counts, such that final counts were greater than initial counts in some low density plots. Although Guo et al. (1998) rescaled their survivorship measures to a maximum of 1 by dividing all values by the maximum ratio of final to initial densities (3.0 for *Eriogonum* and 2.1 for *Haplopappus*), this was not done for our analyses.

The model used by Guo et al. (1998) is equivalent to  $S = N_f (N_i)^{-1} = c_f (N_i)^{-1}$ , where  $S$  is the ratio of final to initial densities,  $c_f$  is a constant that is a final density specific to the species and environment,  $N_i$  is the initial plant density, and  $N_f$  is final plant density. If the exponent is fixed at  $-1$ , then this model implies that an estimate of  $c_f$  should be made from  $N_f$  final density. Unfortunately, an equation of this form, where one variable, initial plant density, occurs on both sides of

the equation, raises a troubling statistical issue that has been debated in the self-thinning literature (Weller 1987, Lonsdale 1990, Osawa and Allen 1993, Petraitis 1995, Guo and Rundel 1998). One simple solution is to modify the equation to allow the exponent to vary rather than to fix it at  $-1$ , similar to suggestions for biomass versus density versions of the self-thinning equation (Weller 1987, Lonsdale 1990). Our model now is  $N_f = c_f (N_i)^{\lambda+1}$ , where  $\lambda$  is the parameter relating the ratio of final to initial density (survival) and initial density, and the  $+1$  in the exponent is due to multiplying both sides by  $N_i$ . This equation can be expressed in typical allometric form for statistical estimation as  $y = \beta_0 X^{\beta_1} \varepsilon$ , where  $y = N_f$ ,  $X = N_i$ ,  $\varepsilon$  is a random error term (more on this below), and  $\beta_0$  and  $\beta_1$  are the constant and exponent to estimate. We can recover an estimate of  $\lambda$  by subtracting 1 from our estimate of  $\beta_1$ . This implies that  $\beta_1 = 0$  if the exponent  $\lambda = -1$ , as in the Guo et al. (1998) formulation. If we assume  $\lambda = -1$ , we can constrain the equation (i.e., constrain  $\beta_1 = 0$ ) and just estimate the constant,  $\beta_0 = c_f$ . Here we consider three alternative models:

$y = \beta_0 X^{\beta_1} \varepsilon$ , estimating  $\beta_0 = c_f$  by constraining  $\beta_1 = 0$ ;  
(1a)

$y = \beta_0 X^{\beta_1} \varepsilon$ , estimating both unconstrained parameters;  
and  
(2a)

$y = \beta_0 X^{\beta_1} e^{\beta_2 X} \varepsilon$ , an exponential form where all  
parameters are unconstrained.  
(3a)

Model (2a) is just the logical unconstrained version of model (1a). Model (3a) is a generalization of the discrete logistic growth function that provides an increasing mortality penalty ( $e^{\beta_2 X}$ ) with increasing initial densities (May 1976, Ricklefs 1990: 359). Our attempts at fitting piecewise linear regressions for model (2a)

indicated the need for a functional form like model (3a) that could increase to an asymptote and then decrease. All models were put in linear form by taking natural logarithms of both sides:

$$\log(y + 1) = \log(\beta_0) + \log(\varepsilon); \quad (1b)$$

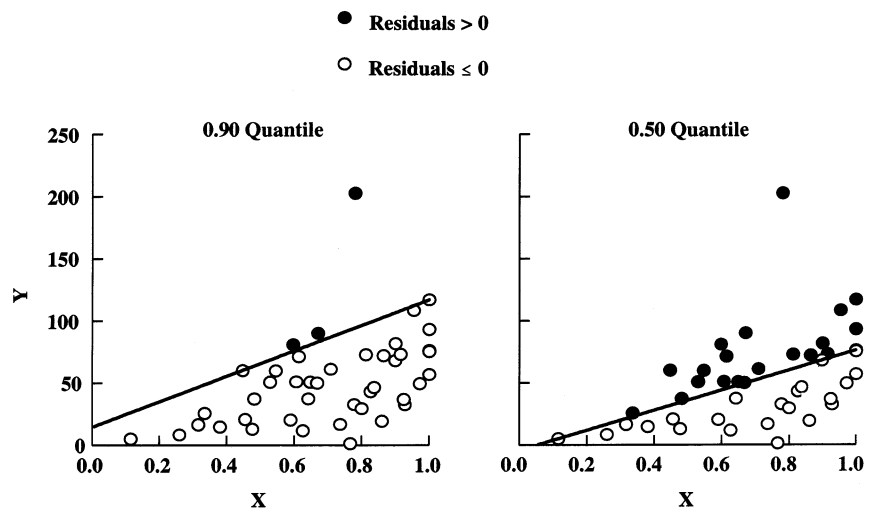
$$\log(y + 1) = \log(\beta_0) + \beta_1 \log(X) + \log(\varepsilon); \text{ and} \quad (2b)$$

$$\log(y + 1) = \log(\beta_0) + \beta_1 \log(X) + \beta_2 X + \log(\varepsilon). \quad (3b)$$

The constant 1 was added to final densities before taking logarithms because there were some zero counts; 1 was the minimum count for initial densities.

