

## Modelling partitioning between structure and storage in sugar beet: Effects of drought and soil nitrogen

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### Abstract

In the UK sugar beet is grown on contrasting soils that vary both in their nutritional status and water-holding capacities. Water shortage and low nitrogen reduce canopy growth and dry matter production, which is compensated in part by an increase in the fraction of assimilates partitioned to storage. Conversely, high nitrogen and ample water encourage growth of the canopy, increase assimilation of carbon dioxide but reduce the proportion of assimilates stored as sugar. This paper sets out to examine simple relationships between sugar yield, total dry matter and soil nitrogen in rain-fed and irrigated sugar beet crops (*Beta vulgaris* L.) from 46 field experiments spanning 12 years and a range of soil types, in order to improve prediction of sugar yields.

Two partitioning functions were fitted to the data. The first represents a useful alternative formulation of the allometric growth function that overcomes some of the difficulties in the interpretation of the parameters. This model adequately described the seasonal progress of sugar yield ( $Y$ ) in relation to total dry matter ( $W$ ), but it was difficult to postulate biological mechanisms as to how the parameters should vary in relation to varying soil nitrogen or to drought. The second partitioning function, given by  $Y = W - (1/k) \log(1 + kW)$ , also described the data well, but had the more useful parameter,  $k$ , the decay rate of the fraction of assimilates partitioned to structural matter. This was shown to be greater in crops which had experienced significant drought and was inversely proportional to the amount of nitrogen taken up by the crops. Relationships between  $k$  and amounts of nitrogen fertilizer applied and/or amounts of residual nitrogen in the soil at sowing, however, were more variable. These could be improved by additionally taking account of soil type and rainfall following nitrogen fertilizer application in late spring. The models are a useful extension to yield forecasting models because they provide a simple means of estimating sugar yield from total dry matter in relation to factors that affect partitioning of assimilates such as drought and soil nitrogen availability.

### Introduction

In the UK sugar beet is grown on contrasting soils that vary both in their nutritional status and water-holding capacities. Much of it is also grown in Eastern England where low summer rainfall means that crops frequently experience drought (Werker and Jaggard, 1998; Jaggard et al., 1998).

The partitioning of assimilates to storage, shoot and root systems are strongly influenced by soil nitrogen dynamics. Relationships between soil nitrogen

concentration and yields of sugar beet crops have been extensively studied, with three notable conclusions on which there is a general consensus.

- (1) In common with many crops, too little nitrogen retards leaf growth (Milford et al., 1985), accelerates leaf senescence (Burky and Biscoe, 1983) and thereby reduces the amount of solar radiation intercepted and the yield. However, this loss in yield is partly compensated by an increase in the proportion of assimilates stored as sugar rather than used for growth (Scott et al., 1994).
- (2) Conversely, too much nitrogen causes over-production of leaves (Milford et al., 1988), even

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when these afford little benefit in additional amounts of radiation intercepted (Scott et al., 1994), causing a decrease in the proportion of assimilates stored as sugar (Milford, 1973). This is accompanied by an increase in the amount of nitrogenous compounds stored in the root, which significantly reduces the processing quality of sugar beet (Pocock et al., 1990).

- (3) Determining optimum fertilizer requirements is confounded by overriding influences of field to field and year to year variation in soil nitrogen dynamics, and in Britain in particular, good correlations between any single measure of available or potentially available soil nitrogen and fertilizer requirement have been singularly lacking (Allison et al., 1996; Greenwood et al., 1986; Greenwood et al., 1984; Last et al., 1983).

Despite the importance of soil nitrogen dynamics in determining total dry matter, sugar concentration and the processing quality of the root, quantitative relationships between soil nitrogen and partitioning in sugar beet are rare. Such relationships could be used to improve yield prediction of sugar beet, which is an important activity of sugar producers. National and regional predictions of yield are used to optimize resources during the harvesting and processing season. In Britain, simple yield prediction models are used, relying either on empiricism (Church and Gnansakthy, 1983) or on the principle that yields in temperate climates are limited by the amount of intercepted radiation (Monteith, 1977; Scott and Jaggard, 1993). However, in areas such as eastern England a shortage of water frequently limits the growth of crops during the summer (Werker and Jaggard, 1998; Jaggard et al., 1998). Others have preferred more physiologically detailed simulation models, usually concerned with potential growth, such as SUCROS (Spitters et al., 1989). Here the problem of partitioning is frequently bypassed by resorting to historic growth analysis data to determine the fractions of assimilates partitioned to numerous plant organs. An alternative approach to modelling growth and partitioning was suggested by Webb et al. (1997) who constructed a model in which soil nitrogen content and solar radiation are used as driving variables to predict shoot, storage root and fibrous root weights. Although the equations required numerical solutions, the model could be fitted to standard growth analysis data from nitrogen response field experiments. The authors demonstrated that there was an optimal soil nitrogen concentration that gave the largest root yield.

