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Simulation of shoot vegetative development and growth of unstressed winter wheat

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ABSTRACT

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Mechanistic crop simulation models can aid in directing research and improving farm management. Recent research on winter wheat (*Triticum aestivum* L.) canopy development was consolidated into a model of aboveground vegetative development and growth called SHOOTGRO 1.0. The model assumes that water, nutrients, and light do not limit development and growth. Initial conditions of cultivar type (dwarf, semidwarf, mid-tall, and tall), seeding rate, planting depth and date, and latitude are inputs. Daily temperature, expressed as growing degree-days, drives SHOOTGRO 1.0. Processes are simulated with a daily time step. Computer code is standard Fortran 77.

The morphological nomenclature used allows each leaf and node plus associated internode to be identified and their appearance, development, growth, and senescence to be followed from planting through completion of main stem flag leaf growth (shortly before booting). Three cohorts of plants are simulated based on time of emergence. Simulated growth of leaves and internodes is a function of leaf number and accumulation of thermal time, as is leaf senescence.

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The model integrates aboveground vegetative development and growth of individual vegetative components into one simulation. SHOOTGRO 1.0 is useful in estimating potential development and growth, and in predicting stage of vegetative development which may be critical in scheduling cultural practices and assisting breeders in selecting traits.

INTRODUCTION

Much research has been directed in the last decade toward understanding the development and growth of winter wheat (*Triticum aestivum* L.). Less attention has been directed towards consolidating this work into a mechanistic model. Dynamic models describing development and growth can aid in understanding system processes, identifying interactions among processes, summarizing diverse research areas, and managing crops (Gandar et al., 1984; Baker et al., 1985; Day and Atkin, 1985; Weir et al., 1984; Ritchie and Otter, 1985). Current mechanistic winter wheat models use photosynthesis submodels to drive developmental and growth submodels, but do not identify individual morphological units in the model. The purpose of the work reported here was to consolidate research on winter wheat canopy development into a simulation model of shoot development and growth that includes specification of all leaves, culms, nodes and internodes.

METHODS

'SHOOTGRO 1.0' simulates the morphogenesis and growth of plant organs using a nomenclature based on the phytomer unit (Fig. 1), and shoot development pattern defined by Klepper et al. (1982) and Masle-Meynard and Sebillotte (1982). Development and growth are assumed not to be limited by supply of photosynthate, nutrients, water, or light. Accumulation of thermal time [growing degree-days (GDD), base 0°C (Gallagher, 1979; Gallagher et al., 1979; McMaster and Smika, 1988)] drives development and growth. Growing degree-days is the sum over some interval of the daily maximum and minimum air temperature divided by 2 minus a base temperature. If the quantity is less than the base temperature, then the quantity is set equal to the base temperature. SHOOTGRO is written in standard Fortran 77 and executes on a Sun and Maascomp (BSD 4.3 UNIX) and a Digital Equipment Corporation microVAX II (VMS 4.7). Copies of the code are available from the corresponding author by sending a 0.5-inch magnetic tape or 5.25-inch floppy disk and requesting the appropriate operating

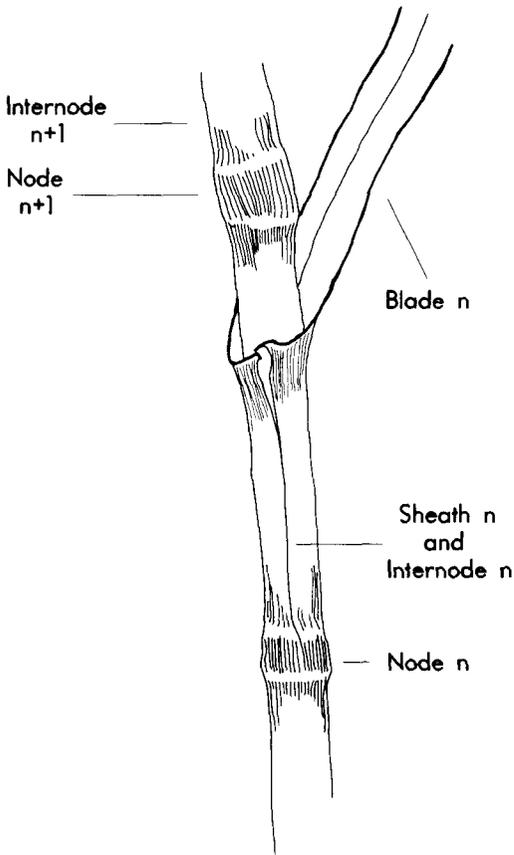


Fig. 1. System for naming nodes and associated internodes. The naming scheme is based on a phytomer unit.

system version (UNIX or VMS). Calculations are done using a daily time step.

