MODELLING TILLERING AND YIELD FORMATION
IN SPRING-SOWN MATA BARLEY

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ABSTRACT

Yield formation in crops such as barley is often described in terms of the yield components plants per unit area, ears per plant, grains per ear and average grain weight. Because this method of analysis has little predictive value, alternative approaches are required. To illustrate ideas, we discuss the construction of population models for tillers, using data on tillering and tiller yields for a crop of spring-sown Mata barley, grown at four levels of applied nitrogen. Population models can be based upon tiller generations, types, ages or sizes. Some difficulties that arise in applying standard population models to tillering are outlined. We conclude that population models involving tiller sizes may enable useful linkages to be made between tiller numbers and crop yield.

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

INTRODUCTION

Yield in crops is often described using yield components. For barley, these components are average numbers of plants per unit area, ears per plant, grains per ear, and average grain weight. Grain yield per unit area, Y, is then expressed as

$$\overline{Y} = \frac{\overline{plants}}{area} \times \frac{\overline{ears}}{plant} \times \frac{\overline{grains}}{ear} \times \overline{grain\ weight} \qquad (1)$$

with the overbars used to emphasise that quantities are averages.

A very large number of agronomic and physiological studies have been based on (1). Studies on cereals have led to a general understanding of the process of yield formation. For barley, it is usually assumed that the components of yield are determined in a temporal order that corresponds to the order of terms on the right-hand side of (1). The number of plants per unit area is set shortly after emergence, there being little plant mortality in most crops. Tillering, and tiller survival determine ear numbers. Peak tiller numbers are reached before ear emergence and ear numbers are set shortly after anthesis. Grain numbers are also set by this time. These first three yield components determine potential yield. Grain filling after anthesis determines grain weights and actual yields.

To carry the analysis of yield formation beyond this qualitative description, predictive models are required. A number of predictive models have been produced for cereals. These range from the simple through to elaborate simulation models. In simple models, such as that of Gallagher *et al.* (1983), only grain yield is predicted. In the more elaborate models, ear and grain numbers are also predicted. For example, in the ARCWHEAT model (Weir *et al.*, 1984) currently under investigation at Lincoln (D.R. Wilson, pers. comm.), tiller number, ear number, grain number and grain weight are all predicted in sub-models.

To predict tiller, ear, or grain numbers some sort of population model is required. For example, in ARCWHEAT the sub-model for tillers involves tiller birth and tiller death. Tillers are born on a weekly basis using a tiller production rate that depends on temperature. Tiller death occurs after the double-ridge stage with the latest-formed tillers being the most likely to die. Tillers surviving at the time of main-stem anthesis are considered to produce ears (Porter, 1984).

This model for tillering is an example of an age-dependent population model, since tillers are grouped into even-aged, weekly cohorts and tiller behaviour varies from cohort to cohort. However, grouping into even-aged cohorts is not the only way in which a tiller population model could be constructed. There is, for example, ample evidence to show that different types of tillers (main-stem, first-leaf, etc.) behave differently (Thorne, 1962; Cannell, 1969; Fraser and Dougherty, 1978), so that tiller type could form a basis for a population model. There is also evidence that tiller size influences tiller survival and yield (e.g. Jones and Kirby, 1977; Kemp and Whingwiri, 1980) so that size could be another basis for a population model.

This raises the question: if different types of population models can be constructed for tillers (and, by implication, for other yield components), which is most appropriate? In this paper, we report an investigation into this question based on data for tillering in spring-sown Mata barley.

SOURCE OF DATA

This investigation was carried out as part of the long-term nitrogen balance experiment described by Gandar and Gregg (1979) and Mohammed (1983). The experiment involved an oats-barley rotation on Tokomaru silt loam (Fragiaqualf) at the DSIR Tiritea Research Area near Palmerston North. This paper is based on data from the barley crop (cv. Mata) grown during the 1978/79 summer.

TABLE 1: Crop development: Mata barley grown at the Tiritea Research Area, Palmerston North.