All parameters were estimated with regression quantiles for the linearized form of the models (1b–3b). Estimates were returned to the nonlinear form (1a–3a) by exponentiation and subtracting the constant 1 added to  $y$ . Estimates of  $\lambda$  due to dividing  $N_f$  by  $N_i$  were obtained by subtracting 1 from the estimate of  $\beta_1$  and an estimate of  $\gamma$  was set equal to the estimate of  $\beta_2$  in model 3a ( $N_f (N_i)^{-1} = c_f (N_i)^{\lambda} e^{\gamma N_i}$ ). Regression quantiles extend the usual univariate concept of quantiles to the linear model (Koenker and Portnoy 1996, Cade et al. 1999) by defining an ascending sequence of planes (lines) that are above an increasing proportion of observations with increasing values of  $\tau$  (Fig. 1). When  $\beta_1$  is constrained to 0 (i.e.,  $\lambda = -1$ ) in model (1a), this estimation process is equivalent to the usual method of estimating univariate sample quantiles. The  $\tau$ th quantile ( $0 \leq \tau \leq 1$ ) of a random variable  $Y$  is the inverse of the cumulative distribution function,  $F^{-1}(\tau)$ , which is defined as the smallest real value  $y$  such that the probability of obtaining smaller values of  $Y$  is greater than or equal to  $\tau$ . The 1-sample quantile definition is formally extended to the linear model  $y = X\beta + v(X)\varepsilon$  by defining the  $\tau$ th regression quantile as  $Q_\tau(\tau|X) =$

Fig. 1. Estimates for 50th ( $\tau = 0.50$ ) and 90th ( $\tau = 0.90$ ) regression quantiles for the linear model  $y = \beta_0 + \beta_1 X_1 + \varepsilon$  for  $n = 43$ . Open circles indicate residuals  $\leq 0$  that are given weights  $= (1 - \tau)$  in the estimation process and filled circles indicate residuals  $> 0$  that are given weights  $= \tau$ . Data were modified from Schroeder and Vangilder (1997).



$X\beta(\tau)$ , where  $\beta(\tau) = \beta + v(\cdot)F_{\varepsilon}^{-1}(\tau)$ ,  $y$  is an  $n \times 1$  vector of dependent responses,  $\beta$  is a  $p \times 1$  vector of unknown regression parameters,  $X$  is an  $n \times p$  matrix of predictors (first column consists of ones),  $v(\cdot) > 0$  is some known function,  $\varepsilon$  is an  $n \times 1$  vector of random errors that are independent and identically distributed (iid), and  $F_{\varepsilon}^{-1}$  denotes the inverse cumulative distribution function of  $\varepsilon$  (Koenker and Bassett 1978, Koenker and Portnoy 1996, Koenker and Machado 1999). The term  $v(X)$  allows the error distribution to change as a function of  $X$  and, thus, various heteroscedastic (inid) and homogeneous (iid) error models are accommodated with regression quantiles (Koenker and Portnoy 1996). If the error distributions are homogenous, then only the intercept parameters,  $\beta_0(\tau)$ , in  $\beta(\tau)$  will differ, i.e., rates of change (slopes) will be the same for all quantiles. If the error distributions are heterogeneous; e.g.,  $v(X) = (\text{diag}(X\gamma))$ , where  $\gamma$  is a  $p \times 1$  vector of unknown scale parameters in the familiar location-scale model of heteroscedasticity; then all parameters in  $\beta(\tau)$  may differ, yielding very different rates of change for different quantiles. Because a  $\tau$ th regression quantile with  $p$  estimated parameters passes through at least  $p$  sample observations ( $p$  residuals equal zero), there are at most  $n\tau$  sample observations below and at most  $n(1-\tau)$  above the regression quantile estimate (Koenker and Bassett 1978, Koenker and Portnoy 1996).

Estimates,  $b(\tau)$ , of  $\beta(\tau)$  were obtained from a simplex linear programming solution by minimizing an asymmetric loss function of absolute values of residuals, where positive residuals are given weights equal to  $\tau$  and negative residuals are given weights equal to  $1-\tau$  (Koenker and Portnoy 1996). Computer routines written in S-Plus by R. Koenker were used to estimate regression quantiles, test hypotheses about parameters, and compute confidence intervals (Cade et al. 1999, Ecological Archives E080-001). We used a regression quantile rank-score test procedure (Koenker 1994, Koenker and Portnoy 1996) implemented in S-Plus to test hypotheses and compute confidence intervals. The quantile rank-score test can be thought of as an extension of the sign test to quantiles other than the 50th (median) and to continuous covariates. Under the null hypothesized model, positive residuals are assigned ones, negative residuals zeros, zero residuals take a value in the interval (0, 1) based on the dual linear programming solution, and a scoring function ( $-(1-\tau)$ ) based on the specified quantile is applied to these values (Koenker 1994). The rank-score test statistic is evaluated with a Chi-square distribution with degrees of freedom (df) equal to the difference between number of parameters in alternative and hypothesized models.

