A MECHANISTIC MODEL OF COMMON RAGWEED BASED ON PHOTOTHERMAL TIME

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WILLIAM DEEN

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Abstract

A MECHANISTIC MODEL OF RAGWEED

BASED ON PHOTO-THERMAL TIME

William Deen — Advisors: Dr. C.J. Swanton

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Implementation of an integrated weed management system requires prediction of the impact of weed competition on crop yield. Predicting outcomes of weed competition is complicated by genetic and environmental variation across years, locations and management. Mechanistic models have the potential to account for this variability. Weed phenological development is an essential component of such models.

Growth cabinet studies were conducted to characterize common ragweed's phenological response to temperature, photoperiod and irradiance. Ragweed development occurred over a temperature range of 8.0 to 31.7C, and this response to temperature was best characterized using a nonlinear function. A maximum leaf appearance rate of 1.02 leaves per day occurred at 31.7C. Ragweed has a short juvenile phase, during which it was not sensitive to photoperiod. Following this juvenile phase, sensitivity to photoperiod was constant and continued until pistillate flowers were observed. Photoperiods of 14 hours or less were optimal and resulted in maximum rates of development. Irradiance level affected ragweed phenological development only when combined with the additional stress of very low temperatures.

Temperature and photoperiod responses derived from the above growth cabinet studies were assessed using phenological development data from a study of common ragweed grown in monoculture at Woodstock, Ontario under field conditions in 1994 and 1995. Photothermal time explained the appearance of phenological events and leaf number of common ragweed emerging at different times under field conditions. Estimated dates of phenological events of common ragweed were within 4 days of recorded values. Interactions between photoperiod and temperature did not need to be considered. Common ragweed seedling density did not influence phenological development indicating that factors affecting ragweed growth do not impact common ragweed phenology. It was shown, however that common ragweed phenological status will impact growth parameters, such as leaf area development, biomass partitioning, and total biomass.

Finally, a mechanistic model for ragweed growth and development based on the generic plant model CROPSIM was developed. Adaptations to the algorithms and parameterization of CROPSIM's development routine was done using the photothermal time concept developed above. Adaptations and parameterization of the growth routine were made based on data from field studies using a single source ragweed grown in monoculture and from the literature. The resulting model accounted for the influence of varying environmental conditions across years, density and emergence timing on leaf number, leaf area, leaf weight, height, and biomass accumulation. Deviations between simulated and measured values generally fell within +/- 25%, the range considered to be acceptable. Deviations greater than +/-25% tended to be associated with ragweed growth shortly after emergence, particularly when temperature and moisture extremes occurred during this time period. Sensitivity of a multi-species competition model to larger deviations at early stages of weed growth will need to be examined and future

versions of the CROPSIM model may need to include more detailed algorithms for upper soil surface layer temperature and moisture conditions, and improved germination and emergence algorithms to reduce these deviations.

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Introduction

Common ragweed is a major weed species in many parts of North America, and is commonly found in corn-soybean-wheat rotations in Ontario. The primary method available currently for controlling common ragweed is use of herbicides. A secondary control method is the use of tillage. Common ragweed frequently escapes herbicide application, particularly in soybeans. Common ragweed causes significant reductions in crop yield, crop quality and harvest efficiency. An integrated weed management (IWM) approach to controlling common ragweed could improve grower returns, and rationalize herbicide use.

IWM involves combining practical weed control strategies such as mechanical, cultural, biological, genetic, and chemical controls along with common crop production practices into an economically and ecologically sustainable systems (Anon., 1989; Swanton et al, 1989; Swanton and Weise, 1991). A basic requirement of any IWM system is a greater understanding of the biological, physiological, and ecological consequences of weed-crop interactions (Swanton and Murphy, 1996).

A major limitation to implementing effective IWM strategies for the control of common ragweed is the lack of understanding of the dynamics of competition between ragweed and other species, and the impact of environmental factors on these dynamics. Competition between ragweed and a crop is dynamic because competition outcomes are influenced by relative responses of the crop and ragweed to moisture, nitrogen, cultural practices such as row spacing, planting date, and by the effects of emergence timing. The interaction of these variables with phenological development of both crop and ragweed is an additional complexity that must be considered in determining the outcome of competition. Finally, the relative competitiveness of the crop and ragweed

at any given point in time will influence the future ability of either species to capture resources. Models have been evaluated as a tool in a IWM system for predicting the impact of weed competition.

Typically, empirical models have been used for this purpose. Unfortunately these models do not consider the dynamic nature of processes underlying weed-crop competition. Also, while they can predict the outcome of weed-crop competition under a narrow range of conditions, they are unable to account for genetic and environmental variation across years, locations and management, and consequently are unable to predict the impact of weed competition on crop performance. Empirical weed competition models cannot account for this variation and therefore, have limited predictive ability. Mechanistic competition models have been suggested to be a better approach.

Mechanistic models of weed-crop competition implicitly consider the dynamic nature of competition. Mechanistic models integrate our current understanding of growth and development of both the crop and weed under competition and enable researchers to evaluate the validity of that understanding. Mechanistic competition models are process-oriented. They consolidate, in mathematical terms, the various physiological and physical processes underlying crop and weed growth and development. They consider relative growth responses to environmental variables through time. These models are designed such that growth-limiting resources are distributed among the species according to the defined underlying physiological processes. Environmental, genetic and management factors affecting these processes are also considered. Consequently, mechanistic models are potentially better able to predict competition

outcomes between ragweed and crops and improve our understanding of the weed-crop competition system.

Simulation of weed phenological development is fundamental in the development of mechanistic weed-crop models. Plant phenological status has a major impact on plant growth processes, such as photosynthesis, partitioning, respiration, and the impact of environmental influences on crop growth. Simulation models need to provide an accurate prediction of phenology under varying conditions, otherwise growth processes of the crop and weed will be simulated inaccurately. This error not only causes simulation inaccuracy at the point of time of the simulation, but also impacts the ability of the model to simulate crop and weed growth at future stages since conditions during each crop growth stage affect the ability of the crop to respond to conditions during later stages. Phenological development could be a major factor determining the outcome of weed-crop competition.

The objectives of this study were to

1. Characterize the phenology of common ragweed in terms of response to temperature, photoperiod, and irradiance.
2. Determine if there were significant interactions between temperature and photoperiod effects on common ragweed phenology
3. Determine if common ragweed phenology under field conditions could be described using photothermal time
4. Develop a model of common ragweed growth and development for subsequent use in competition models.

Literature Review

Mechanisms of Weed-Crop Competition

Weeds interact with crops in various ways. The primary negative impact of weeds on crops is through competition for limited resources upon which the plant depends to achieve the maximum growth set by its hereditary potential (Zimdahl, 1980). Other interactions, such as allelochemical interference and harbouring of crop pests, are of secondary importance. The factors that determine the intensity of competition include the species of weed, weed density, spatial distribution, and duration of growth of both the weed and the crop (Bleasdale, 1960). These factors are modified by the physical environment and environmental conditions to which the weed and crop are exposed. Factors that influence plant growth affect the ability of both weeds and crops to exploit environmental resources.

The outcome of weed-crop competition is determined by the ability of the competing species to capture limited resources; irradiance, moisture and nitrogen being the most important. It is also determined by how efficiently each species uses the resources they capture (Berkowitz, 1988). A species that captures a disproportionate amount of a resource but uses it inefficiently will lose its competitive advantage. Similarly, a competitive advantage for one resource could confer a competitive advantage for the other resources (Carlson and Hill, 1986; Liebeman and Robichaux, 1990; Di Tomaso, 1995)

i. **Competition for Irradiance:** Irradiance is considered the environmental resource for which plants and weeds compete most and is the resource most likely to determine the outcome of weed and crop competition (Donald, 1963; Zimdahl, 1980;

Stoller and Wooley, 1985; Holt and Orcutt, 1991, Aldrich, 1986, Goudriaan and Monteith, 1990). Its importance has been demonstrated in competition studies between soybean, jimsonweed and common cocklebur (Pike et al., 1990), soybean and velvetleaf (Akey et al.,1990; Munger et al.,1987;Begonia et al., 1991), and soybean and shattercane (Fellows and Roeth, 1992). Unlike nitrogen and water, no reservoir of irradiance exists in the soil or plant. Irradiance is either captured and converted to chemical energy, reflected, or dissipated as heat.

Quantity and quality of irradiance incident on weeds and crop varies with solar angle, photoperiod, prevailing weather, time of day, canopy architecture and relative height of species (Holt, 1995). The impact of radiation environment on crops and weeds has been reviewed by Holt (1995), Patterson (1995), Aldrich (1984), Patterson (1982a, 1982b), Patterson (1985), Radosavich and Holt (1984). Shading by a plant canopy reduces available energy and alters the spectral distribution of irradiance by increasing the ratio of far-red to red light (Casal and Smith, 1989). Plant morphological responses (Patterson, 1978) to minimize shading are thought to be mediated by phytochrome (Casal and Kendrik, 1993; Smith et al., 1990).

The outcome of crop and weed competition is determined by direct competition for irradiance. Competitive ability is a function of plant architecture effects on the penetration and distribution of radiation within canopies (Caldwell et al., 1983). Visible radiation has a rapid extinction rate in plant canopies (Saeki, 1963), and consequently, the ability of a plant to place foliage in upper canopy layers should improve competitive ability. Crop and weed proportions of the total canopy leaf area index, and the vertical distribution of those proportions largely determines competitive ability (Legre and

Schreiber, 1989; Pike et al., 1990; Radosavich and Holt, 1984: Begonia et al. 1991, Regnier and Stoller, 1989).

Another aspect of light penetration important in weed-crop competition is the crop and weed leaf angle (Aldrich, 1984). Plant characteristics that appear to confer an ability to compete for irradiance are a high leaf area index, a leaf angle and leaf arrangement that maximizes interception of light, and leaf placement by one species over the other (Gonzalez et al., 1996; Stoller et al., 1987; Teasdale, 1998)

Competitive advantage, in terms of light interception, can be associated with temporal differences in crop and weed leaf area index (Joenje and Kropff, 1987). Temporal differences, such as an initial advantage in stem height or leaf placement early in the season, may confer an advantage throughout the period of competition (Radosavich and Holt, 1984: Berkowitz, 1988). Also, differences in leaf duration or differences in stem growth duration may determine when a species is the dominant light competitor (Berkowitz, 1988). This is reflected in studies showing the importance of time of weed emergence relative to crop emergence (Bosnić and Swanton,1996; Chikoye et al.,1995; Kropff et al., 1992).

Competition for irradiance can also be approached from the perspective of shade tolerance and photosynthetic utilization of intercepted irradiance (Beyschlag et al., 1990. Plants adapt to shade in various ways and possess varying degrees of abilities to adapt or tolerate low irradiance levels (Paterson, 1985; Regnier et al., 1988; Stoller and Myers, 1989). Adaptive measures include increases in chlorophyll content and photosynthetic efficiency (Patterson et al., 1978), increases in leaf area ratios (Patterson, 1982a; Stoller and Myers, 1989) and alterations in biomass allocation (McGiffen et al, 1992; Stoller and Myers, 1989). Commonly demonstrated alterations in morphology stemming

from changes in biomass allocation include, decreased root to shoot ratios, decreased reproductive allocation, increased leaf biomass allocation, and decreased lower branching.

Competition for light influences the ability of weeds and crops to compete for water and nitrogen (Salisbury and Chandler, 1993). A competitive advantage aboveground conferred the same advantage belowground (Ampong_Nyarko and De Datta, 1993). This has been attributed to reductions in photosynthate availability for root growth (Kramer and Kozlowski, 1979) and decreased root/shoot ratios (Patterson, 1979).

ii. Competition for Nitrogen and Water: The soil profile contains reservoirs of nitrogen and water that are temporally and spatially variable in distribution. Vertical and horizontal moisture and nitrogen gradients exist in the soil profile that are determined by precipitation patterns, row orientation and row spacing, and fertilization methods (Di Tomaso, 1995). Competition for nitrogen and water is dependent on the ability of plants to exploit this variably distributed resource before another species has the opportunity. It is also dependent on the species ability to tolerate deficiencies during the season.

Competition for below ground resources depends on the relative growth rate of weed and crop roots, and relative rates of root extension (Harper, 1983). Species with high growth rates are better suited to exploit regions in the soil containing nitrogen and water.

Competition for nitrogen is usually more significant than competition for the other major plant nutrients (Blackman and Templeman, 1938; Moody, 1981). In plants, nitrogen deficiency causes reductions in leaf expansion and photosynthetic efficiency due to reduced chlorophyll concentrations (Schepers et al.,1996). The relative ability of

crops and weeds to obtain soil nitrogen and the relative ability to tolerate soil nitrogen deficits determines the outcome of competition for this resource. Species vary in their ability to obtain and utilize soil nitrogen. For example, added nutrients often favour weed growth over crop growth (Carlson and Hill, 1986; Liebman, 1989; Sindel and Michael, 1992; Qasem, 1992a).

Water stress occurs when transpiration water loss exceeds water uptake through the roots. Results of water stress include reduced stomatal conductance (Yang-Jian et al., 1995), reduced leaf area expansion (Tafur et al., 1997), and reduced chlorophyll synthesis (Schepers et al.,1996) and decreased net photosynthesis (Iqbal and Wright, 1998). Weeds reduce the amount of soil moisture available to plants and thereby hasten the onset of or accentuate the water stress experienced by the crop.

Water use efficiencies, transpiration rates, and responses to soil moisture deficits vary among species and, consequently, influence the process of competition (Geddes et al., 1979; Patterson and Flint, 1983). Cocklebur, for example, during drought stress maintained a lower stomatal resistance and higher transpiration rate than soybean, thus depleting soil moisture more rapidly (Scott and Geddes, 1979). Similarly, compared to velvetleaf, soybean stomatal closure is initiated at a higher leaf water potential, however, under field conditions soybeans are able to exploit moisture from greater soil depths (Munger et al., 1987). Iqbal and Wright (1998) concluded that *Chenopodium album* was able to recover from a period of drought stress whereas Phalaris minor could not. Weise and Vandiver (1970) concluded that, similar to soil nitrogen, the relative ability of crops and weeds to obtain soil moisture and the relative ability to tolerate soil moisture deficits determines the outcome of competition for this resource

Temporal and spatial moisture and nitrogen variability in the soil influences weed-crop competition outcomes (Goodwin and Jones, 1991). Degree of sensitivity of a given species varies with development stage. Soybeans, for example, are more sensitive to drought stress at the time of flowering than earlier in the season (Eaton et al., 1976). Spatial variability in weed-crop competition is a factor if one species is able to avoid or reduce stress by accessing moisture or nitrogen from regions in the soil where another species has not yet reached (Munger et al., 1987; Kirkland and Beckie, 1998.)

Modelling Weed-Crop Competition

Models, in general terms, are simplified representations of systems. Jeffers (1982) provides a formal definition of the term model. He defines model as "a formal expression of the relationship between defined entities in physical or mathematical terms." Physical models are common in disciplines such as chemistry and engineering. In crop physiology, however, crop simulation models are primarily mathematical representations.

Models used to simulate crop growth consist of mathematical expressions. These mathematical expressions quantify how individual components of a system behave and interact with each other. Mathematics is used as a tool that enables scientists from a range of disciplines (crop physiology, soil science, agroclimatology etc.) to express their ideas so that quantitative prediction possible. Mathematics provide symbolic logic which is capable of describing ideas and relationships of considerable complexity. Models based on mathematics are precise and, thus, enable predictive statements to be derived that can be checked against reality by experiment or survey. The intent behind mathematical modelling of complex systems is to simplify, but not

distort underlying relationships within a system. Unfortunately because they are a simplification, models necessarily do not give a perfect representation of a system.

Numerous models have been developed to describe the impacts of inter-plant competition. Two general types of modelling strategies have been used: strictly empirical models and mechanistic models.

i. **Empirical models:** In most quantitative studies on weed-crop competition empirical models are used that describe the outcome of competition at a single time with a regression equation. Most often yield loss has been regressed against weed density . Cousens (1985a, 1985b) adopted this approach when he related weed density to crop loss using the rectangular hyperbola model. This model has subsequently been modified to include information on time of emergence (Cousens et al., 1987), and relative leaf area (Kropff, 1988; Kropff and Spitters, 1991) in an attempt to account for emergence date impacts in light interception.

Empirical models are useful for quickly determining competition effects in a particular experiment in which only weed density is varied and for interpolating between data points. However, the growth rate of the crop and the weed will not be the same when soil, crop husbandry practices or weather are varied. Large differences in parameter estimates can result from such differences (Lindquist et al., 1996a; Bauer et al., 1991). In theory, it is possible to derive the required parameters from many field trials. In practice, however, many variables influence growth patterns, thus making accurate quantification for all conditions impractical.

Efforts to develop weed-crop competitive indices for use in decision support systems have assumed parameter stability. Parameters are only stable for a given set

of data or under a very narrow range of conditions. Lindquist et al. (1996a) suggests that the use of a single set of competitive indices is inadequate since parameters vary with years, locations, planting dates and other variables.

ii. Mechanistic Models: A mechanistic weed-crop competition model (also referred to as explanatory or ecophysiological models) dynamically simulates resource capture and use efficiency by weed and crop based on knowledge of underlying physiological processes governing photosynthesis and morphological development. Caldwell et al. (1995) outline five ecophysiological intercropping models: GROWIT, ALMANAC, CropSys, INTERCOM and Ecosys. This approach to weed-crop competition modelling was first introduced by Spitters and Aerts (1983). Since their introduction, competition or intercropping models have undergone further testing and development (Kropff and van Laar, 1993; Wilkerson et al., 1990; Graf et al., 1990; Grant, 1994; Ball and Shaffer, 1993; Barbour and Bridges, 1995; Debaeke et al.,1997; Kiniry et al., 1995.; Caldwell et al. 1995 ; Olesen et al. 1997; Lindquist and Mortensen, 1997; Chikoye et al., 1996). All the models used are based on the principle that competition is a dynamic process that can be understood from the distribution of the growth determining (light) or growth limiting (water and nutrients) resources over the competing species and the efficiency with which each species uses these resources.

Mechanistic models attempt to explicitly represent causality between system variables. Mathematical equations in these models represent the mechanisms that relate the variables and explain their behaviour. Mechanistic models consist of mathematical descriptions of the operation of a system. These models consist of several main components: 1) state variables, 2) rate variables, 3) functional relationships, 4) driving variables and 5) parameters. A time period of one day or a

fraction of a day is usually used for the integration step. Driving variables are measured for this time period and are used as input for the model. Although the input is discrete, it allows for continuous simulation of the system.

Dent and Blackie (1979) identified four features common to any system being modelled. First, a system is fully defined by a set of identifiable entities and interconnections between them and by the limits to their organizational autonomy. Second, a system is a hierarchical structure comprising a number of subsystems each capable of autonomous definition; in turn subsystems similarly embody the next layer of detail in autonomous sub-subsystems. The point of entry into the hierarchy in any systems study is related to the objectives for which the system is being studied. Third, the most important characteristics of systems emerge over time so that the understanding of systems requires explicit consideration of time and rate of change. Finally, systems are sensitive to the environment in which they exist. This environment is usually unpredictable and certainly variable.

Loomis et al. (1979) and Thornley et al. (1990) identified the hierarchical levels present in any cropping system. Levels of interest to crop physiology generally include crop, plant, and organs. Tissue, cells, organelles and lower levels generally are not considered in crop physiology modelling efforts. The reason for this is that factors affecting crop, plant and organ simulation models are unlikely to affect the proper functioning of lower hierarchical levels.

Initial efforts were directed at simulating single processes within cropping systems. Over time, efforts were directed towards combining single process models into complex crop system models. Currently there are numerous crop system models. In many cases multiple models exist for a given crop. Hesketh and Alm (1992), for

example, provide citations for nine different cotton models, nine wheat models and eight potato models.

Current efforts in crop simulation revolve around refining, adapting or expanding existing models. Submodels are being improved and existing models are being calibrated and validated for a wider range of conditions, to include such things as weed competition and pest infestations (Kropff et al., 1995).

Mechanistic models have two potential advantages over a strictly empirical modelling approach. First, parameters derived for mechanistic models are potentially more stable than those developed for descriptive models. Mechanistic models are better suited to predict yield losses for a range of environmental and management conditions. Second, mechanistic models can provide insight into competition effects observed in experiments and may aid in seeking ways to manipulate competitive relations using IWM systems.

The weed-crop competition system is very complex. The number of state variables that may be distinguished in such a system is exceedingly large. It is not feasible to construct a model that accounts for all the physical, biological and chemical phenomena that occur. Intuitively one might think that the greater the number of state variables the better that the model simulates reality. This, however, is not the case. For each objective their is an optimum number of state variables. At first, increasing the number of state variables increases the models representation of the weed-crop system. Eventually the addition of more variables diverts attention from more important state variables. Information currently available to estimate rate variables, functional relationships etc. is currently limiting. Inclusion of a large number of state variables would require assumptions and approximations unless sufficient resources are available

for generating necessary data. The more unverified hypothesis and approximations in the model the less accurate it is likely to be.

Kropff and Spitters (1992a, 1992b) define weed-crop competition as the growth reduction of a plant brought about by the capture of growth limiting resources by competing species. As discussed previously, these resources are primarily irradiance, water, and nitrogen, with irradiance capture being the most important indicator of competitive ability. de Wit and Penning de Vries (1982) have developed a classification system to assist in conceptualizing crop-production systems. They proposed four levels of system complexity:

Level 1: Water and nutrients are available in ample supply. Crop growth is determined by irradiance, temperature and species characteristics.

Level 2: Crop growth and production are limited by water supply for at least part of the growing system.

Level 3: Water and nitrogen are limiting crop growth and production for at least part of the growing season

Level 4: Water, nitrogen and other nutrients are limiting for at least part of the growing season.

As Kropff (1993) notes, weed competition can be incorporated into the system at any one of these levels. Mechanistic models of competition developed to date fall into one of the first three levels of system complexity. Nutrients, other than nitrogen, have not been considered in any models given their limited importance to weed-crop competition. The majority of simulation models can be categorized as level one complexity. This degree of system simplification, again, is consistent with the

observations that irradiance competition frequently determines competitive outcome and with current limitation in understanding of below ground processes. Models that incorporate competition for water and/or nitrogen have been developed by Grant (1994), Ball and Shaffer (1993), Debaeke et al. (1997) and Graf et al. (1990a, 1990b).

a. Mechanistic Weed-crop models - irradiance competition:

Competition for irradiance, at a given point in time, is determined primarily by the leaf area index of crop and weeds, vertical distribution of the leaf area, and extinction properties. ALMANAC (Agricultural Land Management with Alternative Numerical Assessment Criteria) for example, simulates competition for light based on Beer's Law, allowing different extinction coefficient (k) for each species. Light is partitioned between species based on k values, LAI values, and heights (Debaeke et al., 1997). Sensitivity analysis of various models has demonstrated that rate of height increase strongly impacts simulation outcomes (Kropff et al, 1992; Spitters and Aerts, 1983; Olsen et al., 1997; Sinoquet and Caldwell, 1995). Various approaches have been used to simulate crop and weed height. Kropff and Van Laar(1993) outline a method based on plant assimilation, minimum stem diameters, and maximum plant heights. Ball and Shaffer (1993), similarly, relate plant height to total dry matter accumulation. Wiles and Wilkerson (1991) simulate height as a linear function of vegetative stage. Graf and Hill (1992) use a logistic function to relate height and age of the plant. To date, no attempt has been made to simulate the impact of canopy architecture and resulting light profile on crop and weed height even though it has been demonstrated that canopy architecture of weeds is altered by the presence of a crop (Legere and Scheiber, 1989; Regnier and Stoller, 1989)

Vertical leaf area distribution is another significant determinant of competition outcomes (Olesen et al., 1997). Parabolic, rectangular (Spitters and Aerts, 1983; Kropff and van Laar, 1993), triangular (Wiles and Wilkerson, 1991), and distributions skewed to the upper portion of the canopy (Graf and Hill, 1992) have been used. As with height growth, no attempt has been made to simulate the impact of canopy architecture and resulting light profile leaf area distribution.

Most simulation models assume a uniform horizontal distribution of leaf area (Kropff and van Laar, 1993; Spitters and Aerts, 1983; Graf et al., 1990a; Grant, 1994; Ball and Shaffer, 1993). At low plant densities or for heterogeneously distributed weeds horizontal distributions may deviate from uniformity. Kropff et al. (1992a) recommends overcoming this problem by distinguishing smaller fields with different weed densities and simulating yield loss for these fields separately. Another approach for accounting for nonuniformity through the use of 'zone of influence' models (Wilkerson et al., 1990; Barbour and Bridges, 1995). In these models, area of influence is a function of weed diameter. The field average of light interception is calculated on the basis of the proportion of the field with and without weed areas of influence.

Other factors affecting competition for irradiance include leaf area development, phenology, partitioning, branching patterns, specific leaf area, assimilate production, moisture and nitrogen limitations, photosynthetic properties etc.

b. Weed-crop models - nitrogen and moisture competition:

Moisture limitations can be accounted for in a number of competition models (Spitters and Aert, 1983; Kropff, 1988). Drought stress effects are accounted for by attaching to the model a water balance for the soil profile. Transpiration and growth rates of crop and weed are reduced when available soil moisture falls below a certain

level. ALMANAC for example simulates competition for soil water and nutrients based on each species' current rooting zone and demand by each species (Debaeke et al.,1997). Competition in these models is driven by above ground competition for light.

Phenological Development

The state of a plant at any point of time is determined by two distinctly different processes; growth and development. These processes must be kept separate because they are affected by different environmental variables (Ritchie, 1991). Hodges (1990) defined plant phenology as the development, differentiation, and initiation of plant organs. Alm et al. (1991) further defined it as the study of periodic effects that occur at different levels of the plant, such as organ, tissue, or cell with the focus of study being the scheduling of events versus the processes causing the events. Growth refers to the increase in weight, volume, height or area of the plant or part of the plant.

While growth processes do not affect phenological processes, the opposite is not true. Plant phenological status has a major impact on plant growth process, such as photosynthesis, partitioning of biomass, respiration, and the impact of environmental influences on crop growth (Wall and Morrison, 1990; Tworkoski, 1992). For example, phenology determined the impact of moisture stress on growth components of potatoes (Lynch et al. 1995). Simulation models require an accurate prediction of phenology under varying conditions, otherwise growth processes of the crop and weed will be simulated inaccurately. This error not only causes simulation inaccuracy at the point of time of the simulation, but also impacts the ability of the model to simulate crop and weed growth at future stages since conditions during each crop growth stage affect the

ability of the crop to respond to conditions during later stages (Frank et al., 1987.; Gardner et al., 1981).

Temperature and photoperiod are the major factors regulating phenological response (Hodges, 1991; Cousens et al., 1993). Phenological processes proceed in direct relation to the accumulated temperature or thermal time experienced by the plant (Ritchie, 1991). Below a base temperature no thermal time accumulates and crop growth ceases. Above this base temperature development rate increases with increasing temperature up to an optimum temperature or optimum temperature range. Above that optimum temperature, development rate decreases with increasing temperature until a maximum temperature is reached beyond which no development occurs. Numerous studies have been conducted to determine cardinal temperatures for various plant species (eg. Patterson, 1995, Flint et al, 1984; Tollenaar et al, 1989; Roche et al., 1997).

Linear and nonlinear algorithms have been developed to calculate accumulated thermal time. Numerous studies have applied growing degree equations to accumulate thermal time linearly above a base temperature (Major et al., 1975). Reservations have been expressed regarding the assumption of linearity of response. Shaykewich (1996), for example, reviewed responses of phenological development of cereal crops and found the response to be sigmoidal. Similarly, Cregan (1995) found that soybeans responded quadratically. Wassink (1974) has demonstrated, however, that inclusion of extreme temperatures provide a curvilinear response while inclusion of only the range of temperatures typically experienced by the plant results in a linear response.

Most crop simulation models utilize a linear response function. Minimum and maximum air temperatures are used to generate temperatures at set intervals throughout the day. From these temperatures thermal time is calculated.

Phenology of most plants responds to photoperiod, or more specifically, to night length. Major and Kiniry (1991) have reviewed the effect of day length on phenological events. Sensitivity to photoperiod was first demonstrated for soybeans by Garner and Allard (1920) and has since been demonstrated for numerous crop and weed species (eg. Kiniry et al., 1983a and 1983b; King et al. 1986; Patterson, 1995; Salisbury, 1963). The photoperiod effect on development only occurs during the inductive phase (Wilkerson et al., 1989). During the pre-inductive or juvenile phase and during the post inductive phase photoperiod, has no effect. For many species, such as maize (Kiniry et al., 1983b) the post inductive phase begins when flowering occurs. This effect of photoperiod differs from temperature which influences plant development throughout the life cycle.

The nature of the response falls into two main categories, long day plants and short day plants (Salisbury and Ross, 1992). A short day plant completes its life cycle in fewer days in short day lengths while a long day plant has a shorter life cycle under long days. Plant response to day length can be described in terms of effects on duration between phenological events , where duration is described in terms of calendar days, thermal time, and leaf number. It can also be described in terms of effect on rate of development, where rate is calculated as the inverse of duration. Rate of development has the advantage that it is more consistent with enzyme kinetics and plant physiology. Another advantage is that the response of duration to day length is frequently nonlinear,

but when rate of development is used, the response frequently becomes linear (Hadley et al., 1983)

Functions characterizing the effect of day length in simulation models generally include two parameters, the threshold photoperiod (DETP) and the photoperiod sensitivity (DESP). A commonly used function is the two straight line function discussed by Major and Kiniry (1991):

$$DFDE = 1 - (DESP*(DETP-DAYL))$$

in which DFDE is the day length factor and DAYL the photoperiodically effective day length (i.e. including twilight). Curvilinear functions include a quadratic response (Ritchie, 1991) and an exponential response (Angus et al., 1981). Changes in daylength at values less (or greater for the exponential) than the threshold have no impact on the development rate.

Several complexities in determining photoperiod and temperature responses have been identified. Yin and Kropff (1996) demonstrated that rice response to day and night temperatures varied over stages of development. Wang (1960) noted that base temperatures vary over the life cycle of a corn plant. Slafer and Rawson (1996) concluded that photoperiod sensitivity can vary with phenological stage in wheat, although this conclusion may not be correct since they compared absolute durations of each phase and not rates of development for each phase. There are genotype by photoperiod interactions, as demonstrated by Wilkerson et al. (1989) in soybeans. Photoperiod and temperature interactions may exist (Yan and Wallace, 1996), although Major and Kiniry (1991) suggest that interactions between photoperiod and temperature

only occur at extreme values for either variable. While these complexities exist, their inclusion may not improve predictive capabilities of phenological models given current modelling limitations such as use of air temperatures, sampling frequency, and sampling location (Ritchie, 1991)

While photoperiod and temperature are the major factors affecting phenology (Masle et al. 1989), other stresses, such as moisture and nitrogen stress, will affect phenology if severe (Major and Kiniry, 1991). Reported impacts of mild stress have been minimal and inconsistent (eg. Bridges and Chandler, 1989; Yegappan, 1986). Under typical Ontario field conditions, water and nitrogen stresses are unlikely to impact plant phenology.

Common Ragweed (*Ambrosia artemisiifolia*)

Basset and Crompton's (1975) and Weaver and William's (1980) reviews of ragweed's biology thoroughly describe the morphology, geographical distribution, habitat, and population dynamics of the plant. Common ragweed is a member of the compositae family and is native to North America. Common ragweed is a C3 plant (Garbutt et al., 1990),and is quantitative short day, photoperiod sensitive (Dickerson and Sweet, 1971; Garner and Allard, 1920). Ragweed is commonly found in cultivated fields, open disturbed habitats, along roadsides, hay fields, fence rows and waste places. Common ragweed is an erect herbaceous plant that can grow up to 200 cm tall. Stems are unbranched to bushy branched, glabrous to rough hairy. Leaves are short stalked, 5-10cm long, mostly opposite below and alternate above, thin, and finely dissected. The blades of the upper most leaves are occasionally unlobed. Flower heads contain either male or female flowers. Male flower heads, 10-100 per plant, hang

down in small clusters at the tip of stems and branches. Bracts of the flower heads are united. Female heads are one-flowered, sessile, inconspicuous in small clusters or single in the axil of the upper leaves. Male and female flower heads are usually in different parts of the same plant. A. artemisiifolia is a hermaphroditic plant. Mckone and Tonkyn (1986) demonstrated that sex expression can vary from all female to 78% male, most plants however express to some degree both male and female flowers. Plants are rarely entirely female. Morphology varies considerably over ragweed ecotypes and also, over phenotypes within ecotypes (Dickerson and Sweet, 1971).

Common ragweed is one of the most troublesome weeds in South-Western Ontario (Frick and Thomas, 1992). It escapes the commonly used herbicides and results in yield losses and quality reductions of the crop. Heavier infestations may also reduce harvest efficiency. In soybeans, Coble et al. (1981) reported that 4 common ragweed plants per 10m of row reduced yields by 8%.