Date	Day	Event
2.10.78	0	sowing
16.10.78	14	emergence
26.10.78	24	onset of tillering
15.11.78	44	stem elongation
6.12.78	65	ear emergence, anthesis
30. 1.79	120	harvest

A summary of the development of this crop is given in Table 1. Urea was applied at sowing at rates of 0, 50, 100 and 200 kg N/ha on four large (100 m x 30 m) blocks. Fifty plants were selected at random within each block and examined every two or three days. Dates of tiller 'birth' (appearance of prophyll or first leaf within the subtending leaf), heading (ear above flag-leaf ligule) and 'death' (all leaves yellow or dead) were recorded for all tillers on these plants. At harvest, culm lengths, floret numbers, grain numbers and total grain weights were recorded for surviving tillers and grain yields were measured from five 0.2 m² quadrat cuts in each block.

TABLE 2: Grain yields and yield components. Yields were determined from hand-harvested, 0.2 m² quadrats. Yield components are means for the 50 marked plants in each treatment.

Quantity	Nitrogen application rate (kg N/ha)			
	0	50	100	200
Yield (kg/ha)	3700	4810	5540	4600
S.E. (n = 5)	190	410	350	420
Plants/m²	335	339	335	322
S.E. (n = 20)	19	11	16	13
Yield/plant (g)	1.14	1.38	1.49	1.33
S.E. (n = 50)	0.10	0.20	0.14	0.17
Grains/plant	29.2	37.3	39.6	40.0
S.E. (n = 50)	2.4	4.7	3.2	4.1
Weight/grain (g)	0.037	0.035	0.036	0.030
S.E.	0.0007	0.0009	0.0010	0.0010
n	106	105	129	117
Ears/plant	2.2	2.4	2.7	2.6
S.E. (n = 50)	0.1	0.2	0.2	0.2
Grains/ear	13.8	17.7	15.0	17.0
S.E.	0.6	0.7	0.6	0.7
n	106	105	129	117

RESULTS AND DISCUSSION

Yields and yield components

Yields and yield components for each treatment appear in Table 2. Quadrat yields increased from 0 to 100 kg N/ha but this trend was not maintained at 200 kg N/ha. To explain the trend we can divide mean yield into the components plants per unit area and yield per plant (cf.

(1)). Since there were no significant differences across treatments in average numbers of plants per unit area at day 24 (Table 2), or in subsequent plant mortalities, differences in yield per unit area must be attributed to differences in yield per plant. This component also increased with rate of applied nitrogen up to 100 kg N/ha and then fell at 200 kg N/ha (Table 2).

To explain this pattern, we can divide yield per plant into two further components, grains per plant and average grain weight. Average grain weight (strictly, an average of the average grain weights for individual ears) was constant in the 0, 50 and 100 kg N/ha treatments and fell in the 200 kg N/ha treatment (Table 2). Thus, in the first three treatments at least, increasing plant yield is associated with increasing numbers of grains per plant (Table 2).

This trend can be examined by dividing grains per plant into ears per plant and grains per ear, as in (1). Although both these components tend to increase with increasing N level (Table 2), in neither case is the trend clear-cut. For example, ear numbers per plant are the same in the 0 and 50 kg N/ha treatments so that any yield advantage in the latter treatment arises from grain numbers per ear. However, the yield increase between the 50 and 100 kg N/ha treatments involves both a slight increase in ear numbers per plant and a decrease in grain number per ear.
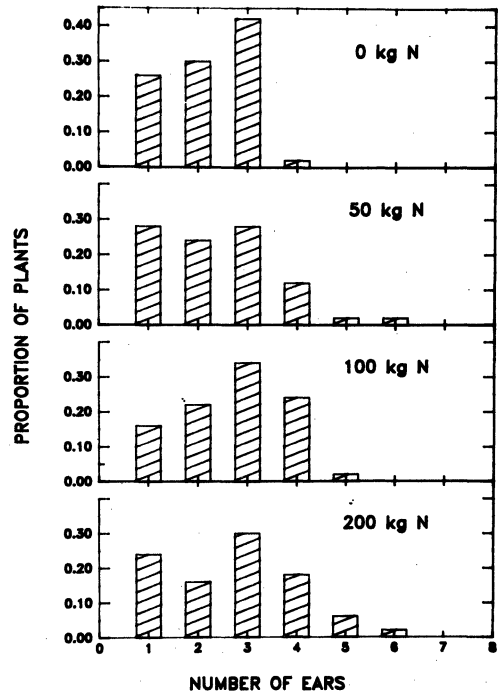