We plotted estimates of  $\beta(\tau)$  for all quantiles as a step function (Koenker and Machado 1999), but focus attention on upper, 90–99th, quantiles for this self-thinning problem. We will use the notation for a 100 $\tau$ th (e.g., 99th) rather than for the  $\tau$ th (0.99th) regression

quantile when convenient. Coefficients of determination for regression quantiles were computed to compare model fits (Koenker and Machado 1999):  $R^1 = 1 - (SUM_{(F)}/SUM_{(R)})$ , where  $SUM_{(F)}$  is the sum of weighted absolute deviations minimized in estimating full parameter models (2b or 3b) and  $SUM_{(R)}$  is the sum of weighted absolute deviations minimized in estimating the reduced parameter model (1b).

Unlike least squares estimates of means, regression quantiles are equivariant to nonlinear monotonic transformations (Koenker and Portnoy 1996). The  $\tau$ th quantile of the transformed data is the transformation of the  $\tau$ th quantile of the original data, i.e., if  $h(\cdot)$  is a nondecreasing function, then for any random variable  $Y$ ,  $Q_{h(Y)}(\tau) = h(Q_Y(\tau))$ . Thus, there is no ambiguity about what is being estimated when back-transforming estimates from the transformed (1b–3b) to the original (1a–3a) data scale as there is when estimating means with least squares regression for nonlinear (e.g., logarithmic) monotonic transformations (Koenker and Portnoy 1996). This is a great advantage for estimation problems such as the self-thinning rule that involve allometric equations that require linearizing with logarithms.

## Results

When the parameter  $\beta_1$  was constrained to 0 (i.e.,  $\lambda = -1$ ), model (1a) estimates for the 99th quantile of final densities of *Eriogonum* were  $b_0 = 40$  (95% CI = 13–67) and for *Haplopappus* were  $b_0 = 97$  (95% CI = 41–153). Estimates for 90th and 99th quantiles in the log scale in which they were estimated (model 1b) are plotted in Fig. 2 and in the original scale (model 1a) in Fig. 3. Returning these estimates to our ratio of final to initial density equation yields functions that are very similar to those graphically fit by Guo et al. (1998) (Fig. 4). But how justified are we in constraining  $\beta_1 = 0$ , and, thus,  $\lambda = -1$ ? Intuitively, the flaw in this model specification is that it will never be possible for upper quantiles of observed final densities to approach the estimated function at low initial germination densities (Figs 2 and 3), thus, indicating lack of model fit. The assumption made by Guo et al. (1998) when fixing the exponent at  $-1$  was that all populations attained the same final summer density, but the data indicated that this was unrealistic when initial germination densities were low (Fig. 2).

Estimates for model (2b) indicated there was little evidence that  $\beta_1 = 0$  for either *Eriogonum* or *Haplopappus* for any quantile (Fig. 5). The slopes for upper quantiles for *Eriogonum* were just below 0.6 (i.e.,  $\lambda = -0.4$ ) and those for *Haplopappus* were just above 0.6 (Fig. 5). Other than the zero slopes associated with the lowest quantiles ( $< 10$ th) corresponding to the zero

