MODELLING TILLERING AND YIELD FORMATION IN SPRING-SOWN KARAMU WHEAT

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ABSTRACT

A weight- and age-dependent model for tillering in cereals is outlined. The model includes terms for tiller growth, tiller birth and tiller death and it can be used to predict tiller weight distributions. Application of the model is illustrated using data on tiller numbers and tiller dry weights from a crop of spring-sown Karamu wheat. We conclude by noting that the model provides a link between plant growth analysis and demographic analysis and that further research is needed into the processes of tiller formation and tiller death and into models for tiller growth.

Additional Key Words: population models, yield components, age-dependent models, size-dependent models.

INTRODUCTION

Although there is a very large literature on growth and yield in cereals, a coherent framework for analysing the process of yield formation is lacking. The old approaches of growth analysis and yield component analysis have failed to provide this framework, although they continue to find advocates (Fraser and Eaton, 1983; Joliffe and Courtney, 1984). Detailed biochemical, physiological and agronomic studies have provided essential insights into aspects of yield formation but cannot provide an overview. Simulation modelling has been used in an attempt to bring ideas together (e.g., Arkin *et al.*, 1976; Weir *et al.*, 1984) but lack of consistency between models demonstrates the inadequacy of this approach.

It is by no means clear, from past research, how an adequate framework for yield formation in cereals should be constructed. However, since yield formation involves population processes for apices, leaves, tillers, grains, etc., population models of one kind or another will be required. In a companion paper, Gandar and Bertaud (1984) considered some possible bases for population models for tillers. One of their conclusions was that tiller size was a promising basis for a tiller population model but no details were given on how such a model might be constructed.

In this paper, we report on an exploratory study of a weight- and age-dependent model for tillering based on data from a spring-sown Karamu wheat crop. The results discussed are preliminary and, in places, tentative. Our objective is simply to open the way for some ideas that deserve more attention from physiologists and agronomists.

SOURCE OF DATA

The data used in this paper were collected from the early-sown (12 October 1983) Karamu wheat crop in the trial described by Withers and Palenski (1984). This trial was situated on the Tiritea Research Area, Palmerston North and involved various nitrogen (N) treatments. Our data came from plots receiving 0, 25 and 100 kg N/ha at sowing. A summary of crop development is given in Table 1.

Tillering and dry weight data were collected from 120 plants selected at random from each of the 0, 25 and 100 kg N/ha plots. Dates of tiller 'birth' (appearance of prophyll or first leaf within subtending leaf), heading (ear above flag-leaf ligule) and 'death' (all leaves yellow or dead) were recorded for all tillers on these plants. Between the onset of tillering and ear emergence (Table 1), 12 marked plants were harvested each week. Dry weights and numbers of live and dead leaves were recorded for all tillers on these plants. At final harvest (Table 1), there remained 36 marked plants in each treatment; total and ear dry weights were recorded for all tillers on these plants, and grain weight:ear weight ratios were determined for samples of ears from each treatment.

TABLE 1: Crop development: Karamu wheat grown at the Tiritea Research Area, Palmerston North.

Date	Day	Event
12.10.83	0	Sowing
21.10.83	9	Beginning of emergence
4.11.83	23	Beginning of tillering
11.11.83	30	Beginning of stem elongation
16.12.83	65	Beginning of ear emergence
8. 2.84	119	Final harvest

Tiller age is used as a basis for analysis in this paper. Ages were determined by dividing tillers into three-day cohorts according to date of appearance or of first record. Thus, tillers appearing on (or recorded on) days 20, 21 and 22 were assigned to cohort I, those appearing on days 23,

24, 25 to cohort II, and so on. Tillers in a cohort were then given a common age measured from the first-day number for each cohort. Note that this procedure is arbitrary for cohort I tillers since these were predominantly main-stem tillers and plants may have appeared several days before day 20 (age 0 for this cohort).

THEORY

The model discussed in this paper is an example of a general, multidimensional population model. The theory underlying such models is discussed by Streifer (1974) and Oster (1977). We shall be concerned with a two-dimensional population model involving weight and age. Models of this sort do not appear to have been applied to plants previously. An application to fish populations is discussed by Thompson and Cauley (1979); our paper parallels theirs in many respects.