This paper reports concurrent work on effects of soil types, seasons and fertilizer application on sugar yield using simple empirical partitioning functions, given known total dry matter. There is little quantitative information on how the proportion of total dry matter stored as sugar changes during the course of the growing season on the wide variety of soils on which sugar beet is grown in the UK and as affected by different rates of fertilizer application and by drought. It is assumed that reliable prediction of total dry matter can be obtained by calculating light interception (Steven et al., 1986; Werker and Jaggard, 1997) and evapotranspiration (Monteith, 1986; Werker and Jaggard, 1998) as a function of foliage cover, solar radiation and available water. The allometric growth function and an alternative model are used, firstly to obtain relationships between sugar and total dry matter during the course of the growing season and, subsequently, to consider the effects of drought, soil type and soil fertility and fertilizer application on relationships between storage and total dry matter.

## Materials and methods

Two simple empirical models were used to relate sugar and total dry matter yields from 46 field experiments. The first is the allometric growth function because it provides a widely used method for describing relationships between plant components. However, an alternative formulation is suggested in which the parameters have a more useful biological interpretation. The second model is proposed because it is more flexible than the allometric function when used to analyse effects of agronomic variables on partitioning. In this analysis total dry matter ( $W$ ) is partitioned either to plant structure ( $G$ ) or to storage ( $Y$ ). A list of the symbols referred to in the following text is given in Table 1.

### *The allometric growth function*

This function is derived from an assumption that the relative growth rates of plant components are proportional and constant. Thus, storage ( $Y$ ) and total ( $W$ ) dry matter may be related by

$$\frac{dY}{dt} \frac{1}{Y} = b \frac{dW}{dt} \frac{1}{W} \quad (1)$$

Equation 1 is usually given as  $\log Y = \log a + b \log W$ , but this formulation posses practical problems when it comes to interpreting the meaning of the regression

Table 1. Definitions and units of symbols referred to in the text

Symbol	Definition	Units
$W$	total dry matter ( $W = Y + G$ )	$\text{g m}^{-2}$
$Y$	storage dry matter (sugar)	$\text{g m}^{-2}$
$G$	structural dry matter	$\text{g m}^{-2}$
$W_0$	initial total dry matter	$\text{g m}^{-2}$
$Y_0$	initial storage dry matter (sugar)	$\text{g m}^{-2}$
$G_0$	initial structural dry matter	$\text{g m}^{-2}$
$\log a$ $b$	intercept and slope of the log transformation of the allometric growth function	—
$\alpha$	partitioning fraction of total dry matter to $Y$	$\text{g g}^{-1}$
$\beta$	partitioning fraction of total dry matter to $G$	$\text{g g}^{-1}$
$\alpha_0$	initial partitioning fraction of total dry matter to $Y$	$\text{g g}^{-1}$
$\beta_0$	initial partitioning fraction of total dry matter to $G$	$\text{g g}^{-1}$
$k$	decay parameter of the fraction of assimilates partitioned to $G$ , with respect to $W$	$(\text{g m}^{-2})^{-1}$
$k_0$	$k$ at a base concentration of soil nitrogen (when $N_a = 0$ or $N_q$ )	$(\text{g m}^{-2})^{-1}$
$r$	magnitude with which $1/k$ increases as $N$ increases	$\text{g m}^{-2} (\text{kg ha}^{-1})^{-1}$
$N$	soil nitrogen concentration	$\text{kg ha}^{-1}$
$N_0$	soil nitrogen concentration at sowing	$\text{kg ha}^{-1}$
$N_u$	total amount of nitrogen taken up by the crop	$\text{kg ha}^{-1}$
$N_a$	total amount of fertilizer nitrogen applied to the crop	$\text{kg ha}^{-1}$
$N_q$	recommended amount of fertilizer nitrogen applied to the crop	$\text{kg ha}^{-1}$

coefficients  $\log a$ , the intercept, and  $b$ , the slope. An alternative formulation can be arrived at by defining a partitioning function,  $\alpha$ , which describes the fraction of total dry matter partitioned to sugar, such that

$$\frac{dY}{dt} = \alpha \frac{dW}{dt} \quad (2)$$

Solving equations 1 and 2 for  $\alpha$  and eliminating the coefficient  $b$  gives the rate of change of the partitioning function  $\alpha$  as

$$\frac{d\alpha}{dt} = \alpha \left( \frac{dY}{dt} \frac{1}{Y} - \frac{dW}{dt} \frac{1}{W} \right) \quad (3)$$

(see appendix). This says that the relative rate of change of the partitioning function  $\alpha$  is equal to the difference in the relative rates of change of  $Y$  and  $W$ . Solving Eqs. (2) and (3) for  $Y$  and defining the initial conditions as,  $\alpha = \alpha_0$ ,  $Y = Y_0$  when  $W = W_0$  gives an alternative formulation of the familiar allometric growth function,

$$Y = Y_0 \left( \frac{W}{W_0} \right)^{\alpha_0 \frac{W_0}{Y_0}} \quad (4)$$

It has coefficients that pertain to the initial conditions and that have a simple biological interpretation.