Figure 1: Number density distributions for the four nitrogen treatments, showing proportions of plants with 1, 2, 3, ... ears.

The yield components in Table 2 provide no more than an after-the-event description of yield under the four treatments. We may speculate about the ways in which nitrogen might have caused trends and interactions, such as that between ears per plant and grains per ear, but there is no way to incorporate any N-dependent growth or development processes into the yield-component analysis.

To overcome this limitation, we need predictive models for yield components. These must be capable of explaining differences or similarities between yield components in different treatments. This is rather more of a challenge than may be appreciated. For example, consider Fig. 1 where the proportions of plants bearing one or more ears at harvest are shown for each of the four N treatments in our trial. It is clear that N tends to increase variability in ear numbers. It is also clear that the distributions of yield components may differ when mean values are the same (for example, the 100 and 200 kg N/ha treatments appear to have dissimilar distributions of ear numbers per plant but similar mean values for this quantity). Thus, population models should take account of variability as well as mean behaviour.

Population models could be constructed for plant, tiller or grain numbers in a barley crop. In all cases, the same principles are involved. We shall centre our discussion on models for tillering in the remainder of this paper.
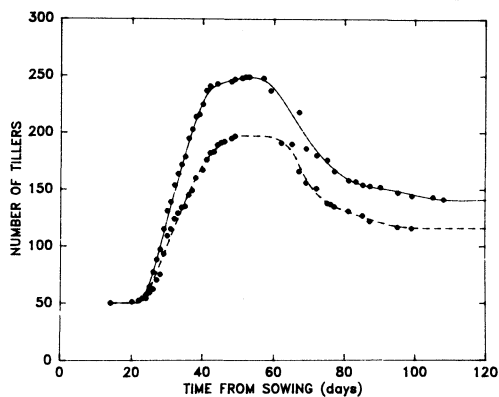

Figure 2: **Total numbers of live tillers on 50 plants plotted against time for the 0 kg N/ha (— — —) and 100 kg N/ha (————) treatments. Lines were fitted to the data using constrained cubic B splines. All plants were assumed to appear at day 14.**

Population models

There are several ways in which population models might be constructed for tillers. The most direct approach is simply to model changes in the total number of tillers as the crop develops. These changes are illustrated in Fig. 2 for the 0 kg N/ha and 100 kg N/ha treatments. The pattern of increase to a maximum tiller number around anthesis (Table 1) followed by a decline to a final ear number is similar in both treatments (and to patterns in the 50 kg N/ha and 200 kg N/ha treatments, which are not shown) and is typical of barley and other cereal crops (e.g. Thorne, 1962; Cannell, 1969; Fraser and Dougherty, 1977).

Modelling these population changes requires an equation that expresses rate of change in tiller numbers in terms of rates of tiller birth and tiller death. These rates are illustrated in Fig. 3 for the 100 kg N/ha treatment. Peak birth and death rates are separated by about 30 days and there is some overlap between birth of late tillers and the onset of tiller death.

