

TOWARDS A DESCRIPTIVE FRAMEWORK FOR THE GROWTH OF ONIONS

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ABSTRACT

The growth of an onion crop can be described in various ways: the average yield, the distribution of different sized bulbs, growth and physiology of cells and organs. The purpose of this paper is to link together these areas. We begin by considering the variability in bulb size that is a feature of the crop. The crop is considered as a population of growing bulbs and for each of the bulbs the change in size can result from changes in leaf number and in leaf size. Thus for each bulb there is a population process and a growth process. These concepts are illustrated with data from a spring sown onion crop grown at Lincoln.

The mean bulb weight at final harvest was 89 g, the standard error was 8.6 g and the distribution skewed. For each bulb leaf appearance and leaf death occurred throughout the season with a flush of new leaves appearing before bulb expansion. No leaves were present throughout the whole season and the final bulb was composed of the ten or so scales which appeared after bulbing.

Harvested bulbs had similar numbers and ages of scales, but varied greatly in the weights of those scales. Variation in leaf numbers between plants arose mainly after bulbing. Within a plant each leaf was unique in its maximum weight and relative proportions of leaf blade and scale which meant that there were thirty fold and sixty fold differences in maximum weight of scales and blades respectively. There was great variability (tenfold) between plants in leaf and scale weights.

We discuss the kinds of models (deterministic and stochastic) which could best describe onion growth and the implications of management during growth on the quality of the plant.

Additional Key Words: Bulb size distributions, variability, population model.

INTRODUCTION

Onion bulbs vary in both shape and size: bulbs can be spherical, elongated or flattened in shape and can range in diameter from 25 to 120 mm at harvest, a six-fold range in size. This variability is of practical concern to growers because returns are affected by bulb size and bulb shape. One goal of research should therefore be to find ways to manipulate the genetic and environmental factors that contribute to this variability. To do this, it is clear that we will require some sort of descriptive framework for the growth of onions which takes account of plant-to-plant variability and of the within-plant factors affecting the size and shape of bulbs.

The growth of an onion crop can be described in various ways. In many studies, description focuses upon average yield (e.g. Brewster, 1982), but in others, information on size distributions is also given (Rogers, 1977; Brewster and Barnes, 1981). There are also detailed studies in which the growth of individual bulbs is examined (Lercari, 1984; Khan, 1981). Although these various approaches contribute to the understanding of onion growth, it is often difficult to link field studies to detailed growth studies and vice versa. Yet these links must be made if we hope to bring scientific insight to the practical concerns of growers. The purpose of this paper is to begin to develop a more comprehensive framework for the description of onion growth, using data collected during a study of flavour precursors in onion bulbs (Lancaster, McCallion and Shaw, 1986).

A FRAMEWORK FOR THE DESCRIPTION OF ONION GROWTH

An onion plant is composed of leaves which arise alternately from a small, flattened stem or base plate, so that older leaves are on the outside and younger leaves on the inside (Fig. 1). Each leaf is composed of a photosynthetic leaf blade and a non-photosynthetic leaf scale. The leaf scales thicken to form the bulb and bulb growth depends on numbers and sizes of scales. A satisfactory framework should link the growth of parts of a plant to bulb growth, and the growth of populations of bulbs to size distributions at harvest, and to yield.

Size distributions and yield

A typical size distribution for onions is illustrated as a histogram in Fig. 2. The smooth number density function (i.e. frequency) fitted to these data can be denoted by $n(w, t_h)$, where w stands for fresh weight and t_h for time of harvest measured in days from date of emergence. The area under this function gives the proportions of onions of different sizes at harvest. For example, 64% of bulbs in Fig. 2 lie between 60 and 100 g dry weight. Mean bulb weight can also be calculated from $n(w, t_h)$ by taking a weighted average: i.e.,

$$(1) \quad w = \int_0^{w_{\max}} w \cdot n(w, t_h) dw$$

where w is mean bulb weight. A similar calculation leads to an estimate of the variance of bulb weights.