The key variable in our weight- and age-dependent model is the proportion of tillers whose weights lie within some range at a given age. This variable is illustrated in Fig. 1 for tillers from cohort I in the 100 kg N/ha treatment at age zero. The proportion of tillers with dry weights lying between any two limits can be found by calculating the area under the smooth curve. For example, the area under the curve between 0.04 and 0.06 (Fig. 1) is 0.33, which means that 33% of the zero-aged tillers in the particular cohort had weights in this range.

Since the area under the curve in Fig. 1 is a proportion, or fractional number, it is clear that the curve itself must have units of fractional number per unit weight, or number density. We shall use the notation $n(w,a)$ to stand for the tiller number density at weight, w, and age, a. For example, $n(0.04, 0)$ stands for the value of the smooth curve at weight 0.04 g in Fig. 1.

The weight- and age-dependent population model is formulated in terms of tiller number densities. The origin of this model can be explained by considering how the proportion of tillers in some weight range, say Δw, changes in time. If there is no birth or death of tillers, we can write that

$$\left\{\begin{array}{l}\text{the rate of change}\\ \text{with age of fractional}\\ \text{number of tillers in}\\ \text{range } w_1 \text{ to } w_2, \text{ i.e.}\\ \Delta w\end{array}\right\} = \left\{\begin{array}{l}\text{rate of inflow by}\\ \text{growth so tiller}\\ \text{weights exceed } w_1\end{array}\right\} - \left\{\begin{array}{l}\text{rate of outflow by}\\ \text{growth so tiller}\\ \text{weights exceed } w_2\end{array}\right\}$$

$$= \left\{\begin{array}{l}\text{net rate of flow of}\\ \text{tillers in } w \text{ direction}\\ \text{caused by growth}\end{array}\right\} \qquad (1)$$

Equation (1) can be written more compactly as

$$\frac{\partial n}{\partial a} = -\frac{\partial ng}{\partial w} \qquad (2)$$

(Thompson and Cauley, 1979). Here n is used as a shorthand for $n(w,a)$ and we introduce g as a growth rate function for tillers. We shall illustrate this function in the next section. The minus sign appears in (2) as part of a sign convention.

Equation (2) can be used to predict the way in which a tiller number density changes as a cohort ages. We shall illustrate this for tillers in cohort I of the 100 kg N/ha treatment in the next section. Equation (2) is not, however, a general model for tiller number density changes because there are no terms for tiller death or tiller birth.

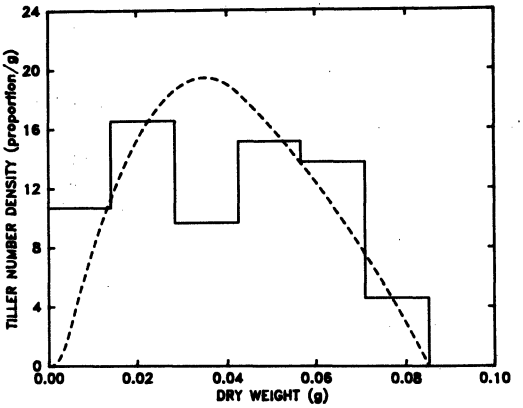

Figure 1: Observed (———) and fitted (— — —) tiller number densities for tillers of age zero in cohort I of the 100 kg N/ha treatment. Areas under curves give proportions of tillers with weights in given weight ranges. The densities are derivatives of the data and fitted curve in Fig. 2.

The death of tillers can be included in (2) by a simple extension of the argument in (1). Consider, once again, the weight range Δw. The fractional number of tillers in Δw at a given age can change due to growth, as before, but it will also change if tillers die and are removed from Δw. To account for death, we modify (2) to

$$\frac{\partial n}{\partial a} + \frac{\partial ng}{\partial w} = -d(w,a) \qquad (3)$$

where $d(w,a)$ is a weight- and age-dependent death function. We shall discuss the form this function may take in the next section.

Tiller birth cannot be accounted for simply by adding another term to (3), for, by definition, all members of a cohort are born at age zero. Thus, birth of a group of tillers is an initial condition required for the cohort model. The link between a cohort of tillers and older parent tillers then becomes interesting. Since new tillers arise from tillers in older cohorts, we can inquire into the rate at which tillers in a cohort give rise to new tillers, the 'maternity rate' for tillers. We shall provide data that indicate the form of this rate in the next section.