Nonetheless, Eq. (4) shows the complex nature of the regression coefficients  $a$  and  $b$ , where  $a = Y_0(1/W_0)^b$  and  $b = \alpha_0(W_0/Y_0)$ .

#### An alternative model

The second model was developed to describe the particular case of partitioning between just two components, structure ( $G$ ) and storage ( $Y$ ), and whose parameters are more amenable to data analysis than those presented by Eq. (4). This model was derived by defining a partitioning function,  $\beta$ , which determines the fraction of total dry matter partitioned to structure ( $G$ ),

$$\frac{dG}{dt} = \beta \frac{dW}{dt} \quad (5)$$

which decays exponentially in relation to the size of the structural material, such that

$$\frac{d\beta}{dt} = -k\beta \frac{dG}{dt} \quad (6)$$

Integrating Eq. (6), substituting  $\beta$  in Eq. (5) and given that  $G + Y = W$ , gives

$$G = G_0 + \frac{1}{k} \log(1 + k\beta_0(W - W_0));$$

$$Y = Y_0 + W - W_0 - \frac{1}{k} \log(1 + k\beta_0(W - W_0)) \quad (7)$$

Various simplifications of Eq. (7) are possible, for example, (i) at crop emergence it may be assumed that,  $Y_0 = 0$ , and  $G_0 = W_0$ , (ii) at this point  $W_0$  may approximate to 0, and (iii)  $\beta_0$  to unity, meaning, initially all the assimilates are partitioned to structure. These conditions reduce Eq. (7) to just one parameter,  $k$ , i.e.

$$G = \frac{1}{k} \log(1 + kW); \quad Y = W - \frac{1}{k} \log(1 + kW) \quad (8)$$

The parameter  $k$  ( $\text{g}^{-1}\text{m}^2$ ) determines how fast the partitioning function  $\beta$  changes from 1 to 0.

Equation 8 can also be derived by considering the rate of growth of structural matter as a function of the reciprocal of total dry matter, thus

$$\frac{dG}{dt} = \frac{dW}{dt} \left( \frac{1}{A + kW} \right);$$

$$\text{where } A = \frac{1}{\beta_0} - kW_0 \quad (9)$$

### Analyses

Two analyses were performed using the general statistical package *Genstat* (Payne et al., 1993). In the first, Eqs (4) and (7) were fitted to sequential measures of sugar ( $Y$ ) and total dry matter ( $W$ ) of crops (cultivar Regina) grown at IACR-Broom's Barn during 1980–91 under standard farm management. This was done to compare Eqs (4) and (7) and to obtain reliable estimates of the parameters and the extent to which they vary from year to year. The data comprised 6–18 repeated measures of  $W$  and  $Y$  during the growing season, except during 1986–88 when they were estimated at final harvest only. Many of the experiments have been described elsewhere (e.g. Werker and Jaggard, 1998; Scott and Jaggard, 1993; Dunham, 1993; Brown et al., 1987; Milford et al., 1985).

In the fitting of Eq. (4),  $Y_0$  was fixed at  $30 \text{ g m}^{-2}$  ( $= 4 \text{ g per plant} \times 7.5 \text{ plants per square metre}$ ). This is the estimated amount of sugar in the crop when secondary thickening of the root has just taken place (Spitters et al., 1990). Also, in order to have a degree of homogeneity between the two models,  $\alpha_0$  in Eq. (4) was replaced by  $1 - \beta_0$  where  $\alpha_0$  and  $\beta_0$  are the initial partitioning coefficients for structure and storage respectively, when  $Y = Y_0$  and  $W = W_0$ .

The second analysis was limited to final yield data, and was designed to test effects of drought and different soil nitrogen concentrations on the parameter  $k$  (Eq. 7). Effects of drought were estimated with data from irrigation response trials at IACR-Broom's Barn between 1980 and 1991 and included seven years when drought caused significant yield losses (1982–1985, 1989–1991). Effects of nitrogen were estimated from data derived from 34 field experiments designed to test effects of fertilizer application rates (0–180 kg/ha of N) on the growth, yield and processing quality of sugar beet. The experiments were carried out between 1986 and 1988 at 12 locations covering major soil types in the sugar beet growing regions of the UK (Allison et al., 1996). The choice of cultivars grown depended on farmers' preferences that varied amongst years and sites. During these years there was little drought. For the purpose of this investigation, the soil types were divided into sandy, silty and clay loams and organic soils (SL, ZL, CL, O). In addition to the amount of fertilizer applied ( $N_a$ ), estimates were also made of the soil nitrogen at sowing ( $N_0$ ) and the total amount of nitrogen taken-up by the crops ( $N_u$ ).