SHOOTGRO is organized by submodels (Fig. 2). Initial inputs and driving variables are listed outside the system boundary box. Broken lines indicate submodels where these inputs have greatest or most direct effect. Driving variables are daily maximum and minimum air temperature. The initial inputs are: (1) latitude, (2) planting date, (3) planting depth, (4) seeding rate, and (5) cultivar height-class (i.e. dwarf, semidwarf, mid-tall, or tall).

The driving variables are input into the Environment submodel, which creates output used by other submodels. Output includes daily GDD, photoperiod, and daily change of photoperiod. The Seedling Emergence and Phyllochron submodels are called only once for each seedling cohort, at the beginning of the simulation. The remaining submodels are grouped within

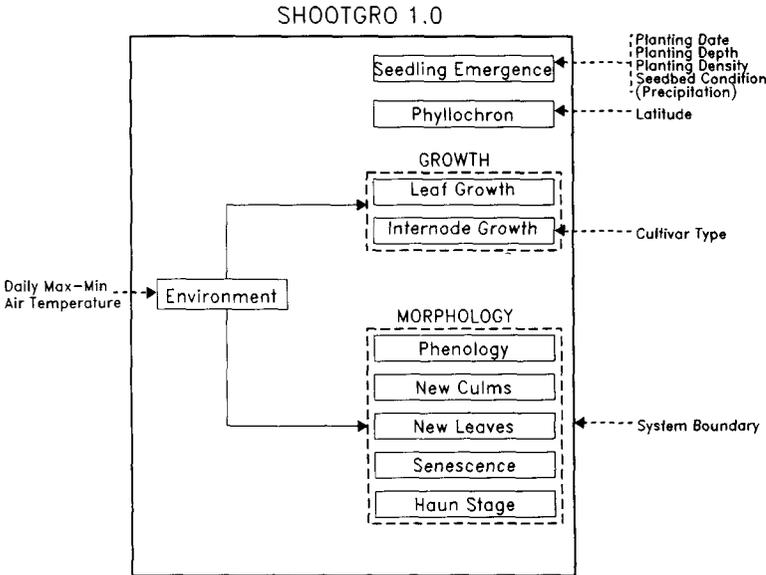


Fig. 2. SHOOTGRO 1.0 submodels. Driving variables and initial inputs are listed outside of the system boundary box. Broken lines indicate submodels where these inputs have greatest or most direct effect.

two general disciplines: growth and morphology. Growth contains two submodels (Leaf Growth and Internode Growth); morphology contains five submodels (Phenology, New Culms, New Leaves, Senescence, and Haun Growth Stage).

Specific plant organs are simulated using the morphological nomenclature of Klepper et al. (1983). Leaves are numbered acropetally on a culm, with the first leaf to appear designated L1. Culms are either the main stem (MS) or tillers. Primary tillers appear in the axils of MS leaves and are given one digit designations. For example, the primary tiller T1 appears in the axil of MS L1. Secondary tillers appear in the axils of primary tiller leaves and are given two digit designations (e.g. T11). The first digit refers to the parent tiller, the second digit is the parent leaf number. Tertiary tillers such as T111 are given three digit designations, where the first two digits signify the parent tillers.

Seedling emergence submodel

The seedling emergence curve is used to introduce population variation into the plant stand simulated by the model. A normal distribution is assumed (Rickman et al., 1983) for the relationship of emerged seedlings to GDD with a coefficient of variation of 0.1 (Fig. 3). The normal curve is