CHAPTER 1: Influence of Temperature, Photoperiod and Irradiance on the Phenological Development of Common Ragweed (*Ambrosia artemisiifolia*)

Abstract. Implementation of an integrated weed management system requires prediction of the impact of weed competition on crop yield. Predicting outcomes of weed competition is complicated by genetic and environmental variation across years, locations and management. Mechanistic models have the potential to account for this variability. Weed phenological development is an essential component of such models. Growth cabinet studies were conducted to characterize common ragweed's phenological response to temperature, photoperiod and irradiance. Ragweed development occurred over a temperature range of 8.0 to 31.7C, and this response to temperature was best characterized using a nonlinear function. A maximum leaf appearance rate of 1.02 leaves per day occurred at 31.7C. Ragweed has a short juvenile phase, during which it was not sensitive to photoperiod. Following this juvenile phase, sensitivity to photoperiod was constant and continued until pistillate flowers were observed. Photoperiods of 14 hours or less were optimal and resulted in maximum rates of development. Irradiance level affected ragweed phenological development only when combined with the additional stress of low temperatures. Data generated in this study can be used for the development of mechanistic weed competition models.

Nomenclature: Common ragweed, *Ambrosia artemisiifolia* L. #[1]

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[1] Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA.

Introduction

Integrated weed management (IWM) combines available weed management practices in a manner that promotes agroecosystem health (Swanton and Murphy 1996; Swanton and Weise 1991). Prediction of the potential impact of weed competition on crop yield could lead to significant improvements in IWM systems. Predicting outcomes of weed competition however, is complicated by genetic and environmental variation across years, locations and management (Dieleman 1996; Knezevic et al. 1994). Predictive models are required in order to account for this variability.

Empirical weed competition models cannot account for this variation and therefore, have limited predictive ability (Kropff and van Laar 1993; Lindquist et al. 1996; Swanton and Murphy 1996). Mechanistic competition models are a better approach. Weed competiton is determined by the ability of the crop and weed to capture and use resources such as light, moisture and nitrogen (Kropff 1988; Weaver et al. 1992; Wilkerson et al. 1990). Mechanistic models integrate our current understanding of growth and development of both the crop and weed under competition. Environmental, genetic and management factors affecting these processes are also considered (Ghersa and Holt 1995; Patterson 1995a). Consequently, mechanistic models are better able to predict weed-crop competition outcomes.

In current efforts to develop a mechanistic weed competition model, the working hypothesis is that phenological development is a major factor determining the outcome of weed-crop competition. Many plant processes are a function of the phenological stage of the plant. Assimilate partitioning, leaf distribution, leaf area development, plant height, and leaf duration for example, are influenced by phenological phase (Ghersa and

Holt 1995; Tworkoski 1992; Wall and Morrison 1990). The impact of phenological phase on these processes in turn, influences the outcome of weed-crop competition. While the importance of phenological development has been stressed (Ghersa and Holt 1995), there have been limited discussions as to how this information can be used in modifying weed management programs. Crop scientists have repeatedly demonstrated that phenological development is critical to our understanding of crop growth and yield potential and that phenological development can be predicted (Chapman et al. 1993; Grant 1989; Miller et al. 1993). A similar understanding must be achieved by weed scientists in order to develop predictive models.

Simulation of weed phenological development is fundamental in the development of mechanistic weed-crop models. Phenological development is primarily controlled by temperature, and photoperiod (Hodges 1991; Patterson 1995b). Other stresses associated with moisture availability, level of nutrition, and plant density can affect phenological development, but under typical field conditions they are of minor importance relative to the effects of photoperiod and temperature (Major and Kiniry 1991; Medd and Lovett 1978; Roché et al. 1997; Slafer and Rawson 1994). For weeds growing under a canopy, low irradiance levels may represent a sufficient stress to affect phenological development and may also require consideration in modelling efforts (McLachlan et al. 1993).

The influence of temperature, photoperiod and irradiance on phenological development was studied using common ragweed. Common ragweed is a major weed species in many parts of North America, and is commonly found in corn-soybean-wheat rotations in Ontario. A complete description of phenological development of common ragweed as influenced by these three factors has not yet been reported.

Materials And Methods

The developmental response of common ragweed to temperature, photoperiod and irradiance was studied in growth cabinets using seed collected in 1992 from Woodstock, Ontario, Canada. Seeds were soaked in water at room temperature for two days then planted at a depth of 0.5 cm in 15 cm pots containing PRO-MIX[2]. Pots were watered as required and supplied weekly with a nutrient solution containing N, P, K, Ca, Mg, and chelated micronutrients. Irradiance was supplied by a sliding bank of Sylvania Cool White and Vita-Lite Duro-test fluorescent lamps and Westinghouse 40W incandescent bulbs. Photosynthetic photon flux densities were measured at the top of the canopy using a point quantum sensor[3].

Temperature response study: Pots were maintained initially in a growth room (22/17C day/night temperature, 16 h day length, and 400 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD)). Emerged ragweed seedlings were thinned to one per pot. At the two leaf stage, 25 pots were selected and arranged in a completely randomized design using five growth cabinets with day/night temperature of 11/2, 17/7, 23/13, 29/19, and 35/25 C. In each cabinet the PPFD was 400 µmol m^{-2} s^{-1} for a duration of 16h daily. Treatments were replicated three times and randomized across the five growth cabinets. The same growth cabinet was not used more than once for a given treatment. Mainstem leaves greater than 1 cm^2 were counted on five plants per replicate (n=15) every third day until the staminate involucre (reproductive phase) was visible. Leaf number 12 on each plant was marked as a reference to account for leaf senescence.

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[2] PRO-MIX BX, Premier Horticulture Inc., Red Hill, PA, 18076

[3] LI-COR 190SB. LI-COR, Inc., Lincoln, NE 68504.

Temperature effects on leaf number were analysed using ANOVA procedures to determine if treatment affected ragweed development. Data from each replicate per treatment was linearly regressed against time (number of days after the 2 leaf stage). Regression slopes provided estimates of leaf appearance rates as affected by temperature. Rates were then regressed against the mean treatment temperature (i.e. 35/25C at a 16/8 day night photoperiod results in a 24h mean temperature of 31.7) using a logistic equation similar to that used by Sinclair et al. (1991):

$$f(T) = LAR_{max}/(1 + \exp(-A(T-T_m)))$$

where LAR_{max} is the maximum leaf appearance rate, A is a regression coefficient and T_m defines the temperature at which $f(T) = .5$. T_m, as discussed by Sinclair et al. (1991), is the midrange temperature in the flowering response and the value A defines the range width. The smaller the value of A, the wider the temperature response range. The model was fitted for a wide range of T_m values in 0.1C increments. The T_m value giving the highest adjusted R^2 ((corrected sums of squares - error sums of squares)/corrected sums of squares) was selected (Kvalseth 1985). To obtain an indication of variability for A and T_m, the above analysis was repeated for each replicate with the only change being that normalized values for leaf appearance rates were used.

Photoperiod response study: Eight pots containing pre-germinated ragweed seed were placed in a growth cabinet. Seedlings emerging on day five after planting were identified and thinned to one per pot to ensure a uniform photoperiod exposure. To ensure that growth did not differ across treatments, each cabinet received a core irradiance of 400 µmol m^{-2} s^{-1} PPFD for 10 hours and photoperiod treatments were then

established using two 40W incandescent bulbs that provided approximately 40 µmol m^{-2} s^{-1} PPFD. The level of irradiance emitted from these two bulbs was high enough to affect photoperiod response but had negligible impact on photosynthesis levels. This design eliminated the potential confounding effect of differing growth rates on phenological development. Photoperiods were initiated and ended with incandescent lighting. The four day/night photoperiod treatments examined were 10/14, 12/12, 14/10 and 16/8h at a constant day and night temperature of 20C. The treatments were replicated three times in a randomized complete block design with treatment order also randomized using three growth cabinets. Main stem leaves were counted (described above) and plants were examined every third day for staminate involucre, pistillate flower (style and stigma visible), and dehiscence initiation. Dates of first appearance were recorded.

Data were subjected to ANOVA to test for significant photoperiod effects on days to staminate involucre. Since development can be more accurately described as a rate, data were converted to rates by calculating the inverse of time taken to reach a particular stage. Development rates for each interval (i.e. staminate involucre to pistillate flower and pistillate flower to dehiscence) were normalized to the maximum rate within each interval. Normalized development rates were compared using Fischer's Protected LSD to determine if sensitivities to photoperiod varied for different development stages.

Juvenile phase study: Juvenile phase length was determined using a long day to short day transfer study. Fifty ragweed plants were established in each of three long-day growth cabinets receiving a core irradiance period of 8 hours at 400 µmol m^{-2} s^{-1} PPFD, at a constant temperature of 20C. The photoperiod in these cabinets was

extended to 20 hours using 40W incandescent bulbs, as described above. Seedlings emerging on day five after planting were identified and thinned to one per pot to ensure a uniform photoperiod exposure. Beginning at emergence, and repeated at three day intervals up to 27 days after emergence, groups of five plants selected randomly were transferred to a short-day growth room with an 8h photoperiod. Irradiance was 350 μmol m^{-2} s^{-1} PPFD, with a constant temperature of 20C. Treatments were replicated three times in a randomized complete block design. Main stem leaves were counted and first appearance dates of phenological events were recorded as described above.

Data were subjected to ANOVA to establish significant effect of time of transfer on days to staminate involucre. Data were analysed using a method similar to that employed by Wilkerson et al. (1989). A series of paired data sets were produced by splitting data (individual replicates) at the 9,12,15, and 18d after emergence treatments. Linear regressions were applied to the various data sets to determine the set that provided the minimized combined sum of squared residuals. For example, linear regressions were first fitted to the 0, 3, 6 and the 9, 12, 15, 18, 21, 24, 27 data, then to the 0, 3, 6, 9 and 12, 15, 18, 21, 24, 27 data, and so on. The point of interception of the two regression lines for which the sum of squared residuals was a minimum was taken as the time when photoperiod sensitivity began (i.e. end of juvenile phase). The mean date when photoperiod sensitivity began was calculated along with an associated standard error.

Irradiance response study: The 17/7, 23/13, and 29/19 C day/night temperature treatments, described above, were repeated at 150 μmol m^{-2} s^{-1} PPFD. Main stem leaves were counted as described above. Data were subjected to ANOVA to test for

irradiance effects on leaf appearance rates. Mean leaf appearance rates were calculate (described above) for the various treatments and were separated using a t-test.

Results And Discussion

Temperature Response: Common ragweed development occurred over a wide temperature range. Leaf numbers increased at mean daily temperatures ranging from 8 to 31.7C (Figure 1). Leaf appearance at day/night temperatures of 29/19 and 35/25C correspond closely with leaf appearance results obtained by Frazee and Stoller (1974) for ragweed seed collected in Illinois and grown at 30/24C. Rate of leaf appearance, obtained from linear regression of data presented in Figure 1, indicated that rate of development increased with temperature (data not shown). At 31.7C the rate of leaf appearance was higher ($P<.05$) than at 25.7C. This suggested that the optimal temperature for rate of leaf appearance was at or above 31.7C. For Ontario conditions, daily average temperatures of 31.7C are seldom exceeded therefore, leaf appearance rates at this temperature were considered to be the maximum rate. By linearly regressing data from individual replicates, the maximum rate of leaf appearance was determined to be 1.02 (+/-.02) leaves per day at 31.7C. While ragweed is typically considered an early season and hardy weed (Gebben, 1966) these results indicated adaptation to a wide temperature range.

Ragweed's adaptation to a wide temperature range requires that the algorithm describing this relationship account for high and low temperatures. Linear algorithms have frequently been used to describe plant development responses to temperature (Shaykewich 1995). Recent work has shown however, that when high and low temperatures were included in the analyses a nonlinear algorithm was more appropriate

(eg. Shaykewich 1995; Sinclair et al. 1991). A nonlinear, logistic function was used to describe the rate of leaf appearance as influenced by temperature (Figure 2). Leaf appearance rates were determined from linear regressions on data in Figure 1. The logistic function was fitted to leaf appearance rates for the five mean daily temperatures (Figure 1), normalized to the maximum rate of 1.02 leaves/day. Parameter values for A and T_m were 0.18 and 15.2C, respectively. Given the appropriateness of this function, the same analysis procedure was conducted on each replicate to obtain an estimate of variability for the midrange temperature, T_m and the parameter, A. The mean midrange temperature was 15.2C (+/- 0.1C) and the mean value for parameter A was 0.18 (+/- .01). The asymptotic characteristics of this equation cannot account for extreme temperatures. It does describe adequately however, the response of ragweed to field temperature conditions.

Extrapolation of this relationship to field conditions requires several considerations. Rate of leaf appearance was estimated using only air temperatures. Plant development rates however, are probably determined by temperatures experienced by plant meristematic tissue (Swan et al. 1987). The temperature of this tissue could be higher or lower than air temperature due to variations in components of the energy budget of the tissue (Pararajasingham and Hunt 1991). Plants absorb radiation energy. Whether plant temperature is higher or lower than air depends on the energy absorbed and the ability of the plant to dispose of this energy through reflection, sensible heat transfer, and transpiration. The differential between leaf and air temperature can be zero or less than zero due to evaporative cooling (Jackson 1984). If water stress occurs, this differential may be greater than zero because of a reduced energy loss through transpiration. Actual and potential transpiration rates may differ

between growth cabinet and field conditions due to differences in moisture levels and resulting transpiration rates, differences in boundary layer thickness, vapour pressure deficits, and long wave radiation inputs (Pararajasingham and Hunt 1991).

Photoperiod Response: Ragweed is a quantitative, short-day species. Phenological development was similar for plants exposed to 10, 12 and 14h photoperiod treatments (Figure 3). The mean numbers of days from emergence to first staminate involucre, first pistillate flower, and first dehiscence were 20.7, 27.0 and 34.7, respectfully. The times required for common ragweed to reach these same phenological stages when exposed to 16 hour photoperiods were longer ($P<.0001$): 40, 56, and 63 days, respectively.

Photoperiod sensitivity of common ragweed was constant until the occurrence of the pistillate flower, after which it was insensitive (Figure 3). The times from emergence to first staminate involucre and from first staminate involucre to first pistillate flower were affected by photoperiod ($P<.0001$). By contrast, time from first pistillate flower to first dehiscence was not affected by photoperiod ($P>.05$). Photoperiod sensitivity ended at the time of appearance of pistillate flowers.

A single photoperiod sensitivity parameter can be used to characterize common ragweed development. When data from Figure 3 was expressed in terms of development rates (i.e. inverse of duration of development) (Table 1) and compared across phenological stage no differences ($P<.05$) between photoperiod sensitivities were found. This finding differs from previous research that has suggested that photoperiod sensitivity varies with growth stage (Slafer and Rawson 1996). This previous work however, compared the impact of photoperiod on durations of growth stages whereas phenological development should be characterized as a rate function.

When extrapolating photoperiod sensitivity results of growth cabinet studies to the field the question of actual photoperiod length in the field arises. Photoperiod length is perceived by plants through the detection of red to far-red light ratio by phytochrome (Papenfuss and Salisbury, 1967). In growth cabinets photoperiod is easily measured, but under field conditions red to far-red ratios vary (Salisbury 1981), making measurement of photoperiod length more difficult. At twilight, far-red light increases very quickly relative to red light and it is this change that plants detect. Salisbury (1981) for example, determined that cocklebur (*Xanthium strumarium*) detected the end of the photoperiod twenty minutes after sunset. Compared to civil twilight, when the sun is 6 degrees below the horizon, cocklebur's "twilight" occurred when the sun was 4 degrees below the horizon. For ragweed, the red to far-red ratio that results in detection of the end of photoperiod is not yet known.

Juvenile Phase Duration: Common ragweed was photoperiod sensitive soon after emergence thereby enabling immediate adjustment of development duration to the photoperiod length. Date of appearance of first staminate involucre, pistillate flower, and dehiscence increased ($P<.0001$) with number of days of exposure to 16h photoperiods (Figure 4). The duration from emergence to the end of the juvenile phase (i.e. beginning of photoperiod sensitivity) using days to first appearance of staminate or pistillate flower was 9.1(+/-1.2) or 8.5(+/-1.3) days ($P<.05$), respectively. Theoretically, the juvenile phase should also account for time from germination to seedling emergence. In this study, this time was estimated to be 3-5 d and this could be added to the former duration to give about a 12-13d juvenile period.

Three phenological phases of common ragweed were identified. These phases and their durations were emergence to staminate involucre (20.7d), staminate involucre

to pistillate flower (6.3d), and pistillate flower to dehiscence (7.7d). Phase durations were based on the initial transfer dates of the juvenile phase study and the 10, 12, and 14h photoperiod treatments of the photoperiod study at 20C. Phase duration estimates obtained from the two studies did not differ (P>.05)(Table 2).

Irradiance Response: Phenological development of ragweed was reduced by a combination of low irradiance and low temperature. Leaf appearance rates were not affected (P>.05) by irradiance level at day/night temperatures of 29/19 and 23/13C (Table 3). However, when the day/night temperature was reduced to 17/7C, leaf appearance rate was lower (P<.05) for the 150 μmol m^{-2} s^{-1} irradiance level than for the 400 μmol m^{-2} s^{-1} level (Table 3). The combined stress of low irradiance and low temperature affected ragweed development possibly by reducing assimilate production. Other research has demonstrated the impact of severe stresses, such as moisture, nitrogen (Major and Kiniry 1991), and shading (Gmelig-Myelig 1973; McLachlan et al. 1993) on plant phenological development. Within a crop canopy, ragweed could experience irradiance levels at or below 150 μmol m^{-2} s^{-1}. McLachlan et al. (1993), for example, found that irradiance transmittance through an established corn canopy at silking was only 8%. The combination of low level of irradiance and temperature which occur under field conditions will affect growth and phenological development of common ragweed.

Understanding phenological development is fundamental in the development of mechanistic models. In this study phenological development of common ragweed was influenced by temperature, photoperiod and irradiance. Ragweed development was adapted to a wide temperature range and was best described by a nonlinear function. Ragweed was photoperiod sensitive shortly after emergnce and remained sensitive until

pistillate flower initiatation. When phenological development was expressed in terms of rate, photoperiod sensitivity did not differ with phase of ragweed development. Interpretation of constant sensitivity to photoperiod will simplify simulation of phenological development in mechanistic models. Low levels of irradiance in combination with low temperatures reduced rate of phenological development.

In future research, the relationships determined in this study need to be incorporated into a photothermal model. The ability of such a model to explain or predict ragweed phenological development under field conditions will determine whether photoperiod-temperature interactions or other stresses need to be considered as factors affecting development of ragweed. If a relatively simple photothermal time model is sufficient for describing ragweed phenological development then there exists a basis for further development of a mechanistic weed competition model.

Table 1: Normalized rate of development to first staminate involucre and pistillate flower for common ragweed. [a]

Photoperiod	Staminate involucre	Pistillate Flower	$LSD_{.05}$; N=3
14 hour	1.00	1.00	
16 hour	.51	.42	
Rate Change	-.49	-.58	.33

[a] Normalized to the maximum replicate value

Table 2: Durations of ragweed phases determined from two separate studies conducted at 20C.

Phase	Phase Duration	
	Juvenile Phase Study [a]	Photoperiod Study [b]
	Number per day (SE)	
Emergence - Staminate Involucre	19.5 (0.3) a	20.7 (0.7) a
Staminate Involucre -Pistillate	6.2 (0.9) a	6.3 (1.2) a
Pistillate Flower - Dehiscence	6.5 (0.9) a	7.7 (0.7) a

Means followed by the same letter within a row are not different (P>.05) according to Student's t-test.

[a] Derived from 0, 3, 6 and 9 days after emergence transfer treatments

[b] Derived from 10, 12, and 14 hour photoperiod treatments

Table 3: Ragweed leaf appearance rates as affected by irradiance and temperature.

	Leaf Appearance Rate	
Day/Night Temperature (C)	150 µmol m^{-1} s^{-1}	400 µmol m^{-1} s^{-1}
	number /day (S.E.)	
17/7	.37 (.01) a	.48 (.01) b
23/13	.68 (.02) a	.66 (.01) a
29/19	.88 (.06) a	.82 (.03) a

Means followed by the same letter within a row are not different (P>.05) according to Student's t-test.

Figure 1: Main stem leaf number (>1.0cm^2) versus time after the 2-leaf stage for common ragweed growing at a day/night temperature of 35/25C (□), 29/19C (⊠), 23/13C (■), 17/7C (●), and 11/2C (▲).

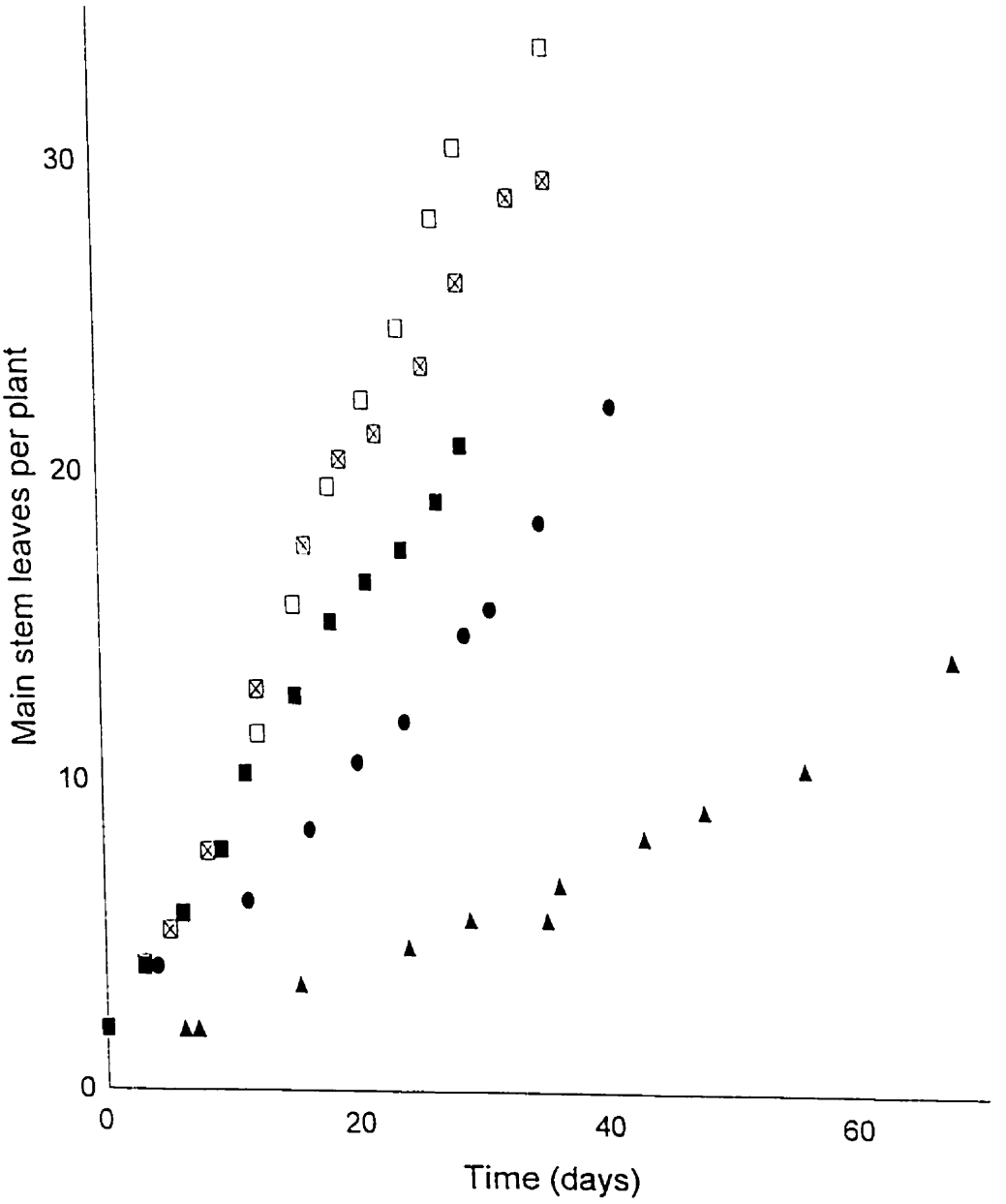

Main stem leaves per plant
30
20
10
0
0
20
40
60
Time (days)

Figure 2:. Effect of mean temperature on common ragweed leaf appearance rate (normalized): observed (●), logistic equation $y = 1.0/(1 + \exp(.18(X-15.2))$ (------), $R^2 = .97$.

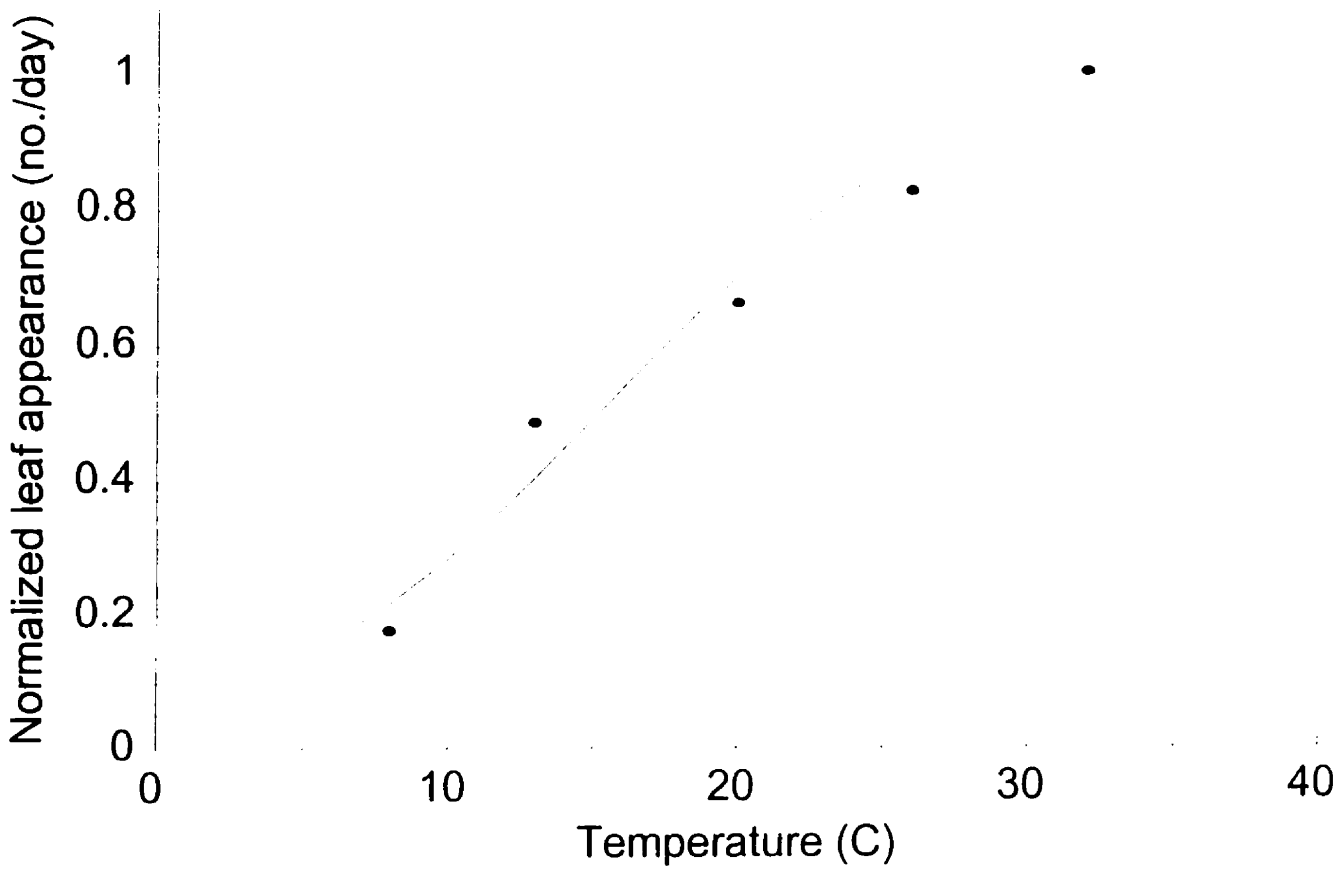

Normalized leaf appearance (no./day)
1
0.8
0.6
0.4
0.2
0
0
10
20
30
40
Temperature (C)

Figure 3: Effect of photoperiod on the days to first appearance of phenological stages: staminate involucre (———), first pistillate flower (- - - -), first dehiscence (- - - - -), and interval from staminate involucre to pistillate flower (— - — - —), and the interval from pistillate flower to dehiscence (— - — - —). Vertical lines represent standard error of means.

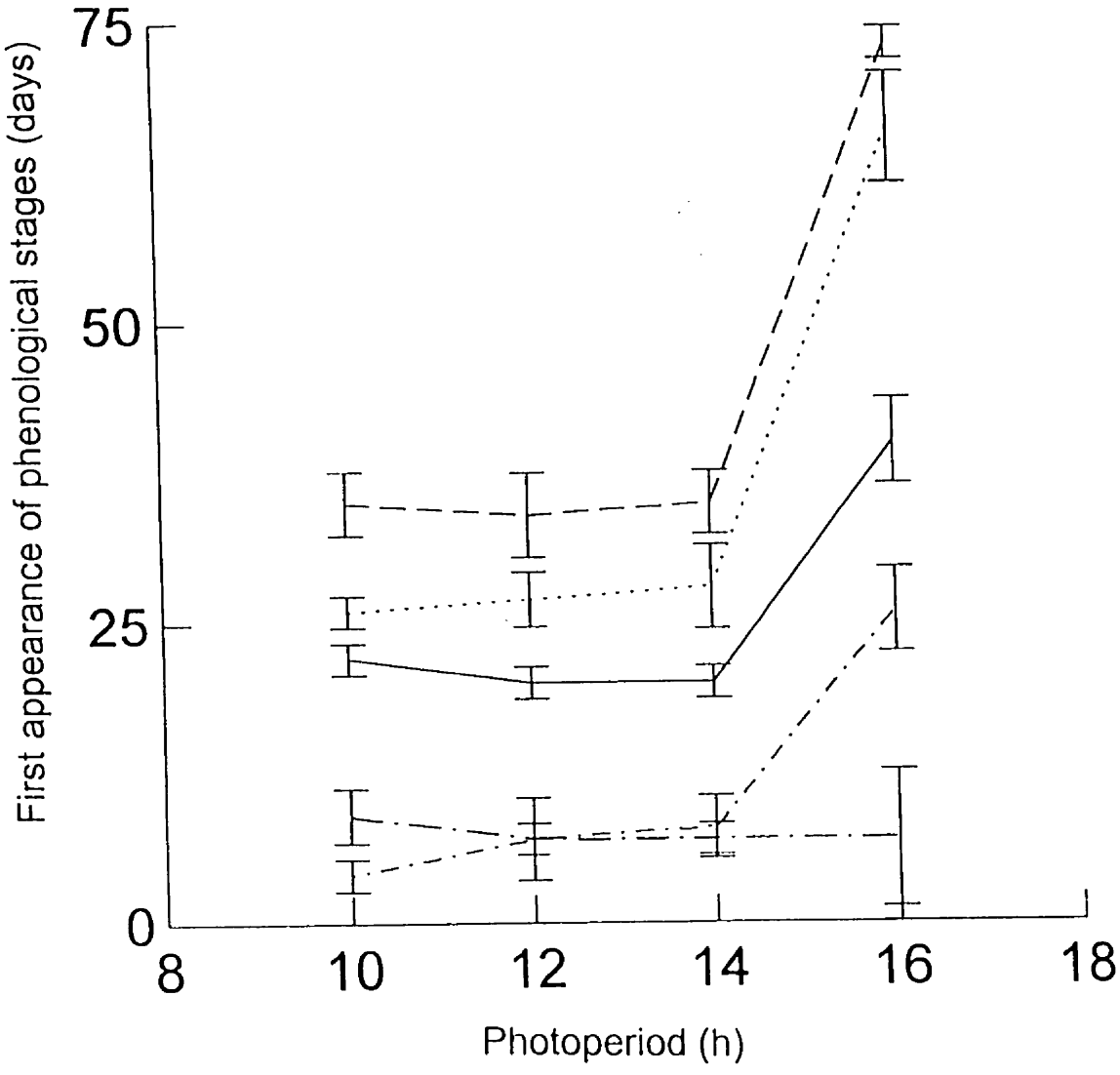
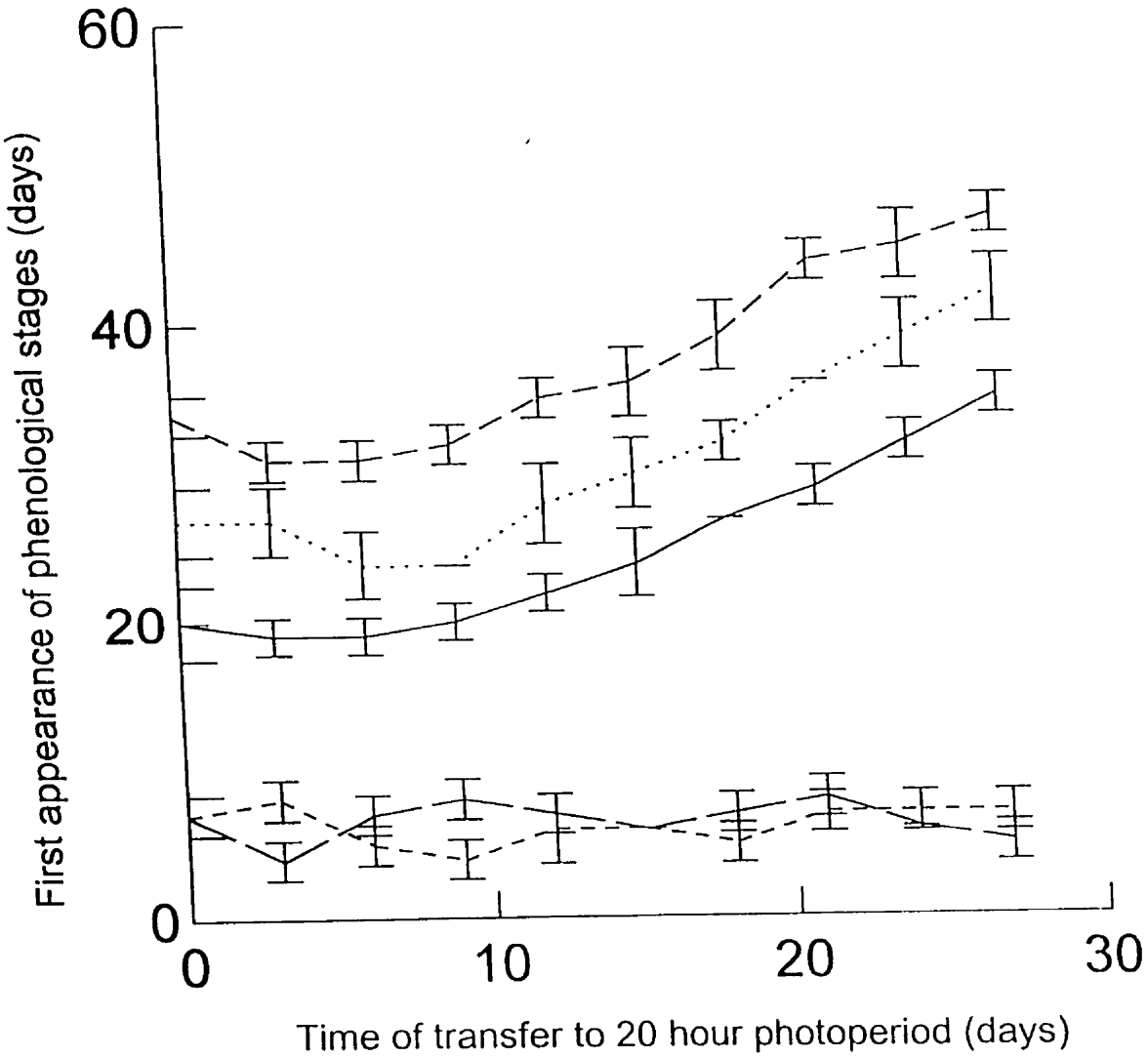

75
50
25
0
First appearance of phenological stages (days)
8
10
12
14
16
18
Photoperiod (h)

Figure 4: Effects of the time of transfer from a long day photoperiod (20 hour) to a short day photoperiod (8 hr) on days to first appearance of phenological stages: staminate involucre (———), first pistillate flower (- - - -), first dehiscence (— — —), and interval from staminate involucre to pistillate flower (- - -), and the interval from pistillate flower to dehiscence (—— —— ——) of common ragweed. Vertical lines represent standard error of means.