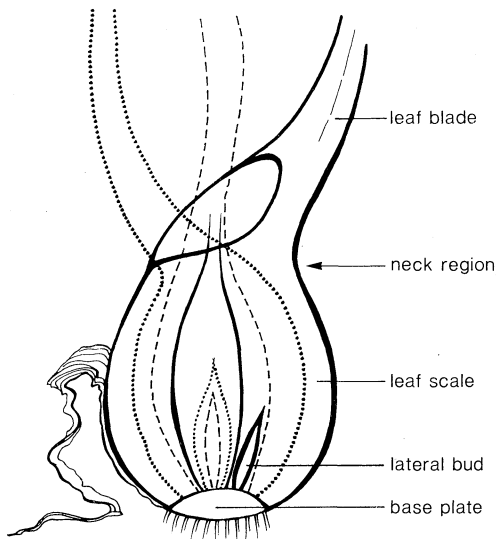


Figure 1: Diagrammatic representation of the relationship between the stem, or base plate, and the leaf blades and scales of an onion plant.

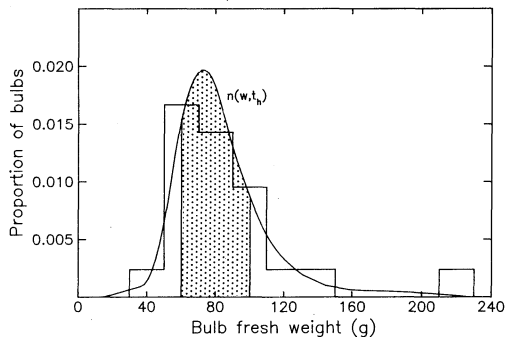


Figure 2: Number density distributions (i.e. frequency) for bulb fresh weights at final harvest (day 168). The histogram is of original data in 20 g size classes. The smooth number density function, $n(w, t_h)$, was obtained as the derivative of a cumulative distribution function fitted to cumulative bulb number data using a constrained B-spline method (Sprigg, 1986). 'Proportion of bulbs' = fractional numbers of bulbs per unit weight = number of bulbs in weight class divided by total number of bulbs divided by width of weight class interval.

Population balances for bulbs

We have chosen $n(w, t_h)$ to represent size distributions, rather than the more familiar histogram (Fig. 2), because

this function can be incorporated into population models for onion bulbs. Prediction of $n(w, t_h)$ using a population balance model would then be a step towards being able to manage the crop so as to maximize the numbers of onions in desirable size ranges. A number balance for onions in an arbitrary size class would be

$$(2) \quad \begin{pmatrix} \text{rate of change of} \\ \text{number of onions} \\ \text{in size class} \end{pmatrix} = \begin{pmatrix} \text{rate of inflow into} \\ \text{size class by} \\ \text{growth of smaller} \\ \text{onions} \end{pmatrix} - \begin{pmatrix} \text{rate of outflow} \\ \text{from size class by} \\ \text{growth of onions} \\ \text{in class} \end{pmatrix} \quad \begin{matrix} (i) \\ (ii) \end{matrix}$$

$$+ \begin{pmatrix} \text{'birth' of new} \\ \text{onions within} \\ \text{size class} \end{pmatrix} - \begin{pmatrix} \text{'death' of onions} \\ \text{already within} \\ \text{class} \end{pmatrix} \quad \begin{matrix} (iii) \\ (iv) \end{matrix}$$

Any size-dependent population model for onions will require terms for onion growth, (i) and (ii), and terms for 'birth' and 'death', (iii) and (iv). In onions, 'birth' is the production of lateral buds to form doubles, and 'death' is death and disappearance of plants. In this paper our main concern will be the growth terms, (i) and (ii). These terms depend upon the numbers and sizes of leaves on onion plants.

Proliferation and growth of leaves

Since bulb growth depends on the number and sizes of scales (see Fig. 2) models for the growth of individual onions should be formulated in terms of numbers and sizes of blades and scales.

The total above-ground weight of an onion plant at time t is

$$(3) \quad W(t) = w_p + \sum_j^{N_t} b_{w_j} + s_{w_j}$$

where w_p is the weight of the base plate, b_{w_j} and s_{w_j} are the weights of the j th blade and j th scale and N_t is the number of leaves present at t .