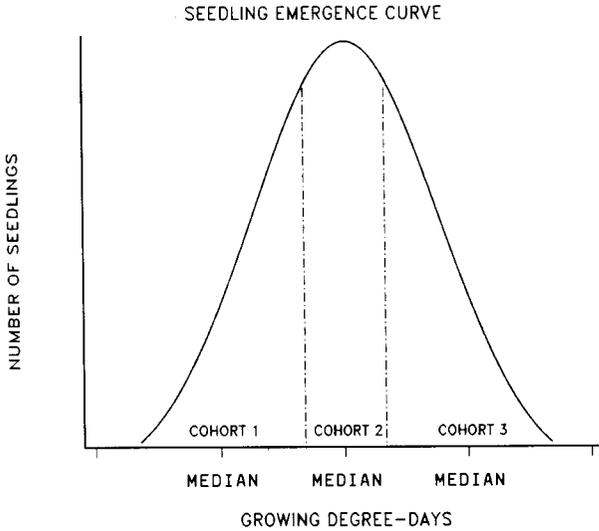


Fig. 3. Seedling emergence as a function of growing degree-days (GDD) using 0°C base temperature. Growing degree-days required for the mean plant of cohort 2 to emerge is determined by GDD required for seed germination plus coleoptile elongation rate per GDD. A coefficient of variation equal to 0.1 controls the variance. The normal curve is divided into three equal-sized cohorts.

derived from estimating seed germination and coleoptile elongation rates based on 80 GDD for germination and 2 GDD mm^{-1} for coleoptile elongation rate (Rickman et al., 1983). We assume 85% of the planted seeds germinate. Seedling emergence is treated similarly for all cultivars as Bauer et al. (1984) found no difference in time to emergence among 16 hard red spring and 3 durum wheat cultivars.

Once the normal curve is generated, the curve is truncated $\pm 3 \text{ SD}$. Then the median GDD for three equal-sized cohorts, based on number of individuals, is determined. The plant emerging at the median GDD for each cohort is simulated, rather than simulating only the mean plant in the field, which would be the median plant in cohort 2. The seedling emergence curve has an impact on development and growth throughout the growing season because each cohort will be at different developmental stages for the climatic conditions encountered. The difference in developmental stages is maintained throughout the growing season (Masle-Meynard, 1981a, b; Rickman et al., 1983). This approach allows the model to simulate the variation observed among plants in the field. This will be especially important when the effects of competition for light and soil resources are considered, as plants in the earliest cohort will have advantages in height, root and shoot development, and so forth.

Phyllochron submodel

The fundamental concept involved in predicting organ morphology is the phyllochron, defined as the time, in growing degree-days (GDD), for successive leaves to pass through the same developmental stage. SHOOTGRO simulates the observed tendency for a constant phyllochron over the life of a plant. Phyllochron has been related to daily change of photoperiod at emergence (Baker et al., 1980). The corrected equation from Baker et al. (1980) is used to calculate the phyllochron:

$$\text{phyllochron} = ((0.026 * \Delta d) + 0.0104)^{-1} \quad (1)$$

Change in photoperiod Δd is determined from the latitude and emergence date using WGEN, and is in hours (Richardson and Wright, 1984). Because each cohort appears on a different day, the phyllochron varies among cohorts. Therefore, each cohort encounters different temperature conditions as various developmental stages are reached. The phyllochron is constant for all culms within a cohort (Friend, 1965; Klepper et al., 1982; Masle-Meynard and Sebillotte, 1981), although some studies have found tillers, especially T0, have longer phyllochrons than the main stem (Kirby et al., 1985b). The phyllochron varies among cultivars (Baker et al., 1986; Kirby et al., 1985a; Syme, 1974), but information is presently insufficient to model such cultivar-related differences.

Leaf growth submodel

One leaf per culm is allowed to grow at a time. Leaf growth is divided into blade and sheath growth. Duration of growth is one phyllochron. Gallagher (1979) and Rawson et al. (1983) have shown an increase in maximum size of successive unstressed leaf blades on a culm. For growth of the first ten blades in SHOOTGRO, the maximum length and width are estimated using exponential functions shown in equations (2) and (3):

$$\text{Maximum blade length (mm)} = 86e^{0.15x} \quad (2)$$

$$\text{Maximum blade width (mm)} = 3.44e^{0.15x} \quad (3)$$

where x is leaf number on any culm (≤ 10), with the first leaf on the culm equal to 1. The first leaf is assumed to be 100 mm long and 4 mm wide (Rawson et al., 1983). Successive blades increase in both dimensions by 15% through L10. Blades after L9 are the same maximum size. Maximum length and width are divided by GDD per phyllochron to get a linear elongation rate in mm per GDD (Gallagher et al., 1979; Hay and Wilson, 1982; Kirby, 1988; Kirby et al., 1985b). Daily growth then becomes a function of the current day's GDD. Blade area (mm^2) is obtained by multiplying length, width, and

0.74 (Clements and Goldsmith, 1924) to account for blade shape, except for L1 on the main stem (MS) which tends to have a more blunt blade tip and therefore is multiplied by 0.83. A constant specific blade weight of 0.03 kg m^{-2} is used to convert area to weight. Sheath weight is set equal to current blade weight.

