MODELLING THE SEASONAL CARBON ECONOMY OF DECIDUOUS TREE CROPS

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Abstract

In this paper, we outline an approach to modelling the carbon economy of tree crops based on the concept that plants grow as collections of semi-autonomous, but interacting organs. The plant genotype, triggered by internal and environmental signals, determines current organ specific growth potentials. Environmental conditions specify the conditional growth capacity and maintenance requirements for each organ. Finally, resource availability determines realised organ growth. A model for one organ type, individual fruit growth, has been developed for peaches. Within the framework of the larger model, this fruit growth model has been used to study factors that limit fruit size and crop yield, and the effect of management practices such as thinning on fruit growth and yield. Comparing the relative growth rate of fruit on normally cropped trees to the potential relative growth rate indicated that fruit growth was source-limited during two periods of growth. The model can be used in similar fashion to evaluate the timing of source limitations on vegetative growth.

Additional Index Words: carbohydrate partitioning, source, sink, fruit growth, peach

1. Introduction

During the last few decades, there have been many attempts to use computer simulation modelling techniques to describe and study the dynamics of crop growth and productivity. Many of these studies have made valuable contributions to our understanding of key factors limiting crop productivity in different environments. These models have emphasised the importance of carbohydrate partitioning in determining crop growth rates and productivity; however, they have provided little insight into how carbohydrate partitioning is achieved. An empirical approach has generally been taken, estimating carbohydrate partitioning from a series of sequential harvests under different growing conditions and/or from asssumptions about the maintenance of a balance between roots and shoots.

Although the high degree of manipulation of tree crops offers the opportunity for implementing management strategies derived from computer simulation models of carbon economy, many fewer models have been developed for tree crops than for annual or biennial crop species. The traditional approaches used for row crops, such as

sequential harvests of total biomass, present a monumental task for tree crops. Furthermore, due to the large number of management variables (such as scion cultivar, rootstock cultivar, tree spacing, pruning and training system, and fertilisation), in addition to the normal environmental variables (such as photon flux, temperature, soil type, and water availability), the value of expending large amounts of time and energy to collect detailed, site-specific data may be questioned.

On the other hand, deciduous tree crops offer certain advantages for developing functionally-based simulation models based on organ specific growth potentials that may be used to study carbon partitioning within the whole plant. Unlike many annual crops, deciduous tree crops such as peach, apple, and pear, begin their growing season with a synchronised bloom in spring following the occurrence of appropriate environmental thresholds. This synchronised bloom allows manipulation of crop load without stimulation of further reproductive development such as subsequent bloom or increases in seed number.

2. Conceptual basis for the model

Our approach to modelling carbohydrate partitioning in deciduous tree crops utilises the observation that plant growth occurs in individual plant organs, including stems, leaves, roots and reproductive organs (Watson and Casper, 1984; Sprugel et al., 1991). Observed carbohydrate partitioning results from the dynamic equilibrium achieved by the competition of individual sink organs for resources (Patrick, 1991) within a framework dictated by the plant genotype, environmental thresholds, and environmental conditions. Competition between growing organs is mediated by the effect that growth has on resource availability and the relative ability of the translocation system to provide resources to the growing organs.

Carbohydrate resources available for growth are provided by current photosynthate and by stored carbohydrates (figure 1). These resources move from their respective places of synthesis or storage (sources) towards individual sinks through the phloem by Münch pressure flow. Resource usage by other organs and translocation resistance, determined by the distance between source and sink and by the nature of the translocation pathways available, dictates the organ specific resource availability for each growing organ. Fruits, stems, and leves are generally closer than roots to photosynthetic sources, and appear to have lower translocation resistance than roots. The relative resistance between fruits, stems and leaves appears to favour fruit growth over stem and leaf growth.

Internal signals, such as the presence of a sink at a particular developmental stage, and environmental thresholds, such as daylength, chilling, and heat accumulation trigger the plant genotype to determine the current organ specific growth potentials (figure 2). Endogenous coordinators such as hormones and differences in water potential (Patrick, 1991) provide communication between the sites of perception of these environmental thresholds and individual organs.

Environmental conditions including ambient temperature and water availability determine the conditional growth capacity and maintenance requirements of each organ based upon the current specific growth potential. Organ specific resource availability determines realised growth. If sufficient resources are available, growth occurs at the level of conditional capacity. If organ specific resource availability is insufficient to support growth and maintenance at the conditional capacity, then realised growth occurs at less than conditional capacity.

In this paper, we describe a model of fruit growth potential for peach that we have developed, show this model can be used to study source- and sink-limited aspects of fruit growth, and indicate our future plans for extending the model to encompass vegetative growth.