60
40
20
0
0
10
20
30
First appearance of phenological stages (days)
Time of transfer to 20 hour photoperiod (days)

CHAPTER 2: Photothermal Time Describes Common Ragweed (*Ambrosia artemisiifolia L.*) Phenological Development and Growth

Abstract. The ability to predict weed phenological development under field conditions is fundamental to the development of mechanistic weed-crop competition models. In this study, phenological development of common ragweed grown under field conditions could be explained using temperature and photoperiod responses derived from growth room experiments. It was also determined that the relationship between phenological development and common ragweed leaf area, dry matter production and partitioning. Phenological development of common ragweed emerging at different times in the field was described by photothermal time based on temperature and photoperiod responses derived from growth room experiments. Estimated dates of phenological events of common ragweed were within 4 days of recorded values. Common ragweed seedling density did not influence phenological development. Common ragweed leaf area development, biomass partitioning, and total biomass were related to photothermal time accumulation. The results of this study are consistent with a hypothesis that phenological development is a major factor influencing the outcome of weed-crop competition. Results obtained from this study could be incorporated into a mechanistic model of weed-crop competition.

Nomenclature: Common ragweed, *Ambrosia artemisiifolia* L. #[4] AMBEL;

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[4]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA.

Introduction

Successful development of mechanistic weed-crop competition models requires prediction of weed phenological development under field conditions. A mechanistic approach to describing weed-crop competition considers environmental variation due to location, year and management (Chikoye et al. 1996; Kropff 1988; Weaver et al. 1992; Wilkerson et al. 1990). As a result, mechanistic models more accurately predict the outcome of weed-crop competition than traditional empirical models. Mechanistic weed-crop competition models are driven by functions describing underlying growth processes. In these models, weed and crop growth processes are determined by phenological development and environmental conditions (Chapman et al. 1993; Ghersa and Holt 1995; Grant 1989; Miller et al. 1993).

Plant phenological development largely determines growth potential through its impacts on processes such as dry matter partitioning. The hypothesis is that photothermal time, through its effects on phenological development, is a major factor influencing the outcome of weed-crop competition (see also Deen et al. 1998). Leaf area development, plant height, leaf area duration, and assimilate partitioning have been described as functions of weed phenological status (Ghersa and Holt 1995;Tworkoski 1992; Wall and Morrison 1990). Weed phenological development, through its effects on these and other growth processes, determines a plant's ability to compete for resources such as irradiance, moisture and nitrogen.

Phenological development is primarily controlled by temperature and photoperiod (Hodges 1991). Plant phenological response can be described by photothermal time which is simply the accumulation of thermal time adjusted by a factor

based on daylength (Hunt and Pararajasingham 1995). This response to temperature and photoperiod has been demonstrated for common ragweed (Deen et al. 1998), redroot pigweed (McLachlan et al. 1993), velvetleaf (Patterson 1995), and several other species (Flint et al. 1984; Patterson 1993). For all species there existed a base temperature below which little or no development occurred. As temperature increased above this base temperature, the rate of development increased with temperature up to an optimum, after which it declined. During the photoperiod sensitive phase of these weed species, duration of day length (i.e. photoperiod), in addition to temperature, determined the rate of phenological development (Deen et al. 1998; Major and Kiniry, 1990; Patterson, 1995). The temperature and photoperiod responses derived in these studies were all determined from controlled environment studies. Whether these responses can be combined using a concept of photothermal functions and applied directly to weeds grown under field conditions has not yet been confirmed. The applicability of these responses and the importance of other factors, such as soil moisture and nitrogen status, on phenological development must be determined under field conditions.

Relative to temperature and photoperiod response, the phenological response of crop plants to moisture, nitrogen, or irradiance levels experienced under field conditions is considered minimal (Major and Kiniry 1991). Previous studies (eg. Bridges and Chandler 1989; Yegappan 1986) have indicated that these stresses must be severe in order for phenological development to be affected. For example, Deen et al. (1998) found that irradiance level will reduce rates of phenological development in common ragweed however, this only occurred at levels of 150 umol m^{-2} s^{-1} in combination with low

temperatures. McLachlan et al. (1993) determined a similar irradiance response for redroot pigweed.

In a previous study (Deen et al. 1998), it was reported that temperature and photoperiod were major environmental variables influencing phenological development of common ragweed grown under controlled conditions. If these results determined in controlled environments can be used to predict phenological development of common ragweed in the field, then development of a mechanistic weed-crop competition model could be possible. Therefore, an objective of the present study was to determine if photothermal time based on temperature and photoperiod responses derived under growth room conditions provides a basis for explaining phenological development of common ragweed grown in the field with differing emergence dates and seedling densities. A second study objective was to determine the impact of phenological development on common ragweed growth as influenced by differing times of emergence and seedling densities.

Materials And Methods

Experimental locations. Field experiments were conducted in 1994 and 1995 at Woodstock, Ontario. Soil type at Woodstock was a Guelph silt loam (Grey Brown Podzolic; 53% sand, 34% silt, 12.5% clay, 3.3% organic matter, pH 7.1). The experimental design was a split plot design with four replicates. The main plot factor was weed density and the split plot factor was emergence date. Treatments consisted of two weed densities and three common ragweed emergence dates.

Weather conditions. Rainfall varied both in total amount and in distribution over the 2 year study period (Table 4). In 1994 and 1995 total rainfall for the growing season (May to September) was 435 mm and 390 mm, respectively. The thirty year average for the region is 370mm per year. Rainfall delayed planting in 1994 compared to 1995. Moisture for the various planting dates was sufficient to allow uniform emergence of all treatments, although the emergence of the third planting date in 1994 appeared to be delayed by a combination of low rainfall and high temperatures.

Experimental procedures. Tillage for both years consisted of spring cultivation. Common ragweed seed were collected in the fall of 1992 from the experimental site and stored at -5 C. Prior to sowing, seeds were soaked in water at room temperature for 48 hours to aid in uniformity of germination. Germination of the seed lot was greater than 85% based on germination tests conducted in 1995. Planting occurred on May 21 and May 8 in 1994 and 1995, respectively. The second and third planting dates were June 2 and June 14, 1994, and May 23 and June 6, 1995. For each planting date, common ragweed seed was seeded to a depth of 1 cm. Common ragweed emergence for the three consecutive planting dates occurred on May 27, June 11, and June 24 in 1994, and May 16, June 1 and June 13 in 1995. Dates were based on 50% emergence. Common ragweed seedlings were thinned at the two true leaf stage to give the desired plant densities of 1.5 and 4.5 plants per m^2. Common ragweed plants were equidistantly spaced in the plot. The plots were 7.0 metres long and 10 rows wide. Inter-row space was kept weed-free by hand-hoeing.

Leaf number, plant height and date of 50% main stem terminal bud appearance (i.e date when 50% of plants had visible terminal buds on the main stem) were measured each year on five plants per plot. In 1995 the date of 50% dehiscence (i.e. date when

50% of plants had visible dehiscence of staminate involucres) was also recorded. Leaves greater than 1 cm^2 in size on the main stem were counted at regular intervals until the reproductive phase was initiated. Reference leaves were marked to ensure accurate counts if leaf senescence occurred.

Above-ground biomass was harvested 2, 4, 6, 8 weeks after seedling emergence. A fifth harvest was obtained 12 and 10 weeks after emergence in 1994 and 1995, respectively. A final harvest immediately followed the first killing frost of the season (-2 C). For each treatment, four common ragweed plants were sampled per plot. Common ragweed plants were partitioned into leaves, stems and, if present, staminate flower parts. Samples were dried at 80 C until dry weights stabilized. Only total above ground biomass was measured at final harvest. Leaf and stem weight ratios were calculated using leaf and stem biomass as a percent of total above ground biomass.

Common ragweed phenological development results were analysed using the CROPSIM model framework (Hunt and Pararajasingham 1995). Phase durations and responses to photoperiod obtained by Deen et al. (1998) were incorporated into this framework. The CROPSIM framework uses a temperature response based on cardinal temperatures. These values were estimated using data from Deen et al. (1998). The model was calibrated using both years of data by adjusting parameter estimates until predicted and measured phenological events were similar. Calibrated parameter values and phase durations used in the CROPSIM model are given in Table 5. To obtain an estimate of model phenological event prediction variability, simulations were conducted for all combinations of three seeding depths (0.5, 1.5 and 2.5 cm) and three soil types (silty-loam, loam, and loam-clay).

Statistical analysis. Data from each year and harvest date were combined and, when necessary, log transformed to equalize variance. Analysis of variance was used to test for treatment main effects, year by treatment interactions, and for density by planting date interactions[5]. Due to the presence of year by treatment interactions and density by planting date interactions, results were presented separately for each year and density. Data were back transformed for presentation. Means for biomass and leaf area were separated using Fischer's Protected LSD at the 5% level of probability. Means and standard errors for simulated and observed phenological results were calculated. Appropriateness of the phenological model was assessed by plotting deviations between mean simulated and recorded values.

Results And Discussion

Photothermal time described phenological development under field conditions: Growth room derived temperature and photoperiod responses (Deen et al. 1998) incorporated into the CROPSIM model provided a good basis for describing phenological development of common ragweed grown under field conditions (Table 6). Cardinal temperatures did not require adjustment, but the photoperiod response required minor changes. Deen et al. (1998) determined that for each 1hr increase in day length the rate of common ragweed development decreased by 49% and 58%, before and after main stem terminal bud, respectively. Values for photoperiod responses before and after main stem terminal bud were adjusted in the model to -50% and -60%, respectively, indicating a slight difference in photoperiod response across phenological stages. Estimates

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5 [SAS] Statistical Analysis Systems. 1990. SAS User's Guide. Version 6.06. Cary, NC: Statistical Analysis Systems Institute.

derived using these adjusted responses were within 4d of the recorded values for phenological development under field conditions. For example, for the first planting date in 1994 recorded and simulated appearance of 50% main stem terminal bud were julian dates 199 and 202, respectively. Residuals (differences between recorded and estimated dates expressed as a percent of recorded dates) were all within 7% of recorded julian dates except for the third planting date in 1994 where residuals exceeded this value (data not shown). For this treatment, at both densities, seedling emergence values were underestimated.

The time of common ragweed seedling emergence was underestimated by 5d for the third planting date in 1994 (Table 6). Thermal time alone did not sufficiently describe seedling emergence. Measured precipitation was minimal for the two weeks prior to this planting date and for approximately 10 day after planting (data not shown). Consequently, for this planting date soil moisture in the upper 2 cm was relatively low. Daily temperatures following planting, however, were close to optimal (Table 4). Simulated emergence occurred rapidly, due to optimal air temperatures whereas recorded emergence was delayed under conditions of limiting soil moisture. This relationship between temperature, osmotic potential, and plant emergence was also demonstrated in work conducted by E. Roman (1998). Roman found that accuracy of simulation estimates of common lamb's-quarter's (*Chenopodium album* L.) emergence was greatly improved when osmotic potential was combined with temperature in a hydrothermal time calculation. Under moist soil conditions, such as occurred for planting date 141 of 1994 and 128 and 157 in 1995 (Table 4), emergence could be described as a function of temperature. For these planting dates, estimated and recorded days of emergence were within one day of each other (Table 6).

Leaf appearance on the main stem, used as an indicator of phenological development (Tollenaar et al. 1984), was a function of thermal time under field conditions (Figure 5). Deen et al. (1998), determined that 1.02 leaves appeared for each biological day, Bd, (i.e. a day at an optimal temperature of 31.7C and an optimal photoperiod). In order to simulate accurately leaf appearance in the field, this value was adjusted to 1.10 leaves/Bd. This adjustment accounted for differences in air versus leaf temperature relationships in the field compared to controlled environment conditions, as discussed by Deen et al. (1998). In addition, the rate of leaf appearance prior to the two true leaf stage was adjusted to 0.37 leaves/per day. This adjustment was made to account for a slower rate of leaf appearance that occurred during the establishment phase of the common ragweed seedling (data not reported). Residual values for leaf number based on these relationships were generally less than 15% (Figure 6).

Final leaf number on the main stem was influenced by emergence date (Table 7). For example, the first planting of common ragweed in 1995 had 35 leaves on the main stem, compared to 26 leaves for common ragweed planted four weeks later. This difference in final leaf number was due to differences in thermal time accumulation during the period from the juvenile phase to the main stem terminal bud. Due to photoperiod effects on phenological development, later emerging common ragweed had a smaller interval between the juvenile phase and main stem terminal bud phase compared to early emerging common ragweed. As a result of this smaller interval, less thermal time was accumulated and fewer main stem leaves were produced.

Phenological development of common ragweed was influenced by planting date but not by seedling density (Table 8). Year and year by planting date interactions also had a significant effect ($P<.01$)(data not shown). Planting date and year by planting date

interactions influenced the temperature and photoperiod conditions experienced by common ragweed and consequently affected photothermal accumulation. Previous studies have also shown phenological development under field conditions was primarily determined by temperature and photoperiod (Goyne and Schneiter 1988; Senseman and Oliver 1993). Density had no impact on temperature and photoperiod conditions and, consequently, did not impact phenological development. The lack of a density effect indicated that phenological development was not influenced by common ragweed growth characteristics or intraspecific plant competition.

Common ragweed leaf area development, biomass partitioning and final biomass was affected by phenological development and photothermal time. Leaf area development of common ragweed ceased once dehiscence was initiated (data not shown). Date of dehiscence for early and late emerging common ragweed did not differ in 1995 (Table 8). The modulating effects of temperature and photoperiod caused a convergence of dehiscence dates and a reduced duration of leaf area development in later emerging common ragweed. Because dehiscence dates did not differ, the maximum leaf area for later emerging common ragweed was significantly less than for early emerging common ragweed.

Phenological development of common ragweed also influenced biomass partitioning patterns (Table 9). For both densities, initial leaf weight and stem weight ratio measurements did not differ (Figure 7 and 8). At time of initial sampling, all plants were partitioning 75-80% of above ground biomass to leaf production. Over time partitioning to leaves decreased and stems increased. For 1.5 common ragweed plants m^{-2} emerging early in 1995 (julian date 147), for example, allocation of above ground biomass to leaves 56 days after emergence was reduced to 57%. Leaf weight ratios

declined and stem weight ratios increased most rapidly over time for later emerging common ragweed (Figure 7 and 8). Later emerging common ragweed developed more quickly due to temperature and photoperiod effects and, consequently, increased biomass allocation to stems more rapidly. Consequently, phenological changes in biomass partitioning also restricted maximum leaf area of late emerging weeds by reducing biomass available for leaf area development.

Phenological development, as affected by photothermal time, influenced the final total biomass of common ragweed emerging on different dates (Table 10). In 1994, for example, early emerging common ragweed (julian date 147) at a low density yielded 5500 kg/ha total biomass versus only 2900 kg/ha for common ragweed emerging four weeks later. This occurred in spite of early emerging common ragweed seedlings having lower rates initially of biomass accumulation compared to later emerging seedlings (Figure 9). In 1995, for example, common ragweed seedlings that emerged early (julian date 136) had accumulated approximately 1000 kg/ha during the first eight weeks of growth compared to compared to approximately 2700 kg/ha for common ragweed emerging 4 weeks later on julian date 164. The rate of biomass accumulation could be attributed to lower temperatures early in the season. Low temperatures reduced leaf appearance rates per chronological day, and could also have influenced leaf expansion rates or assimilate production available for leaf area development. Flint et al. (1984) demonstrated similar effects of temperature on leaf area development and biomass production in three weed species. Lower initial rates of biomass accumulation for early emerging common ragweed were offset by an increased duration of leaf area development and greater biomass partitioning to leaves.

This study indicated that temperature and photoperiod were the main factors affecting phenological development of common ragweed grown under field conditions. Responses to these environmental factors were taken from a previous growth room study and combined using the concept of photothermal time. These responses required only minor calibration within the CROPSIM model to provide a good description of the development of common ragweed grown under field conditions with differing times of emergence and seedling densities. Interactions between temperature and photoperiod were not considered and do not appear to be significant over the range of photoperiods and temperatures experienced during this study. Once common ragweed had emerged, moisture status and seedling density did not affect common ragweed development. Prior to emergence however, moisture stress was an important factor in determining developmental processes leading up to emergence.

This study confirmed that temperature and photoperiod responses derived from growth room studies can be used to simulate common ragweed phenological development in the field. The results from this study also support the hypothesis that phenological development is a major factor influencing the outcome of weed-crop competition. It was demonstrated that phenological development influenced biomass accumulation by determining leaf number, leaf area development, and biomass partitioning. Biomass accumulation is an indicator of a plant's ability to capture resources, such as light, moisture and nutrients. As such, biomass is also an indicator of the potential competitive ability of the weed. Results obtained from this study can be incorporated into a mechanistic model of weed-crop competition.

Table 4: Average daily temperature and precipitation in 1994 and 1995 at Woodstock, Ontario.

Month	Temperature (C)			Precipitation (mm)		
	1994	1995	30 year average	1994	1995	30 year average
May	11.6	12.8	12	124	96	70
June	19	19.7	18	95	78	78
July	20.5	20.7	20	124	51	80
August	17.5	21.5	19	71	138	70
September	15.6	13.7	15	21	27	74
Total	-	-	-	435	390	372

Table 5: Calibrated parameter values used in the CROPSIM model.

Parameter	Value
Cardinal temperatures (C)	
Minimum	0.9
Optimal	31.7
Maximum	40
Photoperiod response	
Maximum optimum photoperiod (h)	14.5
Photoperiod sensitivity (%/h)	
- juvenile phase to main stem terminal bud	-50
- main stem terminal bud to pistillate flower	-60
Phase durations (biological days[a])	
Germination [b]	3.5
Germination to end of juvenile phase [c]	7
Germination to main stem terminal bud [d]	11.5
Main stem terminal bud to pistillate flower [d]	4.5
Pistillate flower to anthesis [c]	4.5
Node appearance rate (no. /biological day)	0.55
Leaves per node (no.)	2
Hypocotyl extension rate (mm/biological day) [e]	90

Table 5 (cont.): Calibrated parameter values used in the CROPSIM model

[a] Days at optimal temperature, photoperiod and no nitrogen or water stress. Phase durations determined by Deen et al. (1998) were adjusted to optimal temperatures using the temperature response function also in Deen et al. (1998)

[b] Required 0.1 mm extractable water per mm depth in the seed zone.

[c] Temperature sensitive

[d] Photoperiod and temperature sensitive

[e] Modified by temperature and water stress.

Table 6: Recorded and estimated julian dates of emergence, main stem terminal bud and dehiscence appearance of common ragweed grown at Woodstock, in 1994 and 1995. [abc]

Year	Planting Date	Recorded Emergence	Estimated emergence[d]	Recorded main stem terminal bud	Estimated main stem terminal bud [d]	Recorded dehiscence	Estimated dehiscence [d]
1994	141 (May 21)	147	148.0(0.7)	202.0(0.7)	199.0(0.2)	-	225.0(0.2)
1994	153 (Jun 2)	162	159.0(0.6)	205.0(0.2)	201.0(0.2)	-	227.0(0.0)
1994	165 (Jun 14)	175	170.0(1.3)	213.0(0.2)	205.0(0.2)	-	229.0(0.3)
1995	128 (May 8)	136	136.0(0.9)	195.0(0.3)	195.0(0.6)	224.0(0.7)	220.0(0.1)
1995	143 (May 23)	152	150.0(0.8)	199.0(0.7)	201.0(0.2)	224.0(0.3)	222.0(0.0)
1995	157 (Jun 6)	164	163.0(0.7)	204.0(1.0)	203.0(0.3)	225.0(0.3)	223.0(0.2)

Table 6. (cont.): Recorded and estimated julian dates of emergence, main stem terminal bud and dehiscence appearance of common ragweed grown at Woodstock, in 1994 and 1995[abc] .

[a] Recorded data averaged over two common ragweed densities (1.5 and 4.5 plants/m^2).

[b] Estimated values are the average of 9 simulations of combinations of 3 planting depths (0.5, 1.5 and 2.5 cm) and three soil types (clay-loam, loam, silt-loam).

[c] Dashes indicate that data was not collected for 50% dehiscence in 1994.

[d] Estimates based on photoperiod and temperature responses assumed in Table 5.

Table 7: Final main stem leaf number for three emergence timings of common ragweed grown at Woodstock, Ontario in 1994 and 1995. [a]

Emergence Date [b]	1994	1995
	final leaf No. (+/-S.E.)	
1	32.0 (0.3) a	35.0(0.9) a
2	32.0 (0.4) a	34.0 (0.9) a
3	29.0 (0.2) b	26.0 (1.0) b

[a] Final leaf numbers within each column followed by the same letter are not different at P<.05 according to Fischer's Protected LSD Test.

[b] 1994 emergence dates were julian date 147(May 27), 162 (June 11), and 175 (June 24) ,respectively. 1995 emergence dates were julian date 136 (May 16),152 (June 1),and 164 (June 13), respectively.

Table 8: Analysis of variance F statistic for effects of year, common ragweed seedling density, planting date, and their interactions on log transformed 50% main stem terminal bud, 50% dehiscence, main stem leaf number, and final main stem leaf number of common ragweed grown in Woodstock in 1994 and 1995. [ab]

Source	Year	Main stem leaf number	Final main stem leaf number	50% main stem terminal bud	50% dehiscence
		F statistic			
Seedling density	1994	0.1	0.1	6.2	-
	1995	0.9	2	0.03	3
Planting date	1994	507.0***	56.7***	219.9***	-
	1995	62.0***	32.2***	35.2***	3.2
Density by planting date	1994	0.9	0.9	3.4	-
	1995	0.5	3.2	0.8	0.04

[a] * P=.05 to .01 , ** P= .01 to .001, *** P<.001

[b] Dashes indicate that data was not collected for 50% dehiscence in 1994

Table 9: Analysis of variance F statistic for effects of year, plant density, planting date, sampling date, and their interactions on log transformed leaf weight ratio, stem weight ratio, above ground dry weight, and above ground dry weight at maturity for common ragweed grown in Woodstock in 1994 and 1995. [ab]

Source	Year	Above-ground dry weight	Leaf weight ratio	Stem weight ratio	Above ground dry weight at maturity
		F statistic			
Seedling density	1994	478.1**	1.5	3.7	22.7*
	1995	291.9**	10.6*	7.8	12.4*
Planting date	1994	141.6***	97.5***	55.3***	15.0*
	1995	493.2***	93.8***	8.9**	5.9*
Density by planting date interactions	1994	3.8	0.6	0.9	3.3*
	1995	4.1*	3.5	0.46	4.6*
Sampling date	1994	3833.***	435.3***	165.4***	-
	1995	3070.***	429.0***	107.4***	-
Density by sampling date interactions	1994	17.3***	0.9	0.5	-
	1995	18.4***	7.9***	1	-

Planting date by sampling date interactions	1994	108.3***	8.4***	8.0***	-
	1995	51.3***	22.2***	4.4**	-
Planting date by sampling date by density interaction	1994	1.5	0.25	0.2	-
	1995	1.7	2.6*	0.14	-

[a] * P=.05 to .01 , ** P= .01 to .001, *** P<.001

[b] Dashes indicate that data was not collected for 50 % dehiscence in 1994 or that sampling date was not a factor.

Table 10: Above ground biomass at killing frost in 1994 and 1995 for two plant densities and three emergence dates of common ragweed grown at Woodstock , in 1994 and 1995. [a]

Emergence	1994		1995	
Date[b]	1.5 plants m^{-2}	4.5 plants m^{-2}	1.5 plants m^{-2}	4.5 plants m^{-2}
	kg ha^{-1} (+/- S.E.)			
1	5500 (288) a	8300 (814) a	6700 (446) a	6300 (549) a
2	5100 (160) a	7300 (1137) a	5900 (681) a	6400 (462) a
3	2900 (114) b	6300 (873) a	4000 (247) b	6100 (557) a

[a] Final canopy weights within each column followed by the same letter are not different at P<.05 according to Fischer's Protected LSD Test.

[b] 1994 emergence dates were julian date 147(May 27), 162 (June 11), and 175 (June 24) ,respectively. 1995 emergence dates were julian date 136 (May 16), 152 (June 1),and 164 (June 13), respectively.

Figure 5: Main stem leaf number (>1.0cm^2) versus days at optimal temperature and photoperiods (biological day) for common ragweed planted on three dates at Woodstock, Ontario in 1994 (julian dates 141-● , 153-○, and 165-■) and 1995 (julian dates 128-●, 143-○, and 157-■).

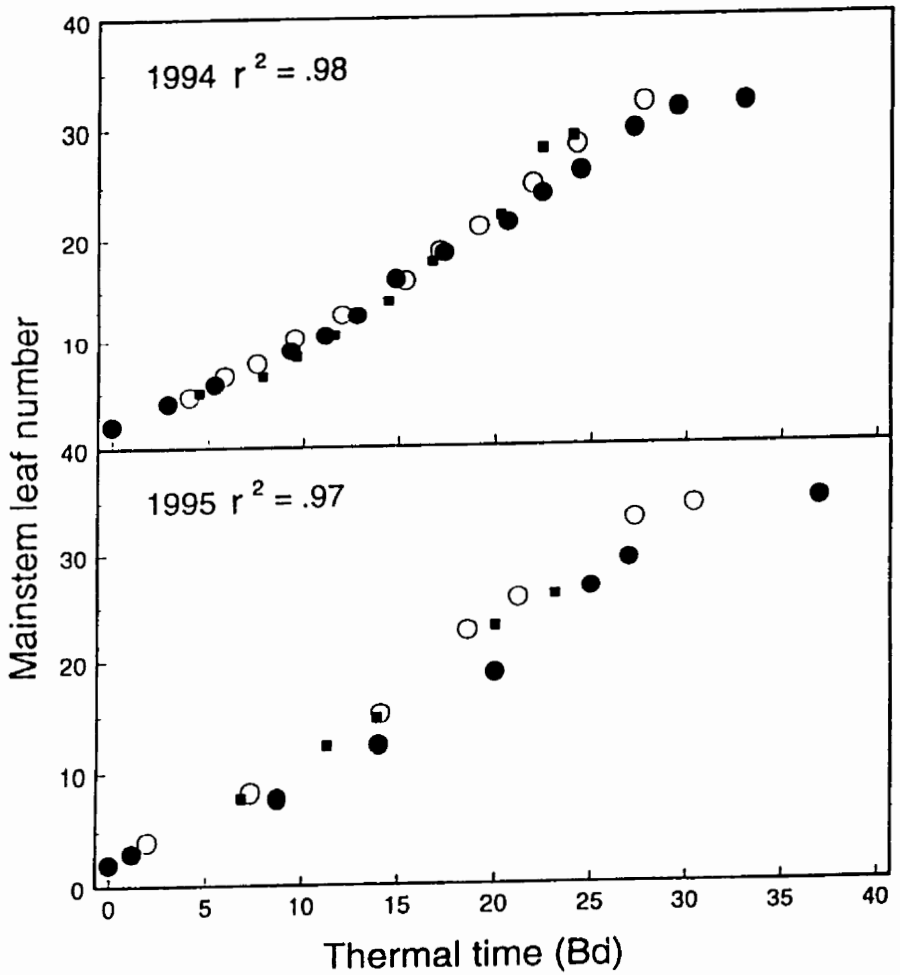

1994 r 2 = .98
1995 r 2 = .97
Mainstem leaf number
Thermal time (Bd)
0
10
20
30
40
0
5
10
15
20
25
30
35
40

Figure 6: Residuals (differences between recorded and estimated main stem leaf numbers expressed as a percentage of recorded leaf numbers) versus days after planting for common ragweed planted on three dates at Woodstock , Ontario in 1994 (julian dates 141-■ , 153- ▾, and 165-●) and 1995 (julian dates 128-□ , 143-▽, and 157-○).