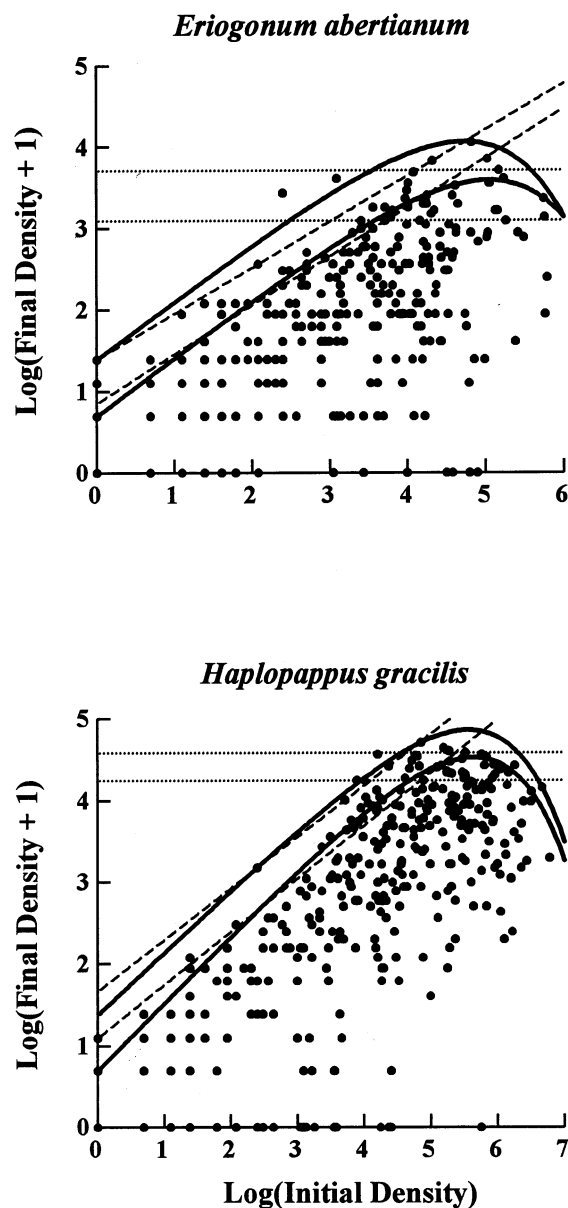


Fig. 2. Final summer and initial winter densities for *Eriogonum abertianum* ( $n = 331$ ) and *Haplopappus gracilis* ( $n = 346$ ) in  $0.25\text{-m}^2$  quadrats at Portal, Arizona (Guo et al. 1998), and estimated 90th (lower lines) and 99th (upper lines) regression quantile functions for model 1b (dotted line), model 2b (dashed line), and model 3b (solid line) in log-transformed scale.

final densities, slope estimates for *Haplopappus* fluctuated somewhat randomly between 0.55 and 0.75 for quantiles  $\geq 10$ th, whereas *Eriogonum* slope estimates gradually increased from 0.25 at the 10th quantile to 0.60 at the 80th quantile (Fig. 5). Model (2b) fit the data better than model (1b) for 90th and 99th quantiles at lower initial plant densities (Figs 2 and 3). Coefficients of determination indicated a 38% ( $R^1 = 0.38$ ) and

28% ( $R^1 = 0.28$ ) reduction in variation for model (2b) compared to model (1b) estimates for 90th and 99th regression quantiles, respectively, for *Eriogonum*. The comparable reductions for *Haplopappus* were 29% ( $R^1 = 0.29$ ) and 18% ( $R^1 = 0.18$ ), for 90th and 99th quantiles, respectively. The estimated rate of change for the 99th quantile of *Haplopappus* ( $b_1 = 0.63$ , 95% CI =  $-0.19-0.83$ ,  $P = 0.150$ ) was more variable than the

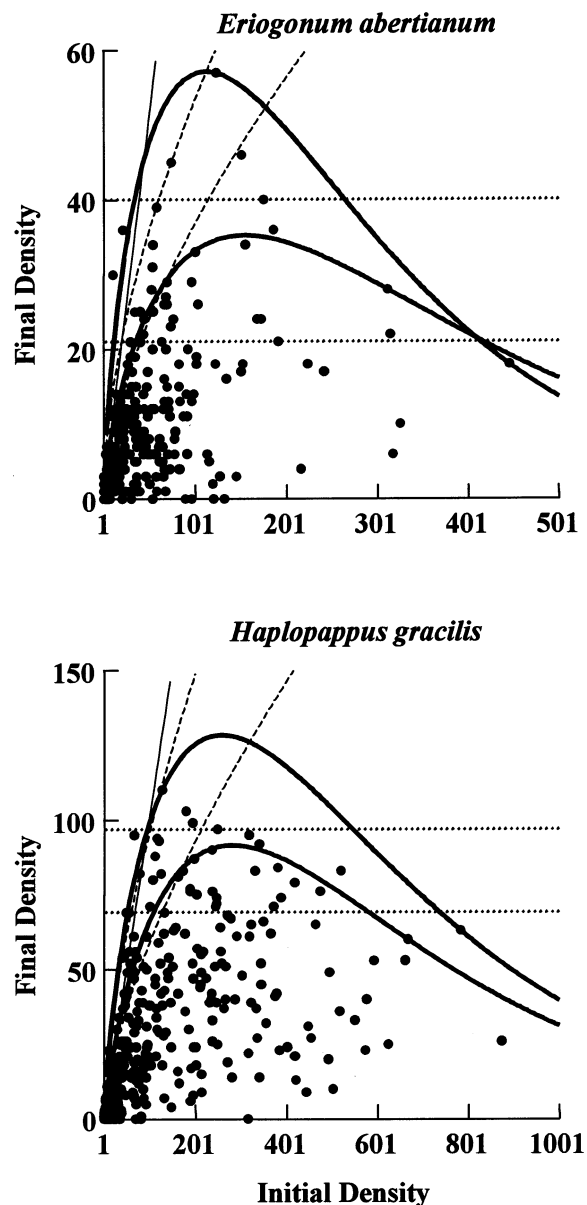


Fig. 3. Final summer and initial winter densities for *Eriogonum abertianum* ( $n = 331$ ) and *Haplopappus gracilis* ( $n = 346$ ) in  $0.25\text{-m}^2$  quadrats at Portal, Arizona (Guo et al. 1998), and estimated 90th (lower lines) and 99th (upper lines) regression quantile functions for model 1a (dotted line), model 2a (dashed line), and model 3a (thick solid line) in original density scale. Thin solid line denotes final summer density = initial winter density.