It is apparent from (3) that the growth rate of an onion depends not only on the growth rates of base plate, blades and leaves but also upon leaf number, N_t , which appears as a summation limit. To calculate growth rates, we change N_t in (3) to N_{max} , a maximum possible leaf number (which may never be realised) and introduce quantities $U(t-t_j)$, known as unit step functions, so that (3) becomes

$$(4) \quad W(t) = w_p + \sum_j^{N_t} U(t-t_j)(b_{w_j} + s_{w_j})$$

In (4), t_j is the time of initiation of the j th leaf and the unit step functions act as switches which are zero while $t < t_j$ and equal to one when $t \geq t_j$. This allows us to write the derivative of (4) as

$$(5) \quad W'(t) = w_p' + \sum_j^{N_t} U(t-t_j)(b_{w_j}' + s_{w_j}') + \sum_j^{N_t} d(t-t_j)(b_{w_j} + s_{w_j})$$

base plate	blade & scale	rate of	initial
growth	growth rates	leaf	size of
rate		initiation	leaf

where W' , wp' etc. are used to indicate growth rates, and the $d(t-t_j)$ are 'impulse' functions, the derivatives of the unit step functions. Eq. (5) expresses the overall growth rate of an onion in terms of the growth rate of the base plate and the growth rates and times of initiation of individual blades and scales, and shows the separate contributions of a population process (formation of leaves on the base plate) and the growth processes for individual leaves. Equation 5 can be extended to account for leaf death, but we will not consider this elaboration here. These are the terms which must be predicted using environmental functions like temperature, and knowledge of the physiological responses, in order to obtain suitable models for growth for use in (2). We shall use (5) as a basis for the analysis and discussion of data for the growth of onions in the field.

MATERIALS AND METHODS

Plant material

Seeds of the brown onion variety Spartan Sleeper (an F1 hybrid) were sown in mid-September, 1981, on a Wakanui silt loam at Lincoln, Canterbury. A base dressing of urea, superphosphate and potassium chloride at a total rate of 1150 kg/ha (to give an N:P:K: ratio of about 100:45:112 respectively) was applied prior to sowing and the crop was also side-dressed with ammonium sulphate at 100 kg/ha in mid-November. A pre-emergence herbicide was used. Seeds were planted in rows 50 cm apart and emergence occurred in the second week of October. We have taken October 10 as a mean emergence date (time, $t=0$). Seedlings were thinned in mid-October to a spacing of 10 cm within rows, and the crop was hand-weeded at regular intervals and irrigated (20-30 mm of water per week) until the end of January.

Selection and measurement

Because the onions were sampled as part of a study of the development of flavour it was necessary to analyse comparable plants at each harvest (Lancaster *et al.*, 1986). To ensure comparability, plants were selected for uniformity of growth rate and size before the start of harvesting (Evans, 1972). To do this, in late October about 400 plants were divided into three size classes on the basis of numbers and lengths of leaf blades, and labelled accordingly. One and two weeks later numbers and lengths of leaf blades were again measured and all plants which had moved from one class to another were discarded. After this selection, 80 plants from the 'medium' class were assigned numbers and used for subsequent growth studies and harvests. Leaf blades on these plants were numbered sequentially, and the appearance and death was recorded at each harvest. Harvests were made at 10 or 11 day intervals starting on November 16 (day 37). At each harvest, three plants were selected at random and leaf scale lengths and fresh weights were recorded individually for all but the smallest (<0.01 g) leaf blades and scales. At harvest 14, the remaining 25 labelled plants were harvested and measured.

RESULTS

Size distributions and plant weights

The mean bulb weight at final harvest was 89.3 g, with

a standard error 8.6 g, but these statistics are insufficient to describe the distribution in Fig. 2, for some measure of skewness is also required. Although the histogram and number density functions in Fig. 2 are based on a small sample, the skewed shapes are quite typical of onion bulb size distributions (cf. de Ruiter, 1986).

The number density distribution (i.e. frequency) at final harvest (Fig. 2) is the outcome of the growth of a set of onion plants. The pattern of growth of individual plants, constructed from sampled data, is illustrated in Fig. 3. Plants were very small and (up to the 5th harvest on day 73) composed mainly of leaf blades. Bulb expansion began about day 100, but until harvest 10 at day 130, total blade weights exceeded total scale weights. Thereafter, the increase in scale weight dominated growth and total blade weights declined until the necks collapsed ('top-down') at day 168. At top down, leaf blades had withered away totally on some plants but were still green on others, so that fresh weights of blades ranged from 0 to 45 g (Fig. 3). Bulb fresh weights ranged from 30 to 225 g (Figs. 2, 3) at the same stage.