Internode growth submodel

Culms elongate as a result of cell enlargement of internodes. Weight associated with the node is included in the internode weight. Elongation rates (mm GDD^{-1}) for each internode are calculated from the maximum internode length divided by the phyllochron. The lower internodes have a

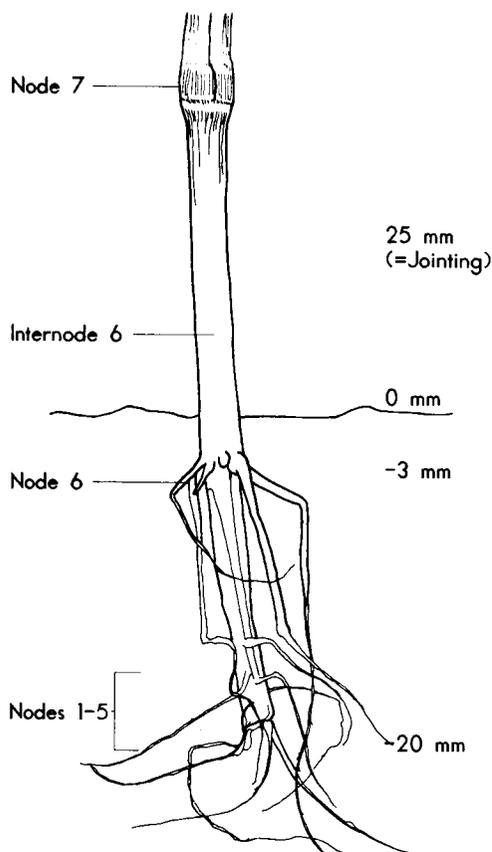


Fig. 4. Diagram of identified nodes and associated internodes and their relationships to the soil surface. In this example, the elongation of internodes 5 and 6 raises node 7 above the soil surface, resulting in jointing as defined by the Feekes Scale.

maximum length of 1 mm. The upper six internodes have maximum lengths calculated from:

$$\text{Maximum internode length} = 10.89(s)(n)^{1.73} \quad (4)$$

where s is a constant related to given cultivar height class (e.g. dwarf, semidwarf, mid-tall, or tall), and n ranges from 1 to 6 where 6 refers to the internode of the penultimate leaf. The peduncle (flag leaf internode) is not simulated because the simulation ends with the completion of main stem flag leaf growth (cohort 2). Elongation of the internode occurs two phyllochrons after the elongation of the leaf at the node. Daily internode elongation is determined from the internode growth rate and daily GDD. SHOOTGRO allows one internode to elongate per culm at any one time, and the duration of elongation for an internode is one phyllochron. Internode weights are estimated by multiplying culm length by unit culm weight (1.5 g m^{-1}). Total culm height is the sum of internode lengths minus crown depth (20 mm, unless planting depth is shallower).

Phenology submodel

This submodel predicts jointing, the time when a node of the main stem can be felt 25 mm above the soil surface [Feekes scale (Large, 1954)]. Jointing is assumed to occur at 470 GDD with 0°C base temperature after 1 January, the mean value which McMaster and Smika (1988) found for four cultivars at seven sites in the Central Great Plains. Equation (4) determines internode length beginning two phyllochrons before 470 GDD after 1 January. A typical arrangement of nodes and internodes with respect to the soil surface is shown in Fig. 4. About 1.5 to 2 phyllochron units are required from the onset of use of (4) for the MS node to rise 25 mm above the soil surface.

Haun growth stage submodel

The Haun growth stage (Haun, 1973) is a scale of phenological development based on the number (and fractions thereof) of fully expanded leaves on a culm:

$$\text{Haun stage} = \frac{L_n}{L_{n-1}} + (n - 1) \quad (5)$$

where L_n is the blade length of the youngest leaf (n) above the collar of leaf $n - 1$, L_{n-1} the blade length of the penultimate leaf ($n - 1$), and n is the number of leaves that has appeared on a culm. The maximum leaf length ratio (L_n/L_{n-1}) is 1.