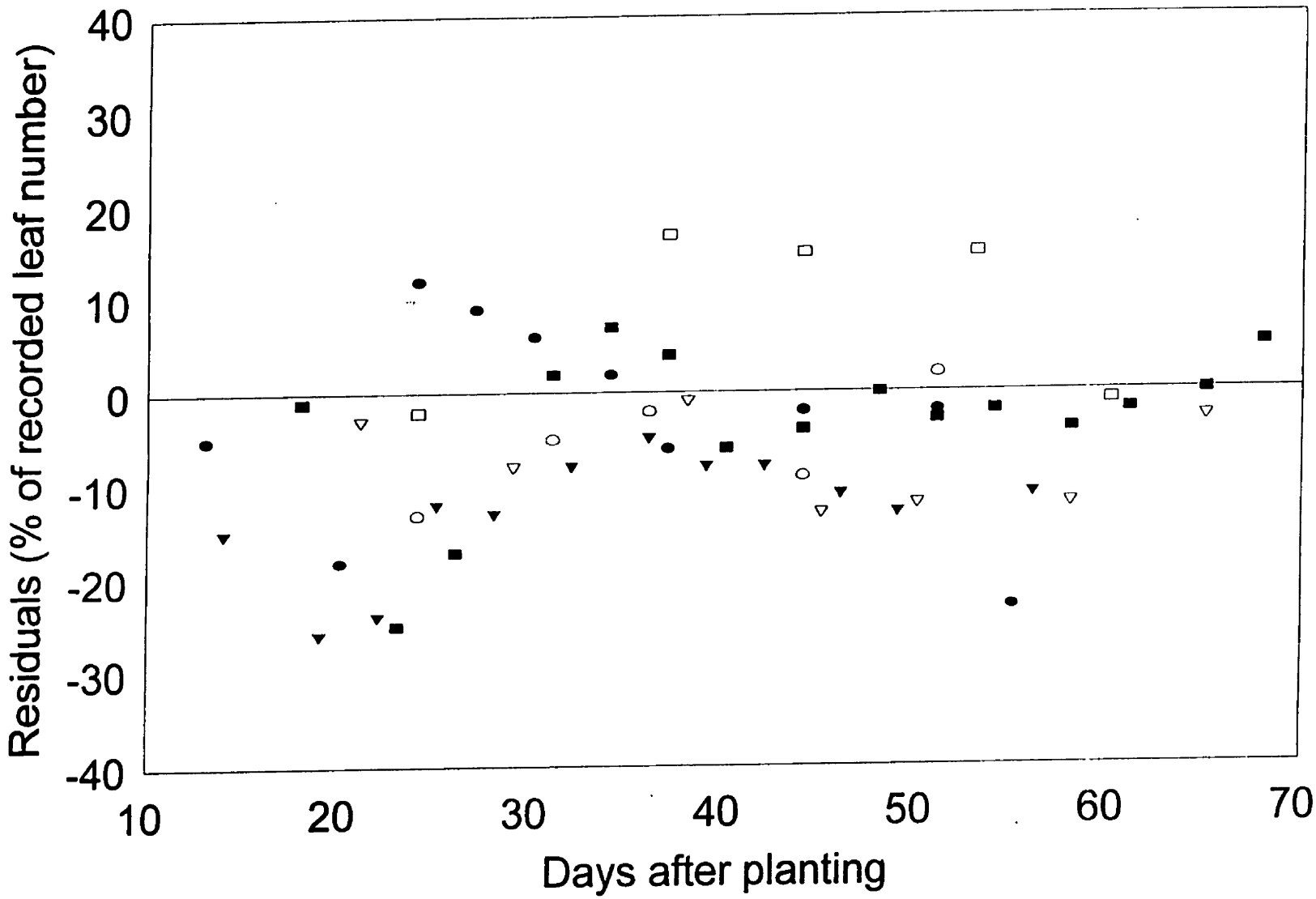

Residuals (% of recorded leaf number)
40
30
20
10
0
-10
-20
-30
-40
10
20
30
40
50
60
70
Days after planting

Figure 7: Leaf weight ratio (leaf biomass divided by total above ground biomass) of common ragweed emerging on three dates and at two densities at Woodstock , Ontario in 1994 (julian dates 147-● , 162--○, and 175-■) and 1995 (julian dates 136-● , 152-○, and 164-■). The same letters within density and days after emergence date indicate that leaf weight ratio means were not different at P<.05 according to Fischer's Protected LSD. NS indicates that the treatment effect was not significant when tested at P<.05 using ANOVA.

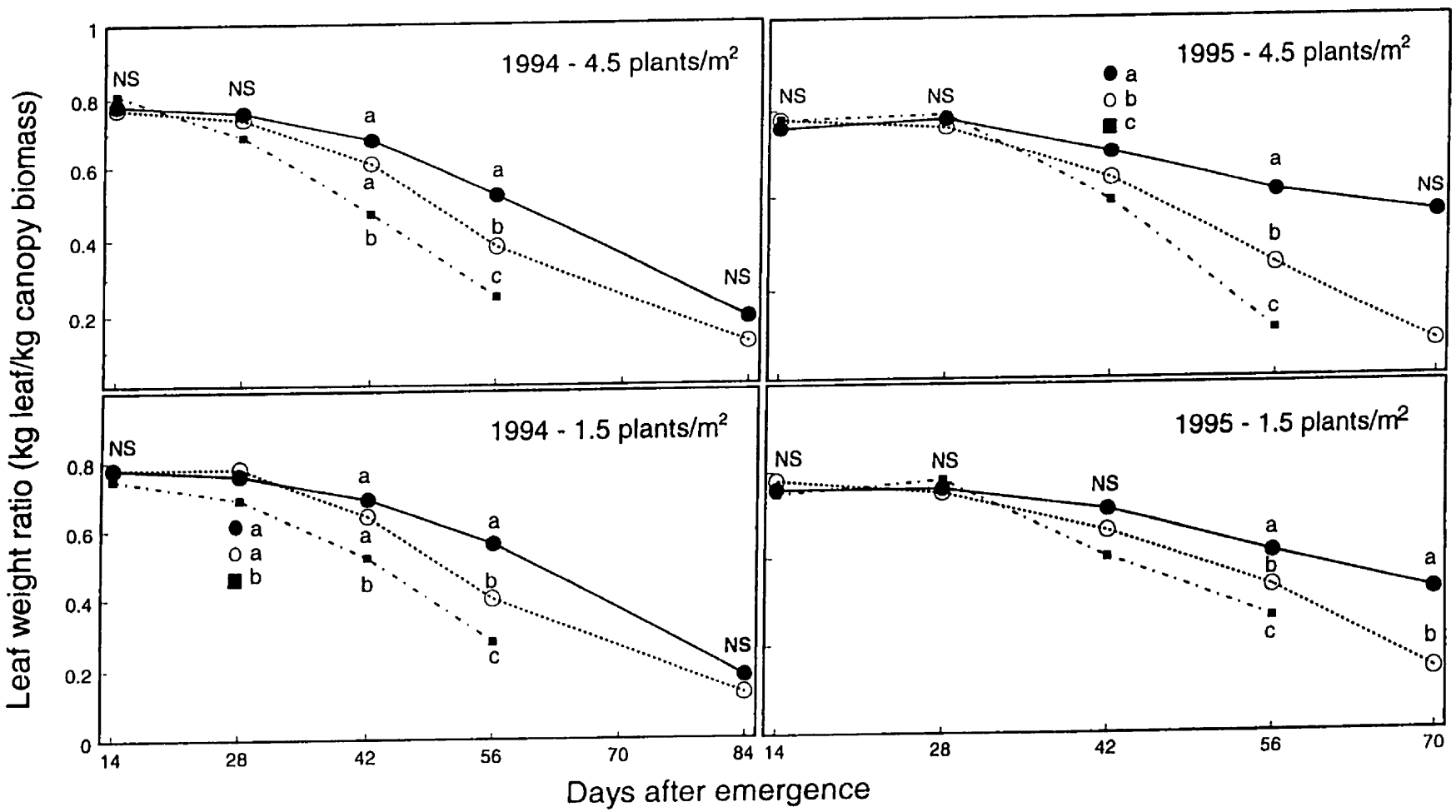

1994 - 4.5 plants/m²
1995 - 4.5 plants/m²
1994 - 1.5 plants/m²
1995 - 1.5 plants/m²
Leaf weight ratio (kg leaf/kg canopy biomass)
Days after emergence
NS
a
b
c
0
0.2
0.4
0.6
0.8
1
14
28
42
56
70
84

Figure 8: Stem weight ratio (stem biomass divided by total above ground biomass) of common ragweed emerging on three dates and at two densities at Woodstock , Ontario in 1994 (julian dates 147-● , 162-○, and 175-■) and 1995 (julian dates 136-● , 152-○, and 164-■). The same letters within density and days after emergence date indicate that stem weight ratio means were not different at P<.05 according to Fischer's Protected LSD. NS indicates that the treatment effect was not significant when tested at P<.05 using ANOVA.

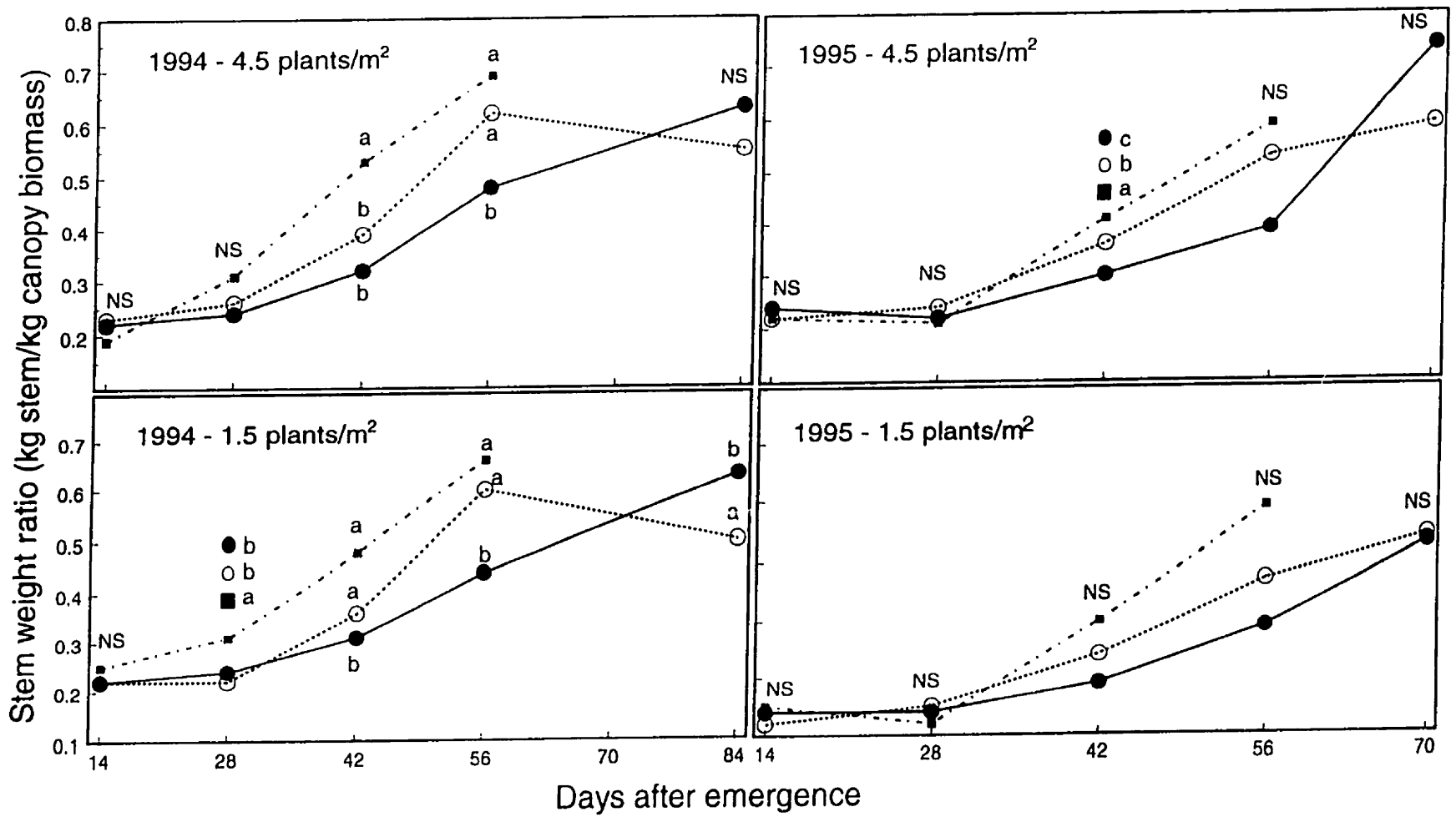
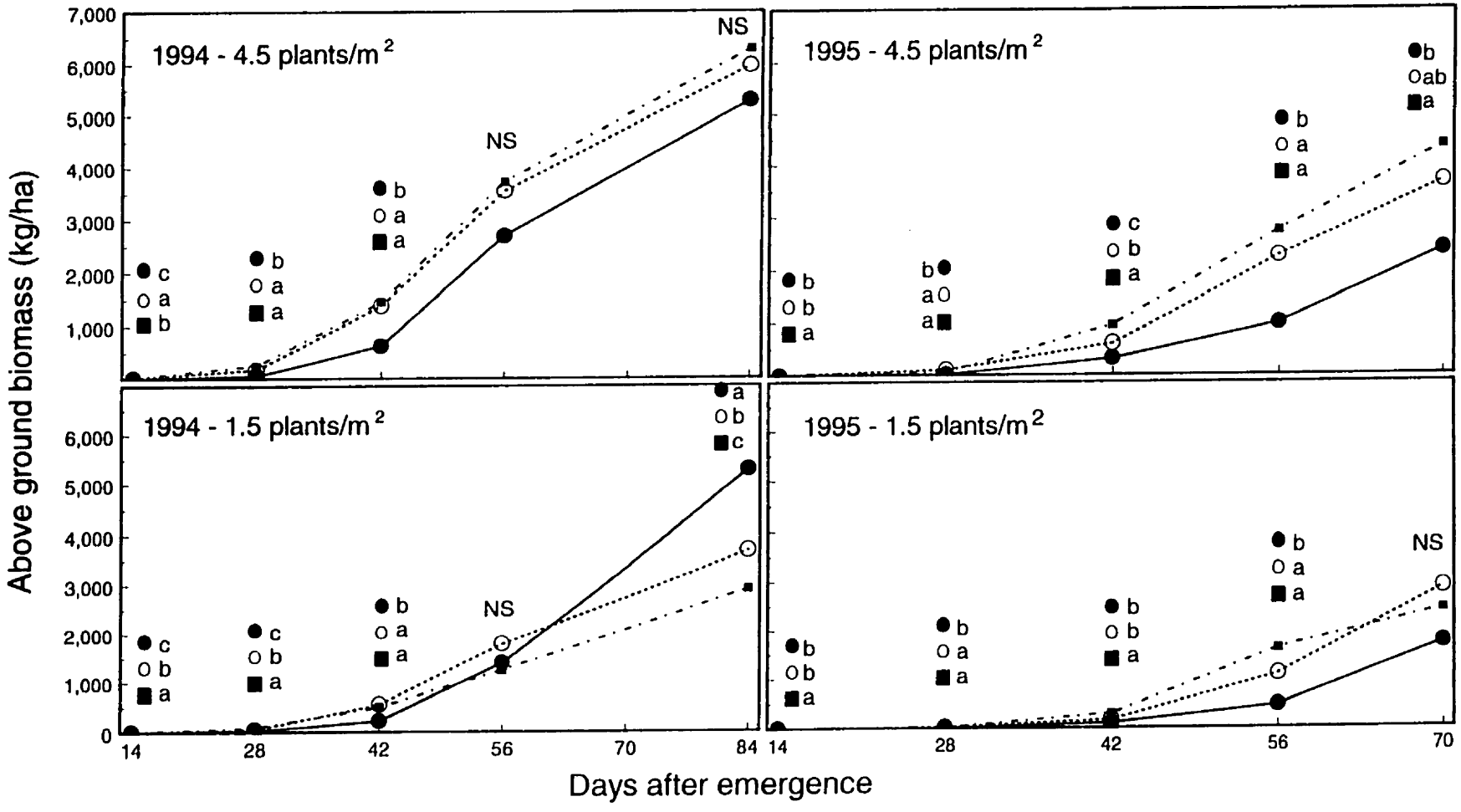

1994 - 4.5 plants/m²
1995 - 4.5 plants/m²
1994 - 1.5 plants/m²
1995 - 1.5 plants/m²
Stem weight ratio (kg stem/kg canopy biomass)
Days after emergence
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
14
28
42
56
70
84
NS
a
b
c

Figure 9: Total above ground biomass versus days after emergence of common ragweed emerging on three dates and at two densities at Woodstock , Ontario in 1994 (julian dates 147-● , 162-○, and 175-■) and 1995 (julian dates 136-● , 152-○, and 164-■). The same letters within density and days after emergence date indicate that above ground biomass means were not different at P<.05 according to Fischer's Protected LSD. NS indicates that the treatment effect was not significant when tested at P<.05 using ANOVA.


1994 - 4.5 plants/m 2
1995 - 4.5 plants/m 2
1994 - 1.5 plants/m 2
1995 - 1.5 plants/m 2
NS
Above ground biomass (kg/ha)
Days after emergence
7,000
6,000
5,000
4,000
3,000
2,000
1,000
0
14
28
42
56
70
84

CHAPTER 3: A Mechanistic Model of Common Ragweed (*Ambrosia artemisiifolia*) Growth and Development.

Abstract. A mechanistic model was constructed for ragweed growth and development based on the generic plant model CROPSIM. Adaptations were made to CROPSIM's growth and development subroutines to enable ragweed growth to be simulated. Data from field studies using a single source ragweed grown in monoculture and from the literature were used to parameterize the model. The influence of varying environmental conditions across years, densities and emergence timing on leaf number, leaf area, leaf weight, height, and biomass accumulation were accounted for by the model. Deviations between simulated and measured values generally fell within a range argued to be acceptable. Deviations outside this range tended to be associated with ragweed growth shortly after emergence, particularly when temperature and moisture extremes occurred during this time period. Sensitivity of a multi-species competition model to larger deviations at early stages of weed growth will need to be examined and future versions of the CROPSIM model may need to include more detailed algorithms for upper soil surface layer temperature and moisture conditions, and improved germination and emergence algorithms to reduce these deviations.

Nomenclature: Common ragweed, *Ambrosia artemisiifolia* L. #1 AMBEL;

Introduction

Weed competition with a crop has been modelled previously, using relatively simple empirical approaches. These models do not consider the dynamic nature of processes underlying weed-crop competition. While they can predict the outcome of weed-crop competition under a narrow range of conditions, they are unable to account for genetic and environmental variation across years, locations and managements (Dieleman et al., 1996; Knezevic et al., 1994; Lindquidst et al., 1996; Swanton et al., 1999). To predict the outcome of weed-crop competition across a wider range of conditions, models must account for the dynamic nature of the competition process. Weed-crop competition is dynamic because competition outcomes are influenced by relative responses of crop and weeds to moisture (Munger et al., 1987), nitrogen (Qasem, 1992; Sindel and Michael, 1992), cultural practices such as row spacing(Malik et al., 1993), planting date (Buchanan et al.,1980), and by the effects of emergence timing (Bosnić and Swanton,1997; Chikoye et al.,1995). The interaction of these variables with phenological development of both crop and weed is an additional complexity that must be considered in determining the outcome of competition. Finally, the relative competitiveness of a species at any given point in time will influence the future ability of that species to capture resources. A mechanistic approach to modelling can address this inherent deficiency of empirical weed-crop competition models.

Mechanistic models of weed-crop competition implicitly consider the dynamic nature of competition (Ball and Shaffer, 1993; Caldwell et al. 1995; Debaeke et al., 1997; Graf et al., 1990; Grant, 1994; Kiniry et al., 1995.; Kropff and van Laar, 1993;

Olesen et al. 1997; Weaver et al, 1992). They are process-oriented and consolidate, in mathematical terms, the various physiological and physical processes underlying crop and weed growth and development. They consider relative growth responses through time to environmental variables (Deen et al., 1998b), and are designed such that growth limiting resources are distributed among the species according to defined underlying physiological processes.

An understanding of the physiological processes involved in competition will improve crop management decisions. For example, Weaver et al. (1994) demonstrated that small differences in the timing of stem extension in winter wheat could have a large effect on outcome of competition with wild oats. Similarly, Dunan et al. (1994) used a mechanistic approach to determine optimal crop density levels that minimized weed competitive effects. Simulation models also represent a potentially powerful tool for predicting yield loss attributable to weed interference. Predictions can be made over a set of average and extreme environmental conditions for a wide range of cultural practices and soil types. "What if" scenarios can provide users with alternative answers or hypothesis for further testing (Kropff et al. 1992: Neeser et al., 1998).

A mechanistic model called CROPSIM, a generic plant model that is capable of simulating competition between 2 or more species is currently being developed. The model follows input standards developed by the International Consortium for Agricultural Systems Applications (ICASA) and is also modular in structure (Timlin et al., 1996). These two characteristics facilitate use of this model in conjunction with other models (eg. Decision Support System for Agrotechnology Transfer (DSSAT) models). CROPSIM also simulates nitrogen and water uptake and soil balances. In this paper adaptations made to the CROPSIM growth and development subroutines to enable

simulation of ragweed growth and development are described. The resulting ragweed model represents the first mechanistic model of ragweed growth and development. While considerable effort has focussed on the development of crop models, few mechanistic weed models have been developed . The utility of a mechanistic modelling approach to describe ragweed growth and phenological development as influenced by year, density and seedling emergence timing is demonstrated.

Materials And Methods

Model description. CROPSIM was developed as a generic mechanistic model of plant growth and development (Hunt and Pararajasingham, 1995). Physiological processes including phenology, leaf area development, dry matter production and partitioning, grain yield, water uptake, nitrogen uptake, and soil moisture and nitrogen balances are simulated on a daily or hourly time step. The model modifies the magnitude of processes occurring in a plant based on development stage, weather conditions and management effects on environment. CROPSIM was developed originally as a wheat model but has since undergone numerous revisions. These included the introduction of a generic format suitable for a wide range of species, a modular structure, generic algorithms for reading input, separation of tasks based on initialization, rate calculations and state variable updates, hourly time steps, ICASA input standards, capability to run multi-year simulations, and the capability to account for competition among species. In this paper the focus was the algorithms and parameters associated specifically with adaptation of CROPSIM for common ragweed growth and development.

Ragweed Development. Vegetative and reproductive development was based on parameters developed by Deen et al. (1998a) and Deen et al.(1998b). In CROPSIM, vegetative and reproductive development are separated into two distinct processes. Phenological development of the crop is assumed to be controlled by two independent variables, one controlling vegetative development and the other reproductive development. The rate of vegetative development is assumed to be affected by temperature alone while the rate of reproductive development (progression toward flowering/maturity) is affected by both temperature and photoperiod.

Vegetative and reproductive processes are assumed to have an identical temperature response based on the cardinal temperatures determined by Deen et al. (1998b). The three cardinal temperatures identified by Deen et al. (1998b) summarized a response curve in terms of a base temperature (0.9C) below which development is zero and above which development rate increases linearly up to an optimum temperature(31.7C) at which the rate of development is at a maximum. Above this optimum temperature, development rate decreases linearly until the highest temperature (40.0C) . At temperatures above this highest temperature development is again zero.

The effect of photoperiod is simulated using a function discussed by Major and Kiniry (1989). The photoperiod response is characterized by two parameters. The threshold photoperiod, expressed in hours, indicates the point at which photoperiod begins to delay development. For a short day species such as ragweed, photoperiods less than this threshold result in maximum development rates. Photoperiods above this threshold cause a reduction in development rate according to a photoperiod sensitivity parameter which indicates the percentage change in development rate. Biological days (Bd) are used to describe the duration of development phases and node appearance.

Biological days (Bd) can be defined as chronological days at optimal temperature and photoperiod with no nutrient or water stress.

Vegetative. Vegetative development stages are planting, germination, emergence, and leaf number on the main stem. For early vegetative development, the model assumes that seed has been stratified and is non-dormant. The period of exposure to cold temperatures (Baskin and Baskin, 1977; Bazzaz, 1974) necessary to overcome primary dormancy is assumed to have occurred. Algorithms for secondary dormancy, which is induced in ragweed if soil temperatures exceeds a maximum (Willemsen, 1975) are not included in the model. Germination in CROPSIM is assumed to occur at the maximum rate if there is more than 0.1 mm extractable water per mm depth in the seed zone. Assuming no further moisture stress, the process of ragweed germination occurrs after 3.5 days at optimal temperatures.

The length of time required for ragweed to emerge once germination has occurred is determined by temperature and moisture availability. At optimal temperatures elongation of the hypocotyl is set at 1.0 cm Bd^{-1} so that time to emergence varies with seed depth. The hypocotyl elongation rate uses the same temperature response described above for development.

Node appearance was shown by Deen et al. (1998a) to be a function of accumulated thermal time. Ragweed leaves were opposite i.e. two leaves per node on the lower main stem and became alternate higher up on the main stem. In this model, it is assumed that all leaves were opposite. Node appearance rate is 7.24 Bd $node^{-1}$ prior to the 2-leaf stage and 1.81 Bd $node^{-1}$ after the 2-leaf stage. The maximum number of nodes on the mainstem is set at 23.

Branch development is initiated once the threshold of 3.5 nodes or 7 main stem leaves is exceeded and ceases at midway point between pistillate flower appearance and beginning anthesis. Similar to leaf appearance, branch development is assumed to be a function of accumulated thermal time. Branches are initiated at a rate equal to the node appearance rate, but as main stem leaf number increases branch appearance rate increases according to a Fibonacci series(Gentry, 1978). Radiation interception by the canopy above 50% is assumed to result in a linear reduction in branch increase rate.

Reproductive development. The main reproductive stages, as specified by Deen et al. (1998b) are germination to end of juvenile phase (7.0 Bd), end of juvenile phase to main stem terminal bud appearance (4.5 Bd), main stem terminal bud appearance to pistillate flower appearance (4.5 Bd), pistillate flower appearance to beginning anthesis (4.5 Bd), and beginning anthesis to physiological maturity (14.5 Bd). Although there can be monoecious and dioecious plants in any ragweed population(Mckone and Tonkyn, 1986), typically only a small percentage of ragweed plants are dioecious. The model assumes that ragweed is a monoecious plant that exhibits all the specified phases.

Increments in development age are calculated as a function of the daily minimum and maximum temperatures and when appropriate the photoperiod status. For ragweed, suboptimal photoperiods are assumed to affect reproductive development from the end of the juvenile phase until the pistillate flower stage. Biological days are summed and as soon as the characteristic number of days for a particular phase are reached the succeeding phase is entered.

Dry Matter Production. CROPSIM calculates potential dry matter production from the daily intercepted photosynthetically active radiation, and radiation use efficiency. Intercepted photosynthetically active radiation is calculated from an exponential function of canopy area index (weed leaf and stem area) and a canopy extinction coefficient. The extinction coefficient for ragweed is assumed to be constant over the depth of the canopy and ranges from 0.90 to 0.75 depending on development stage. A radiation use efficiency of 2.2 g dry matter MJ^{-1} at 10 MJ m^{-2} d^{-1} is used as a standard. Radiation use efficiency is assumed to be a function of daily incident photosynthetically active radiation as described by Goudriaan and van Laar (1978). CROPSIM calculates potential dry matter accumulation by multiplying the radiation use efficiency by the amount of photosynthetically active radiation intercepted by the canopy. For ragweed potential dry matter accumulation is set at a maximum prior to the midway development point between main stem terminal bud appearance and pistillate flower appearance, decreases linearly above this point, and decreases at an accelerated linear rate once beginning of anthesis occurrs. CROPSIM adjusts potential dry matter accumulation by CO_2 concentration and by the minimum of factors representing the effects of temperature, vapour pressure deficit, water deficit, and nitrogen deficit.

Dry Matter Distribution. Dry matter is partitioned to roots and the canopy using root/canopy partitioning coefficients that are a function of growth stage. Initial values for this coefficient were taken from Gleeson (1986). Calibrated coefficient values range from 0.6-0.95 depending on developmental stage of ragweed.

Ragweed canopy assimilates are partitioned to leaves, stems and reserves. Assimilates for leaf growth are determined by subtracting stem and reserve assimilates

from total above ground assimilates. Initial coefficients for assimilate partitioning to stem, and reserves were again based on work done by Gleeson (1986). Calibrated values are based on developmental stage and canopy interception of photosynthetically active radiation (Begonia et al.,1991; McGiffen et al, 1992; Stoller and Myers, 1989). Assimilate partitioning to stems and reserves is the greatest during the period from the end of the juvenile phase to the terminal bud stage, a period roughly corresponding with stem elongation. Percentage of assimilates allocated to stem and reserve growth increases by .004% for each 1% increase in canopy interception above 50%. Reserves fraction decreases by .004% for each 1% increase in canopy interception above 50%. Stem growth continues until the median point between end of pistillate flower and beginning of anthesis stage. After this point all assimilates accumulate in a reserve pool.

Leaf Expansion and Growth. CROPSIM computes daily increments in main stem leaf area as a function of leaf appearance rate. For ragweed, the potential area of the first main stem leaf is 1.0 cm^2. Subsequent ragweed leaves on the main stem are potentially 60 % larger than the potential size of the previous leaf. The maximum leaf area size on the main stem is 65 cm^2. CROPSIM further adjusts actual leaf size by temperature, water deficits, and nitrogen deficits. Ragweed main stem potential leaf area continues to increase until the appearance of ragweed's terminal bud.

Leaf area on the branches of ragweed is a function of daily increment in main stem leaf size, branch number, and plant competition. Leaf growth potentials for branches one to seven, eight to sixteen and greater than 17 are of 0.8, 0.6 and 0.4 times the main stem leaf area potential, respectively. Potential branch leaf area decreases by 33% for each 10 % increase in canopy photosynthetically active radiation

interception above 60%. Leaf expansion of ragweed branches continues until the beginning of the pistillate flower stage.

Ragweed leaf dry matter accumulation is calculated from the potential leaf area on the mainstem and branches and the average specific leaf area which is set at 250 cm^{-2} g^{-1}. This value is adjusted by a factor which accounts for the impact of low temperatures. It is also increased by 25 % when canopy interception of photosynthetically active radiation exceeds 40%.

Leaf Senescence. CROPSIM records the age, dry matter, and area of the cohort of leaves produced on each day. Potential longevity of leaves produced on a given day are assumed not to vary with stage of ragweed development. Under ideal conditions, any given ragweed leaf has an expected longevity of 10.5 Bd.

Canopy Height. The rate of ragweed canopy height increase is assumed to be a function of development stage. Rate of height increase varies from .1 cm d^{-1} from emergence to the end of the juvenile phase, to 2 cm d^{-1} from mainstem terminal bud to the pistillate flower phase. These stage dependent rates are modified by factors accounting for PAR transmission through the canopy (i.e. an indicator of competition), as well as temperature and water stress. Both Dickerson (1968) and Gebben (1966) demonstrated that low to moderate levels of competition for light increased ragweed height whereas high levels of light competition decreased height probably due to assimilate limitations.

Stem Growth. CROPSIM computes potential stem dry matter accumulation from a defined ratio of the stem to the total canopy dry matter. Ragweed stem growth ceases at the midway point between pistillate flower appearance and beginning anthesis. Ragweed stem area is estimated from the stem dry weight using a standard area weight ratio factor of 10 $cm^2\ g^{-1}$.

Seed Production. Staminate and pistillate flowers are considered separately in the model reflecting the fact that ragweed is both a monoecious or dioecious plant (McKone and Tonkyn, 1986). Weight of each component is taken as a proportion of total above ground biomass (leaf, stem, and reserve biomass), with the proportion determined as a function of growth stage (Gleeson, 1986). The pistillate flower component at physiological maturity, for example, is assumed to be 25% of total above ground biomass. Seed production is estimated by multiplying pistillate flower biomass by a seed weight factor of 125 seeds g^{-1}.

Model calibration and statistical analysis. Field data on the effect of emergence timing and seedling density on common ragweed growth and development were used to calibrate the model. These data were from experiments conducted in 1994 and 1995 at Woodstock, Ontario. The experimental design was a split plot design with four replicates. The main plot factor was weed density and the split plot factor was emergence date. In each year, three ragweed emergence timings were evaluated, May 27, June 11, and June 24 in 1994, and May 16, June 1 and June 13 in 1995. These emergence dates were based on 50% emergence. In each year, ragweed seedlings were thinned to two densities, 1.5 and 4.5 plants m^{-2}. Plots were sampled five or six

times during the season for determination of leaf and stem biomass accumulation, leaf area index and height. Details of this experiment have been reported previously (Deen et al., 1998b). Data were subjected to log transformation to equalize variance and analysis of variance. Using these data, the model was calibrated by adjusting parameters which summarize plant morphological response to environment. These adjustments were made to minimize deviations, where deviations were defined as differences between measured and simulated values divided by measured values and expressed as a percentage (Mitchell and Sheehy, 1997).

The method based on the evaluation of deviations as advocated by Mitchell and Sheehy (1997) was used to assess the ability of the model to describe the data. In this evaluation an acceptable deviation level of 25% was used. As Mitchell and Sheehy (1997) indicated, ultimately, what constitutes an acceptable deviation can only be determined by evaluating the model for the purpose intended, in this case, for use as a component of a competition model. The level of accuracy required eventually will be determined through further testing. Deviations for ragweed leaf appearance, leaf are index, canopy height, canopy dry matter, and leaf weight are presented.

Results and Discussion

The CROPSIM model adapted for ragweed was able to account for significant effects of year, emergence timing, seedling density, and interactions of these factors on ragweed growth. Leaf area, canopy height, leaf weight, and canopy weight were all affected by year, emergence timing and density (Table 11). The CROPSIM model was run on a hourly time step using actual rainfall and temperature data as input and was therefore, able to account for the fact that environmental conditions varied across

treatments. For example, during August of 1995 temperatures were higher than in the same month in 1994 (Table 12). In 1994, however, there was more rainfall in the months of May, June, and July than during those same months in 1995. Ragweed growth was limited by temperature, precipitation stresses, and the timing of these stresses.