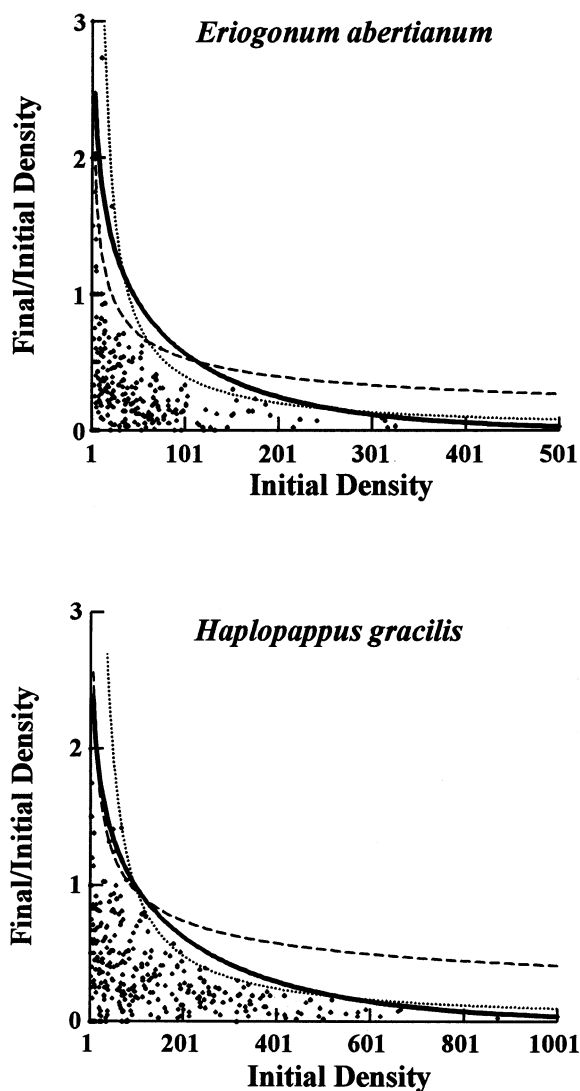


Fig. 4. Ratio of final summer to initial winter densities against initial densities for *Eriogonum abertianum* ( $n = 331$ ) and *Haplopappus gracilis* ( $n = 346$ ) in 0.25-m<sup>2</sup> quadrats at Portal, Arizona (Guo et al. 1998), and estimated 99th regression quantile functions from model 1a (dotted line), model 2a (dashed line), and model 3a (solid line).

estimate for *Eriogonum* ( $b_1 = 0.56$ , 95% CI = 0.14–0.81,  $P = 0.017$ ). Although the 99th quantile estimate for *Haplopappus* did not differ from zero because of large sampling variation, estimates for quantiles just below the 99th, e.g., 98th (Fig. 5), provided similar estimates with greater precision that differed from zero ( $P < 0.02$ ). Estimates for 90th quantiles, although slightly farther away from the boundary of the distribution, fit the trend in the data well (Fig. 2) and differed from zero for both species (Fig. 5).

Recovering estimates of  $\lambda$  from our estimates of  $\beta_1$  in model (2b) for the 99th regression quantiles, resulted in

functions that did not fit the higher initial densities of *Eriogonum* and *Haplopappus* as well as the constrained parameter model (1b) (Fig. 4). This is perhaps more obvious by comparing estimates of final density as a function of initial density (Figs 2 and 3), where estimates for model (1b) (flat dotted lines) deviated from observed final densities less than estimates for model (2b) (sloped dashed lines) when initial densities were  $> 100$  for *Eriogonum* ( $e^{4.6} \approx 101$ ) or  $> 150$  for *Haplopappus* ( $e^5 \approx 148$ ). The linear function of model (2b) fit better than model (1b) for lower initial densities (Figs 2 and 3), although this was less obvious in allometric form when expressed as a ratio of final to initial density (Fig. 4). The appearance of a better fit with estimates from the constrained parameter model (1b) was due to a combination of scale compression associated with multiplying the left-hand side of the equation,  $N_j$ , by  $N_i^{-1}$ , and because the small initial densities where model (2b) fit better were only 25% of the data range on the original density scale (compare Figs 2 and 3).

The obvious flaw in model (2b) was that it assumed a constant rate of change along the boundary of the final density distribution which was only reasonable at lower initial germination densities (Fig. 3). The exponential form of model (3b) fit the summer plant density changes similar to model (2b) at low initial densities but fit substantially better than model (2b) at higher initial densities (Figs 2 and 3). Coefficients of determination for model (3b) for *Eriogonum* ( $R^1 = 0.41$  for 99th and  $R^1 = 0.29$  for 90th) were slightly larger than those for model (2b), indicating only minor improvement in fit. Coefficients of determination for model (3b) for *Haplopappus* ( $R^1 = 0.38$  for 90th and  $R^1 = 0.29$  for 99th) were larger than those for model (2b), indicating more substantial improvement in fit. The difference in relative improvement in model fit between the two species occurred because there were fewer observations of *Eriogonum* at the higher initial densities where the estimated function for model (3b) was decreasing (Fig. 3). Both species had similar patterns of increasing coefficients for  $b_1$  and decreasing coefficients for  $b_2$  with increasing quantiles (Fig. 6). However, increases in  $b_1$  with increasing quantiles for *Haplopappus* were less than for the estimates for *Eriogonum* (Fig. 6). Decreases in  $b_2$  with increasing quantiles for *Haplopappus* were less than for the estimates for *Eriogonum*; precision of the estimates were poorer for *Eriogonum* and there was weaker evidence that they differed from zero compared to estimates for *Haplopappus* (Fig. 6). Estimates for the 90th regression quantile for *Eriogonum* were  $b_0 = 0.698$  (95% CI = 0.698–1.079),  $b_1 = 0.715$  (95% CI = 0.584–0.722), and  $b_2 = -0.005$  (95% CI =  $-0.005 - (-0.001)$ ) ( $P < 0.001$ ). Rates of change for the 99th quantile,  $b_1 = 0.716$  and  $b_2 = -0.006$ , were not estimated as precisely but were similar to those for the 90th quantile (Fig. 6) and were used for graphical comparisons. Estimates for the 90th regression quantile for