The effect of nitrogen ( $N$ ) on partitioning was analysed by allowing the parameter  $k$  to vary with respect to nitrogen supply according to,

$$k = \frac{1}{1/k_0 + rN} \quad (10)$$

Because  $k$  determines how fast the proportion of total dry matter allocated to structure decays as the amount of structure increases, it would be expected to be inversely proportional to nitrogen concentration. Four measures of  $N$  were used: (1)  $N = N_u$ ; (2)  $N = N_a$ ; (3)  $N = N_0 + N_a$ , which is the total  $N$  available excluding mineralization and leaching; (4)  $N = N_a - N_q$ , the deficit or surplus  $N$  in relation to the recommended fertilizer requirements,  $N_q$ . In this case  $k_0$  more usefully describes the value of  $k$  when the amount of nitrogen applied is equal to the amount recommended ( $N_a = N_q$ ), and  $r$  ( $\text{g m}^{-2}$  per  $\text{kg ha}^{-1}$ ) is a measure of response in partitioning, in terms  $k$ , when fertilizer applications exceed or fall below the recommended amount. The parameter  $k_0$  was allowed to vary with respect to years, soil type and locations to test whether variation could be accounted for in addition to that due to nitrogen supply and uptake.

Table 2. Estimates of parameters, residual sums of squares (rss), degrees of freedom (df) and percentage variation accounted for (%VA) on fitting the partitioning functions (Eqs 4 and 7) to sequential measures (irrigated crops) and final yields (irrigated and unirrigated crops) of sugar ( $Y$ ) and total dry matter ( $W$ ) in sugar beet grown at IACR-Broom's Barn during 1980 to 1991. Figures in square brackets represent ranges of estimated values amongst years

Model	Conditions on the parameters		Parameters estimated				
	fixed	varying amongst years	$k$ ( $\text{g}^{-1} \text{m}^2$ , $\times 10^{-3}$ )	$\beta_0$	$W_0$ ( $\text{g m}^{-2}$ )	rss ( $\times 10^5$ ) (df)	% VA
$Y=Y_0\left(\frac{W}{W_0}\right)^{(1-\beta_0)W_0/Y_0}$	$Y_0=30$	—		0.774	202	4.784 <sup>a</sup> (97)	97.6
		$\beta_0$		[0.76 – 0.78]	193	2.692 (90)	98.5
$Y=Y_0+(W-W_0)$ $-\frac{1}{k}\log(1+k\beta_0(W-W_0))$	$Y_0=30$	—	1.21	0.805	220	4.957 (96)	97.5
		$\beta_0$	1.16	[0.65 – 1.00]	173	2.684 (89)	98.5
		$k$	[0.79 – 1.94]	0.816	198	2.637 (89)	98.5
	$Y_0, W_0 = 0$	—	1.18	0.989	—	4.871 (97)	97.5
		$\beta_0$	1.17	[0.78 – 1.16]	—	2.665 (90)	98.6
		$k$	[0.88 – 1.71]	0.985	—	2.571 (90)	98.6
	$Y_0, W_0 = 0$ and $\beta_0 = 1$	—	1.20	—	—	4.873 (98)	97.5
		$k$	[0.91 – 1.75]	—	—	2.574 (91)	98.6
		—	1.50	—	—	0.573 <sup>b</sup> (11)	89.1
	[final yields of irrigated crops] [final yields of drought stressed crops]	—	1.89	—	—	0.2076 <sup>c</sup> (6)	91.0

(a) Total ss =  $4.540 \times 10^7$  (99)

(b) Total ss =  $1.740 \times 10^7$  (12)

(c) Total ss =  $0.825 \times 10^7$  (7)

## Results

The seasonal progress of sugar ( $Y$ ) against total dry matter ( $W$ ) for sugar beet crops grown under standard farm management was described equally well by either the allometric growth function (Eq. 4) or the new model (Eq. 7). The equations described >97% of the variation in  $Y$  within and amongst eight growing seasons (Figure 1, Table 2). However, significant additional variation could be accounted for by allowing either  $\beta_0$  (Eq. 4 & 7) or  $k$  (Eq. 7) to vary amongst years (Table 2). With respect to Eq. 7, it was better to allow  $k$  to vary rather than  $\beta_0$  because in certain years  $\beta_0$  (the initial fraction of dry matter partitioned to structure) exceeded unity, which was not consistent with the biology of the system. The analyses also showed that equally good fits could be obtained by assuming zero initial weights of sugar ( $Y_0$ ) and total dry matter ( $W_0$ ), when it could also be assumed that  $\beta_0 = 1$ . This reduced the number of parameters for estimation to just one,  $k$ , with a mean estimated value of  $1.20 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$ , but ranging between  $0.91 – 1.75 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$  amongst years (Table 2).