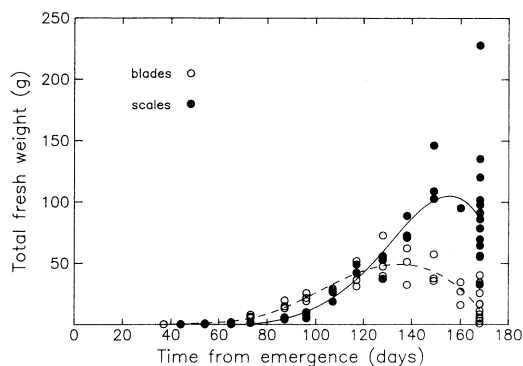


Figure 3: Total fresh weights for leaf blades (○) and leaf scales (●) from harvested plants (sample size, n , equals three except at day 168 when $n=25$). Smoothed curves through data fitted using constrained B-splines (Spriggs 1986).

Proliferation of leaves

Variability in fresh weights between plants could arise from variability in leaf numbers, in leaf weights, or both. The pattern of leaf appearance and death on a typical plant is illustrated in Fig. 4. Dates of leaf appearance are defined as the harvest dates at which leaves attained weights greater than or equal to 0.01 g and dates of leaf death as the harvest dates by which leaves had withered away and disappeared. At harvest 1 (day 37), plants typically had two leaves larger than 0.01 g. These leaves persisted until about day 60 before they withered and were sloughed off and disappeared. Further leaves appeared through the season until top-down at day 168, with a 'flush' of leaf appearance between day 80 and day 100 (Fig. 4), prior to bulb expansion (Fig. 3). Leaves appearing during this flush, and thereafter, persisted until top-down and their scales formed the bulbs

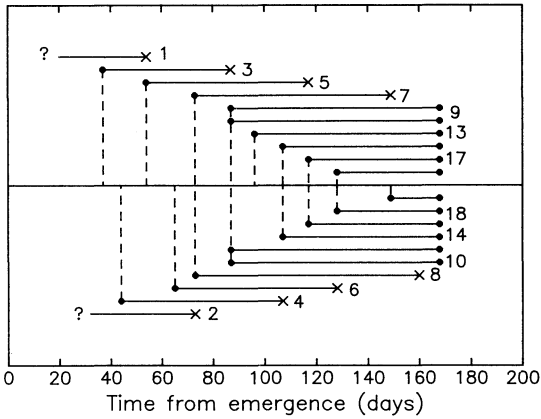


Figure 4: Pattern of leaf appearance and death on a typical onion plant. Time of appearance (●) and death (×) are observed times (corresponding to sampling days), rather than true times. The scales of leaves 9-19 were present in the bulb at top-down.

(Fig. 4). Leaf death also occurred throughout the season. All leaves formed prior to bulb expansion disappeared before top-down, so that no leaves were present throughout the season. Thus, onion bulbs were composed, on average, of the ten or so leaf scales which appeared between days 85 and 149.

Cumulative and net leaf numbers for harvested plants are shown in Fig. 5. Until day 107 (harvest 8) sampled plants had identical numbers of leaves. Variability in the number of scales in bulbs therefore arose only during the latter part of the season. At top-down, bulbs were made up of between 8 and 12 surviving scales (Fig.5).

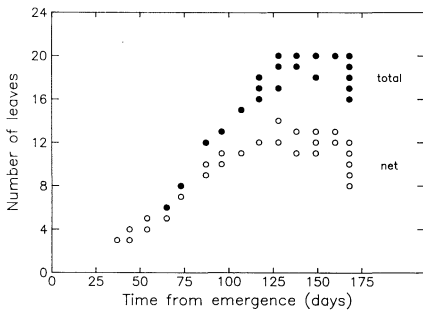


Figure 5: Cumulative (●) and net (○) leaf numbers on harvested plants throughout the season.