*Haplopappus* were  $b_0 = 0.696$  (95% CI = 0.696–1.065),  $b_1 = 0.826$  (95% CI = 0.765–0.842), and  $b_2 = -0.003$  (95% CI =  $-0.003 - (-0.002)$ ) ( $P < 0.001$ ). Rates of change for the 99th quantile,  $b_1 = 0.765$  and  $b_2 = -0.003$ , were not estimated as precisely but were similar to those for the 90th quantile (Fig. 6) and, therefore, used for graphical purposes.

Exponentiating model (3b), subtracting the constant due to adding 1, and multiplying both sides of the equation by  $N_i^{-1}$ , yielded estimates for the function  $N_f(N_i)^{-1} = c_f(N_i)^\lambda e^{\gamma N}$  of  $\lambda = -0.28$  and  $\gamma = -0.006$  for *Eriogonum* and  $\lambda = -0.23$  and  $\gamma = -0.003$  for *Haplopappus*. This model fit the ratio of final to initial densities (survival) against initial plant densities reasonably well (Fig. 4). The functional form of model (3a) was characterized by a positive rate of change in final densities that was nearly a one-to-one function of initial germination densities when they were low, followed by a shift to negative rates of change at higher initial germination densities where self-thinning occurred (Fig. 3).

## Discussion

Our regression quantile estimates indicated that the Guo et al. (1998) data for *Eriogonum* and *Haplopappus* were

not consistent with a simple allometric self-thinning equation with an exponent of  $-1$ . Estimated rates of change in our model (2) indicated exponents were closer to  $-0.44$  and  $-0.37$ , respectively. However, the exponential form of model (3) fit *Eriogonum* and *Haplopappus* densities better than the simpler allometric form of model (2). Our analyses and graphs highlight the deceptive similarity of the functions when transformed to survival rates expressed as a ratio of final to initial plant densities (compare Figs 3 and 4). This reinforces a warning made thirty years ago by Eberhardt (1970) about interpreting hyperbolic functions involving ratios of population parameters conditioned on one of those parameters as evidence of density dependence. We believe that directly exploring the functional relations between final and initial plant densities provides more insight on appropriate functional forms and interpretations of relevant ecological processes.

Our exponential model (3) was consistent with an interpretation that final summer densities of *Eriogonum* and *Haplopappus* were constrained by initial germination densities when they were low ( $< 40$  per  $0.25 \text{ m}^2$  for *Eriogonum* or  $< 100$  per  $0.25 \text{ m}^2$  for *Haplopappus*), but were constrained by self-thinning due to intraspecific competition at higher germination densities (Fig. 3).