TABLE 1

Model relationship between main stem development and culm appearance

MS Haun	Culm class	Culms that appear
0.0	1	MS
1.9	2	T0
2.7	3	T1
3.3	4	T2, T00
4.0	5	T3, T10, T01
5.0	6	T4, T20, T02, T11, T100, T010, T000, T30

New culms submodel

Under unstressed conditions, tillers appear in an orderly and predictable pattern (Klepper et al., 1982; Masle-Meynard and Sebillotte, 1981; Rickman et al., 1983). Tiller appearance is related to MS Haun stage as shown in Table 1 (Kirby et al., 1985b; Klepper et al., 1982). For example, tillers T3, T01, and T10 will appear when MS has four leaves that have fully expanded, or a Haun stage of 4.0. Because the first tiller leaf is hidden by the sheath of the subtending leaf on the parent tiller, the model predicts the appearance of each tiller about 0.3 phyllochrons before it is visible in the field. A tiller can appear only at a specific MS Haun stage. No new culms appear following jointing (Kirby et al., 1985b; Rawson, 1971). SHOOTGRO limits the maximum number of culms that can appear to the 16 noted in Table 1.

New leaves and internodes submodel

A new leaf appears on a culm each phyllochron. The phyllochron is the same for all leaves on all culms of a cohort (Klepper et al., 1982; Klepper et al., 1983; Masle-Meynard and Sebillotte, 1981). No more than 20 leaves are allowed to appear on any culm. Two new leaves are allowed to appear after jointing. If the unlikely situation occurs where jointing is reached when 19 or 20 leaves have appeared on the culm, then 20 leaves still is the maximum number of leaves allowed to appear on a culm. Each node subtends its associated internode (Fig. 1).

Senescence submodel

The model assumes that leaf senescence begins 6.5 phyllochrons after appearance (Klepper, McMaster, Rickman, unpublished data), therefore a maximum of 6.5 green leaves may be on a culm at any one time. A linear senescence rate with GDD is used. The model assumes that senescence

occurs over one phyllochron, therefore, only one leaf on a culm senesces at any one time, and then at the same rate (in thermal time) at which it grew. Dead leaf dry weight is set equal to 80% of live leaf dry weight.

Tillers that have produced fewer than four visible leaves on the day of jointing are likely to abort during jointing (Masle, 1985; Masle-Meynard, 1981b; Rickman et al., 1985). SHOOTGRO aborts all tillers with fewer than four leaves on the day of jointing.

RESULTS AND DISCUSSION

Model performance

The model was evaluated by changing the initial conditions and driving variables to determine their effect on model output. Output and patterns were then compared with our a priori expectations.

Two sites were selected for examining model output for various initial conditions: Amarillo, Texas (35°14' N lat) and Akron, Colorado (40°0' N lat). Average (30-year) monthly maximum and minimum air temperatures at Amarillo and Akron are 22 and 17 (max), and 7 and 2°C (min), respectively. Initial inputs were first set at: 1 September planting date, 145 seeds m⁻², 30 mm planting depth, and a semidwarf cultivar.

Plant development rates such as leaf and tiller appearance rates are primarily controlled by the phyllochron and pattern of GDD accumulation. Sites such as Amarillo have higher mean daily GDD than Akron, and therefore plant development should proceed faster at Amarillo than Akron. The model simulated greater MS Haun stage and number of culms per square meter (Fig. 5) at Amarillo than Akron. SHOOTGRO 1.0 limits maximum culm number on a plant to 16 (Table 1), and this accounts for the Akron site having the same final number of live culms per plant and culms per square meter as at Amarillo. The phyllochron is correlated with change in photoperiod at seedling emergence (Baker et al., 1980; Kirby et al., 1985a), which is a function of latitude and time of year. For the 1 September planting date, the phyllochrons were 108 and 104 GDD for Amarillo and Akron, respectively. The slower development rate observed at the Akron site is the result slower accumulation of GDD.

Slower plant development results in lower biomass and LAI at any point in time as shown in Fig. 5. The aboveground live biomass and LAI for the Akron site are much lower than for the Amarillo site. Since the model assumes unlimited supplies of light, water, nutrients, etc., simulations for Akron show biomass and LAI over typically observed field values. For example, simulated maximum biomass was about 3000 g m⁻², where values over about 1200 g m⁻² are rarely observed for dryland field conditions.