RESULTS AND DISCUSSION

Predicting tiller number densities

To use (2) to predict changes in tiller number densities with age, three pieces of information are required. The first is a simple 'boundary condition': we made the reasonable assumption that no tillers have zero weight. The second and third are an 'initial condition' for tiller number density, and a 'growth law' for tillers. We shall illustrate these for cohort I from the 100 kg N/ha treatment.

'Initial conditions' serve as starting points for models. We used the smooth curve in Fig. 1 to set starting values for the tiller number density in cohort I of the 100 kg N/ha treatment. This curve is the derivative of the curve smoothed through data in Fig. 2 for the cumulative proportion of tillers with weights less than, or equal to, a given value.

The observed density distribution in Fig. 1 is, likewise, the derivative of a curve obtained by joining the data points in Fig. 2.

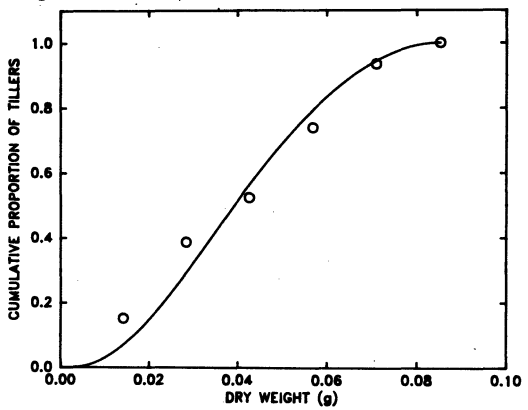

Figure 2: Observed (o) and fitted (— — —) cumulative distributions by weight for tillers of age zero in cohort I of the 100 kg N/ha treatment. The data show the cumulative proportion of tillers with weights less than or equal to 0.14, 0.28, 0.42 g ... in cohort I at day 20. The smooth curve was fitted using constrained cubic B splines.

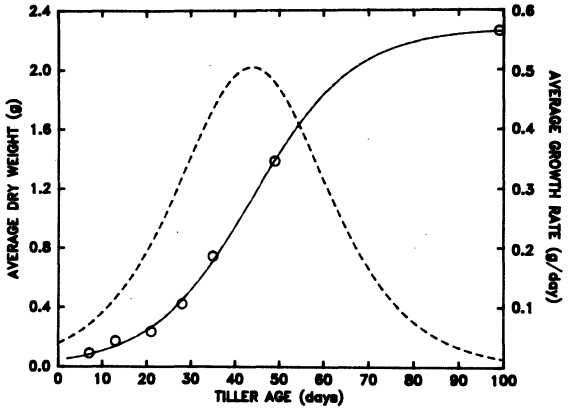

Figure 3: Dry weight accumulation and growth rate for tillers in cohort I, 100 kg N/ha treatment. Data (o) are average dry weights of cohort I tillers in weekly and final harvests. The equation $w = 2.275/[1 + 48.955 \exp(-0.089a)]$ was fitted using nonlinear least squares. The growth rate (— — —, and g in equation (2)) is the derivative of this equation.

The growth function used for cohort I (100 kg N/ha treatment) is illustrated in Fig. 3. We fitted a logistic equation to the average tiller dry weights obtained at each harvest using a nonlinear least-squares method. The derivative of this curve, the growth rate, links rate of change of size to tiller age, as required by equation (1).

Equation (2) applied to tiller cohorts in the absence of death. The mortality in cohort I of the 100 kg N/ha treatment was less than 4% which we assumed to be negligible. Equation (2) can therefore by 'solved' for this cohort using the fitted initial condition and growth-rate function shown in Figs. 1 and 3. By 'solving' (2) we mean obtaining predictions (using computer-based numerical methods) of tiller number densities for the cohort at ages greater than zero.