A common method for obtaining a quantitative measure is to plot simulated vs measured data for comparison against a 1:1 line (Mitchell and Sheehy, 1997), and to provide statistics on goodness of fit. Time course plots of ragweed leaf area index (Figure 10) and canopy height (Figure 11) showed reasonable agreement between simulated and measured data across years, emergence timing, and densities. While many studies use these methods of presenting model performance, this method does not give a quantitative assessment of performance. Mitchell and Sheehy argue that they flatter the model because the eye tends to assess the distance between the plotted point and the nearest point on the line and not the vertical gap between the point and the line. They argue that the better method for model assessment is to plot deviations between measured and simulated values . This method gives a better indication of model strengths, weakness, and biases. Identification of model weaknesses and biases is critical to the ongoing development process of models in that it indicates aspects of the model requiring improvement and further research and development.

Deviations for leaf area index, leaf number, leaf weight, canopy height and canopy dry matter tended to fall within a 25% limit, which was considered an acceptable starting target; indicating that the model was able to account for the effect of year, emergence timing, density and interaction effects (Figures 12-16, respectively). Fifty percent of deviations were within the acceptable range for simulated and observed data of leaf area, leaf number, leaf weight, and canopy weight as emergence timing was

delayed (Figure 12,13,14, and 16). This was consistent with expectations since leaf area development ended at the beginning of the pistillate flower stage of ragweed (Deen et al., 1998a, 1998b). In addition, 77% of canopy height deviations fell within the acceptable range (Figure 15). Consistent with recorded data, simulated canopy height decreased as emergence was delayed and increased with increasing density. Deviations which were greater than the acceptable range were primarily associated with measurements taken shortly after emergence, for the last planting date in 1994, and the first planting date in 1995. Sources of these deviations can be used to determine aspects of the model requiring further work

Deviations between simulated values and measured were greater at early stages for all variables (Figure 12-16). For example, leaf numbers (Figure 13) demonstrated greater deviations at early stages. Larger deviations at early stages occurred for several reasons. First, simulation errors and measurement errors as a percentage of actual values tended to be larger. Also, deviations were further accentuated at early stages by deviations between simulated and observed emergence timings. These two factors caused higher deviations at early stages of weed growth.

Higher deviations at early stages of weed growth will be important in a multi-species competition model. Competition outcome between crops and weeds is determined early in the growing season. Relative time of emergence of crops and weeds, for example, has been shown to be an indicator of potential yield loss from weeds (Bosnic and Swanton, 1997; Chikoye et al., 1995; Knezevic et al., 1995). The species that emerges first obtained the advantage for water, light and nutrients . Research must be conducted to determine the importance of higher deviations at early growth stages on the simulated outcome of crop and weed competition.

The model also overestimated leaf area index, leaf weight and canopy weight at both densities for the last planting date in 1994. This was attributed to the model's inability to simulate seedling emergence date. The observed date of 50% emergence was June 24 whereas the simulated emergence date was June 18. Two factors contributed to this lack of accuracy. First, prior to planting the last appreciable rainfall had occurred fourteen days previously, as a result the soil was relatively dry at the time of planting. Accentuating the drought was the fact that the ragweed seed was only planted 1.0 cm deep, a soil depth that is particularly prone to drought conditions. While the CROPSIM model accounted for the effects of dry soil on germination, the models ability to simulate moisture conditions for the upper 1.0 cm soil layer were probably limiting. The other factor reducing model accuracy was the use of air temperatures to determine germination and emergence from the soil. For a period of four days following planting the maximum air temperature was approximately 35C. Under dry soil conditions soil temperature to a depth of 1.0 cm may have exceeded the maximum temperature of 40 C set within the model. Accurate simulation of weed seedling emergence relative to the crop is required in competition models (Bosnic and Swanton, 1997; Chikoye et al., 1995; Knezevic et al., 1995; O'Donovan et al., 1985; Weaver et al., 1992) . Given the importance of emergence timing and the fact that many small seeded weed species, such as ragweed tend to emerge from the upper 1.0 cm soil layer (Dickerson, 1968; Willemsen, 1975), inclusion of more complex algorithms to simulate temperature and moisture conditions in the upper 1.0 cm of soil may be warranted.

Deviations also tended to be higher than the acceptable range under low soil temperature conditions. Minimum air temperatures were between 0C and 5 C for approximately two weeks following the first ragweed planting date at both high and low

seeding densities in 1995 (data not shown). Although the upper 1.0 cm soil layer may have been warmed sufficiently for germination and seedling emergence, cool soil temperatures may have reduced early season ragweed root growth. The effects of soil temperature on root growth of weed seedlings needs to be incorporated into the CROPSIM model. In addition, the model was developed using ragweed from a single source in Ontario. As a result, the model implicitly assumes that ragweed biotype differences can be ignored. This may not be a valid assumption. Certain biotypes may be more competitive than others and may require specific parameters to be effectively used in a competition model.

In summary, a mechanistic model called CROPSIM, a generic plant model that is capable of simulating competition between 2 or more species is currently being developed. The objective of this work was to use this model to examine the effects of competition between crops and weeds. In this paper are described the changes made to the growth and development subroutines to enable simulation of ragweed growth and development.The resulting ragweed model accounted for the influence of environmental conditions across years, density, and emergence timing on ragweed leaf number, leaf area, leaf weight, height, and biomass accumulation. It was found that deviations between simulated and measured values tended to be greatest for early season ragweed growth, particularly when temperature and moisture extremes occurred during this time period. The sensitivity of a multi-species competition model to large deviations at early stages will need to be examined. Simulation accuracy at these early stages could be improved if future versions of the CROPSIM model included more detailed algorithms for upper soil surface layer temperature and moisture conditions, and improved germination and emergence algorithms.

Table 11: Analysis of variance F statistic for effects of year, ragweed density, planting date, and their interactions on log transformed leaf weight (Lwad), leaf area index (Lai), above ground dry weight (Cwad), above ground dry weight at maturity (Fcwad), canopy height (Chgt), leaf number on the mainstem (Lnum), and final leaf number (Flnum).[a]

Source	Lwad	Lai	Cwad	Fcwad	Chgt	Lnum	Flnum
	---------- F statistic ----------						
Year	59.4***	272.5***	341.6***	0.8	919.8***	198.6***	3.9
Density	13.0**	340.1***	342.0***	47.3***	35.19***	0.8	1.4
Year*density	0.1	0	0.3	14.2**	0.01	0.7	2.6
Planting date	190.8***	251.1***	590.3***	20.2***	594.83***	158.1***	54.2***
Year*planting date	8.7**	37.0***	30.7***	1.5	77.51***	5.0*	13.2***
Planting date*density	1.3	1.5	3.3	7.3**	4.12**	0.74	3.6*
Year*planting date*density	2.2	4.9*	4.0*	0.5	2.06	0.3	2.5

[a] * P=.05 to .01 , ** P= .01 to .001, *** P<.001

Table 12: Average daily temperatures and precipitation in 1994 and 1995 at Woodstock, Ontario.

Month	Temperature (C)			Precipitation (mm)		
	1994	1995	30 year average	1994	1995	30 year average
May	11.6	12.8	12	124	96	70
June	19	19.7	18	95	78	78
July	20.5	20.7	20	124	51	80
August	17.5	21.5	19	71	138	70
September	15.6	13.7	15	21	27	74
Total	-	-	-	435	390	372

Figure 10: Leaf area index of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 measured LAI for julian planting dates 141-■ , 153-▲, and 165-●, 1994 simulated LAI for julian planting dates 141 - ——, 153- - - - -, 165 - ▬▬, 1995 measured LAI for julian planting dates 128-■, 143-▲, and 157-●, 1995 simulated LAI for julian planting dates 128 - ——, 143- - - - -, 157 - ▬▬) .

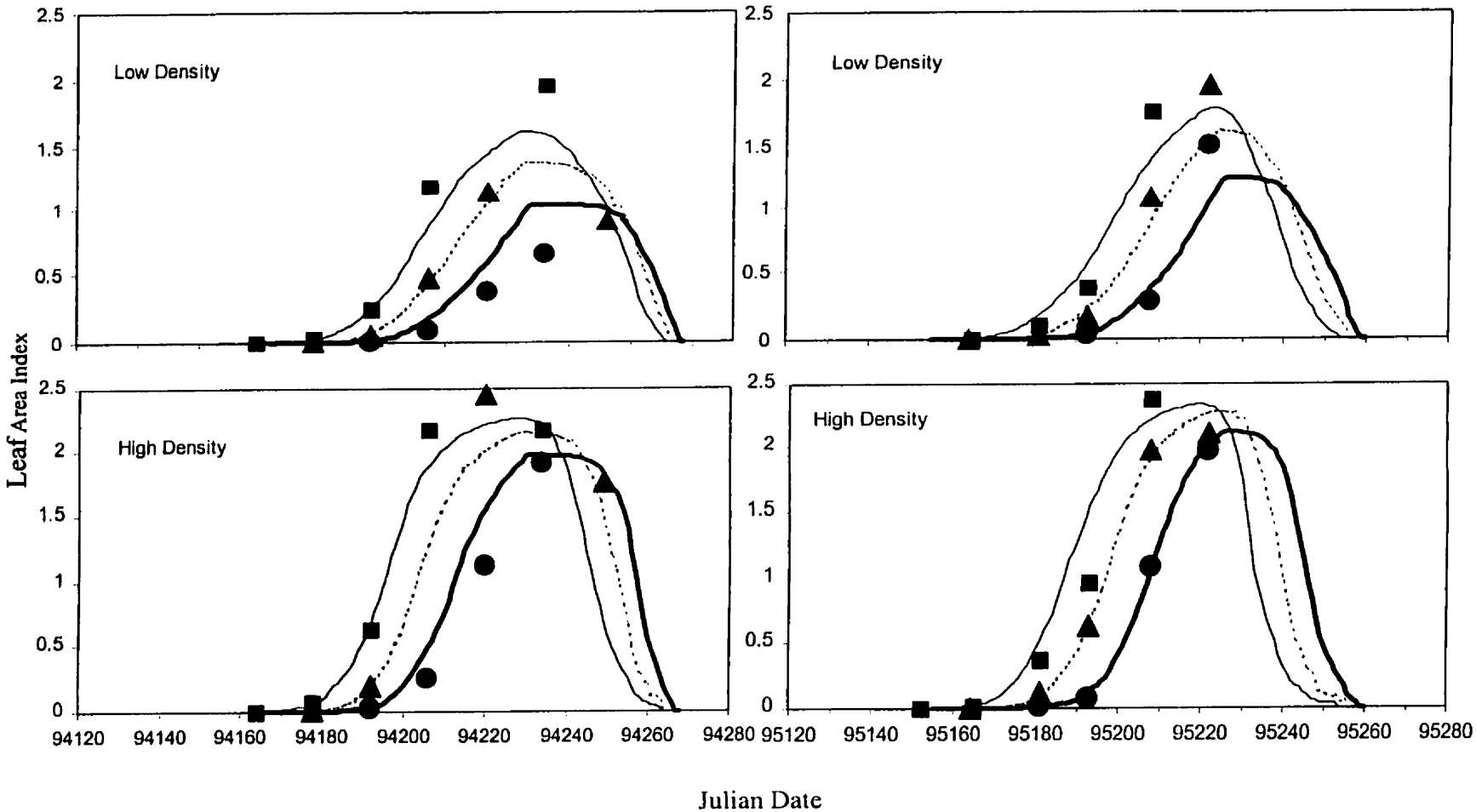

Low Density
Low Density
High Density
High Density
Leaf Area Index
Julian Date
2.5
2
1.5
1
0.5
0
94120
94140
94160
94180
94200
94220
94240
94260
94280
95120
95140
95160
95180
95200
95220
95240
95260
95280

Figure 11: Canopy height of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 measured canopy height for julian planting dates 141-■ , 153-▲, and 165-●, 1994 simulated canopy height for julian planting dates 141 ———, 153- - - - -, 165 - ▬▬▬, 1995 measured canopy height for julian planting dates 128-■, 143-▲, and 157-●, 1995 simulated canopy height for julian planting dates 128 - ———, 143- - - - -, 157 - ▬▬▬) .

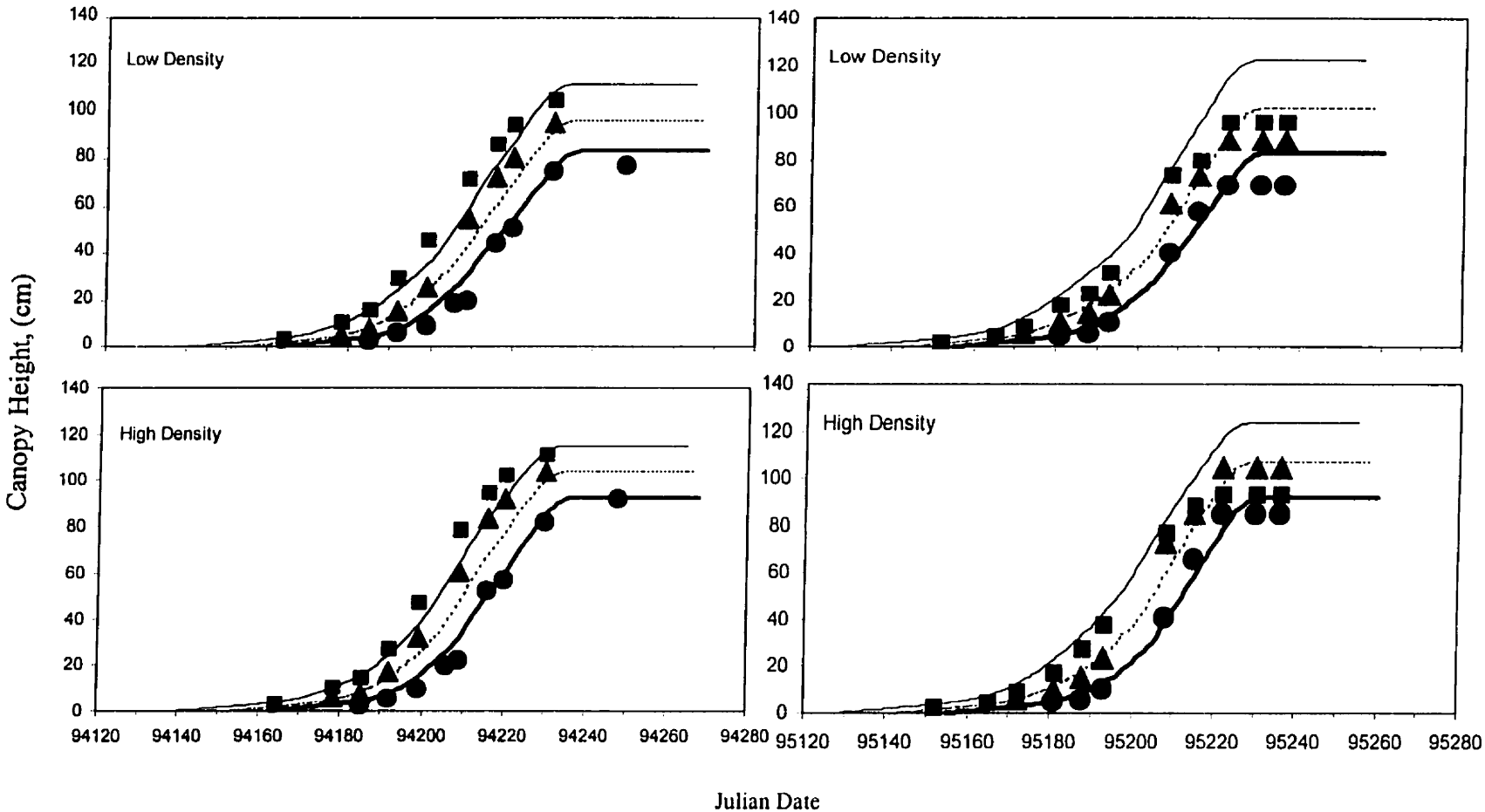

Low Density
Low Density
High Density
High Density
Canopy Height, (cm)
Julian Date
0
20
40
60
80
100
120
140
94120
94140
94160
94180
94200
94220
94240
94260
94280
95120
95140
95160
95180
95200
95220
95240
95260
95280

Figure 12: Deviations between measured and simulated leaf area index of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 julian planting dates at 1.5 ragweed m^{-2} 141-◆, 153-▲, 165-+; 1994 julian planting dates at 4.5 ragweed m^{-2} 141-□, 153-■, 165-●; 1995 julian planting dates at 1.5 ragweed m^{-2} 128-◆, 143-▲, 157-+; 1995 julian planting dates at 4.5 ragweed m^{-2} 128-□, 143-■, 157-●)

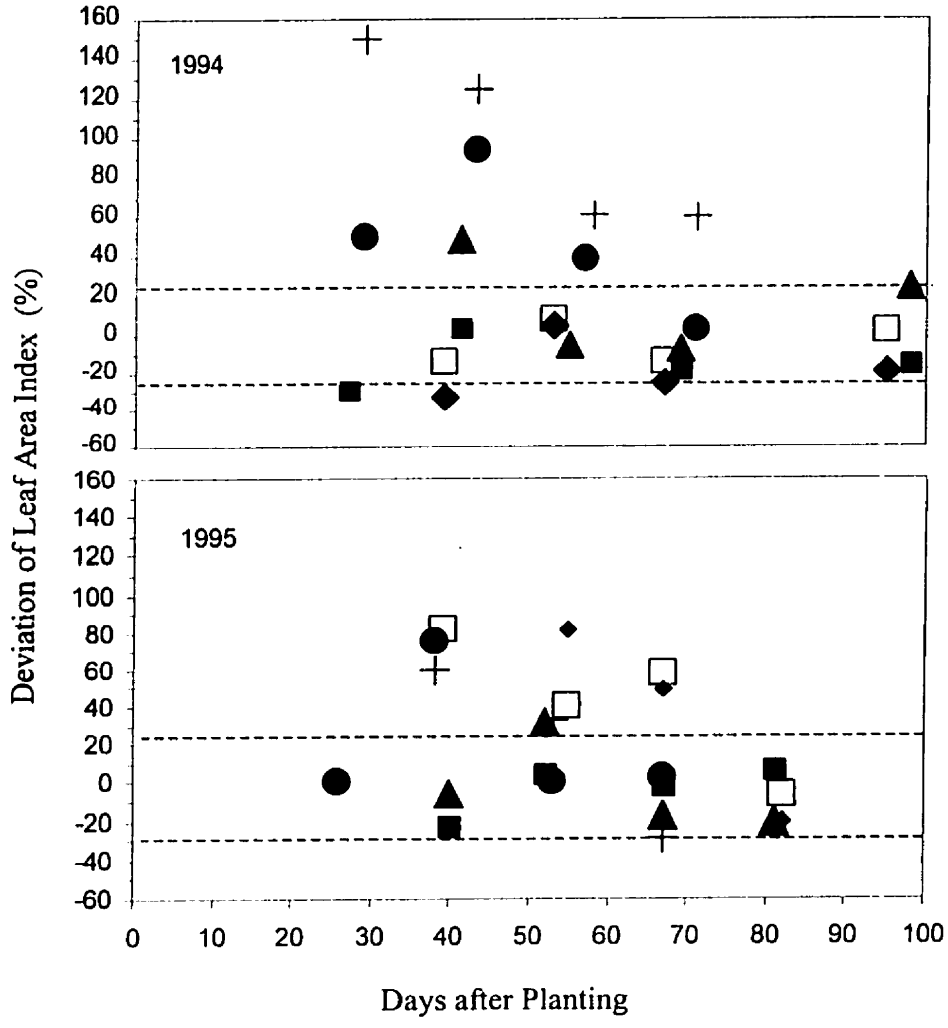

1994
1995
160
140
120
100
80
60
40
20
0
-20
-40
-60
0
10
20
30
40
50
60
70
80
90
100
Deviation of Leaf Area Index (%)
Days after Planting

Figure 13: Deviations between measured and simulated mainstem leaf number of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 julian planting dates at 1.5 ragweed m^{-2} 141-◆, 153-▲, 165-+; 1994 julian planting dates at 4.5 ragweed m^{-2} 141-□, 153-■, 165-●; 1995 julian planting dates at 1.5 ragweed m^{-2} 128-◆, 143-▲, 157-+; 1995 julian planting dates at 4.5 ragweed m^{-2} 128-□, 143-■, 157-●)

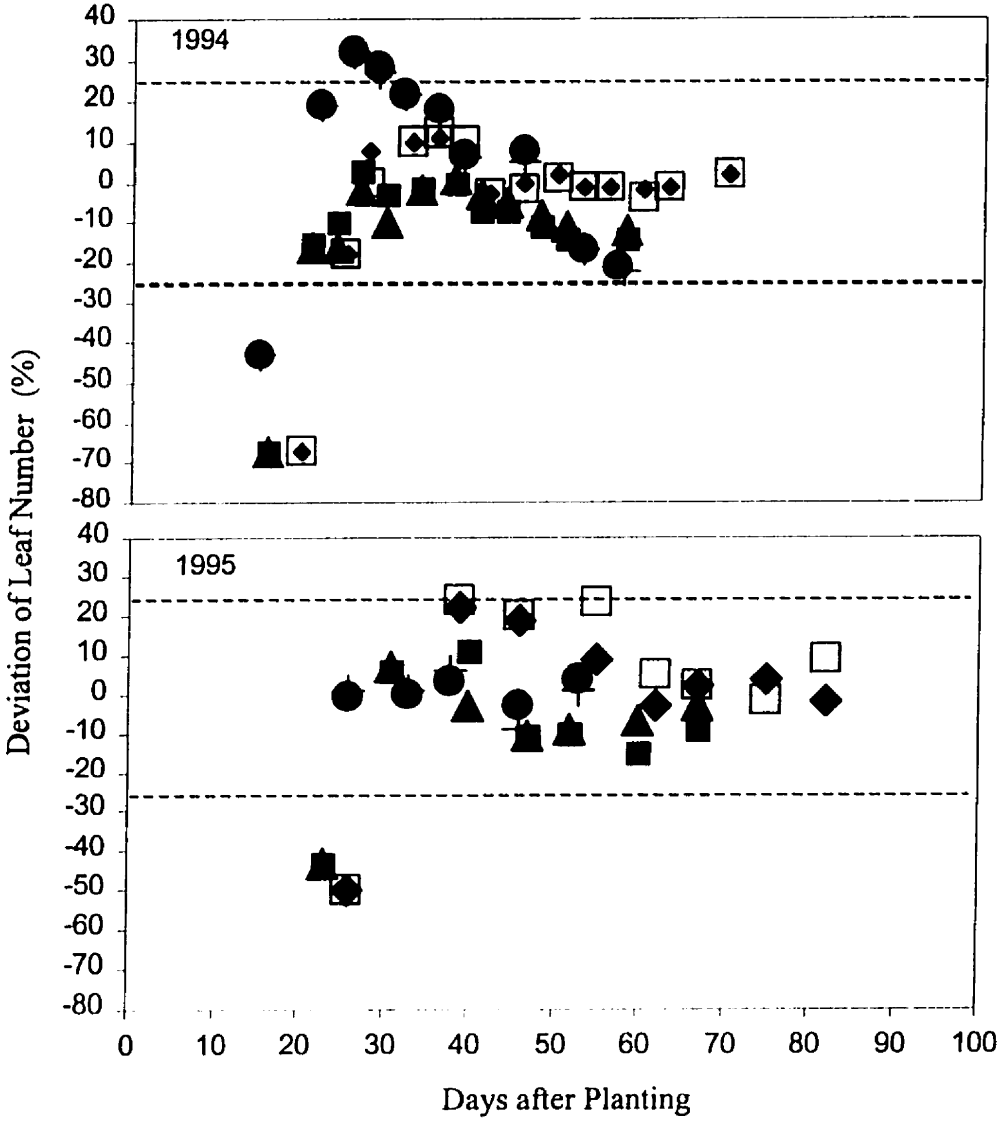

1994
1995
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
0
10
20
30
40
50
60
70
80
90
100
Deviation of Leaf Number (%)
Days after Planting

Figure 14: Deviations between measured and simulated leaf weight of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 julian planting dates at 1.5 ragweed m^{-2} 141-◆, 153-▲, 165-+; 1994 julian planting dates at 4.5 ragweed m^{-2} 141-□, 153-■, 165-●; 1995 julian planting dates at 1.5 ragweed m^{-2} 128-◆, 143-▲, 157-+; 1995 julian planting dates at 4.5 ragweed m^{-2} 128-□, 143-■, 157-●)

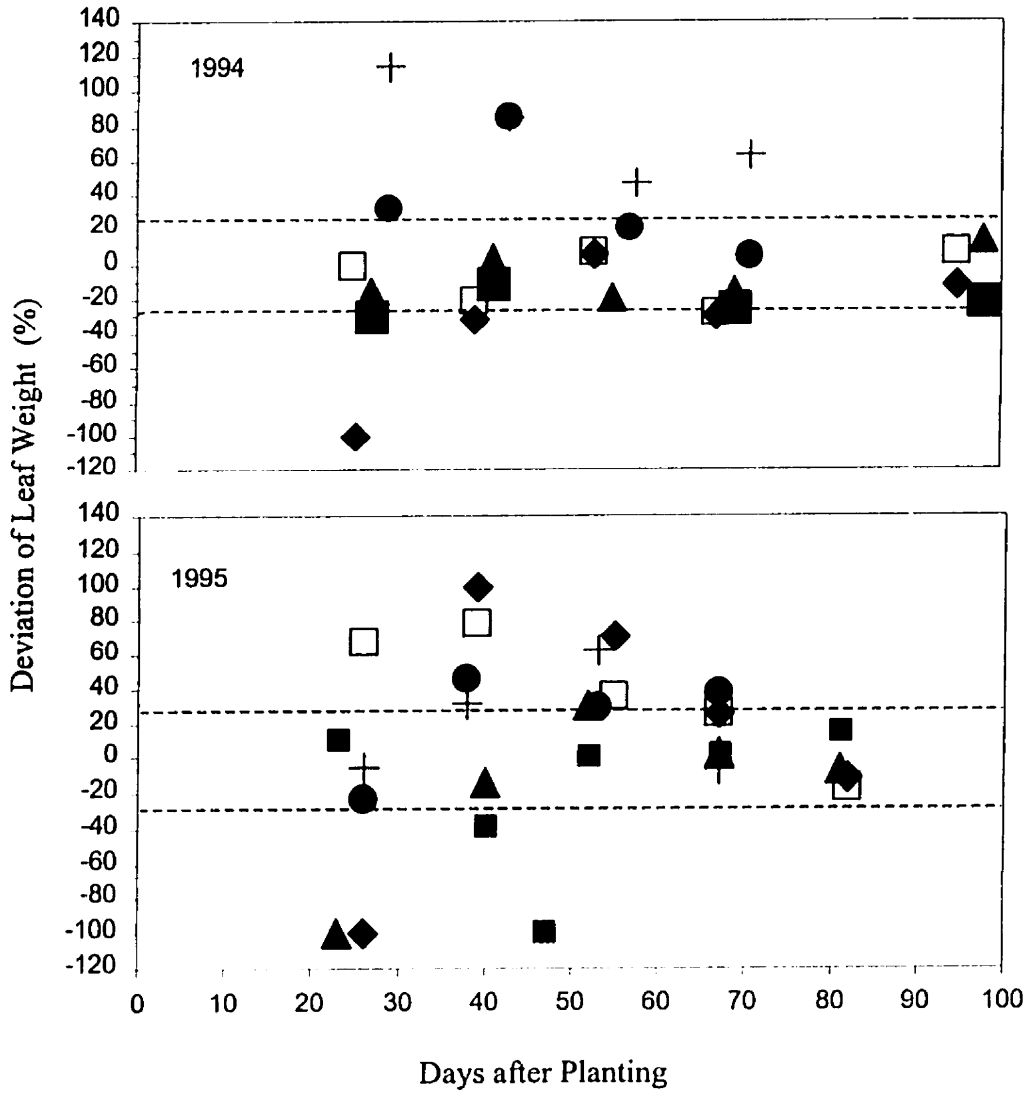

1994
1995
140
120
100
80
60
40
20
0
-20
-40
-60
-80
-100
-120
0
10
20
30
40
50
60
70
80
90
100
Deviation of Leaf Weight (%)
Days after Planting

Figure 15: Deviations between measured and simulated canopy height of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 julian planting dates at 1.5 ragweed m^{-2} 141-◆, 153-▲, 165-+; 1994 julian planting dates at 4.5 ragweed m^{-2} 141-□, 153-■, 165-●; 1995 julian planting dates at 1.5 ragweed m^{-2} 128-◆, 143-▲, 157-+; 1995 julian planting dates at 4.5 ragweed m^{-2} 128-□, 143-■, 157-●)

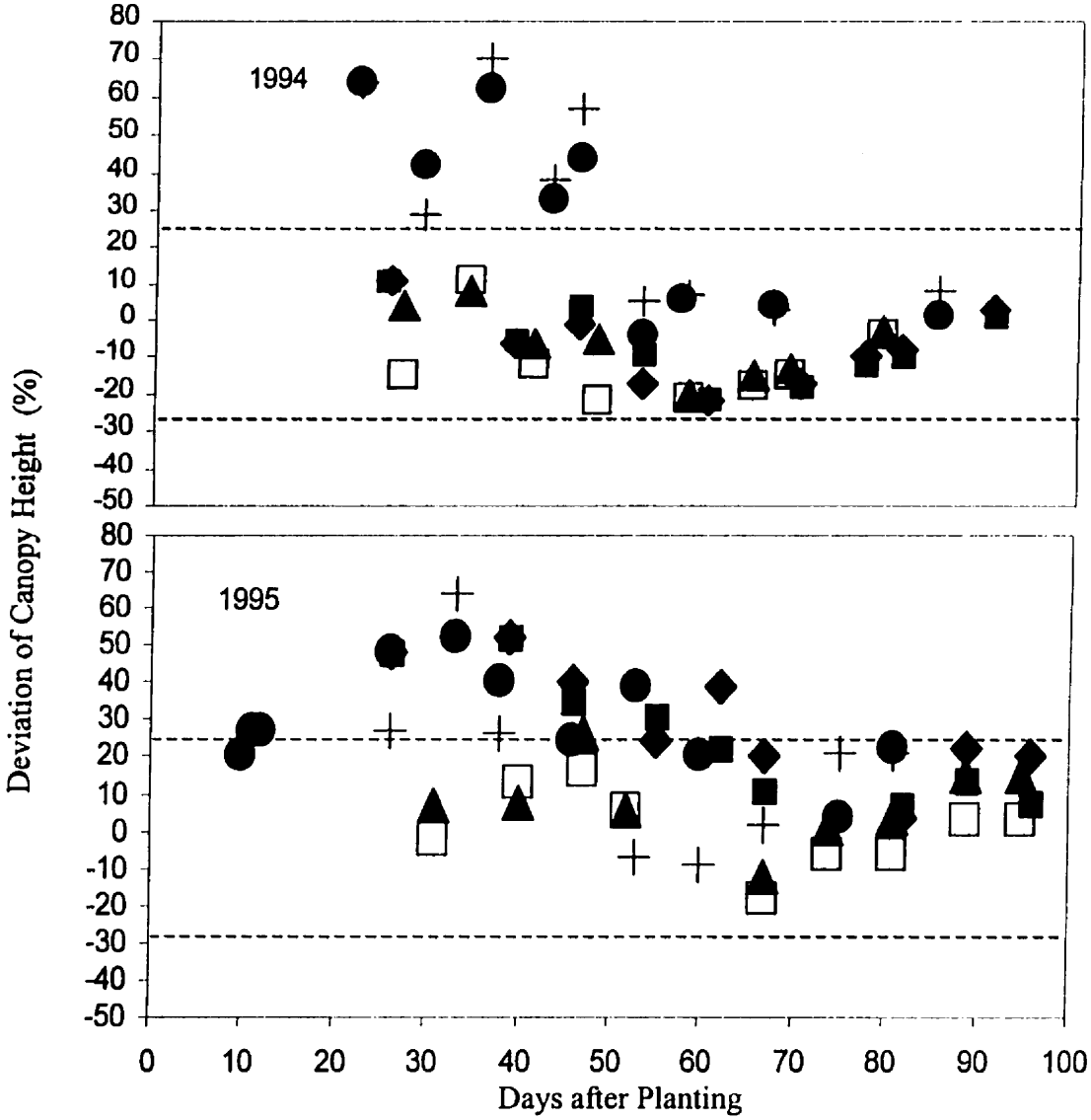
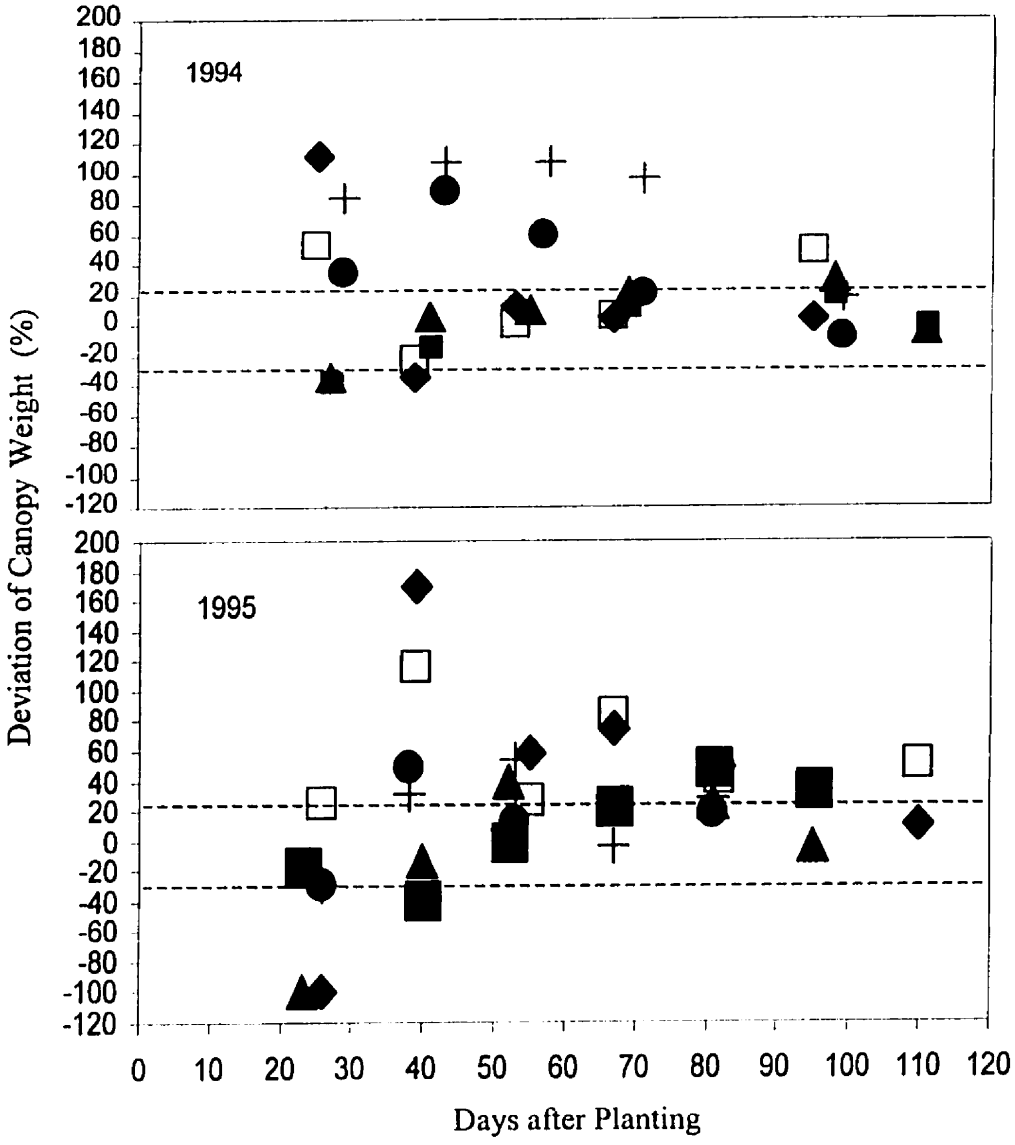