3. Model of peach fruit growth potential

The initial models of individual peach fruit growth potential were developed from dry weight fruit growth data collected on early and late maturing freestone peach cultivars (June Lady and O'Henry respectively; DeJong et al., 1987). Using these data, DeJong and Goudriaan (1989a) plotted the natural logarithm of fruit relative growth rate against degree-days after bloom. They discovered that the typical, double sigmoid curve of peach fruit growth could be simulated with a combination of two log-linear equations describing the seasonal pattern of fruit relative growth rate (figure 3). Subsequent research indicated that a single exponential equation describing the seasonal pattern of fruit relative growth rate can be used to satisfactorily model the fruit growth potential of additional cultivars of peach as well as apple (Pavel, 1991). Furthermore, cubic spline functions can be used to provide a better fit to the observed data (Grossman and DeJong, 1992a).

The relative growth rate model not only represents a convenient means of mathematically describing fruit growth rates under minimal cropping conditions, but also provides a functional model of the fruit growth potential of individual fruit at any point during the growing season. Potential relative growth rates were determined for early and late maturing peach cultivars by heavily thinning the trees at the time of bloom. On unthinned trees, the relative growth rate was much lower than the potential relative growth rate due to the heavy crop load. Time and level of thinning studies indicated that, when the crop was thinned, the fruit relative growth rate increased to a level closer to the potential relative growth rate thn the rate prior to thinning (Pavel, 1991); Grossman and DeJong, 1992b). This indicates that potential final fruit size of any individual fruit is a function of fruit size at that point and the potential relative growth rate for the remainder of the season.

The model of peach fruit growth based upon potential relative growth rates also allows a straight-forward means of estimating fruit respiration requirements. Respiration rates have generally been shown to be correlated with the relative growth rates in plants (Amthor, 1989). Similar correlations have been established for peach fruits (DeJong and Goudriaan, 1989a) and kiwifruit (Walton and DeJong, 1990). Thus, the total potential seasonal carbohydrate costs of growing peach fruits can be simulated

using the relative growth rate model of fruit growth potential and environmental data (DeJong and Walton, 1989). In addition, the total carbohydrate availability for crop growth can also be estimated (Grossman and DeJong, 1992a).

4. Source and sink limitation on crop productivity

After development of a fruit growth potential model from data collected under sink-limited conditions (very lightly cropped trees), this model has been used to study source and sink limitations on crop productivity using crop simulation models. We have developed a simulation model of seasonal canopy photosynthesis in peach to estimate carbohydrate supply. This model has been linked to the fruit growth potential model in order to estimate the total carbohydrate supply and crop demand for each day in the growing season. Insight into questions regarding the effect of periods of high temperature or cloudy days on crop carbohydrate demand and total photosynthesis supply can be gained from these simulations. Models of this type can also be used to develop understanding of fruit growth and crop responses to cultural manipulations such as thinning (DeJong and Goudriaan, 1989a). For example, the model predicted that under the environmental conditions experienced near Yuba City, California, during the summer of 1988, the estimated carbohydrate requirement for clingstone peach fruit growth exceeded the estimated photosynthate supply prior to thinning and just before harvest of three cling peach cultivars (DeJong et al., 1990). Similar results were obtained for the freestone peach cultivar, O'Henry (DeJong and Goudriaan, 1989b). The importance of an accurate estimate of whole tree respiration during the very hot portions of the summer at this location also became apparent in the analysis of these data.

The fruit growth potential model can also be used to study source-sink relatioships experimentally. By comparing the fruit relative growth rates throughout the entire season on trees carrying different crop loads, periods of sink-limited fruit growth can be distinguished from periods of source-limited fruit growth. Studies of this type can be used to answer old questions regarding the timing of source and sink limitations on cro yield, and provide insight into the non-linearity of the fruit size vs. crop yield phenomenon. Studies by Pavel (1991) and Grossman and DeJong (1992a,b) indicate that, on normally cropped, late-maturing peaches, fruit growth tends to be source-limited during the early and late periods of fruit development, but tends to be sink-limited during the mid-period of fruit growth. The non-linearity of the fruit size vs. crop load relationship (Cain and Mehlenbacher, 1956) is apparently a function of the ratio of time that the fruits are source-limited or sink-limited and the extent to which the carbohydrates are limiting growth during the source-limited periods.

5. Interactions between reproductive and vegetative growth

Although it has been well established that crop load can have a significant influence on vegetative dry matter production (Lenz, 1974; Heim et al., 1979; Forshey and Elfving, 1989), the timing and nature of these interactions are largely unknown.