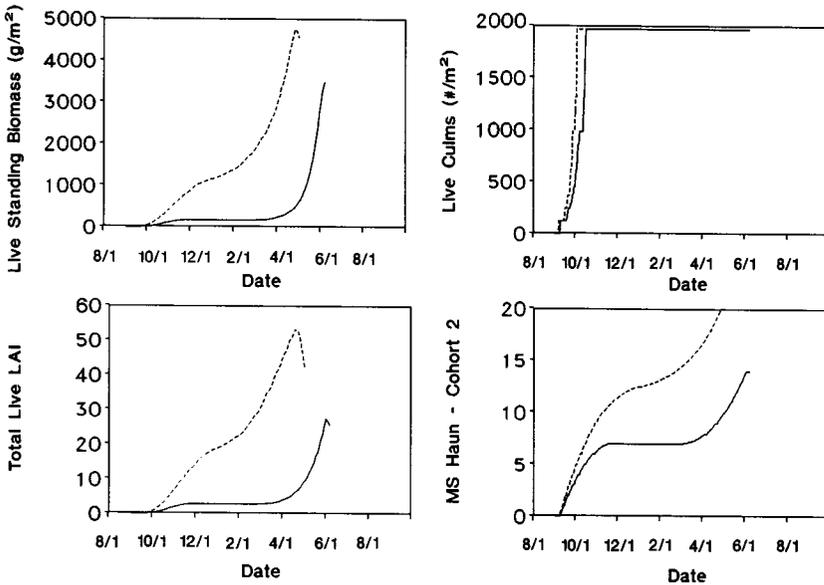


Fig. 5. Outputs for simulations at Akron, Colorado (solid line) and Amarillo, Texas (dashed line), using 30-year averages of climate data. Initial inputs are 1 September planting date, a semidwarf cultivar, 145 seeds m^{-2} , and 30 mm planting depth. All seedling cohorts are combined, except for the main stem (MS) Haun growth stage which is for Cohort 2.

Amarillo was also well above observed stressed field values. Both sites showed the same patterns over time, and the patterns match reported literature through early booting.

Simulations for latitudes varying from Austin, Texas ($30^{\circ}18'$ N latitude) to Swift Current, Saskatchewan, Canada ($50^{\circ}17'$ N latitude) and for planting dates from 1 August to 1 November gave a range of phyllochron values from 84 to 115. Difference among cohorts for a simulation was usually less than 2 GDD's.

Longer phyllochrons and slower accumulation of GDD results in fewer culms on a plant and leaves on a culm, which in turn reduces the maximum potential yield. As planting date is delayed or latitude increased, a greater proportion of plant development and growth will occur in the spring. Delaying tiller appearance, and therefore having tillers with lower Haun stage, increases the proportion of small tillers present at the time of jointing. Tillers that have not produced at least four leaves by jointing will abort, thereby reducing the potential maximum number of spikes. Further, these small tillers will have lower root and shoot biomass and LAI.

Altering plant population produced predictable changes. Individual plant development and growth component patterns stayed identical, only absolute values per square meter changed. This result is logical given the basic

assumption with this model of nonlimiting water, nutrients, light, and photosynthate.

Similar model response to planting depth was found. Planting depth affects crown depth and the seedling emergence curve. Crown depth and planting depth minimally influence culm height, and have no effect on system dynamics. The major influence of deeper planting depth is delaying emergence of each seedling cohort, but this delay showed little effect on plant development and growth.

Varying initial conditions and driving variables resulted in patterns typically observed for wheat development and growth through time. The magnitude of the patterns needs to be evaluated as well. The most direct technique is to compare simulated output to observed values for a given set of initial conditions and driving variables. Three criteria are necessary for validation data sets. First, the validation data must be for conditions where water, nutrients, and light are never limiting. Greenhouse and growth chamber conditions are normally at reduced light intensities. Field conditions rarely are continually optimal for water, nutrients, and light (e.g. cloudy days and most wheat is grown under dryland conditions). Second, knowledge of initial inputs and driving variables is necessary. As shown above, planting date, plant density, and daily temperature are important initial conditions and driving variables in SHOOTGRO. Third, the validation data collected with the first two criteria must be of sufficient detail. For example, information on which culms are present and specific data on each culm (e.g. Haun stage, organ dimensions and weights, phyllochron) must be collected over time. We know of no validation data sets that meet these three criteria. The vast majority of data sets do not collect/report the necessary data and emphasize the life-cycle during the time from heading to physiological maturity. It would be possible to collect reasonably suitable validation data sets. One solution, until validation data sets can be collected, is to compare simulated results to maximum observed values from high yielding areas and expect simulated values to exceed observed values. This approach was tried for a site in England. Thirty-year means for monthly maximum and minimum air temperatures for Heathrow airport (London) were used to calculate daily temperatures. It was assumed that the error by using Heathrow air temperatures was minimal compared to the error of not using specific data sets for a particular year at a specific site.