1994
1995
80
70
60
50
40
30
20
10
0
-10
-20
-30
-40
-50
0
10
20
30
40
50
60
70
80
90
100
Deviation of Canopy Height (%)
Days after Planting

Figure 16: Deviations between measured and simulated canopy weight of common ragweed planted at two densities and three dates at Woodstock, Ontario in 1994, and 1995 (1994 julian planting dates at 1.5 ragweed m^{-2} 141-◆, 153-▲, 165-+; 1994 julian planting dates at 4.5 ragweed m^{-2} 141-□, 153-■, 165-●; 1995 julian planting dates at 1.5 ragweed m^{-2} 128-◆, 143-▲, 157-+; 1995 julian planting dates at 4.5 ragweed m^{-2} 128-□, 143-■, 157-●)


1994
1995
Deviation of Canopy Weight (%)
Days after Planting
200
180
160
140
120
100
80
60
40
20
0
-20
-40
-60
-80
-100
-120
0
10
20
30
40
50
60
70
80
90
100
110
120

Discussion and Conclusions

Summary of Findings

Growth cabinet studies were conducted to characterize phenological response of a common ragweed biotype obtained at Woodstock, Ontario, to temperature, photoperiod and irradiance. Leaf appearance occurred over a wide range of temperatures. Common ragweed is a temperate species and leaf appearance occurred at the lowest temperature evaluated (11/2C). A maximum leaf appearance rate of 1.02 leaves per day occurred at the 35/25C (31.7C) temperature. Common ragweed appeared to be adapted to a wide temperature range. Leaf appearance response to temperature was best characterized using a nonlinear function. Photoperiods of 14 hours or less were optimal and resulted in maximum rates of development. Sensitivity to photoperiod did not differ with phase of ragweed development. Ragweed becomes photoperiod sensitive shortly after germination (12-14 days at 20C). Following this juvenile phase, sensitivity to photoperiod was constant and continued until pistillate flowers were observed. Irradiance level affected ragweed phenological development only when combined with the additional stress of the low temperatures. The lifecycle of common ragweed was broken down into a number of phases whose durations were described in terms of biological days (days at optimal temperatures and photoperiods): germination 3.5 Bd, germination to end of juvenile phase 7 Bd, germination to main stem terminal bud 11.5 Bd, main stem terminal bud to pistillate flower 4.5 Bd, pstillate flower to anthesis 4.5 Bd.

Photoperiod and temperature were the major determinants of development of common ragweed development under field condition and interactions between these factors had minimal impact relative to the independent effects. Temperature and

photoperiod responses, as well as phase durations, were incorporated into a model using the concept of photothermal time (accumulation of thermal time adjusted by a factor based on daylength). When germination and emergence of ragweed was not limited by soil moisture, the photothermal model described accurately phenology of common ragweed grown at different densities and emergence timings in field experiments located in Woodstock, Ontario in 1994 and 1995. Under these conditions, other factors which may be experienced under typical field conditions, such as competition from other plants or nitrogen stress, are of minor importance relative to the effects of photoperiod and temperature. Also, these results indicated that interactions between photoperiod and temperature do not need to be considered to adequately simulate phenology of common ragweed under field conditions.

Common ragweed germination and emergence were not adequately described based on temperature alone. If moisture stress conditions occurred prior to emergence, photothermal time estimates of common ragweed phenology were poor. Subsequent models of ragweed phenology will need to incorporate more detail on the effect of moisture on germination and emergence.

Common ragweed leaf area development, biomass partitioning, and total biomass accumulation could be explained based on photothermal time accumulation and resulting ragweed phenology. This suggested that photothermal time and phenological development were major factors influencing the outcome of weed-crop competition. By determining length of vegetative period and resulting leaf area development and biomass accumulation, phtotothermal and phenological development time can be an indicator of ragweed's ability to capture resources, such as light, moisture, and nutrients.

Using the photothermal time model as a basis, a mechanistic model for ragweed growth and development was constructed. The model was developed from the generic plant model CROPSIM, a model which is capable of simulating competition between two or more species. Adaptations were made to CROPSIM's growth and development subroutines to enable ragweed growth to be simulated. Data from field studies using a single source ragweed grown in monoculture, and from the literature were used to parameterize the model. The resulting ragweed model accounted for the influence of environmental conditions across years, density and emergence timing on leaf number, leaf area, leaf weight, height, and biomass accumulation of ragweed grown in monoculture. Larger deviations tended to be associated with ragweed growth shortly after emergence, particularly when temperature and moisture extremes occurred during this time period.

Contributions to the Discipline of Weed Science

This study provided a number of concrete contributions to the discipline of weed science. Common ragweed phenology was characterized in terms of its response to temperature and photoperiod. It was determined that temperature and photoperiod responses generated using controlled environment studies could be combined in a concept of photothermal time and that photothermal time was adequate for characterizing ragweed growth in the field. Interactions and other factors did not significantly affect ragweed phenology. Finally, a mechanistic model of ragweed growth and development was constructed that can subsequently be used in multispecies competition models.

A more abstract contribution of this study is that it explicitly attempts to relate potential competitive ability of a weed with its phenological development. This is not a

concept which has been pursued in the weed science discipline. Numerous studies have characterized the phenological development of weed species, but few have attempted to relate phenological development to competitive ability. In this study it was shown that phenology can potentially influence competitive ability. This further demonstrates that the use of empirical models to describe the effects of weeds on potential yield is limited. The mechanistic ragweed model developed in this study, when used in future work in a multi-species competition model, will implicitly capture this concept.

Future Research Requirements

While the concept of incorporating photothermal time into a mechanistic weed-crop modeling approach appeared to have merit in this study, several areas require further research and development. In this study, the ragweed model was assessed using data from ragweed grown in monoculture. The ability of the model to adequately describe ragweed growth in competition with a crop needs to be assesses. Leaf area distribution, specific leaf area, and plant height of ragweed grown in competition with a crop may differ from ragweed grown in monoculture.

The model implicitly assumes a uniform distribution of ragweed plants in the field. While this assumption is valid for most crops it is not valid for weed populations. Weed infestations are typically not uniform. Subsequent weed competition models would need to account for this lack of uniformity

As demonstrated in this study, estimation of germination and emergence under extreme conditions (eg. drought) is poor. Accurate estimation of emergence timing is required for determining potential weed-crop competition outcomes. Sensitivity of a multi-species competition model to larger deviations at early stages will need to be

examined and future versions of the CROPSIM model may need to include more detailed algorithms for upper soil surface layer temperature and moisture conditions, and improved germination and emergence algorithms to reduce these deviations.

Finally, the model was developed using ragweed from a single source in Ontario. As a result the model implicitly assumes that ragweed biotype differences can be ignored. This may or may not be a valid assumption. Certain biotypes may be more competitive than others and may require specific parameters to be effectively used in a competition model. The validity of the model for a range of ragweed biotypes must be tested. Furthermore it needs to be determined whether the model is valid for ragweed plants that escape herbicide treatment and possibly have a reduced level of vigor. Testing the model across a wider range of data sets would identify weaknesses in the model which may provide additional refinements to increase model confidence.

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Appendix 1: Common ragweed species file (RWSIM980.SPE)

*SPECIES_COEFFICIENTS: RWSIM980 RAGWEED - CROPSIM MODEL

@CODE DESCRIPTION
AGE Age (Biological days)
CO2 Co2 (Vpm)
CTDR Cold tolerance (Fr.of max.rate)
DE1R Development before Zadoks 80 (Fr.of max.rate)
DE2R Development after Zadoks 80 (Fr.of max.rate)
DPTH Depth (cm)
DSTG Developmental stage (Zadoks)
ECPL PAR extinction coeff.,canopy area index basis (#)
L#IR Leaf number increase,relative (Fr.of max.rate)
LEXR Leaf expansion,relative (Fr.of max.rate)
GEMR Germination and emergence,relative (Fr.of max.rate)
GRFR Grain filling (Fr.of max.rate)
GRNR Grain N filling (Fr.of max.rate)
LNCN Leaf nitrogen content,minimum (fr)
HT Height (cm)
LAWR Leaf area/weight ratio (Fr.of max value)
LNCX Maximum leaf N (%)
LRSS Leaf resistance,stomates,standard (s m-1)
PAR Photosynthetically active radiation (MJ m-2 d-1)
PHOR Photosynthesis,canopy (Fr.of rate at 330 vpm)
RGFR Root growth factor (0-1)
RNCX Maximum root N (%)
RUER Radiation use efficiency (Fr of Rue at 10MJ m-2 d-1)
SNCX Maximum stem N (%)
TEMP Temperature (C)
VRNR Vernalization rate (Fr.of max.rate)
WIND Windspeed (m s-1)

@SPEX	SPEY	SPEXY1	SPEXY2	SPEXY3	SPEXY4	SPEXY5	SPEXY6	SPEXY7	SPEXY8	SPEXY9
TEMP	GEMR	0.9,0.0	31.7,1.0	31.7,1.0	40.0,0.0	.	.	.	.	.
TEMP	L#IR	0.9,0.0	31.7,1.0	31.7,1.0	40.0,0.0	.	.	.	.	.
TEMP	LEXR	0.0,0.0	11.0,.50	14.0,1.0	28.0,1.0	40.0,0.0	.	.	.	
TEMP	DE1R	0.9,0.0	31.7,1.0	31.7,1.0	40.0,0.0	.	.	.	.	.

```
TEMP  DE2R  0.9,0.0   31.7,1.0   31.7,1.0   40.0,0.0  .     .     .     .     .     .
TEMP  GRFR  0.0,0.0   7.0,0.00   26.0,1.0   34.0,1.0   40.0,0.0  .     .     .     .
            .
TEMP  GRNR  0.0,0.0   7.0,0.00   26.0,1.0   34.0,1.0   40.0,0.0  .     .     .     .
            .
TEMP  PHOR  0.9,0.0   13.0,0.4   26.0,1.0   34.0,1.0   40.0,0.0
TEMP  VRNR  -4.75,0.0 5.2,1.0    26.6,0.0   .     .     .     .     .     .     .
TEMP  CTDR  -3.5,0    -3,.17     -2,.4      -1,.6      0,.76      1,.88      2,.96      3,1.0      5,1.0
            10,0.
PAR   RUER  1.0,2.8   2.0,2.6    3.0,2.4    4.0,1.9    5.0,1.2    6.0,1.15   7.,1.08    10.,1.     16.,.9
            20.,.88
CO2   PHOR  100,.3    230,.7     330,1.0    400,1.1    500,1.2    600,1.3    800,1.4    900,1.5    1000,1.6
            1100,1.75
CO2   LRSR  50,0.54   150,.70    250,.84    350,1.0    450,1.16   550,1.3    650,1.46   750,1.6    850,1.76
            1000,95
WIND  CRAR  0.5,2.0   1.,1.      1.5,.66    2.,.5      2.5,.4     3.,.33     3.5,.29    4.,.25     5.,.21
            7.,.14
HT    CRAR  10.,2.5   20.,1.8    30.,1.4    40.,1.2    50.,1.0    70.,.7     100,.5     140,.3
            160,.2
DPTH  RGFR  5.0,1.0   15.0,0.9   30.0,0.75  45.0,0.65  60.0,0.55  90.0,0.45  120,0.35
            150,0.05
TEMP  LAWR  0.9,0.7   13.0,0.9   23.0,1.0   31.7,1.0   40.0,0.5
AGE   DI1R  7.0,1.0   10.0,0.9   14.0,0.8   17.0,0.66  20.0,0.6   60.0,0.58  .     .     .
TEMP  DI1R  0.0,0.    5.0,0.14   10.0,0.3   15.0,0.4   20.0,0.7   22.0,1.0   25.0,1.0   30.0,0.0
TEMP  DI2R  10.0,0.0  17.0,1.0   25.0,1.0   30.0,0.0   .     .     .     .     .     .
TEMP  DI3R  10.0,0.0  20.0,1.0   30.0,1.0   40.0,0.0   .     .     .     .     .     .
TEMP  DI4R  10.0,0.0  20.0,1.0   26.0,1.0   30.0,0.0   .     .     .     .     .     .
DSTG  LNCX  10,3.0    20,3.0     30,3.0     40,3.0     50,3.0     60,3.0     70,3.0     80,3.0
            90,3.0
DSTG  SNCX  10,1.0    20,1.0     30,1.0     40,0.75    50,0.5     60,0.5     70,0.5     80,0.5
            90,0.5
DSTG  RNCX  10,2.0    20,2.0     30,2.0     40,2.0     50,2.0     60,2.0     70,2.0     80,2.0
            90,2.0
DSTG  ECPL  10,.90    20,0.90    30,0.90    40,0.85    50,0.85    60,0.85    70,0.75    80,0.75
            90,0.75
```

@SPEC SPVAL
CRAS 18.0
CT1U -6.0
CT2H -5.0
CTSP 1.0
CTD1 20.0
CTD2 12.0
DETP 14.8
DI1R 0.25
DI2R 0.14
DI3R 0.10
DI4R 0.10
DTVR 50.0
DFDN 0.0
DFEN 60.0
FDYX 5.00
GTYP 3.0
H#PT 300.
H#RT 0.05
H#TT 43.0
HINX 55.0
L#EF 1.6
L#SE 40.6
L#SX 25.0
LALX 65.0
LFLB 10.5
LFLC 50.0
LNFL .10
LNFM 1.0
LNFV 0.0
LNCN 0.003
LSLC 0.00
LSLF 0.60
LDFD 0.30
LDFA 0.00
LRSS 50.0
RUFX 10.0
RLAT 20.0

PHSV -.15
PHTV 2.0
PRIF 1.5
PRRF 4.0
PRNP 3.0
RESPF 0.90
RTGF 30.0
RLWS 25000
RNCN 0.002
RSRS .005
RSTR 0.05
RSUR 0.00
RSAF 0.03
RTDX 250.
RWUX 0.04
S#PE 65.0
S#PI 1.0
S#PF 80
S#PS .40
SDNP .0006
SNCN 0.002
STSS 300.
VETT 25.0
VFMN .001

Appendix 2: Common Ragweed Cultivar file (RWSIM980.CUL)

*CULTIVAR_COEFFICIENTS: RWSIM980 RAGWEED - CROPSIM MODEL

@CODE DESCRIPTION
AWNS Awn score (0-1.0;0=none,1=long and active)
CT1H Cold tolerance,stage-1 hardened (C)
DSV1 Development,sensitivity to vernalization(%change in dev rate/Vday)
DSP1 Development sens.to photoperiod,phase1 (ge-dr;%change/h,threshold)
DSP2 Development,sens.to photoperiod,phase2 (dr to ts;%Change per h)
DSP3 Development,sens.to photoperiod,phase3 (ts to ll;%Change per h)
DUP0 Duration of phase0,juvenile phase (B.days)
DUP1 Duration of phase1,end of juvenile to double ridges (B.days)
DUP1 Duration of phase1,end of juvenile to double ridges (B.days)
DUP2 Duration of phase2,double ridges to terminal spikelet (B.days)
DUP3 Duration of phase3,terminal spikelet to last leaf expanded (B.days)
DUP4 Duration of phase4,last leaf expanded to spike emergence (B.days)
DUP5 Duration of phase5,spike emergence to anthesis (B.days)
DUP6 Duration of anthesis phase (Bday)
DUP7 Duration of lag phase (Bday)
DUP8 Duration of phase8,grain filling (B.days)
G#WB Grain number per unit biomass at anthesis (# g-1)
GP%S Grain protein concentration,standard (%)
GW#X Grain weight,maximum (mg grain-1)
HFLR Host factor,leaf rust (0-1.0;0=resistant,1=fully susceptible)
HFLS Host factor,leaf spot (0-1.0;0=resistant,1=fully susceptible)
HFPM Host factor,powdery mildew (0-1.0;0=resistant,1=fully susceptible)
HFSC Host factor,scab (0-1.0;0=resistant,1=fully susceptible)
LA1X Leaf area,first leaf,maximum (cm2)
LALI Leaf area increase factor (leaf-1)
LAWS Leaf area/weight ratio,standard (cm2 g-1)
PHYL Phyllochron (Bday)
RUES Radiation use efficiency,standard (G MJ-1 PAR)
S#IF Shoot number increase factor (=leaf #/plant at which tillering=0)
S#DF Shoot number decrease factor (= linear decrease to 0 at factor value)

@CUL#	CULTIVAR_NAME.....	ECO#	DUP1	DUP2	DUP3	DUP4	DUP5	DUP6	DUP7
UC0001	Ontario ragweed	ONEC1	4.5	0.0	0.0	4.50	0.00	4.5	0.0

DUP8	DUP0	PHYL	DSP1	DSP2	DSP3	DSV1	LA1X	LALI	LAWS	RUES
14.5	10.5	1.81	-50.2	-60.0	10.00	0.00	2.5	1.60	250.0	2.80

S#IF	S#DF	G#WB	GW#X	GP%S	AWNS	CT1H	HFPM	HFLR	HFLS	HFSC
50.0	60.00	35.	35.	40.	0	0.0	0.0	0.0	0.0	0.0

Appendix 3: Common Ragweed Ecotype file (RWSIM980.ECO)

*ECOTYPE_COEFFICIENTS: RWSIM980 RAGWEED - CROPSIM MODEL

@CODE DESCRIPTION
CTOF Cold tolerance,organs,factor (0=no kill;1=leaves;2=leaves+roots)
DUEM Duration of emergence phase (Bday/cm)
DUGI Duration of germination,initial,no dormancy (Bday)
LDWC Leaf death,water stress,critical Wfg for accelerated ageing (Fr)
LDWF Leaf death,water stress,factor to accelerate ageing (Fr of normal)
NFPL Nitrogen factor 1,lower bound (Fr of leafN range)
NFPU Nitrogen factor 1,upper bound (Fr of leafN range)
RERS Root elongation rate,standard (cm/Bd)
RUEF RUE factor for stems (Fr of standard)
SAWS Stem area to weight ratio,std (cm2 g-1)
SELE Stem elongation ends (Rstage)
S#PI Shoot number per plant,initial value (#)
S#IS Shoot number production start (leaf #)
WFPI Water factor,phs,intercept (Fr;relates to Extractable/Capacity)
WFGI Water factor,growth,intercept (Fr;relates to Extractable/Capacity)
L#SFN Leaf number per shoot,minimum produced after floral initiation (#)
L#SFF Leaf number per shoot,factor to calculate final leaf# (#/Haun)

@ECO#>	ECONAME.....	NFGI	NFPU	NFPL	WFPI	WFGI	LDWC	LDWF
ONEC1	CANADIAN HRS(L)	1.0	.85	.00	1.10	1.20	0.90	1.00

RERS	SELE	RUEF	CTOF	L#SFN	L#SFF	S#PI	S#IS	SAWS	DUEM	DUGI
4.0	65.0	1.0	0.0	6.0	3.25	1.00	3.5	10	1.0	3.5

DSTG Development stage (Zadoks,BBCH scale)
CFRX Canopy fraction,maximum (fr)
SFRX Stem fraction,maximum (fr)
RSFRX Reserves fraction,maximum (fr)

@ECO#	ECOX	ECOY	ECOXY1	ECOXY2	ECOXY3	ECOXY4	ECOXY5	ECOXY6	ECOXY7
ONEC1	DSTG	CFRX	10,.60	15,.78	40,.82	60,.95	100,.95	.	.

.

ONEC1 DSTG SFRX	10,.25	15,.30	40,.15	65,1.0	100,1.0	.	.
	.						
ONEC1 DSTG RSFRX	10,0.0	15,0.0	40,0.1	65,1.0	100,1.0	.	.
	.	.					