Variation in  $k$  amongst years in irrigated sugar beet crops was correlated with rainfall during late spring (Figure 2), but this was not as a consequence of drought, which normally occurred during the middle of the summer. Crops which later were affected by drought partitioned more dry weight to sugar than irrigated crops ( $k = 1.89$  and  $1.50 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$  respectively, Figure 1, Table 2). The discrepancy between the estimated mean value of  $k$  derived from sequential data and that derived from final harvest data (Table 2) may be due to an under-estimation of foliage dry matter in plots assigned to final harvests, in which senesced and senescing leaves that became detached from the crown during toping were not weighed. In the smaller and more meticulously sampled plots assigned to intermediate harvests, all of the foliage was recovered for weighing. The discrepancy in  $k$  may also have arisen because  $k$  varies from year to year. Some of this variation can be accommodated by the model when there are no intermediate data to constrain the fitting process, causing an increase in the value of  $k$ . Therefore, the appropriate value for  $k$  will depend on how  $W$  is estimated, whether account is taken of leaf

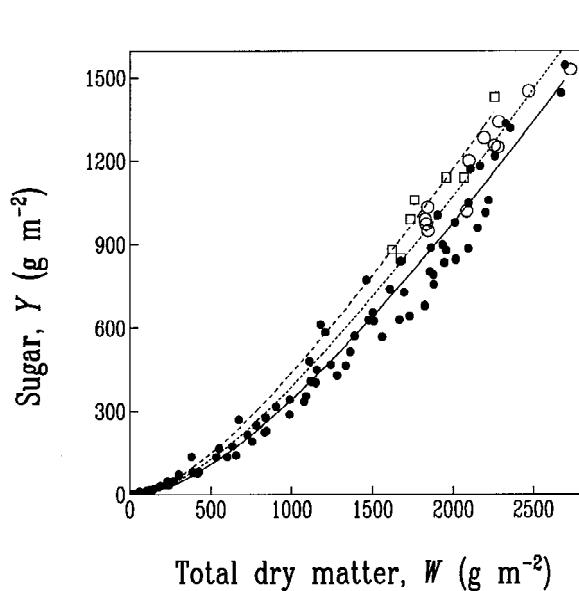


Figure 1. Observed and fitted relationships ( $Y = W - \frac{1}{k} \log(1+kW)$ ) between sugar yields ( $Y$ ) and total dry matter ( $W$ ) of sugar beet crops from irrigation experiments conducted at IACR-Broom's Barn, UK during 1980 to 1991: (closed circles and solid line = intermediate samples from irrigated crops,  $k = 1.20 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$ ; open circles and dotted line = final harvests from irrigated crops,  $k = 1.50 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$ ; open squares and dashed line = final harvests from droughted crops,  $k = 1.89 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$ ).

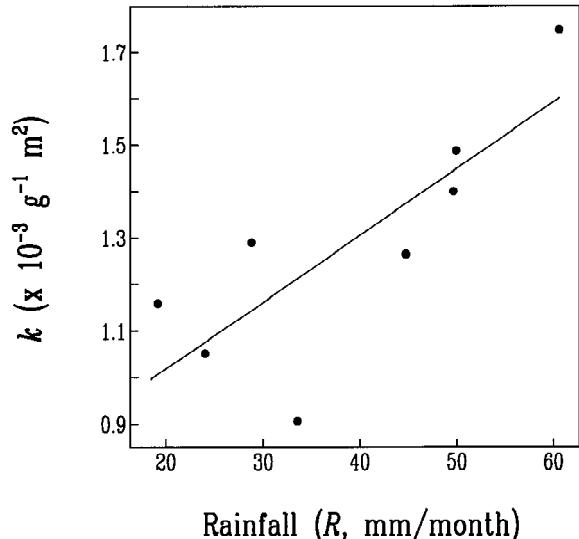


Figure 2. Correlation between the value of  $k$  for irrigated sugar beet and the mean monthly rainfall during May and June ( $R$ ): the fitted line is described by  $k = 0.73 + 0.014R$ .

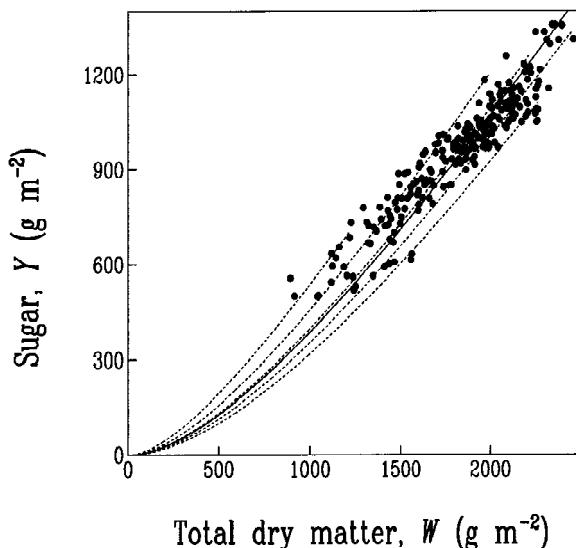


Figure 3. Observed and fitted relationships ( $Y = W - \frac{1}{k} \log(1+kW)$ ) between final sugar yields ( $Y$ ) and total dry matter ( $W$ ) of sugar beet crops in 34 nitrogen response trials in the UK during 1986-88: solid line represents the mean response and dashed lines represent different partitioning trajectories for crops that take up 60, 120, 180, 240 and 300  $\text{kg ha}^{-1}$  nitrogen ( $N_u$ ), where  $k = k_0/(1 + rk_0N_u)$ ,  $k_0 = 5.42 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$  and  $r = 2.53 \text{ g m}^{-2} (\text{kg ha}^{-1})^{-1}$ .

senescence, and whether intermediate estimates of  $Y$  for a specific crop, or whether only final estimates of  $Y$  for numerous crops are required.