The birth and death rates illustrated in Fig. 3 are keys to population modelling, for we can write

$$\left\{ \begin{array}{c} \text{rate of change} \\ \text{of tiller number} \end{array} \right\} = \left\{ \begin{array}{c} \text{rate of birth} \\ \text{of tillers} \end{array} \right\} - \left\{ \begin{array}{c} \text{rate of death} \\ \text{of tillers} \end{array} \right\} (2)$$

Tiller birth and death rates are clearly functions of environmental factors and of plant factors. Modelling tiller dynamics amounts to finding relationships between these factors and tiller birth and tiller death that are suitable for use in (2).
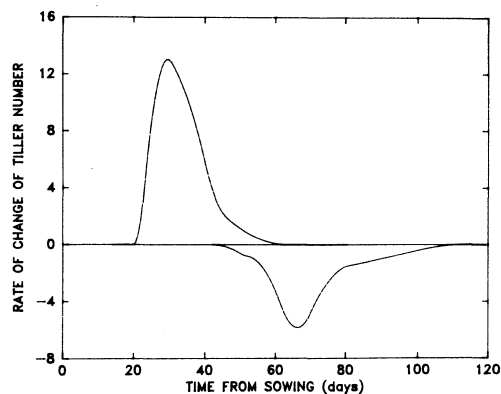

Figure 3: **Birth and death rates for tillers in the 100 kg N/ha treatment. These are the derivatives of constrained cubic B splines fitted to data for tiller appearance and number of dead tillers.**

The number of factors that affect tiller birth and death is large. It is clear from Fig. 2 that N is one environmental factor and we should also expect temperature, radiation, photoperiod and water stress to have effects (Gallagher *et al.*, 1983). Tiller birth and tiller death are also affected by plant factors such as the ages, types and sizes of tillers and it is on these factors that we shall focus in the remainder of this paper. We do this in the belief that tiller birth and death functions must have an adequate biological basis: incorporation of the effects of environmental factors can follow once this basis is established.

Models for tillers

The pattern of tillering recorded for a barley plant in the 100 kg N/ha treatment is shown in Fig. 4. There is a 'branching process' of tillers with the main stem giving rise to primary tillers, and primary tillers giving rise to secondary tillers. Obviously, different plants will have different tillering patterns; in fact, there appear to be no exact matches amongst the 200 branching patterns recorded in our experiment (we have not made an exhaustive comparison!).
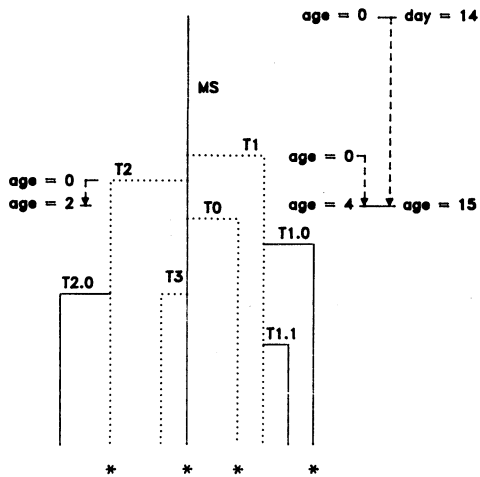
Figure 4: A representation of tillering in one of the barley plants in the 100 kg N/ha treatment. Dotted lines denote second generation tillers. MS denotes the main stem, T0 the tiller in the axil of the coleoptile, T1 the tiller in the axil of the first leaf, T1.0 the tiller in the axil of the prophyll on tiller 1, etc. * denotes a tiller which produced an ear. Time is measured in days from appearance of the main stem (i.e. 14 days after sowing).

This variety of branching patterns raises a question about the sort of mathematics that should be employed in population models. There are two choices: stochastic models, in which probabilistic birth and death 'laws' are used to estimate means and variances of populations, and deterministic models, in which the birth and death laws are fixed and the focus is usually upon mean numbers. For tillering, stochastic models could accommodate the variety of branching patterns in different plants while deterministic models would deal with the behaviour of an average plant.