Appendix 4: CROPSIM Development Subroutine (CRSIMCD.FOR)

```
C CROPSIM CROP DEVELOPMENT SUBROUTINE

      SUBROUTINE Development(cswtstep,cfltask,hour,doy,iyr,yer,
     X rotc,roto,trt,spp,
     X nfg,wfg,
     X parip,tmin,tairhr,sh2o,dayl,
     X CFLSTAGE,CFLSTSPP,MESSAGE,STNAME,DAG,DAP,
     X DSTAGE,DSTAGESP,VSTAGE,RSTAGE,RDSUMP,
     X LNUMSG,
     X LNUMSD,LNUMSS,SNUMPP,SNUMPSGT,
     X VDRATE,RDRATE,
     X STAGEDAT,DASTAGE,PYR,EDAT,PRNUMSS,PDOY,RSTNAME)

      IMPLICIT NONE

      INCLUDE 'Crsimcd.icc'                    ! Communication variables
      INCLUDE 'Crsimcd.icd'                    ! Driving variables
      INCLUDE 'Crsimcd.ici'                    ! Input variables
      INCLUDE 'Crsimcd.icr'                    ! Rate variables
      INCLUDE 'Crsimcd.ics'                    ! State variables
      INCLUDE 'Crsimcd.ict'                    ! Temporary variables

      INCLUDE 'Crsimcd.icu'                    ! File unit names and numbers

      IF(cswtstep.LT.24)THEN
       IF(hour+cswtstep.LT.25.AND.vstage.LT.1)RETURN
      ENDIF

      IF(cfltask.EQ.'i'.OR.cfltask.EQ.'b')THEN
       CALL Stormame(trt,spp,rotc,roto,'cdi',FNAMEST)
       OPEN(fnumst,FILE=fnamest,FORM='UNFORMATTED')
       READ(fnumst)
     X  detp,dfdn,dfen,dtvr,dsvrn,duge,dugi,dugx,dugp,
     X  duph,dspps,gtyp,hdatm,lnumef,lnumirs,lnumsff,lnumse,
     X  lnumsfn,lnumsx,prif,prnump,prrf,pstmn,pstmx,rstend,
```

```
X  rstname,duem,snumdf,snumif,snumis,snumpe,tdev1,tdev2,
X  tgemr,tlnumir,tvrn1,vett,vfmn,sdul,sldl,slll,
X  page,pdoy,pldp,pldpu,plly,plme,pyri,cswplant,cswswb,cswtem,
X  pfrst,ph2od,ph2ol,ph2ou,plast
 CLOSE(fnumst)
 ENDIF

 IF(cfltask.EQ.'z'.OR.cfltask.EQ.'b')THEN
  cflstage=0                          ! Control flag,stage change
  DO l=1,5
   cflstspp(l)=0                      ! Control flag,st.change,spp
   dstagesp(l)=0                      ! Development stage,species
  ENDDO
  cflplant=0                          ! Control flag,planting
  cflpldoy=0                          ! Control flag,pl.day
  dap=0                               ! Days after planting
  dag=0                               ! Days after germination
  dog=0                               ! Day of germination
  dstage=0                            ! Developmental stage
  dastage=0                           ! Days after last stage
  emfd=0                              ! Emergence fraction,cum
  gefd=0                                    ! Germinated fraction,cum
  lnumsd=0                            ! Leaf # per axis (#)
  lunitsd=0                                 ! Leaf units from germ
  prnumsd=0                           ! Primordia # per axis (#)
  rdsump=0.0                          ! Reproductive dev sum,phase
  rstage=0.0                          ! Reproductive stage
  rstagep=0                           ! Reproductive stge,principal
  rstages=0.0                         ! Reproductive stge,secondary
  snumpp=0                            ! Branch # (total produced)
  snumpsgt=0.0                        ! Shoot # senescence,total
  tcnum=0                             ! Tiller cohort number
  vstage=0                            ! Vegetative stage
  vdsump=0.0                          ! Vegetative dev sum,phase
  vrndaysm=0.0                        ! Vernalization sum
  DO l=0,9
   stagedat(l)=0
  END DO
```

```
 DO l=1,dogx
  stlc(l)=0.0                                    ! Stem length of gm cohort
 ENDDO
 DO l=0,4
  lnumss(l)=0                                    ! Leaf # per axis (#)
  prnumss(l)=0                                   ! Primordia # per axis (#)
 ENDDO
ENDIF

IF(cfltask.EQ.'r')THEN                           ! If to calculate rates
 eproductive development
 IF(rstage.GT.0)THEN                             ! If processes active
  IF(rstage.LT.70)THEN

   tfrdev=Tfachr(cswtem,tdev1,tairhr(hour),degday)
   IF(cswtstep.EQ.24)tfrdev=Tfac(cswtem,tdev1,tairhr,degday)
  ELSE
   tfrdev=Tfachr(cswtem,tdev2,tairhr(hour),degday)
   IF(cswtstep.EQ.24)tfrdev=Tfac(cswtem,tdev2,tairhr,degday)
  ENDIF
  IF(rstage.LT.30)THEN                           ! If before terminal spk
   tfvrn=Tfac(cswtem,tvrn1,tairhr,degday)        ! NB Needs change to hour
   vfde=1.0-dsvrn*0.01*(dtvr-vrndaysm)           ! Vernalization factor
   vfde=AMIN1(1.0,AMAX1(vfmn,vfde))              ! Vernalization factor,limit
  ELSE
   vfde=1.0                                      ! Vfactor after terminal spk
  ENDIF
  IF(rstage.LE.20)THEN                           ! Before double ridges
   dspp=dspps(1)                                 ! Pp sensitivity
  ELSEIF(rstage.GT.20.AND.rstage.LT.60)THEN      ! staminate flower to pistillate flower
   dspp=dspps(2)                                 ! Pp sensitivity
  ENDIF
  IF(dspp.GT.0.AND.dayl.LT.detp)THEN             ! If daylength < threshold
   dfde=1.0-dspp*0.01*(detp-dayl)                ! Daylength factor-LDP,linear
  ELSEIF(dspp.LT.0.AND.dayl.GT.detp)THEN                 ! If daylength > threshold
   dfde=1.0-dspp*0.01*(detp-dayl)                ! Daylength factor-SDP
  ELSE
   dfde=1.0
```

```
 ENDIF
 dfde=AMIN1(1.0,AMAX1(dfdn,dfde))          ! Daylength factor-limited
 IF(vstage.LT.10)dfde=0.0                  ! Dfactor prior to emergence
 IF(rstage.LT.10)THEN                      ! If in juvenile phase
  dfde=1.0                                 ! Dfactor,juvenile phase
  vfde=1.0                                 ! Vfactor,juvenile phase
 ENDIF
 IF(rstage.GE.dfen)dfde=1.0                      ! Dfactor after end stage
 rdrate=(tfrdev/24.0)*cswtstep*
X  AMIN1(dfde,vfde)                        ! Reproductive dev.rate(0-1)

 IF(rstage.GE.20)rdrate=AMAX1(.01,rdrate)  ! Dfactor after end stage
 ELSE                                            ! Processes not active
 rdrate=0.0
 ENDIF

 ! Vegetative development
 lnumsgs=0.0                               ! Leaf # inc,standard
 vdrate=0                                  ! Vegetative dev rate
 IF(vstage.GE.1)THEN
  tfvdev=Tfachr(cswtem,tlnumir,tairhr(hour),degday)
  IF(cswtstep.EQ.24)tfvdev=Tfac(cswtem,tlnumir,tairhr,degday)
  IF(vstage.LT.10)THEN
   IF(hour.EQ.1)tfgemday=0.0
   tfgem=Tfachr(cswtem,tgemr,tairhr(hour),degday)
   IF(cswtstep.EQ.24)tfgem=Tfac(cswtem,tgemr,tairhr,degday)
   tfgemday=tfgemday+(tfgem/24.0)*cswtstep
   IF(vstage.LT.5)THEN
    vdrate=(tfvdev/24.0)*cswtstep
   ELSE
    vdrate=(tfvdev/24.0)*cswtstep
   ENDIF
  ELSEIF(vstage.GE.10)THEN
   vdrate=(tfvdev/24.0)*cswtstep
   IF(rstage.GE.65)THEN
    vdrate=rdrate
   ENDIF
```

```
 IF(gtyp.EQ.3)THEN
  IF(lnumsd.LT.0.75)THEN
   lnumsgs=vdrate*lnumirs/4
  ELSE
   lnumsgs=vdrate*lnumirs
  ENDIF
 Else
  IF(cswtstep.EQ.24)lnumsgs=lnumsgs*0.95
 ENDIF
ENDIF

lnumsg=lnumsgs*lnumif                          ! Leaf # increase lvs/day
snumir=lnumsg                                  ! Shoot# increase rate

snumpg=0.0                                     ! Branch no increase = 0
IF(rstage.LT.snumpe) THEN                      ! If tillering possible
 IF(lnumsd.GE.snumis)THEN                      ! If leaf number > threshold
  IF(lnumsd.GE.snumis.AND.lnumsd.LT.snumis+3)THEN
   tfibonum=1                                  ! Fibonacci series number
  ELSEIF(lnumsd.GE.snumis+3.AND.lnumsd.LT.snumis+4)THEN
   tfibonum=2
  ELSEIF(lnumsd.GE.snumis+4.AND.lnumsd.LT.snumis+5)THEN
   tfibonum=3
  ELSEIF(lnumsd.GE.snumis+5.AND.lnumsd.LT.snumis+6)THEN
   tfibonum=4
  ELSEIF(lnumsd.GE.snumis+6.AND.lnumsd.LT.snumis+7)THEN
   tfibonum=6
  ENDIF

  IF(wfg.GT.0.5)THEN                           ! If no h2o stress
   IF(tmin.GT.-10)THEN                         ! If temperature ok
    snumpg=tfibonum*snumir                     ! Branch no increase
    IF(parip.GT.50.0)THEN
     snumpg=snumpg*AMAX1(0.3,1.0-(parip-50.0)/(80.0-50.0)) ! PAR effect
    ENDIF
    snumpg=snumpg*AMAX1(0.0,(1.0-snumpp/snumif))
    IF(dstage.GT.snumpe-5)snumpg=snumpg*0.2
   ENDIF
```

```
  ENDIF
 ENDIF
 ENDIF
 snumpg=snumpg*nfg                                    ! N effect on tillering
ELSE
 tfgem=0.0
ENDIF
ENDIF


IF(cfltask.EQ.'s')THEN                               ! State variables
 IF(hour.EQ.1.AND.cflstage.LT.999)cflstage=0                ! Reset stage flag
 IF(rstagep.EQ.9)go to 9999                                 ! NB Temporary to stop!!!!!

 IF(vstage.LT.1) THEN                                ! If not yet planted
  cflpldoy=0
  IF(cswplant.EQ.'A')THEN                                   ! If automatic planting
   IF(doy.GE.pfrst.AND.doy.LE.plast)THEN
    cflplant=1
    IF(sh2o(1).LT.ph2ol*0.01*slll(1).
x    OR.sh2o(1).GE.slll(1)+ph2ou*.01*(sdul(1)-slll(1)))RETURN
    pyr=iyr
    pdoy=doy
    cflpldoy=1
   ELSE
    IF(cflplant.GT.0)THEN
     message=' Too late to plant ! '
     stname= 'Termination  '                         ! Stage name
     cflstage=999
     cflstspp(spp)=cflstage
     stagedat(9)=(iyr*1000)+doy                             ! Final date
     cflplant=0
     RETURN
    ELSE
     RETURN
    ENDIF
   ENDIF
  ENDIF
```

```
      IF(doy.NE.pdoy)RETURN                          ! If not at planting day
      IF(yer.EQ.1.AND.iyr.NE.pyri)RETURN             ! If<pl year
      cflpldoy=1                                     ! Planting day flag
      pyr=iyr
     ENDIF

     IF(vstage.LT.1.and.cflpldoy.LT.1)THEN           ! If not at planting date
      RETURN
     ELSEIF(vstage.LT.1.and.cflpldoy.GT.0)THEN             ! If planted
      vstage=1                                       ! Planting,start imbibition
      stname='Planting'                              ! Stage name
      IF(page.LE.0)THEN                              ! If no transplant
       IF(page.LE.-99)page=0.0                               ! If not missing value
       duge=duge-page                                ! Duration,gm,specific  dday
       duge=amax1(0.0,duge)
      ENDIF
      dugp=amin1(dugp,duge)
      IF(plme(1:1).EQ.'t'.OR.plme(1:1).EQ.'2')THEN         ! If transplanting
       stname='Transplanting'                        !  - Stage name
      ENDIF
      IF(cflstage.LT.999)cflstage=1                         ! Phase change indicator
     ELSEIF(vstage.GE.1)THEN                         ! If planted
      IF(hour.EQ.1)dap=dap+1                               ! Days after planting
      IF(hour.EQ.1)dastage=dastage+1                 ! Days after phase change
      IF(hour.EQ.1.AND.vstage.GE.5.0)dag=dag+1
      IF(dap.GT.400)THEN
       message=' 400 dap! problem?  '
       stname='Termination  '                        ! stage name
       cflstage=999
       stagedat(9)=(iyr*1000)+doy                           ! Final date
      ENDIF
     ENDIF

C    Vegetative development

     IF(rstage.LT.lnumse)THEN                              ! If producing leaves
      IF(vstage.LT.10) THEN                          ! If not emerged
```

```
!Water stress factors before emergence
IF(plly.EQ.1.AND.sh2o(1).LT.sh2o(2))THEN
 sh2os=sh2o(1)+(pldp/sldl(1))*(sh2o(2)-sh2o(1))    ! H2O around seed
ELSE
 sh2os=sh2o(plly)
ENDIF
swfg=0.5*(sdul(plly)-slll(plly))                   ! Soil water for max germ
IF(sh2os.GT.slll(plly)+swfg)THEN
 wfg=1.0
ELSEIF(sh2os.GT.slll(plly))THEN
 wfg=(sh2os-slll(plly))/swfg
ELSE
 wfg=0.0
ENDIF

IF(cswswb.EQ.'0')wfg=1.0
vdsump=vdsump+(tfgem/24.0)*cswtstep                ! Veg.dev sum for phase

IF(hour+cswtstep.GT.24)THEN                        ! If at end of day
 IF(vdsump.GE.duge-dugp)THEN                       ! If germ started
  IF(gefd.LT.1)THEN                                ! If germ not complete
   dog=dog+1                                       ! Day of germination
   IF(dugp.GT.0)THEN
    dog=MIN0(dogx,dog)
    gefc(dog)=tfgemday/dugp                        ! Germination on day (fr)
    gefc(dog)=AMIN1(1.0,gefc(dog))
    gefd=AMIN1(1.0,gefd+gefc(dog))                 ! Germination,cumulative fr
   ELSE
    gefc(dog)=1.0
    gefd=1.0
   ENDIF
  ENDIF
  emsd=0.0
  emfd=0.0
  DO l=1,dog
   stlc(l)=stlc(l)+tfgemday/duem                          ! Stem length of gm cohort
   emfdtmpu=1.0-AMAX1(0.0,((pldpu-stlc(l))/pldpu))
```

```
  emfdtmpl=1.0-AMAX1(0.0,((pldp-stlc(l))/pldp))
  emsd=AMIN1(1.0,emsd+gefc(l)*(emfdtmpu+emfdtmpl)/2.0)                !
                                                                      Emergence
  IF(emfdtmpu.EQ.1)emfd=emfd+gefc(l)/2.0
  IF(emfdtmpl.EQ.1)emfd=emfd+gefc(l)/2.0
 ENDDO
 ENDIF
ENDIF

IF(vstage.LT.5)THEN                          ! If not fully germinated
 IF(duge.GT.0)THEN
  vstage=1.0+(vdsump/duge)*4.0
  vstage=AMIN1(5.0,vstage)
 ELSE
  vstage=5.0
 ENDIF
 IF(vdsump.GE.duge)THEN                      ! If vdsump > germ phase
  stname='Germination 100%'                  ! Stage name
  IF(cflstage.LT.999)cflstage=1                    ! Stage change indicator
 ENDIF
ENDIF

IF(vstage.GE.5)THEN                          ! If germinated,not emerged
 IF(pldp.GT.0)THEN
  vstage=5.0+(emsd*5.0)                      ! Vstage
 ENDIF
 IF(emfd.GE.1.0) THEN                        ! If fully emerged
  stname='Emergence 100%'                    ! Stage name
  vstage=10.0                                ! Vstage
  edat=(iyr*1000+doy)                        ! Emergence date
  IF(cflstage.LT.999)cflstage=1                    ! Stage change indicator
  lnumsd=0.0                                 ! Leaf number at emergence
  snumpgc=0.0                                ! Tiller cohort at emergence
 ENDIF
 lunitsd=lunitsd+lnumirs*vdrate                    ! Leaf # from germination
 prnumsd=prnumsd+lnumirs*vdrate*prif         ! Primordia # increase if gm
ENDIF
```

```
 ELSEIF(vstage.GE.10)THEN                    ! If emerged
  lnumsd=lnumsd+lnumsg                              ! Haun scale leaves
  IF(gtyp.EQ.1.and.lnumss(4).GT.0)
X   lnumsd=AMIN1(lnumss(4),lnumsd)
  IF(lnumsd.GT.lnumsx)THEN                  ! If leaf number > max
   WRITE(*,*)' Warning. leaf number greater than maximum'
   message=' Too many leaves !'
   stname='Termination     '                ! Stage name
   cflstage=999
  ENDIF
  lunitsd=lunitsd+lnumirs*vdrate                    ! Leaf # from germination
  IF(rstage.LT.20)THEN                      ! If still initiating leaves
   prnumsd=prnumsd+lnumsg*prif              ! Primordia #
  ELSEIF(rstage.GE.20.AND.rstage.LT.30)THEN
   prnumsd=prnumsd+lnumsg*prif*prrf         ! Primordia #
  ENDIF
  vstage=10.0+lnumsd                        ! Vstage
 ENDIF
ENDIF

IF(rstage.LT.snumpe) THEN                   ! If tillering possible
 IF(snumpg.GT.0)THEN
  snumpp=snumpp+snumpg                      ! Branch # - total produced
  snumpgcn=0.3
  snumpgc=snumpgc+snumpg                    ! Branch # - new cohort
  IF(snumpgc.GE.snumpgcn)THEN               ! New cohort
   IF(tcnum.LT.tcnumx)THEN
    tcnum=tcnum+1                           ! Tiller cohort number
    tcsize(tcnum)=snumpgc
    snumpgc=0.0
    tclnum(tcnum)=lnumsd
    tcdag(tcnum)=dag
   ELSE
    tcsize(tcnum)=tcsize(tcnum)+snumpg
    tclnum(tcnum)=lnumsd
    tcdag(tcnum)=dag
   ENDIF
  ENDIF
```

```
      ENDIF
     ELSE
      IF(gtyp.LT.3.AND.snumpsgt.LE.0)THEN          ! Tiller death for cereals
       DO l=tcnum,1,-1
        IF(lnumsd-tclnum(l).GT.snumdf)EXIT
        snumpsgt=snumpsgt+tcsize(l)                ! Tillers that will die
       ENDDO
       snumpsgt=snumpsgt+snumpgc                   ! Tillers that will die
      ENDIF
     ENDIF

C    Reproductive development

     IF(vstage.GE.5.0)THEN                              ! If germinated
      vrndaysm=vrndaysm+tfvrn                           ! Vernalization age
      rstagep=INT(rstage/10.0)                  ! Reproductive stage,primary
      rstages=rstage/10-AINT(rstage/10.0)       ! Reproductive stage,primary
      rdsump=rdsump+rdrate                              ! Rep dev sum for phase
      IF(rdsump.GE.duph(rstagep))THEN
       rdsump=rdsump-duph(rstagep)              ! Reprod sum for next phase
       IF(rstagep.EQ.6)rdsump=0                         ! No carryover into filling
       IF(rstagep.LE.4)lnumss(rstagep)=lnumsd   ! Leaf # at end of phase
       IF(rstagep.LE.4)prnumss(rstagep)=prnumsd ! Primordia #,end of phase
       IF(rstagep.EQ.3)prnumss(3)=ANINT(prnumss(3)+0.5)
       stagedat(rstagep)=(iyr*1000+doy)         ! Date at end of phase
       IF(cflstage.NE.1.AND.cflstage.LT.999)THEN        ! If not changed or failed
        cflstage=1                              ! Phase change indicator
        stname=rstname(rstagep)                         ! Stage name
       ENDIF
       rstagep=rstagep+1                        ! Reproductive stage
       IF(rstagep.GT.rstagepx)THEN
        WRITE(*,*)'No.of principal stages over maximum of: ',rstagepx
        WRITE(*,*)'Species that working with was: ',spp
        STOP
       ENDIF
      ENDIF

      IF(duph(rstagep).GT.0)THEN
```

```
 rstages=rdsump/duph(rstagep)                    ! Reproductive stage,2ndary
ELSE
 rstages=0.0
ENDIF
rstage=(rstagep+rstages)*10.0                    ! Reproductive stage
IF(rstage.LE.0.0.AND.vstage.GE.5.0) rstage=0.0001

IF(rstage.GE.rstend)THEN
 cflstage=99                                     ! Control flag - maturity
 stagedat(9)=(iyr*1000)+doy                              ! Harvest date
ENDIF

IF(rstage.LT.20)THEN                             ! If before final lf# set
 IF(gtyp.EQ.1)THEN                               ! If growth type=wheat
  IF(lnumef.LE.0)lnumef=1.6                              ! If emergence factor 0
  lnumif=1.0+AMAX1(0.0,((3.0-lnumsd)/3.0)*(lnumef-1.0))
  IF(cswtstep.EQ.24)lnumif=lnumif*0.95
 ELSE
  lnumif=1.0
 ENDIF
ENDIF

IF(rstage.GE.20.AND.lnumss(4).LT.1)THEN                  ! If to set final leaf #
 IF(gtyp.EQ.1.0)THEN
  lnumss(4)=lnumsfn+lnumsff*lnumsd               ! # from Haun at floral in.
  lnumss(4)=anint(lnumss(4))                             ! Round out leaf#
  lnumif=((lnumss(4)-lnumsd)/                            ! Leaf app factor (#)
x   (duph(2)-rdsump+duph(3)))/lnumirs
 ELSEIF(gtyp.EQ.2.0)THEN
  ! Algorithms to calculate durations if leaf rate held fixed
  treal1=(lnumss(4)-lnumsd)/lnumirs              ! Duration of phases 2+3
  treal2=duph(3)/duph(2)                         ! Ratio of phase durations
  duph(2)=(treal1+rdsump)/(1.0+treal2)           ! Duration of phase 2
  duph(3)=duph(2)*treal2                         ! Duration of phase 3
 ENDIF
ENDIF

ENDIF                                            ! End of states
```

```
C     Harvest
      IF(hdatm.GT.0)THEN                          ! If harvest date specified
       IF((iyr*1000+doy).GE.hdatm)THEN            ! If specified date reached
        stname='Specified harvest'                ! Stage name
        stagedat(8)=(iyr*1000)+doy                    ! Maturity date
        stagedat(9)=(iyr*1000)+doy                    ! Harvest date
        cflstage=99                               ! Control flag - harvest
       ENDIF
      ENDIF

C     Developmental stage
      ! 'Developmental' stage (Zadoks/BBCH) = Vstage until tillering
      !                       = f(tiller#) after tillering
      !                       = f(rstage) once reproductive
      IF(rstage.LT.20)THEN
       ! 01=begining of seed imbibition (assumed to be at planting)
       ! 05=germination (assumed to be when the radicle emerged)
       ! 09=coleoptile thru soil surface
       ! 10=first leaf emerged from the coleoptile (taken as emergence)
       ! 11=first leaf fully expanded
       ! 20=first tiller appeared on some plants
       IF(snumpp.LE.0)THEN
        dstage=AMIN1(19.9,vstage)
       ELSEIF(snumpp.GT.0)THEN
        IF(snumpp.LE.1.0)THEN
         treal1=AMIN1(19.9,vstage)
         dstage=AMAX1(treal1,11.0+10.0*snumpp)
        ELSE
         dstage=AMIN1(29.9,20.0+snumpp)
        ENDIF
       ENDIF
      ELSEIF(rstage.GE.20.0.AND.rstage.LT.30.0)THEN  ! If after dr,before ts
       dstage=AMIN1(29.9,20.0+snumpp)
       IF(rstage.GT.22)THEN
        dstage=AMAX1(dstage,rstage)
       ENDIF
      ELSEIF(rstage.GE.30.0.AND.rstage.LT.40.0)THEN  ! If after ts,before ll
```

```
      dstage=rstage
     ELSEIF(rstage.GE.40.0.AND.rstage.LT.70)THEN     ! If after ll,before ea
      dstage=rstage
     ELSEIF(rstage.GE.70.0.AND.rstage.LT.80)THEN     ! If after ea,before lgf
      dstage=70.0+0.4*(rstage-70.0)
     ELSEIF(rstage.GE.80.0)THEN                      ! If in linear fill
      dstage=74+1.6*(rstage-80.0)
     END IF

     cflstspp(spp)=cflstage
     dstagesp(spp)=dstage

 9999  continue

    ENDIF


     CALL Storname(trt,spp,rotc,roto,'cdm',FNAMEST)

     RETURN

     END
```