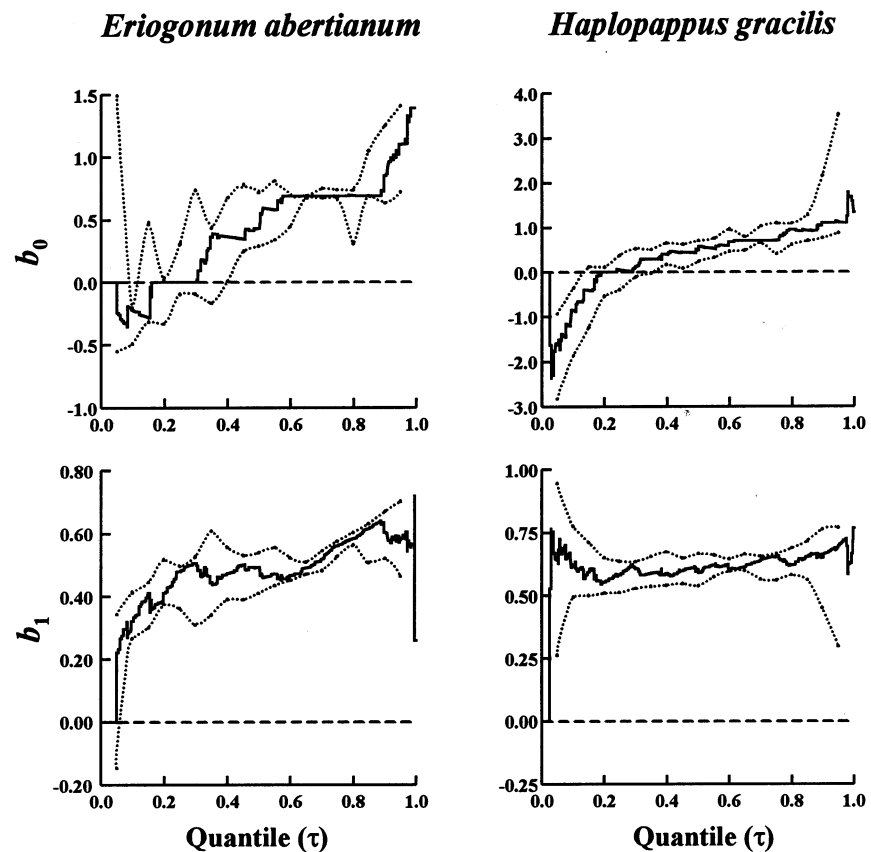


Fig. 5. Parameter estimates for model (2b) for *Eriogonum abertianum* ( $n = 331$ ) and *Haplopappus gracilis* ( $n = 346$ ) for all regression quantiles relating final summer to initial winter densities in  $0.25\text{-m}^2$  quadrats at Portal, Arizona (Guo et al. 1998). Solid line is step function of estimates by quantiles, and dotted lines are lower and upper bounds connecting 95% confidence intervals from inverting a quantile rank-score test for  $\tau = 0.05\text{--}0.95$  by increments of 0.05.

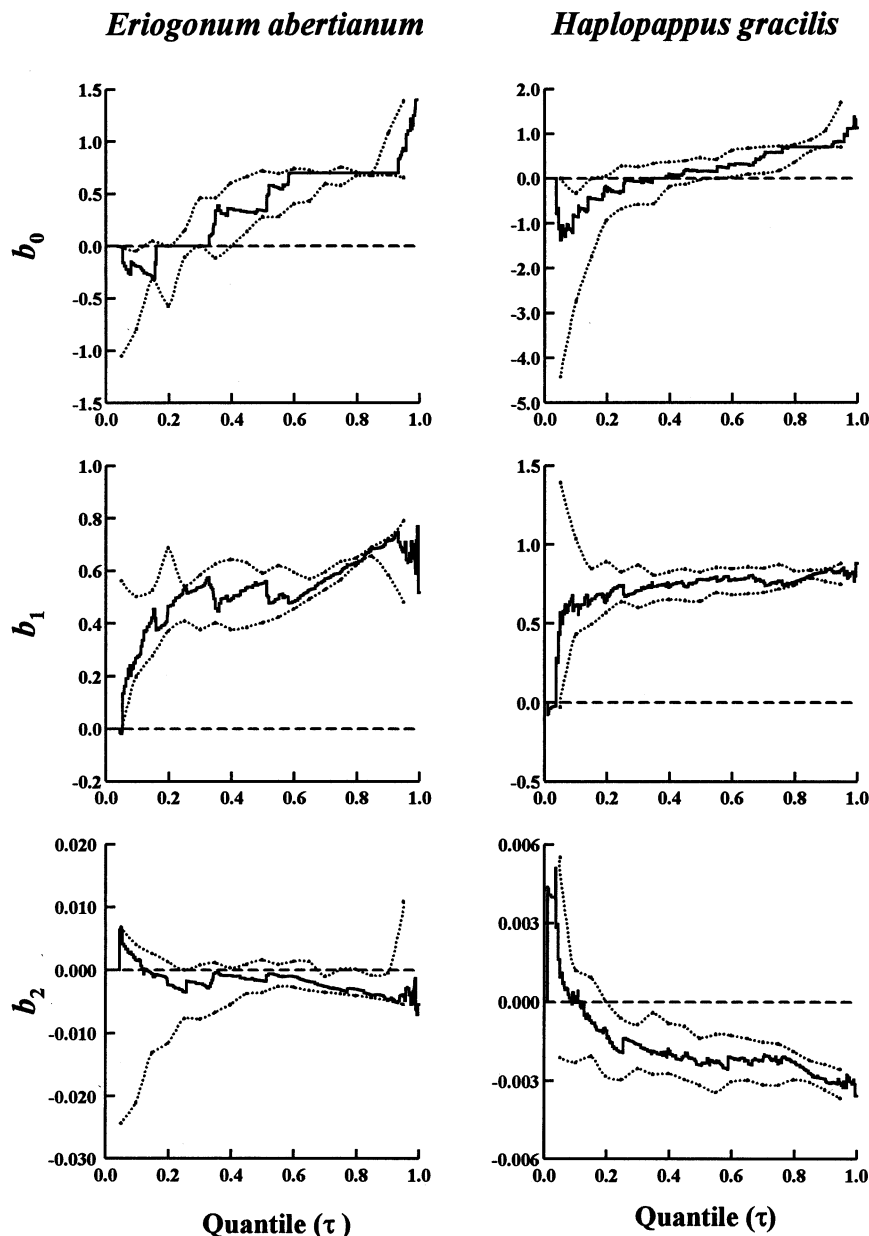


Fig. 6. Parameter estimates for model (3b) for *Eriogonum abertianum* ( $n = 331$ ) and *Haplopappus gracilis* ( $n = 346$ ) for all regression quantiles relating final summer to initial winter densities in 0.25-m<sup>2</sup> quadrats at Portal, Arizona (Guo et al. 1998). Solid line is step function of estimates by quantiles, and dotted lines are lower and upper bounds connecting 95% confidence intervals from inverting a quantile rank-score test for  $\tau = 0.05-0.95$  by increments of 0.05.