Leaf growth

The second source of variability in total plant weights lies in the weights of individual leaves. Patterns of growth of leaf blades and scales for a selection of leaves are illustrated in Fig. 6 (leaf 5 is typical of leaves 1-5, leaf 8 of

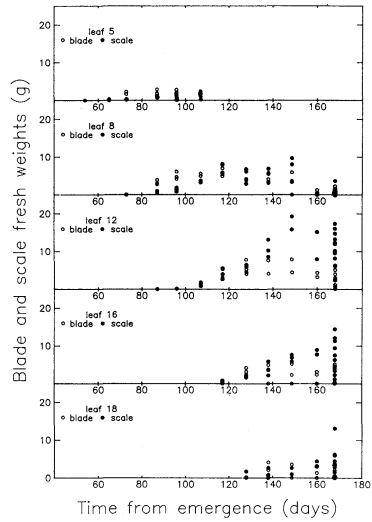


Figure 6: Fresh weights of some leaf blades (○) and leaf scales (●) of plants harvested throughout the season.

leaves 6-9, leaf 12 of leaves 10-13, and leaves 16 and 18 of remaining leaves).

For each leaf there was an appearance, a period of fresh weight increase, a peak fresh weight and then for all leaf blades and some leaf scales a period of senescence, during which fresh weight was lost which ended ultimately in death. However, each leaf behaved differently from its neighbours in its maximum weight (with a 30 fold and 60 fold range for scales and leaves respectively) and in the relative proportions of the blade and scale. Early leaves (1-5) were largely blades, whereas in leaf 8 the maximum weights of the blade and scale were comparable. In subsequent leaves the scale predominated.

Plant to plant variability in leaf size is a feature of the data. Identically numbered leaves on different plants differed in size by a factor of up to 10. Although the variability was greatest from bulbing onwards, it was present throughout all harvests. At the final harvest individual scales were at different stages of growth. Outer, older scales were senescing, middle ones were at maturity and inner, smaller scales were developing.

Distribution of scale weights in bulbs

The contributions of the weight and number of scales to bulb weights at top-down are illustrated in Fig. 7 for a selection of bulbs. The pattern of scale weights within individual bulbs was unimodal, with the third-to-oldest scale typically the heaviest. There was some variation in the numbers of scales, bulbs had either nine (20%), then (25%), eleven (30%) or twelve (25%) scales. However, the main source of variation between bulbs was variation in scale weights. The weight of the largest scale in the samples shown varied between 5 g and 45 g.

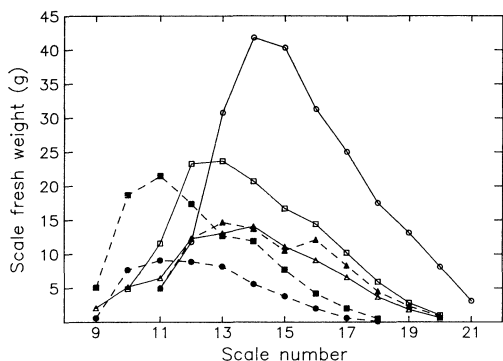


Figure 7: Scale fresh weights vs. scale number for a random sample of onions at day 168 (final harvest).

DISCUSSION

Variability is a feature of the data in this paper despite the fact that the onions used were an F1 hybrid and that plants were selected for uniformity at the outset of the experiment. Greater variability could be expected in open-pollinated, commercial crops. This poses a challenge to agronomists and physiologists studying the crop, and to those who attempt to model onion growth.

In simple models for onion growth, variability is ignored and only mean growth is predicted (e.g. de Ruiter, 1986). To model bulb size distributions, a number balance similar to equation (2) is required as a starting point. In most onion crops, it will be possible to ignore birth terms for lateral buds and death terms for whole plants, leaving prediction of the growth rates of plants as the key input for models of size distributions.

Various approaches can be used to model plant growth rates. One approach is to model mean growth rates and then assume that the variance of growth rates is proportional to the mean, a method used in Sands and Regel's (1983) potato model. This approach works only when size distributions are symmetrical. If bulb size distributions are skewed, as suggested by Fig. 1 and the data of de Ruiter (1986), it is unlikely to be a useful approach for onions.