Bases for stochastic and deterministic models are illustrated in Fig. 4. Tillers on plants may be classified by generations with main stems forming the zeroth generation, T0, T1, T2 etc. forming the first generation, and T1.0, T1.1, T2.0 etc. forming the second generation (Fig. 4). Another basis for models is classification of tillers by types, MS, T0, T1, ..., T1.0 ..., and a third is classification by ages measured from dates of appearance (Fig. 4). In each of these cases, the mathematics of appropriate stochastic and deterministic models have been studied extensively (Jagers, 1975; Pielou, 1977), so that we may ask how useful these models might be for tillering.

This question can be answered from several viewpoints. Models based on tiller generation or tiller type have appeal because they reflect the fundamental development process of barley plants. There is also ample evidence to show that different tiller generations and types contribute differently to plant yields (Table 3; Thorne, 1962; Cannell, 1969; Fraser and Dougherty, 1978), so that a population model based on these variables might link nicely

TABLE 3: Contributions of tillers classified by generation, type or age to grain yield. Zeroth generation tillers are main-stem tillers and also the tillers that appeared between days 14 and 18 (the 14-18 age cohort).

Grain yield (g/tiller)	Generation		
	0th	1st	2nd
mean	0.69	0.54	0.40
S.E.	0.05	0.03	0.07
n	37	78	13

	Tiller type					
	MS	T0	T1	T2	T3	T1.0
mean	0.69	0.57	0.61	0.53	0.33	0.42
S.E.	0.05	0.26	0.05	0.06	0.06	0.08
n	37	3	36	28	10	11

	Age cohort					
	14-18	19-28	29-33	34-38	39-43	44-48
mean	0.69	0.64	0.45	0.41	0.40	0.56
S.E.	0.05	0.05	0.05	0.06	0.09	0.11
n	37	39	32	14	4	2

to a yield model. On the other hand, collection of data on tiller generations or types requires much effort and this is a major drawback.

It is somewhat simpler to collect data on tillers when they are grouped by age into cohorts and there is also a good relationship between the ages of tillers and their grain yields (Table 3). The demographic changes that an age-based model would have to mimic are illustrated in Figs. 5, 6, and 7. Early-formed tillers dominate the tiller population at final harvest (Fig. 5) because there is a progressive increase in the mortality of successive tiller cohorts (Fig. 6). Early-formed tillers also dominate in the production of further tillers because there are marked decreases in the 'maternity' rates (tillers/parent tiller/day) of successive cohorts (Fig. 7).
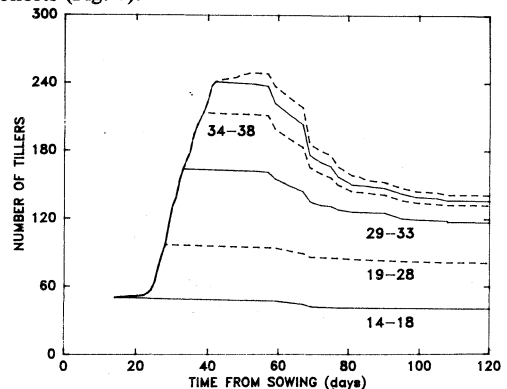

Figure 5: Contributions of various cohorts to total tiller number in the 100 kg N/ha treatment. Cohorts were formed by grouping all tillers that appeared within the specified ranges of days.
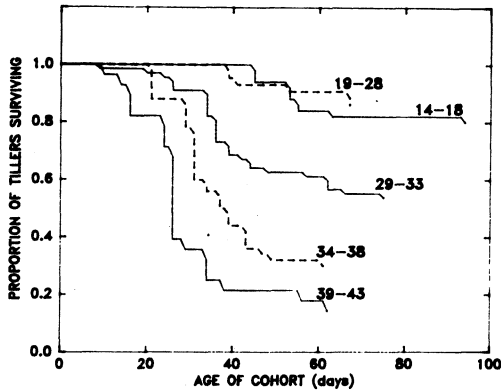
Figure 6: **Survival patterns for tillers in the cohorts shown in Fig. 5. Ages of cohorts are measured from the beginning day of the appearance-day range for each cohort.**