The restrictions  $Y_0, W_0 = 0$  and  $\beta_0 = 1$  forced Eq. (7) to take a biologically realistic trajectory when no intermediate data were available. This was a useful property in the analyses of final sugar and total dry matter yields obtained from nitrogen response trials. Here, the mean estimated value for  $k$  was  $1.48 \times 10^{-3} \text{ g}^{-1} \text{ m}^2$ , which accounted for 79% of the variation in  $Y$  (Table 3), which was close to the value obtained when fitting the model to only final yields from IACR-Broom's Barn (Table 2). Relating  $k$  to nitrogen uptake ( $N_u$ ), by linking Eqs 7 and 10, accounted for > 93% of the variation in  $Y$  (Table 3). Figure 3 shows partitioning trajectories for crops with nitrogen uptake values ranging between 60 and 300  $\text{kg ha}^{-1}$ .

Normally the nitrogen uptake of a crop is not known before harvest. Instead, relating  $k$  to the amount of applied nitrogen ( $N_a$ ) provided a small but significant improvement to the goodness of fits by comparison to those when no account of nitrogen application was taken (Table 3). Nonetheless, these fits were not as good as those with  $k$  dependant on  $N_u$ . Taking account of the amount of residual nitrogen in the soil at sowing (thus,  $N = N_0 + N_a$ ) or the amount of recommended

Table 3. Estimates of parameters, residual sums of squares (rss), degrees of freedom (df) and percentage variation accounted for (% VA) on fitting the partitioning function,  $Y=W-\frac{1}{K}\log(1+kW)$  (Eq. 7) to estimates of final yield of sugar ( $Y$ ) and total dry matter ( $W$ ) of sugar beet crops from 34 nitrogen response trials in the UK during 1986 to 1988 grown on sandy (SL), silty (ZL), clay (CL) and organic (O) soils. Figures in square brackets represent ranges of estimated values

definition of $N$ in	Variables for which separate $k_0$ were estimated		parameters estimated		rss <sup>a</sup> ( $\times 10^6$ )	% VA
			$k_0 \times 10^{-3}$ $\text{g}^{-1} \text{m}^2$	$r$ $\text{g m}^{-2} (\text{kg ha}^{-1})^{-1}$	(df)	
$k = \frac{1}{1/k_0+rN}$						
$N = 0$	—	—	1.48	—	1.698 (237)	79.0
$k = k_0$ , k is independent of N	years	86, 87, 88	1.58, 1.45, 1.42	—	1.619 (235)	79.8
	soil type	SL, ZL, CL, O	1.51, 1.50, 1.48, 1.27	—	1.625 (234)	79.6
	years $\times$ soils	11 levels	[1.20 – 1.75]	—	1.385 (227)	82.1
	sites	12 levels	[1.27 – 1.72]	—	1.342 (226)	82.6
$N = N_u$	—	—	5.42	2.53	0.5280 (236)	93.4
$k \propto$ total N uptake by crop	years	86, 87, 88	7.42, 5.14, 4.52	2.53	0.4117 (234)	94.8
	soil type	SL, ZL, CL, O	5.91, 8.10, 5.41, 7.43	2.65	0.4889 (233)	93.8
	years $\times$ soil	11 levels	[4.45 – 14.54]	2.58	0.3391 (226)	95.6
	sites	12 levels	[4.40 – 9.33]	2.59	0.4242 (225)	94.4
$N = N_a$	—	—	1.83	1.35	1.198 (236)	85.1
$k \propto$ applied fertilizer N	years	86, 87, 88	1.98, 1.78, 1.74	1.34	1.120 (234)	86.0
	soil type	SL, ZL, CL, O	1.90, 1.86, 1.81, 1.50	1.37	1.104 (233)	86.1
	years $\times$ soils	11 levels	1.40 – 2.33	1.40	0.8415 (226)	89.0
	sites	12 levels	1.5059 – 2.236	1.40	0.7982 (225)	89.6
$N = N_0 + N_a$	—	—	2.01	1.18	1.238 (236)	84.6
$k \propto$ residual N in spring + applied fertilizer N	years	86, 87, 88	2.56, 2.15, 1.91	1.41	1.003 (234)	87.4
	soil type	SL, ZL, CL, O	2.01, 1.00, 1.98, 1.78	1.13	1.222 (233)	84.6
	years $\times$ soils	11 levels	[1.70 – 2.83]	1.35	0.8373 (226)	89.1
	sites	12 levels	[1.68 – 2.29]	1.06	0.9932 (225)	87.1
$N = N_a - N_q$	—	—	1.46	1.21	1.250 (236)	84.5
$k \propto$ deficit or surplus fertilizer	years	86, 87, 88	1.55, 1.45, 1.40	1.19	1.184 (234)	85.2
	soil type	SL, ZL, CL, O	1.49, 1.47, 1.47, 1.24	1.23	1.158 (233)	85.4
$N$ applied in relation to recommended N	years $\times$ soils	11 levels	[1.14 – 1.77]	1.34	0.8439 (226)	89.0
	sites	12 levels	[1.24 – 1.71]	1.27	0.8601 (225)	88.8