An alternative approach is to assume that plant growth rates depend, in part, upon initial sizes, a method followed by Gandar *et al.* (1984) in their study of wheat tillers. This approach means that size order is maintained during growth of a set of plants, with the smallest plants remaining the smallest, and so forth. We cannot assess the suitability of this approach here because our data were collected on different sets of plants (cross-sectionally) rather than by repeated measurements on the same plants (longitudinally). Evidence from elsewhere is ambiguous: while the data of Triggs, Lancaster and Barrett (1986) suggest that size order is maintained from bulbing onwards, those of de Ruiter (1986) suggest that size order can change.

Models for growth rates could also be based on models for the growth and proliferation of blades and scales, as suggested by eq. (5). Our data show that leaf proliferation in onions could be modelled as a birth and death process, since leaf appearance and leaf death occurred over most of the season (Figs. 4-5). Leaf proliferation models may be deterministic or stochastic (i.e. models based on the probabilities of events such as leaf appearance rather than on the events themselves). In deterministic models, average rates of leaf proliferation are modelled (e.g. de Ruiter, 1986) and variability between plants is ignored.

The branching pattern in Fig. 4 can be viewed as an illustration of the outcome of a stochastic process of leaf proliferation (ignoring the fact that appearance dates in this figure are really dates of first observation), and is, therefore, an example of the sort of data that might come out of an appropriate stochastic model. The step and impulse functions in equation (5) can also be viewed as outputs from an appropriate stochastic model.

Several requirements for stochastic models are apparent from data. There appears to be 'flush' of leaf production prior to bulb expansion (Fig. 4), which could create mathematical difficulties since some model parameters would have to be treated as functions of time. An analysis of the data in Fig. 5 showed that this difficulty could be overcome by treating leaf numbers as functions of thermal time, rather than ordinary time. Cumulative and net leaf numbers are then linearized, and the flush of leaf production disappears (cf. de Ruiter, 1986). This suggests that thermal time should be used as the independent variable in stochastic models for onion leaf production (cf. Chalabi and Day 1986).

It is apparent from Fig. 5 that leaf appearance terminates about day 125, and although the mechanism for this cessation is not known its occurrence would need to be accommodated in a model. The approach of Chalabi and Day (1986) which uses a probabilistic 'stopping time' would be appropriate. Our data show that leaf death is important and this will have to be included in proliferation models. Leaf life appears to be a function of birth order (e.g. Fig. 4) so that order-dependent survivor functions might be a useful approach. In the discussion above we have focussed on leaf birth and death. This is appropriate because for most of the season leaves behave as units, with blade and scale senescing and disappearing together. However, at top-down a different behaviour appeared as blades senesced and scales remained. To account for this leaf proliferation models (and equation (5)) would have to be elaborated with separate survivor functions for blades and scales.

However, there is very little variability in leaf numbers between plants up to day 120 (Fig 4 and 5) and the variability in leaf numbers after bulbing is due to the small inner leaves. It may be appropriate to a first approximation to assume a deterministic model of leaf proliferation, so that average rates of leaf proliferation are modelled and variability between plants ignored.

The second component of models for growth rates is the growth of the individual blades and scales which make up the onion bulb. From Fig. 6 it can be seen that each leaf

differs from its neighbours in its final weight and in the relative proportions of blade and scale. It is difficult to find either a unifying pattern of growth or a suitable empiricism to encompass these differences.

A key feature of Fig. 6 was the large plant to plant differences in the weight of identically numbered leaves. This is in contrast to the small differences in leaf numbers between plants. The same plant to plant variation in the weight of scales could be seen in the data on the harvested bulbs (Fig. 7). The variability in the size distribution of the harvested bulbs was due mainly to the variability in the weights of the individual scales within a bulb.

Understanding the environmental factors and physiological behaviour of the plant which produces blade and scale size is necessary to understanding how bulb size is produced. At final harvest the bulb is made up of scales at different stages of their individual development and thus different physiological ages. Each scale reflects the particular biochemical and physiological process appropriate to its developmental stage. Hence scale to scale differences are found in carbohydrate content (Derbyshire, 1978), dry matter percentage (Lancaster and Kelly, 1984) and in the content of flavour precursors (Lancaster *et al.*, 1986). It can be seen that the kind of management of the crop during its growth is linked in to the quality of the bulb through the growth patterns of the leaf blades and scales.

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