Appendix 5: CROPSIM Growth Subroutine (CRSIMCG.FOR)

```
C CROPSIM CROP GROWTH

      SUBROUTINE Growth(cswtstep,cfltask,cflstage,
     X hour,run,doy,iyr,das,dap,dag,
     X message,stname,rotc,roto,trt,
     X spp,ppop,dstage,vstage,rstage,
     X awpg,lnumsg,hwpga,hwpgrs,resprs,
     X lnumsd,lnumss,snumpp,snumpsgt,hwpd,hwad,hwnumd,hnumad,
     X vdrate,rdrate,
     X nfg,nfp,rtdlw,rtdln,sradhr,parips,paripsa,
     X pard,parip,tairhr,tmin,sh2o,wf,vpd,sno3,co2,dayl,
     X SFRD,CWPGAA,RSWPDA,RWPGA,RWPGR,RWPGS,RDWPG,LDWPG,
     X LRSWPG,SDWPG,STRSWPG,
     X CAID,CAIDSL,ECPC,LAIDL,LAIDLA,
     X LAP,LAPD,LFCIDAG,LFCNUM,LAPP,LAPS,
     X RLAD,RLV,
     X CWPD,LBWPD,LWPCRIT,RWPD,RWAD,SBWPD,SNUMPD,VWPD,
     X WFP,WFG,
     X CWAD,HIAD,LAID,LAIX,SNUMAD,TWAD,WFGPSUM,WFPPSUM,AFLEXSML,
     X DAYLEXSM,TFLEXSML,NFLEXSML,WFLEXSML,LAWGSUM,VWAD,LALD,LALP,
     X SEEDWAP,RUEA,RUEM,PARC)

      IMPLICIT NONE

      INCLUDE 'Crsimcg.ica'                    ! Array dimensions

      INCLUDE 'Crsimcg.icc'                    ! Communication variables
      INCLUDE 'Crsimcg.icd'                    ! Driving variables
      INCLUDE 'Crsimcg.ici'                    ! Input variables
      INCLUDE 'Crsimcg.icr'                    ! Rate variables
      INCLUDE 'Crsimcg.ics'                    ! State variables
      INCLUDE 'Crsimcg.ict'                    ! Temporary variables

      INCLUDE 'crsimht.inc'

      INCLUDE 'Crsimcg.icu'                    ! File unit numbers and names
```

```
 IF(cfltask.EQ.'i'.OR.cfltask.EQ.'b')THEN
  CALL Storname(trt,spp,rotc,roto,'cgi',FNAMEST)
  OPEN(fnumst,FILE=fnamest,FORM='UNFORMATTED')
  READ(fnumst)
X cswfro,cswnit,cswswb,cswtem,
X ename,rname,sname,sppnumo,tn,tname,gtyp,
X pldp,plrs,
X awns,
X cphc1,ctof,
X drgf1,
X duph,
X la1x,lali,lalx,laws,lnumse,ldfa,ldfd,ldwc,ldwf,lflb,
X lnumlrs,lslc,lslf,
X phsv,phtv,
X rers,rlws,rsaf,rsrs,rstr,rsur,rtdx,rtgf,
X rrue1,rues,ruesf,
X saws,seedwap,sele,snumpe,snumpf,snumpi,
X scfrx,secpl,srsfrx,ssfrx,
X tlaw1,tlexr,tphc1,tdev1,
X wfgi,wfpi,
X sdul,slbl,sldl,slll,slnl,srgf
  CLOSE(fnumst)

  IF(gtyp.EQ.3)THEN
   CALL CANHGA(cfltask,cswtstep,wfg,tairhr,
x   parips(spp),parips(spp),rstage,cwpd,CHT,MWPD,FWPD)
  ENDIF
 ENDIF

 IF(cfltask.EQ.'z'.OR.cfltask.EQ.'b')THEN
  DO I=1,50
   lald(I)=0.0
   lalp(I)=0.0
   lapl(I)=0.0
  ENDDO
  DO I=1,200
   laps(I)=0.0
   lap(I)=0.0
```

```
 lwp(l)=0.0
 lage(l)=0.0
enddo
DO l1=1,5
 DO l2=1,30
  caidsl(l1,l2)=0.0
 ENDDO
ENDDO
DO l=1,15
 rlv(l)=0.0                          ! Rt length/volume (cm/cm3)
ENDDO

parlp=0.0                            !par effect on branch leaf area
parlaws=0.0                          !par effect on specific leaf area
aflex=0
tflex=0
lawg=0
aaid=0.0                             ! Awn area index (m2 m-2)
aapd=0.0                             ! Awn area (cm2 p-1)
aapg=0.0                             ! Awn area growth(cm2 p-1)
aapsg=0.0                            ! Awn area senescence (cm2/p
snumps=0.0                           ! Shoot #,senesced (# p-1)
hiad=0.0                             ! Harvest index
laid=0.0                             ! Leaf area index (m2 m-2)
laix=0.0                                    ! Leaf area index,maximum
lapgc=0.0                            ! Lf area gr,cohort (cm2/p)
ldwpd=0.0                            ! Leaf dead wt (g/p)
lbwpd=0.0                            ! Leaf basic wt (g p-1)
lrwpd=0.0                            ! Leaf reserve wt (g p-1)
ldwpd=0.0                            ! Leaf dead wt (g/p)
ldwpdgf=0.0                          ! Leaf dead wt,gr fill (g/p)
lfcnum=0                             ! Leaf cohort #
lnum=0                               ! Leaf #,mature per axis (#)
wfp=1.0                              ! H2O factor,photosynthesis
wfg=1.0                              ! H2O factor,growth
parc=0.0                             ! PAR,int,cumulative (MJ/m2)
rlad=0.0                             ! Root length (cm m-2)
rswpd=0.0                            ! Reserve wt (g p-1)
```

```
lrswpg=0.0
strswpg=0.0
lwpgr=0.0
swpgr=0.0
rwpgr=0.0
rtdd=0.0                ! Root depth (cm)
rtdgsum=0.0             ! Root depth growth sum (cm)
rwpd=0.0                ! Root wt (g p-1)
rdwpd=0.0               ! Root dead wt (g p-1)
ruea=0.0                ! Radiation use effic (g/Mj)
said=0.0                ! Stem area index (m2 m-2)
sapd=0.0                ! Stem area (cm2/p)
srwpd=0.0               ! Stem reserve wt (g p-1)
sbwpd=0.0               ! Stem basic wt (g p-1)
sdwpd=0.0               ! Stem dead wt (g p-1)
sbwsd=0.0               ! Shoot wt per tiller (g)
spwpd=0.0               ! Spike wt per plant (g)
caix=0.0                ! Canopy area index,maximum
cfrd=0.0                ! Canopy fraction (fr)
caid=0.0
said=0.0
swad=0.0
rswad=0.0
sbwad=0.0
cwad=0.0
rwad=0.0
twad=0.0
cdwad=0.0
snumad=0
hiad=0.0
rtdd=0.0
cfrd=0.0
rlad=0.0
parc=0.0
vpdfph=0.0
tfph=0.0
snumpd=0.0
snumps=0.0
```

```
      ENDIF

      IF(cfltask.EQ.'h'.OR.cfltask.EQ.'b')THEN

C The following 3  lines are only for output file names
       ciyr=inchar(iyr)
       ctrt=inchar(tn)
       fncg=fncg(1:4)//ciyr//ctrt(1:lentrimg(ctrt))//'.out'

       unit='$GROWTH ASPECTS OUTPUT FILE  '
       symbol='G'
        cluster='@DATE  CDAY  L#SD  GSTZ  RSTD  CAID  LAID  SAID  LWAD
     x SWAD RSWAD SBWAD  HWAD  CWAD  RWAD  TWAD CDWAD  S#AD  H#AD  HW#D

     x CHGT  RTDD  CFRD  RLAD  RL1D  RL3D  RL6D  RL7D  PARC  TFPD  VFPD
     x WFPD  WFGD  NFPD  NFGD PARIP  RUEA  AWPP SEEDP LAMPD  HIAD     '
       CALL Outputh(run,sppnumo,tn,ename,tname,rname,sname,
     x fnumcg,fncg,unit,symbol,cluster)
       unit='$GROWTH ASPECTS,HR,OUTPUT FILE'
       symbol='G'
       cluster=' '
       cluster(1:102)='@HOUR  SRAD  TAIR  AWPP  WFPH  TFPH  LAPG  WFGR
     X                                  '
       CALL Outpuths(run,tn,ename,tname,rname,sname,
     x fnumcgh,fncgh,unit,symbol,cluster)
       RETURN
      ENDIF

      IF(ppop.EQ.0)RETURN                                  ! If fallow
      IF(vstage.LT.1)RETURN                                ! If not planted

      IF(lnum.GT.0.AND.lalp(lnum).GT.0)THEN          ! Potential leaf area  cm2
       lapgcmin=lalp(lnum)                           ! Minimum size of leaf cohort
      ELSE
       lapgcmin=0.8                                  ! Minimum size of leaf cohort
      ENDIF
      IF(cfltask.EQ.'r')THEN                         ! If to calculate rates
```

```
C     Water stress factors
      IF(cswswb.NE.'0')THEN                          ! If water to be simulated
       IF(wf.LT.wfpi)THEN
        wfp=AMAX1(0.2,AMIN1(1.0,wf/wfpi))            ! NB limit of 0.2
        IF(rstage.GT.80)wfp=1.0-(0.3*(1.0-wfp))      ! Less sensitivity in gf
       ELSE
        wfp=1.0
       ENDIF
       wfg=AMAX1(0.0,AMIN1(1.0,wf/wfgi))             ! NB limit of 0.0
       wfghr(hour)=wfg+0.8*(1.0-wfg)                 ! Water factor,growth
       IF(spp.EQ.1)THEN
        ! Accumulators for phase outputs
        Wfppsum=Wfppsum+Wfp/24.0*cswtstep            ! Water factor,phs-phases
        Wfgpsum=Wfgpsum+Wfg/24.0*cswtstep            ! Water factor,gr-phases
       ENDIF
      ELSE
       wfg=1.0
       wfp=1.0
      ENDIF

      anasg=0.0
      cwpga=0                                        ! Canopy gr,assim
      lapg=0.0
      ldwpg=0.0
      lfcnumsg=0                                     ! Leaf cohort,senesced,new
      lrswpg=0.0
      lwpg=0.0
      lwpga=0.0
      lwpgr=0.0
      lwpgs=0.0
      rdwpg=0                                        ! Root dead wt,growth
      rtdg=0                                         ! Root depth growth (cm)
      rwpga=0                                        ! Root growth from assim
      rwpgr=0                                        ! Root growth from reserves
      rwpgs=0                                        ! Root growth from seed
      sapg=0.0                                       ! Stem area,growth
      sapsg=0.0
      sdwpg=0.0                                      ! Stem weight,senesced,gr
```

```
      snumpsg=0.0                                    ! Shoot #,senesced,growth
      spwpg=0.0
      strswpg=0                                      ! Stem to reserves at death
      swpg=0                                         ! Stem weight growth
      swpga=0                                        ! Stem weight growth,assim
      swpgr=0                                        ! Stem weight growth,from rs
      swpgs=0                                        ! Stem weight growth,from sd
      IF(hour.EQ.1)THEN
       DO I=1,24
        lapghr(I)=0.0
       ENDDO
      ENDIF

      IF(vstage.GT.10)THEN                                ! If emerged
       rswpda=rswpd
C      Dry matter accumulation
       parfrue=Yfactor('rrue1',rrue1,pard)                ! Par effect on RUE
       rue=parfrue*rues                               ! Radn use efficiency g/MJ.p
       IF(said+laid.GT.0)THEN
        rue=((rue*ruesf*said)+(rue*laid))/(said+laid)     ! Stems less effective
       ENDIF

       IF(ppop.GT.0)THEN
        IF(hour.EQ.12)THEN
         treal1=(sradhr(11)+(sradhr(12)-sradhr(11))*0.5)
        ELSE
         treal1=sradhr(hour)
        ENDIF
        awpphr(hour)=(paripsa(spp)*0.01)*treal1*0.5*rue/ppop  ! Assim,pot
       ENDIF

       IF(cswtstep.EQ.24)THEN
        awpphr(hour)=(paripsa(spp)*0.01)*pard*rue/ppop        ! Assim,pot
       ENDIF

       if(hour.eq.1)awpp=0.0
       awpp=awpp+awpphr(hour)*60.0*60.0*1.0E-6*cswtstep
       if(hour.eq.24)awpp=awpphr(hour)
```

```
      IF(gtyp.EQ.3)THEN
       IF(rstage.gt.60)THEN
        awpphr(hour)=awpphr(hour)*(1.0-(rstage-60)/rstage)
        IF(rstage.GT.80)THEN
         awpphr(hour)=awpphr(hour)
     X     *AMAX1(0.0,1.0-(.17+(rstage-80.0)/40))
        ENDIF
       ENDIF
      ENDIF

      IF(co2.LT.329.OR.co2.GT.331)THEN              ! Adjust assim rate for co2
       awpphr(hour)=awpphr(hour)*Yfactor('cphc1',cphc1,co2)
      ENDIF

      tfphhr(hour)=Tfachr(cswtem,tphc1,tairhr(hour),degday)
      IF(sradhr(hour).EQ.0)tfphhr(hour)=0.0
      IF(hour.EQ.12)tfph=tfphhr(hour)
      IF(cswtstep.EQ.24)THEN
       tfphhr(hour)=Tfacd(cswtem,tphc1,dayl,tairhr,degday)
       tfph=tfphhr(hour)
      ENDIF
      awpphr(hour)=awpphr(hour)*tfphhr(hour)        ! Adjust for temperature

      vpdfph=Factor(phsv,phtv,vpd)                      ! Vapour deficit factor,phs

      awpphr(hour)=awpphr(hour)*vpdfph              ! Adjust for vapour press

      wfa=wfp
      IF(rstage.GE.80)THEN
       IF(awns.GT.0)THEN
        wfa=wfp+0.5*(1.0-wfp)                       ! Water factor,assimilation
       ENDIF
      ENDIF
      wfphr(hour)=wfa+0.8*(1.0-wfa)                 ! Water factor,assimilation
      awpphr(hour)=awpphr(hour)*wfphr(hour)         ! Adjust for water status
      awpphr(hour)=awpphr(hour)*nfp                 ! Adjust for N status

      treal1=Yfactor('scfrx',scfrx,rstage)              ! Canopy fraction,max for st
```

```
      cfrx=treal1

      srfrd=Yfactor('ssfrx',ssfrx,rstage)                    ! Stem (incl reserves) fr
      IF(parip.GT.50.0.AND.rstage.LT.65.0)srfrd=srfrd+(parip-50)*.004
      lfrd=1.0-srfrd

      rsfrd=Yfactor('srsfrx',srsfrx,rstage)                  ! Reserves fraction
      IF(parip.GT.50.0.AND.rstage.LT.65.0)rsfrd=rsfrd-(parip-50.0)*.004
      rsfrd=AMAX1(0.0,rsfrd)

      sfrd=AMAX1(0.0,srfrd*(1.0-rsfrd))                      ! Stem fraction

      awpg=awpphr(hour)*60.*60.*1.E-6*cswtstep               ! g/p.period
      IF(cswtstep.EQ.24)awpg=awpphr(hour)

C     Canopy and Root Growth Potential

      rwpga=(1-cfrx)*awpg                                    ! Root gr,from assim
      cwpga=awpg-rwpga                                       ! Canopy gr,pot,from assim
      cwpgaa=cwpga

C     Leaves
      ! Growth
      lnum=INT(lnumsd)

      IF(rstage.LT.65.AND.srfrd.LT.1)THEN
       IF(lnumsd.LT.1)THEN
       lalp(1)=la1x                                          ! Potential leaf area  cm2
       ELSE
       lalp(lnum+1)=lalp(lnum)*lali                          ! Potential leaf area  cm2
       lalp(lnum+1)=AMIN1(lalp(lnum+1),lalx)                 ! Restrict to maximum
       ENDIF
       tflex=Tfachr(cswtem,tlexr,tairhr(hour),degday)
       IF(cswtstep.EQ.24)tflex=Tfac(cswtem,tlexr,tairhr,degday)

       lamgp=lalp(lnum+1)*lnumsg*tflex                       ! Potential dla/stem.period

       IF(cswtstep.EQ.24)lamgp=lamgp*1.1                     ! Adjustment,24h step
```

```
IF(hour.EQ.1)lamgpd=0.0                          ! Daily sum
lamgpd=lamgpd+lamgp
lamgp=lamgp*wfg                                  ! Adjust for h2o stress
latsgp=0.0

DO I=2,int(snumpd)                               ! Adjust,complete cohorts
 IF(I.GT.1.AND.I.LE.4)THEN
  latgp=lamgp*0.80                               ! La of tiller 1 (80% main)
 ELSEIF(I.GT.4.AND.I.LE.8)THEN
  latgp=lamgp*0.60                               ! La of tiller 1 (60% main)
 ELSEIF(I.GT.8.AND.I.LE.12)THEN
  latgp=lamgp*0.40                               ! La of tiller 1 (40% main)
 ELSEIF(I.GT.12.AND.I.LE.16)THEN
  latgp=lamgp*0.40                               ! La of tiller 1 (40% main)
 ELSEIF(I.GT.16)THEN
  latgp=lamgp*0.40                               ! La of tiller 1 (40% main)
 ENDIF
 latsgp=latsgp+latgp
END DO

I=int(snumpd+1)                                  ! Adjust,incomplete cohort
IF(I.GT.1.AND.I.LE.4)THEN
 latgp=lamgp*0.80                                ! La of tiller 1 (80% main)
ELSEIF(I.GT.4.AND.I.LE.8)THEN
 latgp=lamgp*0.60                                ! La of tiller 1 (60% main)
ELSEIF(I.GT.8.AND.I.LE.12)THEN
 latgp=lamgp*0.40                                ! La of tiller 1 (40% main)
ELSEIF(I.GT.12.AND.I.LE.16)THEN
 latgp=lamgp*0.40                                ! La of tiller 1 (40% main)
ELSEIF(I.GT.16)THEN
 latgp=lamgp*0.40                                ! La of tiller 1 (80% main)
ENDIF

latsgp=latsgp+latgp*(snumpd-int(snumpd))         ! Add la,incomplete cohort

IF(gtyp.EQ.3)THEN
 IF(parip.GT.60.0)THEN
  parlp=AMAX1(0.0,1.0-(parip-60.0)/(90.0-60.0))  !Pareffect on branch leaf area
```

```
      ELSE
       parlp=1.0
      ENDIF
      latsgp=latsgp*parlp
     ENDIF

     IF(parip.GT.40.0)THEN
      parlaws=AMAX1(1.25,1.0+(parip-20.0)/(100.0-20.0))      !Pareffect on specific leaf
                                                              area
     ELSE
      parlaws=1.0
     ENDIF

     tflaw=Tfachr(cswtem,tlaw1,tairhr(hour),degday)
     IF(cswtstep.EQ.24)tflaw=Tfac(cswtem,tlaw1,tairhr,degday)
     lawg=laws*tflaw*parlaws

     IF(wfg.GT.0)lawg=lawg*AMAX1(0.6,wfg)          ! Leaf area to weight ratio
     IF(lawg.GT.0)lwpgp=(lamgp+latsgp)/lawg        ! Leaf gr,potential
     IF(rstage.GT.lnumse)lwpgp=(latsgp)/lawg

     IF(lwpgp.GT.cwpga*lfrd)THEN                   ! If pot lf > assim
      lwpga=cwpga*lfrd                             !  - use all avail assim

      IF(rswpda*rsaf/24.0*cswtstep.
    X  GT.(lwpgp-lwpga))THEN                       !  - if reserves>need
      lwpgr=lwpgp-lwpga
      ELSEIF(rswpda*rsaf.GT.0)THEN                 !  - if reserves<need
       lwpgr=rswpda*rsaf/24.0*cswtstep
      ENDIF
      rswpda=rswpda-lwpgr

      IF(lwpgp.GT.(cwpga*lfrd+lwpgr))THEN          ! If pot lf gr > assim+res.
       IF(seedwpd.GT.(lwpgp-(cwpga*lfrd+lwpgr)))THEN! If seed wt > demand
        lwpgs=lwpgp-(lwpga+lwpgr)
       ELSEIF(seedwpd.GT.0)THEN                    ! If seed wt < demand
        lwpgs=seedwpd
       ENDIF
```

```
 ENDIF
ELSEIF(lwpgp.LE.cwpga*lfrd)THEN                ! If pot lf gr < assim
 lwpga=lwpgp                                   ! Assim for leaves
ENDIF

lwpg=lwpga+lwpgr+lwpgs                                  ! Leaf components

lapg=lwpg*lawg                                 ! Leaf area growth
lapghr(hour)=lapg/cswtstep
IF(lapg.LE.0)THEN
 lapg=0.0
 lwpg=0.0
 lwpga=0.0                                     ! Leaf components
 lwpgr=0.0                                     ! Leaf components
 lwpgs=0.0                                     ! Leaf components
ENDIF

IF(lwpgp.GT.0)THEN
 aflex=lwpg/lwpgp                              ! Assimilate factor,leaf ex
ELSE
 aflex=1.0                                     ! Assimilate factor,leaf ex
ENDIF

IF(lnumsg.GT.0.AND.lamgp.GT.0)THEN
 lapgmfr=lamgp/(lamgp+latsgp)                  ! Main stem lf fr
 IF((lnumsd+lnumsg).GT.(lnum+1))THEN
  lapgofr=((lnum+1.0)-lnumsd)/lnumsg           ! Older gr leaf fr
 ELSE
  lapgofr=1.0                                          ! Older gr leaf fr
 ENDIF
 IF(lnum+1.GT.lnumss(4).AND.lnumss(4).GT.0.0)lapgofr=1.0  ! Last leaf .. no new leaf
 ENDIF
ELSE                                                    ! After leaf growth
 lamgp=0.0
 lamgpd=0.0
ENDIF                                          ! End of leaf growth section

! Death
```

```
! Life expectancy calculated before kill leaves
IF(rstage.LT.lnumse)THEN                          ! Before last leaf
 lflife=(lflb/lnumirs)                            ! Leaf life expectancy bd
ELSE                                              ! After last leaf

 IF(gtyp.LT.3)THEN
  IF(duph(8).GT.100)THEN
   lflife=(duph(4)+duph(5)+duph(6)+duph(7)+duph(8)-20)
  ELSE
   lflife=(duph(4)+duph(5)+duph(6)+duph(7)+duph(8)-1.0)
  ENDIF
 ELSE
  lflife=(lflb/lnumirs)                           ! Leaf life expectancy bd
 ENDIF

ENDIF
DO l=lfcnum,1,-1                                  ! From youngest to oldest
 IF(lwp(l).GT.0)THEN
  IF(lage(l).GE.lflife)THEN                       ! Kill leaves if too old
   ldwpg=ldwpg+lwp(l)*ldfd
   lrswpg=lrswpg+lwp(l)*(1.0-ldfd)
   lfcnumsg=MAX0(lfcnumsg,l)
  ENDIF
 ELSE
  EXIT
 ENDIF
END DO


C     Awn growth
IF(rstage.GE.70.AND.rstage.LT.75)THEN
 aapg=10.0*awns                                   ! Awn area,growth (cm2 p-1)
ELSE
 aapg=0.0
ENDIF

C     Awn senescence
IF(rstage.GE.80)THEN
```

```
      aapsg=(aapx*rdrate/duph(8))                    ! Senescence of awn area
      ELSE
       aapsg=0.0
      ENDIF

C     Anther growth
      anumsx=50                                      ! Anther #,max (#/s)
      ana=0.0
      anasg=0.0
      IF(rstage.GE.60.AND.rstage.LT.70)THEN
       anasg=anumsx*ana*rdrate                       ! Anther area,growth (cm2/pd
      ELSE
       anasg=0.0
      ENDIF

C     Anther senescence
      IF(rstage.GE.60)THEN
       ansnfr=(rdrate/(duph(7)+0.4*duph(8)))              ! Sen,anthers (fr)
      ELSE
       ansnfr=0.0
      ENDIF

C     Stems


      IF(rstage.LT.lnumse.AND.lfrd.GT.0)THEN
       swpgp=lwpgp*(srfrd/lfrd)                      ! Stem gr potential
       swpgp=AMIN1(swpgp,(sfrd*cwpga)+
     X   (rswpd*rsaf/24.0*cswtstep))

       ELSE
       IF(rstage.LE.sele)THEN                        ! If stem still growing
        swpgp=(sfrd*cwpga)+
     X    (rswpd*rsaf/24.0*cswtstep)                       ! Stem growth potential
       ELSE
        swpgp=0.0
       ENDIF
      ENDIF
```

```
      IF(swpgp.GT.cwpga*sfrd)THEN                    ! If pot stem > assim
       swpga=cwpga*sfrd                              !  - use all avail assim
       IF(rswpda*rsaf/24.0*cswtstep.
     X  GT.(swpgp-swpga))THEN                        !  - if reserves>need
       swpgr=swpgp-swpga
       ELSEIF(rswpda*rsaf.GT.0)THEN                  !  - if reserves<need
       swpgr=rswpda*rsaf/24.0*cswtstep
       ENDIF
      ELSEIF(swpgp.LE.cwpga*sfrd)THEN                ! If pot stem gr < assim
       swpga=swpgp                                   ! Assim for stems
      ENDIF
      IF(rstage.GE.sele-15)swpgr=swpgr*0.8           ! Reduced stem growth
      IF(rstage.GE.sele-5)swpgr=swpgr*0.4            ! Reduced stem growth
      rswpda=rswpda-swpgr
      swpg=swpga+swpgr                               ! Stem components

C     Stem senescence (tiller death)

      sdwpg=0.0                                      ! Stem weight,senesced,gr
      strswpg=0                                      ! Stem to reserves at death
      snumpsg=0.0                                    ! Shoot #,senesced,growth
      IF(rstage.GE.snumpe.AND.rstage.LT.snumpf)THEN! If>tillering<anthesis
       IF(duph(INT(rstage/10.0)).GT.0)THEN
       snumpsg=((snumpsgt/(snumpf-snumpe))*
     X  (rdrate/duph(INT(rstage/10.0))*10)*2.0)
       ENDIF
       IF(rstage.LT.snumpe+5)THEN
       snumpsg=snumpsg*0.5                                  ! Slower initially
       treal1=0.7
       ELSEIF(rstage.GE.snumpe+5.AND.rstage.LT.snumpf-10)THEN
       snumpsg=snumpsg                               ! Reduced tiller death
       treal1=0.4
       ELSEIF(rstage.GE.snumpf-10.AND.rstage.LT.snumpf-5)THEN
       snumpsg=snumpsg*0.5                                  ! Reduced tiller death
       treal1=0.0
       ELSEIF(rstage.GE.snumpf-5)THEN
       snumpsg=snumpsg*0.2                                  ! Reduced tiller death
       treal1=0.0
```

```
      ENDIF
      IF(nfg.GE.1.0)snumpsg=snumpsg*0.7
      snumpsg=AMIN1(snumpsg,snumpp-snumps)
      sdwpg=AMAX1(0.0,snumpsg*sbwsd*ldfd*treal1)    ! Weight loss (stem only!)
C     strswpg=AMAX1(0.0,snumpsg*sbwsd*(1.0-ldfd)*treal1)    ! Stem to reserves
      ENDIF


C     Stem area
      sapg=0.0                                      ! Stem area,growth
      IF(rstage.LE.sele)THEN                        ! Stem area to end stem gr
       sawd=saws
       IF(rstage.LT.50)THEN
        sapg=swpg*sawd
       ELSEIF(rstage.GE.50.AND.rstage.LT.sele)THEN
        sapg=1.0*swpg*sawd
       ENDIF
       sapsg=0.0
      ENDIF
      ! Stem area senescence
      IF(rstage.GT.80)THEN
       sapg=0.0
       IF(nfg.GE.1.0)THEN
        IF(rstage.LT.89)THEN
         sapsg=0.0                                  ! Senescence,adequate N
        ELSE
         sapsg=(0.5*sapgf*rdrate/duph(8))           ! Senescence,adequate N
        ENDIF
       ELSE
        sapsg=(sapgf*rdrate/duph(8))                        ! Senescence,normal
       ENDIF
       IF(rstage.LE.84)THEN                         ! Reduced senescence early
        sapsg=sapsg*0.3
       ELSEIF(rstage.GT.84.AND.rstage.LE.86)THEN
        sapsg=sapsg*0.6
       ENDIF
      ENDIF
```

```
      ELSE                                          ! Vstage < 10
       cwpga=0.0
       hwpga=0.0
       rwpga=0.0
       lapg=0.0
       lwpg=0.0
       lwpga=0.0
       lwpgr=0.0
       lwpgs=0.0
      ENDIF                                         ! End of vstage>10 section

C     Root growth
      ! Depth
      tfvdev=Tfachr(cswtem,tdev1,tairhr(hour),degday)
      IF(cswtstep.EQ.24)tfvdev=Tfac(cswtem,tdev1,tairhr,degday)
      IF(vstage.GE.5)                               ! If germinated
     x rtdg=tfvdev*(rers/24.0)*cswtstep             ! Root extension growth
       rtdl=slbl(slnl)                                  ! Depth limit,soil
       IF(rtdln.GT.0.AND.rtdlw.GT.0)
     X rtdl=AMIN1(rtdln,rtdlw,rtdl)                 ! Depth limit,supply OK
       IF(rtdx.GT.0.AND.rtdl.GT.rtdx)rtdl=rtdx      ! Depth limit,species
       IF(rtdl.GT.rtdd)THEN
        rtdg=AMIN1(rtdg,rtdl-rtdd)
       ELSEIF(rtdl.LE.rtdd)THEN
        rtdg=0.0
       ENDIF
      ! Dry matter
       IF(vstage.LT.11)THEN                         ! If not emerged
        rwpgn=rtgf*rtdg/rlws                        ! Root growth,minimum
       ELSE
        rwpgn=rwpga                                 ! Root growth,minimum
       ENDIF
       IF(rwpga.LT.rwpgn)THEN                           ! If few assim for roots
        rwpgs=AMIN1((rwpgn-rwpga),seedwpd-lwpgs)    ! Root growth from seed
       ENDIF
       IF(rswpd*rsaf/24.0*cswtstep-
     X  lwpgr-swpgr.GT.rstr*(lbwpd+sbwpd))THEN          ! If res avail
        IF(rstage.LE.30)THEN                        ! - and can be for root
```

```
  rswpt=rstr*(lbwpd+sbwpd)                    ! - set threshold
  rwpgr=AMAX1(0.0,(rswpd-lwpgr-swpgr-rswpt)*
X   rsur/24.0*cswtstep)                       ! - use reserves
 ENDIF
ENDIF
! Length
rlag=(rwpga+rwpgs+rwpgr)*rlws*ppop*0.0001     ! Root length,growth
! Distribution pattern
sldc=0.                                       ! Soil depth,cumulative down
rldfsum=0.
DO l=1,slnl
 rldf(l)=0.0
ENDDO
DO l=1,slnl
 IF(drgf1(1,1).GT.0)THEN
  IF(l.EQ.1)THEN
   sllc=slbl(l)/2
  ELSE
   sllc=slbl(l-1)+(slbl(l)-slbl(l-1))/2
  ENDIF
  crgfsp=Yfactor('drgf1',drgf1,sllc)          ! Crop root growth factor
 ENDIF
 IF(cswswb.NE.'0')THEN                        ! If soil water ON
  crgfw=AMAX1(0.5,(sh2o(l)-slll(l))/(sdul(l)-slll(l)))
  crgfw=AMIN1(1.0,crgfw)
 ELSE
  crgfw=1.0
 ENDIF
 IF(cswnit.NE.'0')THEN                        ! If N ON
  crgfn=AMAX1(0.5,1.0-exp(-0.03*(sno3(l))))
  crgfn=AMIN1(1.0,crgfn)
 ELSE
  crgfn=1.0
 ENDIF
 rldf(l)=crgfw*crgfn*sldl(l)                  ! Distribution
 sldc=sldc+sldl(l)                            ! Cumulative depth
 IF(vstage.GE.1.AND.rtdd.EQ.0)THEN            ! If planted,no roots yet
  IF(pldp.GT.0)THEN
```

```
        rtdtmp=pldp+rtdg
       ELSE
        rtdtmp=rtdg
       ENDIF
      ELSE
       rtdtmp=rtdd+rtdg
      ENDIF
      IF(sldc.GT.rtdtmp)THEN                          ! If depth > rooting depth
       IF(rtdtmp.GT.0.and.sldl(l).GT.0)
     X  rldf(l)=rldf(l)*(1.-(sldc-rtdtmp)/sldl(l))
       rldfsum=rldfsum+rldf(l)
       EXIT
      ENDIF
      rldfsum=rldfsum+rldf(l)
     END DO
     DO l=1,slnl
      crgf(l)=rldf(l)/rldfsum                         ! Overall root growth factor
     ENDDO

C    Root senescence
     rdwpg=0                                          ! Root dead wt,growth
     IF(vstage.GT.20)                                 ! If ready for root death
     X rdwpg=rwpd*(rsrs/24.0)*cswtstep                ! Root - new dead material
      IF(tmin.LT.(-20.0).AND.ctof.GT.1)THEN           ! Arbitrary root kill, cold
       rdwpg=rwpd*(0.9/24.0)*cswtstep
      ENDIF

      IF(gtyp.EQ.3.AND.(cswtstep+hour).GT.24)THEN
       CALL CANHGA(cfltask,cswtstep,wfg,tairhr,
     x parips(spp),parips(spp),rstage,cwpd,CHT,MWPD,FWPD)
      ENDIF
     ENDIF

     IF(cfltask.EQ.'s')THEN
      IF(vstage.GE.10)THEN

C     Dry matter distribution ratio
      IF(awpg.GT.0)cfrd=cwpga/awpg                    ! Canopy fraction
```

```
C     Leaves
      ! Growth
      IF(lapg.GT.0)THEN
       lald(lnum+1)=lald(lnum+1)+lapg*lapgofr*lapgmfr     ! Older leaf

       lapl(lnum+1)=lapl(lnum+1)+lapg*lapgofr             ! Older lvs
       lald(lnum+2)=lapg*(1.0-lapgofr)*lapgmfr            ! Young leaf
       lapl(lnum+2)=lapg*(1.0-lapgofr)                    ! Younger lv
       IF(lfcnum.EQ.300-2)THEN
        WRITE(*,*) 'Leaf cohort number approaching maximum! '
        WRITE(*,*) 'Array bounds will thus be exceeded.    '
        WRITE(*,*) 'Program will stop to allow you to check.'
        WRITE(*,*) ' '
        STOP
       ENDIF
       lapgc=lapgc+lapg                                   ! Leaf area growth,cohort
       lwpgc=lwpgc+lwpg                                   ! Leaf weight growth,cohort
      ENDIF

       IF(gtyp.EQ.3)THEN
        treal1=60.0
       ELSE
        treal1=lnumse
       ENDIF
       IF(lapgc.GT.lapgcmin.OR.lapgc.GT.0.AND.rstage.GE.treal1)THEN
       lfcnum=lfcnum+1                                    ! Leaf cohort number
       lfcidag(lfcnum)=dag                                ! Leaf cohort init date
       lap(lfcnum)=lapgc                                  ! Leaf area in cohort
       lwp(lfcnum)=lwpgc                                  ! Leaf wt in cohort
       lapgc=0.0
       lwpgc=0.0
      ENDIF

      ! Extinction coefficients
      ecpl(spp)=Yfactor('secpl',secpl,dstage)             ! Extinction coeff,leaves
      ecpc(spp)=ecpl(spp)                                 ! Extinction coeff,canopy
```

```
! Ageing and death
DO l=lfcnum,1,-1                                  ! From youngest to oldest
 IF(lwp(l).GT.0)THEN
  ! Ageing
  IF(gtyp.EQ.3.AND.rstage.LT.60)THEN
   lage(l)=lage(l)+vdrate*0.5                     ! Leaf age,normal  bdays
  ELSE
   lage(l)=lage(l)+vdrate                         ! Leaf age,normal  bdays
  ENDIF
  ! Death
  IF(l.LE.lfcnumsg)THEN
   laps(l)=lap(l)
   lap(l)=0.0
   lwp(l)=0.0
   lage(l)=0.0
  ENDIF
 ELSE
  EXIT
 ENDIF
END DO

! Dead matter
ldwpd=ldwpd+ldwpg                                 ! Leaf dead wt  g/p
IF(rstage.GE.70)ldwpdgf=ldwpdgf+ldwpg*(1-ldfa)    ! Leaf dead wt,gr fill

C     Awns
aapd=AMAX1(0.0,aapd+aapg-aapsg)                   ! Awn area (cm2 p-1)
aapx=AMAX1(aapx,aapd)                             ! Awn area,max (cm2 p-1)

C     Anthers
ansdelay=MAX0(0,ansdelay-1)
IF(anasg.GT.0)THEN
 IF(hour.EQ.1)ancnum=ancnum+1
 IF(ancnum.GT.20)then
  WRITE(*,*)' Anther cohort number > limit of 20!!!'
  WRITE(*,*)' Press Enter to exit '
  PAUSE
  STOP
```

```
      ENDIF
      anaix(ancnum)=anaix(ancnum)+anasg*ppop*0.0001*snumpd ! Anther area
      anai(ancnum)=anaix(ancnum)                    ! Anther area,cohort (cm2)
      ansdelay=2
     ENDIF
     IF(ancnum.GT.0.AND.anai(ancnum).GT.0)THEN
      anaid=0.0
      DO I=1,ancnum
       IF(I.LE.ancnum-ansdelay)
     x  anai(I)=AMAX1(0.0,anai(I)-anaix(I)*ansnfr)  ! Anther area,co (cm2)
       anaid=anaid+anai(I)
      ENDDO
     ENDIF

C     Shoots
     sbwpd=sbwpd+swpg-sdwpg-strswpg                 ! Stem weight+growth-sen
     sdwpd=sdwpd+sdwpg                                    ! Stem dead wt
     IF(RSTAGE.GT.65)THEN
      sapg=0.0
     ENDIF

     sapd=AMAX1(0.0,sapd+sapg-sapsg)                ! Stem area
     IF(rstage.LE.80)sapgf=sapd                           ! Stem area at start of lag

     snumps=snumps+snumpsg
     snumpd=snumpi+snumpp-snumps                    ! Shoot (tillers+main) #
     IF(snumpd.GT.50)snumpd=50.                     ! Upper tiller limit
     IF(snumpd.LT.1)snumpd=1.                       ! Lower tiller limit

C     Spike
     spwpd=spwpd+spwpg

     IF(GTYP.EQ.3)THEN
      hwpga=0.0
      hwpgrs=0.0
      resprs=0.0
     ENDIF
```

```
C     Reserves
      rswpd=rswpd+(cwpga-lwpga-swpga-hwpga)+(lrswpg+strswpg)-
     x  (lwpgr+swpgr+rwpgr+hwpgrs)-resprs
      IF(rswpd.LT.0)rswpd=0.0

C     Cumulatives
      IF(hour+cswtstep.GT.24)THEN
       parc=parc+parips(spp)*0.01*pard                ! Cumulative par  mj m-2
      ENDIF

      ENDIF                                           ! End of vstage>10 section

C     Roots
      rwpd=rwpd+rwpga+rwpgs+rwpgr-rdwpg               ! Root wt;+growth-loss
      rlad=rlad+(rwpga+rwpgs+rwpgr)*rlws*ppop*0.0001  ! Total root length
      rdwpd=rdwpd+rdwpg                               ! Root wt - senesced
      rtdgsum=rtdgsum+rtdg                            ! Root depth growth sum
      rtdd=pldp+rtdgsum                               ! Root depth

      DO l=1,slnl
       rlv(l)=rlv(l)+(crgf(l)*rlag/sldl(l))           ! Add new roots
       rlv(l)=rlv(l)-rlv(l)*(rsrs/24.)*cswtstep       ! Root length-dead
       IF(tmin.LT.(-20.0).AND.ctof.GT.1)THEN
        IF(l.LE.2)THEN
         rlv(l)=rlv(l)*0.2                                  ! Arbitrary cold kill
        ELSE
         rlv(l)=rlv(l)*0.0                                  ! Arbitrary cold kill
        ENDIF
        rtdd=slbl(2)
       ENDIF
       IF(rlv(l).LT.0)rlv(l)=0
       rldf(l)=0.0
      END DO

C     Seed
      IF(vstage.EQ.1.and.ppop.GT.0)THEN
       seedwpd=(seedwap/ppop)*0.1                     ! Seed wt in g
       lwpgs=0.0
```

```
      rwpgs=0.0
      swpgs=0.0
     ENDIF
     seedwpd=seedwpd-(lwpgs+swpgs+rwpgs)                    ! Seed weight

C    Leaves
     lapd=0
     lbwpd=0.0
     lapc=0.0
     lwpc=0.0
     lapcrit=0
     lwpcrit=0
     DO l=lfcnum,1,-1                                       ! From youngest to oldest
      IF(lwp(l).GT.0)THEN                                   ! If leaf wt>0
       lapd=lapd+lap(l)
       lbwpd=lbwpd+lwp(l)
       lapc=lapc+lap(l)                                     ! Leaf area/plant,cumulative
       lwpc=lwpc+lwp(l)                                     ! Leaf wt/plant,cumulative
       IF(exp(-ecpc(spp)*lapc*ppop*.0001).GT.0.05)THEN! If par > cr
        lapcrit=lapcrit+lap(l)                              ! Leaf area,critical
        lwpcrit=lwpcrit+lwp(l)                              ! Leaf wt,critical
       ENDIF
      ENDIF
     END DO
     lapd=lapd+lapgc

     lbwpd=lbwpd+lwpgc

C    Area indices
     laid=lapd*ppop*.0001                                   ! Leaf area index
     said=sapd*ppop*.0001                                   ! Stem area index
     aaid=aapd*ppop*0.0001                                          ! Awn area index
     caid=laid+said                                         ! Canopy area index
     laix=AMAX1(laix,laid)                                  ! Leaf area index,max
     caix=AMAX1(caix,caid)                                  ! Canopy area index,max

C    Leaf area distribution
     CALL Layers(spp,ppop,lfcnum,caid,laid,lap,lapp,laps,
```

```
     X  CAIDSL,LAIDL,LAIDLA)

C     Shoots
      IF(snumpd.LE.0)THEN
       IF(snumpi.GT.0)then
        snumpd=snumpi
       ELSE
        WRITE(*,*)' Shoot number <= 0 !!!'
        STOP
       ENDIF
      ENDIF
      IF(snumpd.LE.2)THEN
       sbwsd=(sbwpd/snumpd)*0.8                    ! Stem wt of tiller 1
      ELSEIF(snumpd.GT.2.AND.snumpd.LE.3)THEN
       sbwsd=(sbwpd/snumpd)*0.6                    ! Stem wt of tiller 2
      ELSEIF(snumpd.GT.3.AND.snumpd.LE.4)THEN
       sbwsd=(sbwpd/snumpd)*0.4                    ! Stem wt of tiller 3
      ELSEIF(snumpd.GT.4)THEN
       sbwsd=(sbwpd/snumpd)*0.2                    ! Stem wt of tiller 4+
      ENDIF

C     Components
      IF(Sbwpd.GT.0)THEN
       Lrwpd=AMIN1(lbwpd*0.30,rswpd)               ! Leaf reserves  g/p
       IF(rstage.GT.lnumse)THEN
        Lrwpd=AMIN1(lbwpd*0.40,rswpd)              ! Leaf reserves  g/p
       ENDIF
       Srwpd=AMIN1(sbwpd*0.30,rswpd-lrwpd)         ! Stem reserves  g/p
       rrwpd=rswpd-lrwpd-srwpd                             ! Root reserves  g/p
      ELSE
       Lrwpd=AMIN1(Rswpd,Lbwpd*0.30)
       rrwpd=rswpd-lrwpd
      ENDIF

C     Totals
      IF(gtyp.LT.3)THEN
       cwpd=lbwpd+sbwpd+rswpd+hwpd+ldwpdgf+spwpd ! Canopy weight (g/p)
       vwpd=lbwpd+sbwpd+rswpd+ldwpdgf            ! Vegetative weight
```

```
      ELSE
       cwpd=lbwpd+sbwpd+rswpd+hwpd+spwpd              ! Canopy weight (g/p)
       vwpd=lbwpd+sbwpd+rswpd                         ! Vegetative weight
      ENDIF
      IF(rstage.GT.0)cwps(INT(rstage/10.0))=cwpd      ! Canopy weight,stage end

C     Calculate canopy height and flower weight for ragweed
      IF(gtyp.EQ.3.AND.(cswtstep+hour).GT.24)THEN
       CALL  CANHGA(cfltask,cswtstep,wfg,tairhr,
     x parips(spp),parips(spp),rstage,cwpd,CHT,MWPD,FWPD)
      ENDIF

C     Crop
      cwad=cwpd*ppop*10                              ! Canopy weight (kg/ha)
      vwad=vwpd*ppop*10                              ! Vegetative wt (kg/ha)
      lwad=(lbwpd+lrwpd)*Ppop*10                     ! Leaf (living) wt (kg/ha)
      swad=(sbwpd+srwpd)*Ppop*10                     ! Stem weight (kg/ha)
      sbwad=sbwpd*ppop*10                                ! Stem basic weight (kg/ha)
      rswad=rswpd*ppop*10                                ! Reservs weight (kg/ha)
      rwad=rwpd*ppop*10                              ! Root wt (kg/ha)
      cdwad=(sdwpd+ldwpd)*ppop*10                    ! Canopy dead wt (kg/ha)
      snumad=snumpd*ppop                                 ! Shoot # (#/m2)
      twad=(cwpd+rwpd+seedwpd)*Ppop*10               ! Total Wt (kg/ha)
      tdwad=(sdwpd+rdwpd+ldwpd)*Ppop*10              ! Total dead weight (kg/ha)

C     Ratios
      Hiad=0.0
      Ruem=0.0                                       ! Tops
      Ruea=0.0                                       ! All assimilation
      IF(Parc.GT.0)THEN
       Ruem=0.1*Cwad/Parc                                ! Tops
       IF(ABS(twad+tdwad-seedwap).GT.2.0E-05)THEN
        Ruea=0.1*(Twad+Tdwad-Seedwap)/Parc               ! All assimilation
       ELSE
        Ruea=0.0
       ENDIF
      ENDIF
      IF(Cwpd.GT.0)Hiad=100*Hwpd/Cwpd
```

```
C    Plant death
     IF(seedwpd.LE.0.0)THEN                          ! If no seed reserves
      IF(vstage.LT.10)THEN                           ! Abort if not emerged
       message=' Seed reserves used !'
       stname = 'Termination   '                     ! Stage name
       cflstage=999
       WRITE(*,*)' Seed reserves used! '
       STOP
      ELSE
       IF(awpg.LE.0.AND.rswpd.LE.0)THEN              ! If no growth,no reserves
        afsum=afsum+1                                ! Sum days w no assim
        IF(afsum.GT.40)THEN                          ! If 40 days no growth
         message = ' No assimilates or reserves ! '
         stname='Termination   '                     ! Stage name
         cflstage=999
        ENDIF
       ELSE
        afsum=0                                      ! Reset assim.factor
       ENDIF
      ENDIF
     ENDIF

     ! Sums over phase
     IF(spp.EQ.1)THEN
      If(vstage.GT.10.AND.rstage.LT.lnumse)then
       aflexsml(lnum+1)=aflexsml(Lnum+1)+aflex       ! Assim.factor
       tflexsml(lnum+1)=tflexsml(Lnum+1)+tflex       ! Temp.factor
       wflexsml(lnum+1)=wflexsml(Lnum+1)+wfg         ! Water factor
       nflexsml(lnum+1)=nflexsml(Lnum+1)+nfg         ! N factor,leaf
       lawgsum(lnum+1)=lawgsum(lnum+1)+lawg          ! Leaf a/wt ratio
       daylexsm(lnum+1)=daylexsm(Lnum+1)+1           ! Days expansion
      Endif
     ENDIF

     ENDIF

     ! Outputs
```

```
      IF(cfltask.EQ.'o')THEN
       IF(cswtstep+hour.GT.24)THEN
        daoutg=daoutg+1                                  ! Days > output
        IF(cswfro.GT.0.AND.INT(daoutg).EQ.cswfro.        ! If OK to write
     x  OR.cflstage.GT.1.AND.daoutg.GT.1.
     x  OR.vstage.EQ.1.OR.das.EQ.1.0)THEN
         WRITE(fnumcg(spp),1025)iyr*1000+doy,
     x  dap,lnumsd,dstage,rstage,caid,laid,said,NINT(lwad),
     x  NINT(swad),NINT(rswad),NINT(sbwad),NINT(hwad),
     x  NINT(cwad),NINT(rwad),NINT(twad),NINT(cdwad),
     x  NINT(snumad),NINT(hnumad),hwnumd,
     X  cht,NINT(rtdd),
     x  cfrd,rlad,rlv(1),rlv(3),rlv(6),rlv(7),NINT(parc),tfph,vpdfph,
     x  wfp,wfg,nfp,nfg,parip,ruea,awpp,seedwpd*1000.0,lamgpd,
     x  NINT(hiad)

1025    FORMAT(I6,I6,F6.1,F6.1,F6.1,F6.2,F6.2,F6.2,I6,
     X  10I6,F6.1,F6.1
     X  I6,6F6.1,I6,3F6.1,
     x  6F6.1,2F6.1,I6)
         daoutg=0.0                                      ! Reset counter
        ENDIF                                            ! End time course

        IF(spp.EQ.1.and.das.EQ.1.or.MOD(FLOAT(das),20.0).EQ.0)THEN
         cghout=cghout+1
         IF(cghout.GT.1)THEN
          WRITE(fnumcgh,*)' '
          WRITE(fnumcgh,156)run,symbol,rname,(iyr*1000+doy)
156       FORMAT('*RUN',I4,' (',A1,'): ',A18,2x,'DATE: ',I5,/)
          WRITE(fnumcgh,'(a102)')
     X   '@HOUR  SRAD  TAIR  AWPP  WFPH  TFPH  LAPG  WFGR
     X                                  '
         ENDIF
         DO hr=1,24,cswtstep
          WRITE(fnumcgh,502)hr,sradhr(hr),tairhr(hr),
     X    awpphr(hr)*60.0*60.0*1.0E-6*ppop,wfphr(hr),tfphhr(hr),
     X    lapghr(hr),wfghr(hr)
         ENDDO
```

```
502   FORMAT(I6,2(F6.1),F6.2,F6.2,F6.2,F6.2,F6.2)
     ENDIF                                          ! End 24h
    ENDIF
   ENDIF                                            ! End outputs

   RETURN
   END
```