Given the initial conditions of 200 seeds m^{-2} , 30 mm planting depth, and a semidwarf, planting dates ranging from 15 September to 8 November gave a simulated range of maximum live LAI of about 30 to 3.5, maximum live standing biomass from about 4800 to 750 g m^{-2} , and a maximum of about 2700 live culms m^{-2} for all planting dates. Observed values for number of ears m^{-2} at maturity were presented for this range of planting dates by Weir

et al. (1984). For dates from 15 September to 23 September, observed mean values were 568 ears m^{-2} at maturity; for dates from 15 October to 8 November 551 ears m^{-2} were observed. SHOOTGRO simulated an average of 2720, 2720, 1360, and 510 live culms m^{-2} , respectively, at early boot stage for these four planting dates, respectively. Comparing observed maximum for these two planting periods to simulated values showed similar results where as planting date was delayed, the observed and simulated maximum LAI were closer. The pattern of simulated LAI development through time matched the observed pattern very closely, only differing in magnitude. Results for comparing live aboveground standing biomass were identical for culm number and LAI. Comparisons to the observed values are obscured by not knowing all the initial conditions and particularly not knowing the seedling emergence date.

Again, similar difficulties of not knowing all initial conditions, specific climatic data, seedling emergence, or clearly equivalent observed values to compare to simulated values existed for comparison with the values of Green et al. (1985) and Kirby et al. (1985a, b). Initial conditions for comparing to Green et al. values were set to 450 seeds m^{-2} , 30 mm planting depth, and a semidwarf cultivar. For 2 and 15 November and 5 December planting dates, the maximum number of culms m^{-2} observed was approximately 1150, 900, and 700, respectively; final culm number at maturity was about 425, 375, and 350, respectively. SHOOTGRO simulated much higher maximums, about 6100 m^{-2} for all three planting dates and culm population at early boot of about 1915, 1149, and 766 culms m^{-2} . Initial conditions were the same for comparison to observed values from Kirby et al. except that the seeding population was 270 seeds m^{-2} . For various planting dates from 10 September through 4 December, observed MS, T1, and T3 Haun growth stage could be compared to simulated values for several different cultivars. For MS, the observed final Haun growth stage decreased as planting date was delayed. SHOOTGRO simulated this pattern, as the simulated MS Haun growth stage for 10 September was 14 and 4 December was 8, as contrasted to 13 and 10 for the observed Haun growth stage for the two planting dates, respectively. The predicted phyllochron was 115.6 GDD; the observed phyllochron was about 119 GDD. Some of the discrepancy may be due to SHOOTGRO not simulating the correct dates of seedling emergence, which is critical in determining the phyllochron, along with incorrect initial conditions.

Model applications

SHOOTGRO 1.0 gives an indication of potential vegetative development and growth for specific sites, which can then be compared to observed

development and growth. For example, at Akron, Colorado planting mid- to late-September with plant populations near 125 plants m^{-2} , culm population at jointing is typically between about 500 and 700 culms m^{-2} and peak standing aboveground biomass is approximately 150 to 500 g m^{-2} varying greatly with climatic conditions (Smika and McMaster, unpublished data). SHOOTGRO estimates approximately 1900 live culms m^{-2} 350 g total biomass m^{-2} (i.e. no sloughing of dead leaves). This comparison suggests that significantly fewer tillers develop than is potentially possible. Numerous studies show that culm yield is largely a function of culm size and age (e.g. Darwinkel, 1983; Kirby et al., 1985b; Shanahan, 1982).

SHOOTGRO can aid managers in determining when the stand will reach particular developmental stages. This is important because many herbicides and pesticides have windows of application related to phenological stage, and optimum application of fertilizer and irrigation is often achieved when the stand is at specific developmental stages. SHOOTGRO 1.0 provides a framework for research investigations because identified morphological units have been simulated and quantitative validation data can be obtained for properties of each morphological unit.

SHOOTGRO 1.0 simulates the potential development and growth of shoot vegetative sources and sinks. This model could be incorporated into a model for field conditions by integrating nutrient and water effects on the potential development and growth of shoot vegetative organs, and by adding photosynthesis and carbon allocation submodels.

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