(a) Total ss =  $2.245 \times 10^8$  (238)

nitrogen fertilizer ( $N = N_a - N_q$ ), did not provide any further improvements (Table 3).

Allowing  $k$  to vary amongst soil types only marginally improved the fits (Table 3) whether nitrogen was included in the model or not. Estimated values for  $k$  marginally decreased with heavier soils, and were appreciably lower with organic soils (Table 3). However, allowing  $k$  to vary amongst soil types and seasons significantly improved the fits, an indication of an interaction between soil types and years. Figure 4 shows the mean response in partitioning when the recommended amount of fertilizer was applied,

and the extent to which partitioning varied amongst years and soil types. It shows that there was appreciable variation which could be attributed to either years or soils. The same amount of variation could also be explained when  $k$  was allowed to vary amongst locations of experiments (Table 3). Allowing  $r$ , or both  $r$  and  $k$  to vary amongst different soil types did not provide better fits. In the latter case estimates for  $r$  varied substantially and had large standard errors. Generally, more consistent results were obtained when  $r$  was kept constant.

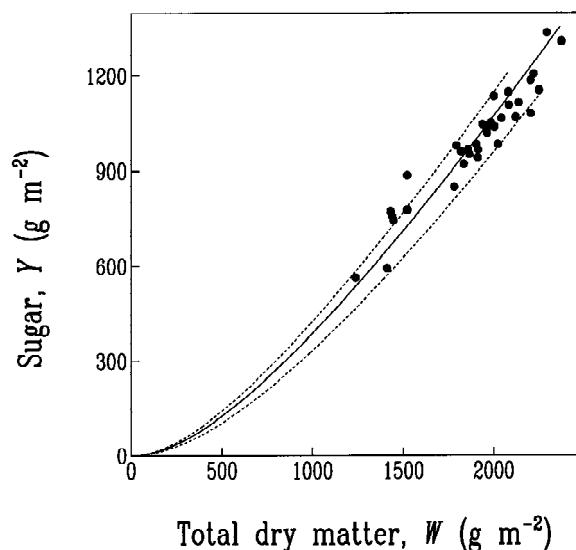


Figure 4. Observed and fitted relationships ( $Y = W - \frac{1}{k} \log(1+kW)$ ) between final sugar yields ( $Y$ ) and total dry matter ( $W$ ) of sugar beet crops receiving the recommended amount of nitrogen fertilizer in 34 nitrogen response trials in the UK during 1986–88: solid line represents the mean partitioning trajectory; dashed lines represent maximum and minimum partitioning trajectories amongst soil types and years.

## Discussion

Two simple empirical functions were derived to describe the partitioning of total dry matter in sugar beet to structure and storage. These were fitted to extensive data obtained from irrigation experiments at IACR-Broom's Barn during 1980–91, and nitrogen response trials during 1986–88 covering a wide range of soil types. Both the allometric growth function and the alternative model (Eq. 7) satisfactorily described the progress of sugar yield against total dry matter. Equation 7 was preferred because the parameters could be restricted, which considerably simplified the analyses. By equating initial weights to zero ( $Y_0, W_0 = 0$ ) and assuming that at this point all matter is partitioned to structure ( $\beta_0 = 1$ ), Eq. (7) was reduced to just one parameter,  $k$ , defined as the relative rate of decay of the fraction of total dry matter partitioning to structure. The value of  $k$  increased in crops experiencing drought and was inversely proportional to nitrogen supply.

The underlying biology of Eq. (7) is reasonable, describing a progressive shift of assimilates from structure to storage. This is consistent with observations by Milford et al. (1988) who disputed the notion of a sudden transition at a specific point in development, put forward by Green et al. (1986). Milford

et al. (1988) suggested that variability in dry matter partitioning is related to factors that limit the size of the shoot, such as nitrogen. Nitrogen encourages the production of larger shoots (Milford et al., 1985) and prolongs the period of foliage dominated growth. However, in the analysis presented here,  $k$  pertains not only to shoot growth, but also to the structural matter in the storage root. This can be justified for sugar beet on the grounds that all structural matter requires nitrogen and all storage matter requires none. It is also supported by observations from Milford and Watson (1971) who noted that nitrogen also increased the proportion of assimilates used for growth of the structural component of the storage root. Thus, high nitrogen not only increases the shoot biomass, but also increases the non-sugar content of the root; together these equate to total structural matter.