The survival patterns of Fig. 6 and the maternity rates of Fig. 7 are closely related to the tiller death and birth rates that would be required in an age-based model. However, the fact of most significance about Fig's 6 and 7 is that survival patterns and maternity rates change with cohort and hence, that birth and death laws must change with time. This creates severe mathematical difficulties; in fact, most literature on age-based population models deals only with time-invariant birth and death laws and is, therefore, of little use when it comes to tillering.
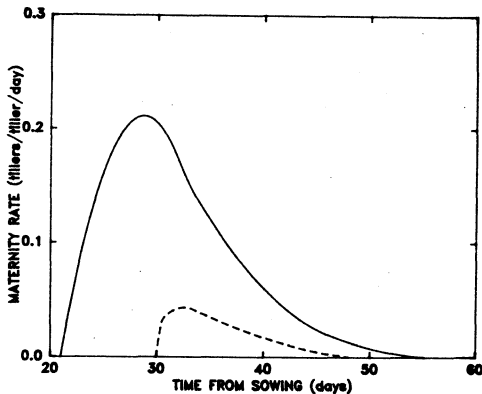

Figure 7: **'Maternity' rates for the 14-18 (———) and 19-28 (— — —) cohorts in Fig. 5. The curves are the derivatives of constrained cubic B splines fitted to data for the cumulative numbers of offspring tillers produced by tillers in each cohort.**

The same is true, although to a lesser extent, of the literature on generation- and type-based models. Tiller birth and death laws change with generation or tiller type.

There are ways to construct stochastic and deterministic models that accommodate these changes (Jagers, 1975; Pielou, 1977) but it is a moot point whether the effort involved would make this worthwhile.

A question of size

Another potential basis for population models is tiller size. An indication of the importance of this quantity is given in Fig. 8, where grain yields from tillers in the 100 kg N/ha treatment are plotted against culm lengths. Overall, some 54% of the variation in tiller yield is associated with variation in culm length and the proportion improves to about 60% when tillers are separated into cohorts, with individual regressions for each cohort (Fig. 8). Similar relationships between tiller yields and tiller weights at anthesis, or at final harvest, can be found in the literature (e.g. Dyson, 1977; Soetono and Donald, 1980). This suggests the possibility of a fruitful link between a population model for predicting numbers of tillers in different size classes and a simple yield-size relationship for predicting yield. Unfortunately, the limitations of our data set prevent us from carrying this idea any further.
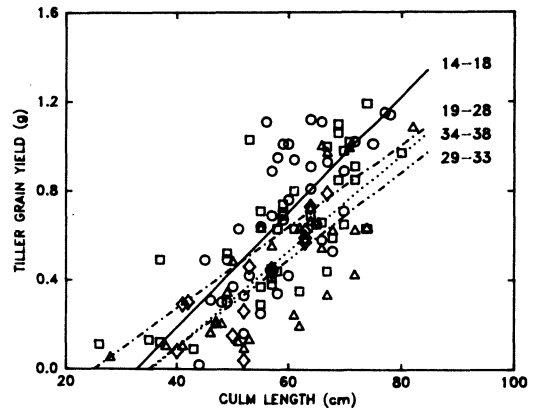

Figure 8: **Tiller yields vs. culm lengths at final harvest for the first four cohorts in the 100 kg N/ha treatment. Symbols: , 14-18 cohort; , 19-28 cohort; , 29-33 cohort, , 34-38 cohort.**

CONCLUDING REMARKS

Our examination of population models for tillering and of the relationship between these models and yield has been little more than a reconnaissance. We cannot give any firm conclusion about a 'best' model. However, we would emphasise three points:

(i) that conventional yield-component analysis is no more than description, and partial description at that, and cannot lead to useful predictive models;

(ii) that difficulties, mathematical and biological, stand in the way of applying many of the standard population models to processes such as tillering; and

(iii) that population models involving tiller size may enable linkage between tiller numbers and crop yield.

This final point is considered in more detail by Gandar et al., (1984).

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