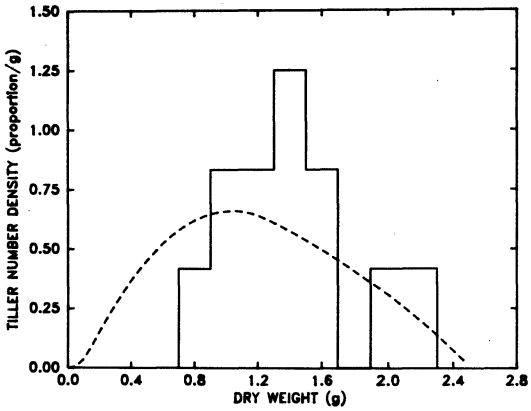

Figure 4: Observed (———) and predicted (— — —) tiller number densities for cohort I, 100 kg N/ha treatment, at age 48 (ear emergence). The observed density is based on weights of 12 tillers. The predicted density was obtained by solving equation (2).

Examples of these predictions, together with observed number densities, appear in Figs. 4 and 5. At ear emergence (age 48 days), the predicted number density overlaps the observed (Fig. 4), while at final harvest (day 99), the two densities coincide more closely. A measure of agreement between the two densities is provided by Table 2 where observed and predicted means and standard deviations are given. At both ages, predicted means are smaller than observed and standard deviations are reasonably close. We consider this agreement between predictions and observations is satisfactory, particulary in view of the fact that the observed densities are based on very small sample sizes (n = 12, Fig. 4; n = 34, Fig. 5). We have also applied equation (2), together with estimates of age-zero number densities and of growth rates, to cohort I in the 0 kg N/ha and 25 kg N/ha treatments. In these cases predictions were less satisfactory, partly because logistic equations fitted the growth data less well, and partly because tiller mortalities were higher.

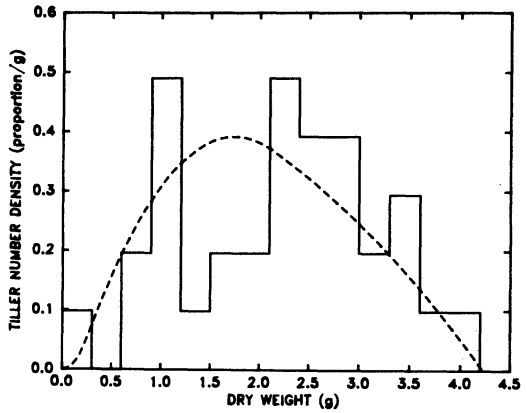

Figure 5: Observed (———) and predicted (— — —) tiller number densities for cohort I, 100 kg N/ha treatment, at age 99 (final harvest). The observed density is based on weights of 34 tillers.

TABLE 2: Observed and predicted means and standard deviations for tiller dry weights, cohort I, 100 kg N/ha treatment.

Age	Mean		S.D.	
	Observed	Predicted	Observed	Predicted
48	1.38	1.19	0.43	0.58
99	2.26	2.00	1.03	0.90

Tiller death

When tiller mortality is no longer negligible, equation (3) must be used in place of (2). Although tillers may die for a variety of environmental (including pests and diseases) and physiological reasons, the bulk of tiller death is associated with stem elongation and the early stages of grain filling (e.g. Thorne, 1962; Fraser and Dougherty, 1977). Tiller death is also strongly hierarchic, with the youngest tillers being most likely to die (e.g. Cannell, 1969; Gandar and Bertaud, 1984).

Tiller death will modify tiller number density patterns within cohorts. To predict this effect using (3), we require information on appropriate weight- and age-dependent death functions. Unfortunately, our method of data collection permitted estimation only of age-dependent death rates and not weight- and age-dependent rates. However, an indication of the form of a weight- and age-dependent death rate is provided in Fig. 6 where the dry weights of all tillers from plants harvested from the 100 kg N/ha treatment are plotted against tiller ages, with data classified on the basis of numbers of live leaves at time of harvest. It is apparent that most of the smaller tillers that were older than 20 days at harvest had three or fewer live leaves. This holds true irrespective of the cohort to which tillers belonged. For example, nearly all the small tillers in cohorts I-IV at day 68 had three or fewer live leaves (Fig. 6).