Good quantitative relationships were obtained between structure, storage and the amount of nitrogen taken up by the crop ( $N_u$ ) (Figure 3). The suspicion here is that crop nitrogen content is closely correlated with structural mass and that the amount of nitrogen taken up merely reflects the size of the crop. In practice, nitrogen concentration was not constant, it increased with increasing structural dry mass, but above all, it was highly variable, ranging between 0.016 and 0.031 ( $\text{g g}^{-1}$ ). Relationships between structure, storage and an accessible measure of soil nitrogen content were not as good unless also the effects of seasons and soil types could be taken into account. Poor correlation between amounts of nitrogen applied and nitrogen taken up by the crop arises from variation in the amounts of nitrogen mineralized, lost through immobilization by soil micro flora, and leached (Allison et al., 1996). Thus the predictability of  $k$  may be improved by relating it to the weather, particularly rainfall in late spring and early summer (Figure 2). Rainfall following nitrogen application enhances leaching and denitrification (Poulson, 1994). However, in the relatively low rainfall regions of Eastern England there is usually too little movement of water down the soil profile to cause substantial nitrogen leaching (Poulson, 1994).

The allometric growth function in the form given by Eq. (4) was less flexible because all its parameters pertain to initial weights and the initial partitioning coefficient. However, it does overcome criticisms of inconsistent dimensions of the parameters when comparing values between crops, environments etc. (Thornley and Johnson, 1990). When these parameters vary amongst soils that differ in their fertility or

available water, which occurs much later during the growing season, it became difficult to argue the validity of the analyses on biological grounds. The new formulation may prove useful in crops where there are distinct growth phases, for example flowering. In this sense, sugar beet is a very simple case for modelling the partitioning process because, with the exception of the 'growing point date' (i.e. the 4g sugar growth stage), it is devoid of these growth phases. The 'growing point date', which occurs very early in the growing season when few data were available, could be ignored as no statistical benefit was noted in its inclusion.

In conclusion, the allometric growth function, given by Eq. 4, and the alternative model, given by Eqs (7) and (8), adequately described the seasonal progress of sugar yield as a function of total dry matter. The alternative model was preferred when it was necessary to account for differences in partitioning patterns in relation to available water and soil nitrogen dynamics. The fraction of assimilates partitioned to sugar progressively increased during the growing season, at a rate that was inversely proportional to the amount of nitrogen taken up by the crops. It also increased in crops experiencing significant drought. Similar, but more variable relationships were obtained between partitioning to sugar and fertilizer application, residual soil nitrogen and the amount of recommended nitrogen fertilizer. The models are a useful extension to simple yield forecasting models that account for effects of drought and soil fertility on total dry matter production, but that resort to a constant conversion coefficient to calculate sugar yields.

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## Appendix – derivation of Eq. (3)

From Eqs (1) and (2),

$$\frac{dY}{dt} \frac{1}{Y} = b \frac{dW}{dt} \frac{1}{W}, \quad \frac{dY}{dt} = \alpha \frac{dW}{dt}$$

it follows that

$$\alpha = b \frac{Y}{W}$$

Differentiating  $\alpha$  with respect to  $t$  gives

$$\frac{d\alpha}{dt} = b \frac{1}{W^2} \left( \frac{dY}{dt} W - \frac{dW}{dt} Y \right)$$

which can be re-arranged, such that

$$\frac{d\alpha}{dt} = b \frac{Y}{W} \left( \frac{dY}{dt} \frac{1}{Y} - \frac{dW}{dt} \frac{1}{W} \right)$$

and since  $\alpha = bY/W$ , therefore

$$\frac{d\alpha}{dt} = \alpha \left( \frac{dY}{dt} \frac{1}{Y} - \frac{dW}{dt} \frac{1}{W} \right)$$

Integrating Eq. (3) with respect to  $t$ , with initial conditions  $\alpha = \alpha_0$ ,  $Y = Y_0$  when  $W = W_0$ , gives

$$\alpha = \alpha_0 \frac{W_0}{Y_0} \frac{Y}{W}$$

and substituting  $\alpha$  in  $dY/dt = \alpha dW/dt$  (Eq. (2)) gives

$$\frac{dY}{dt} \frac{1}{Y} = \left( \alpha_0 \frac{W_0}{Y_0} \right) \frac{dW}{dt} \frac{1}{W}$$

This is the derivative of the allometric growth function with  $b = \alpha_0(W_0/Y_0)$  which integrates with respect to  $t$  to give eqn 4, given the initial conditions  $Y = Y_0$  when  $W = W_0$ ,

$$Y = Y_0 \left( \frac{W}{W_0} \right)^{\alpha_0 \frac{W_0}{Y_0}}$$

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