The data and model (3) provided strong evidence that initial germination density served as the primary constraint on final summer densities up to some moderate level of germination (the peak of the functions in Fig. 3). The evidence was not as strong for decreases in summer densities as germination densities increased to higher levels (the declining portion of the function to the right of the peaks in Fig. 3) because of the low number of sample plots with high initial germination densities, especially for *Eriogonum*. Additional samples at high initial germination densities will be required to more accurately estimate the self-thinning function be-

yond the peak of maximum summer densities and establish whether densities decrease or remain constant. More complicated nonlinear functional forms that cannot be linearized via transformation could be estimated with nonlinear regression quantile estimators (Koenker and Park 1996), although these currently are more delicate to implement and have less well developed inferential procedures than the linear regression quantile estimators. Barrowman and Myers (2000) present a nonlinear model of density dependence in salmonid spawner-recruitment that involves smoothing of a piecewise linear regression. This model might be ex-



tended to nonlinear regression quantiles for estimating effects of density dependent processes in plants.

Regression quantiles are a useful statistical procedure for estimating quantities in allometric relations where the rates of change of interest are associated with the upper boundary of the data distribution. We believe that evaluations of the  $-3/2$  ( $-1/2$ ) or  $-4/3$  self-thinning rules of plant mass as a function of density of plants (Weller 1987, Lonsdale 1990, Niklas 1994: 183–188) would benefit from analyses with regression quantiles. By using regression quantiles, we completely avoid the arbitrary decisions about which data to use for estimating the function, which is required by other regression methods (Weller 1987). Furthermore, the complicated back-transformation procedures required to compute unbiased estimates for mean regression functions estimated on logarithmic transformed data (Beauchamp and Olson 1973) are not required with regression quantiles. The statistical theory associated with regression quantiles also provides a method for comparing parameter estimates (hypothesis tests and associated confidence intervals) among self-thinning relations developed for various taxa.

It is tempting to consider the maximum (100th) regression quantile as the estimate to use for a self-thinning constraint because when viewed as an absolute constraint we would expect no data values outside this boundary (Guo et al. 1998). We do not advocate this approach for several reasons. The data used in estimation are a sample from a population and it is unreasonable to believe that functions that fit the absolute boundary of the sample distribution are better estimates for the population, especially if our interest is on rates of change rather than predicted values. Some amount of measurement error and variation in initial conditions across replicate plots will always likely occur and, thus, it is unreasonable to expect an empirical absolute constraint, even though a theoretical absolute constraint may make sense. Sampling variation of estimated slope parameters for the maximum (100th) quantile may be quite large. Our current implementation of confidence intervals based on inverting the rank-score test does not even allow us to estimate this variation because the asymptotic variance of the test statistic goes to zero for  $\tau = 1$  or  $\tau = 0$  (Cade et al. 1999). Some improvements in this regard are being investigated by implementing permutation versions of the rank-score statistic.

The rather large confidence intervals associated with our estimates for the 99th regression quantiles may appear disheartening, but it is simply not possible to estimate parameters near extremes of data distributions with as much precision as those parameters near the center of distributions (Cade et al. 1999), especially given the inherent variation that occurs in plant densities. Considerable improvement in precision for similar slope estimates often were obtained simply by moving

to a quantile slightly less than the 99th. We recommend estimating the entire regression quantile process and considering estimates for a range of upper quantiles. The local density of values near selected upper quantiles can greatly impact precision of the estimates such that a quantile slightly greater or less than one initially selected may be estimated with better or worse precision. Estimating the entire regression quantile process allows us to examine the entire pattern of variation in rates of change, preventing an analysis from being overwhelmed by selecting a quantile that is estimated less precisely than others in its neighborhood.

We limited our application of regression quantiles to estimating relations between final and initial densities of individual plant species (Guo et al. 1998), where initial germination densities were an antecedent condition for final summer densities. Final summer densities were reasonably considered to be the dependent variable and initial densities the independent variable in our regression models. Guo et al. (1998) proposed other mechanistic relations describing interspecific competition between plant species where there is no clear argument for considering one species as dependent on another. One possible solution for using regression quantiles for estimating effects of interspecific competition is to perform two regressions, considering each species as the dependent variable in turn. The estimated slopes from these two regression quantile models for a given quantile,  $\tau$ , could then be combined into a single estimate by taking the geometric mean of one slope estimate and the reciprocal of the other slope estimate, similar to one formulation of geometric mean regression (Ricker 1984, Legendre and Legendre 1998). Our initial attempts with this procedure provided functions that appeared to be reasonable fits. The statistical properties and theoretical justification for combining estimates this way for regression quantiles are a topic for additional research.

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