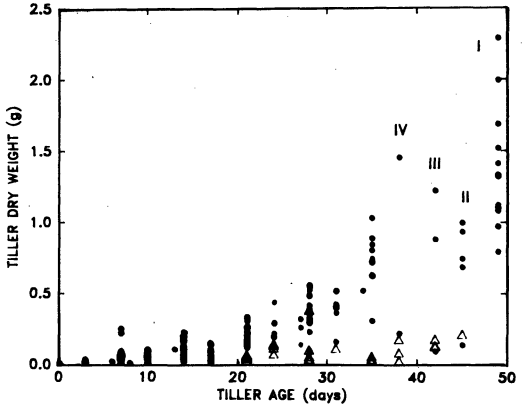

Figure 6: Tiller dry weights vs. tiller ages for all tillers from plants harvested up to day 68 in the 100 kg N/ha treatment. Symbols: △, tillers older than 20 days with three or fewer live leaves at harvest; ●, all other tillers. Roman numberals identify cohorts harvested on day 68 (and therefore, of different ages).

We infer that many, if not all, of these tillers were dying at the time of harvest, since our observations showed that similar tillers on plants remaining in the field eventually died. Thus, Fig. 6 suggests the existence of a 'death zone', perhaps bounded by dry weights of about 0.3 g at ages greater than 20 days, with the tillers that grow into this zone dying and those growing outside it surviving. More research will be required to establish the reality of this idea, for we can go no further with our data. However, it is interesting to note that work of Ong *et al.* (1978) and Masle-Meynard (1982) also points to a critical tiller size of about three leaves.

Tiller birth and maternity rates

The new (age zero) tillers that set the initial conditions for the model form on earlier-formed tillers. The rate at which older tillers give birth to new tillers, the maternity rate, has units of tillers per parent tiller per unit time. Gandar and Bertaud (1984) showed that the maternity rates of barley tiller cohorts varied with age, first rising to a peak and then declining with the onset of stem elongation. We might also expect maternity rates to depend on tiller weights.

Evidence for this effect is shown in Fig. 7, where the maternity rates of tillers in the uppermost and lowermost weight quartiles of cohort I, 100 kg N/ha treatment, are plotted. It is evident that the heavier, upper quartile tillers had substantially higher maternity rates throughout. Rates also vary with age in a manner similar to that observed in barley (Gandar and Bertaud, 1984). Thus, maternity rates appear to be both weight- and age-dependent. The question of why this should be so remains open, but our result is in accord with other work showing that size (of plants, tillers or ears) is an important determinant of productivity in cereals (e.g. Dyson, 1977; Soetono and Donald, 1980).

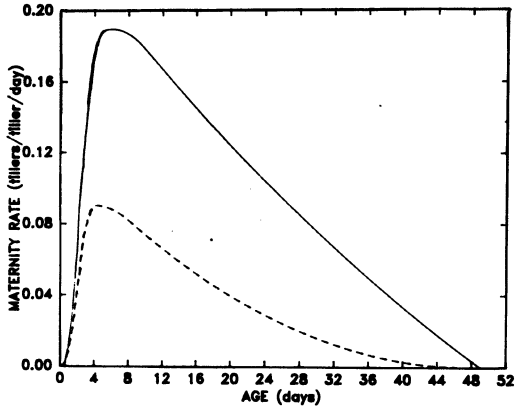

Figure 7: Maternity rates for tillers in the uppermost (———) and lowermost (— — —) quartiles by weight within cohort I, 100 kg N/ha treatment. The rates shown are derivatives of curves fitted to data for cumulative numbers of tillers formed on tillers within each quartile.

Predicting yield

These are various ways in which the weight- and age-dependent tillering model could be linked to crop yield. One approach is illustrated in Fig. 8. Using the linear relationship between ear weight and total tiller weight from this figure and a grain:ear ratio of 0.59 (estimated from a sub-sample of ears), we can convert the predicted mean weight for cohort I tillers at final harvest (Table 2) into a predicted grain yield of 0.67 g per ear. This method for relating tiller weights to grain yield is appealing in its simplicity and deserves further investigation.

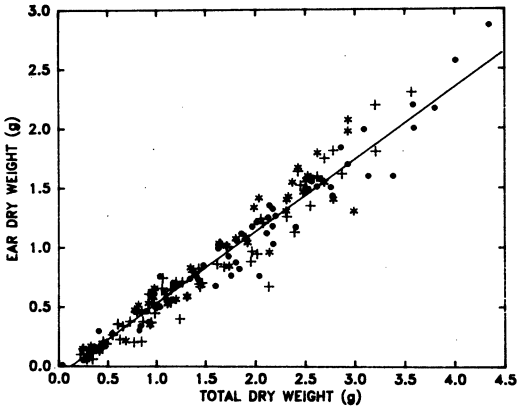

Figure 8: Relationship between ear and total dry weights for all tillers at final harvest. Symbols: *, 0 kg N/ha; +, 50 kg N/ha; ●, 100 kg N/ha. Regression: $y = -0.07 + 0.61x$, $r^2 = 0.90$.

CONCLUDING REMARKS

The main advantage of the model outlined in this paper is that it links the disparate approaches of plant growth analysis and demographic analysis. There has been some search for this link (Hunt, 1978; McGraw and Wulff, 1983). Models in the form of (3), or of elaborations thereon, which include terms for both growth rates and demographic rates, provide the connection. To our knowledge, such models have not been applied to plants previously.

Our results suggest several avenues for future research into weight- and age-dependent models for tillering. The need for a closer examination of tiller death has already been mentioned. Research into tiller birth could focus on relationships between maternity rates in older cohorts and the initiation of a new cohort so that successive cohorts can be linked together. The greatest challenge though, lies in formulating models of tiller growth for use in the population model. The logistic equation we have used is an empiricism with no virtues beyond simplicity. In its place we require a growth model which has a sound physiological basis and which is 'driven' by environmental factors.

REFERENCES

Arkin, G.F., Vanderlip, R.L., Ritchie, J.T. 1976. A dynamic grain sorghum growth model. *Transactions of the American Society of Agricultural Engineers 19:* 622-626, 630.

Cannell, R.Q. 1969. The tillering pattern in barley varieties. I. Production, survival and contribution to yield by component tillers. *Journal of Agricultural Science, Cambridge 72:* 405-422.

Dyson, P.W. 1977. An investigation into the relations between some growth parameters and yield of barley. *Annals of Applied Biology 87:* 471-483.

Fraser, J., Dougherty, C.T. 1977. Effects of sowing rate and nitrogen fertilizer on tillering of Karamu and Kopara wheats. *Proceedings Agronomy Society of N.Z. 7:* 81-87.

Fraser, J., Eaton, G.W. 1983. Applications of yield component analysis to crop research. *Field Crop Abstracts 36:* 787-797.

Gandar, P.W., Bertaud, D.S. 1984. Modelling tillering and yield formation in spring-sown Mata barley. *Proceedings Agronomy Society of N.Z. 14:*

Hunt, R. 1978. Demography versus growth analysis. *New Phytologist 80:* 269-282.

Joliffe, P.A., Courtney, W.H. 1984. Plant growth analysis: additive and multiplicative components of growth. *Annals of Botany 54:* 243-254.

McGraw, J.B., Wulff, R.D. 1983. The study of plant growth: a link between physiological ecology and population biology in plants. *Journal of Theoretical Biology 103:* 21-28.

Masle-Meynard, J. 1982. Elaboration du nombre d'epis d'un peuplement de ble d'hiver en situation de competition pour l'azote. II. Modelisation du nombre d'epis. *Agronomie, 2:* 17-24.

Ong, C.K., Marshall, C., Sagar, G.R. 1978. The physiology of tiller death in grasses. 2. Causes of tiller death in a grass sward. *Journal British Grassland Society, 33:* 205-211.

Oster, G. 1977. Lectures in population dynamics. *Lectures in Applied Mathematics 16:* 149-190.

Soetono, Donald, C.M. 1980. Emergence, growth and dominance in drilled and square-planted barley crops. *Australian Journal of Agricultural Research 31:* 455-470.

Streifer, W. 1974. Realistic models in population ecology. *Advances in Ecological Research 8:* 199-266.

Thompson, R.W., Cauley, D.A. 1979. A population balance model for fish population dynamics. *Journal of Theoretical Biology 81:* 289-307.

Thorne, G.N. 1962. Survival of tillers and distribution of dry matter between ear and shoot of barley varieties. *Annals of Botany 26:* 37-54.

Weir, A.H., Bragg, P.L., Porter, J.R., Rayner, J.H. 1984. A winter wheat crop simulation model without water or nutrient limitations. *Journal of Agricultural Science, Cambridge 102:* 371-382.

Withers, N.J., Palenski, F. 1984. An evaluation of the nitrate sap test for cereals. *Proceedings Agronomy Society of N.Z. 14.*