Examination of the fruit growth potential models has indicated the relatively autonomous bahaviour seasonal fruit growth potential. It is now possible to quantify the interaction of fruit growth and vegetative growth. Measurements of seasonal shoot growth on defruited trees are being used to develop a stem and leaf growth potential model (Grossman, unpublished data). Comparison of stem and leaf growth on differentially cropped trees to the stem and leaf growth potential will yield insight into the timing and extent of competition between reproductive and stem and leaf growth. Similar work is needed to quantify the growth potentials for secondary growth and root growth.

A study of moderately cropped mid-season peaches indicated that stem extension growth was suppressed during the period of final fruit growth and resumed following harvest (DeJong et al., 1987). Such analysis of fruit growth potential and stem and leaf growth potential data, together with experimental work, can yield information on the relative translocation resistances to these organs throughout the growing season.

Additional information is necessary to the environmental controls and carbohydrate requirements of vegetative sinks. Preliminary work is currently in progress to begin modelling the seasonal and dirunal patterns of stem growth. The indeterminate nature of stem extension growth adds a layer of complexity to this analysis.

6. Conclusion

In modelling the carbon economy of deciduous tree crops, we have utilised the idea that plants are collections of semi-autonomous but interacting organs. Plant growth occurs according to organ specific growth potentials mediated by environmental conditions and resource availability. Our programme has developed models of fruit growth potential for peach, and has used these models to study source- and sink-limited aspects of fruit growth. Similar work on vegetative growth is in progress.

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CARBON SUPPLY MODEL

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CANOPY PN ──► PHOTOSYNTHATE ────► STORED CARBOHYDRATES

                    CARBOHYDRATE
                     RESOURCES
                                          TRANSLOCATION
                                            RESISTANCE

FRUIT SPECIFIC
RESOURCE AVAILABILITY

                    STEM AND LEAF SPECIFIC
                    RESOURCE AVAILABILITY

                         FEEDBACK?      ROOT SPECIFIC
                                        RESOURCE AVAILABILITY
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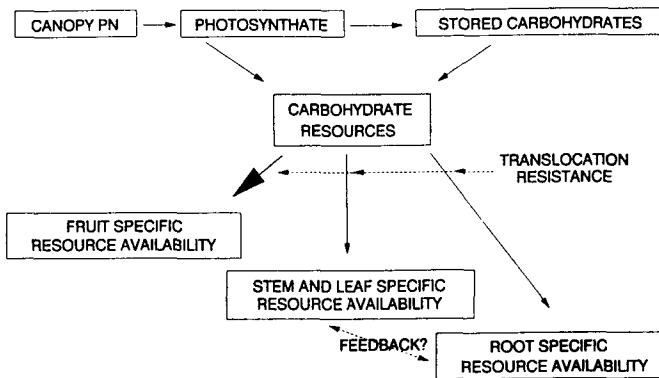
Figure 1. A diagram of the sources of carbon available to growing organs. Estimates of relative translocation resistance are represented by the length and width of the arrows connecting the carbohydrate resources box to the organ specific resource availability boxes. (Shorter, heavier arrows indicate lower resistances than do longer, lighter arrows.) The possibility of feedback between stem and leaf, adn root specific resource availabilities is indicated.

SINK DEMAND MODEL

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                                    GENOTYPE

INTERNAL AND          ENDOGENOUS
ENVIRONMENTAL SIGNALS  REGULATORS
                                    CURRENT ORGAN-SPECIFIC
                                    GROWTH POTENTIAL

ENVIRONMENT (AMBIENT
TEMP, WATER AVAIL, ETC.)
                                    CONDITIONAL GROWTH CAPACITY
                                    AND MAINTENANCE REQUIREMENTS

ORGAN SPECIFIC
RESOURCE AVAILABILITY
                                    REALIZED GROWTH AND
                                    MAINTENANCE OF ORGAN
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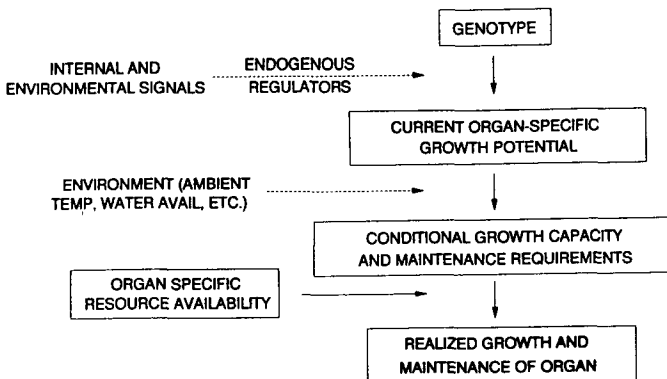
Figure 2. A diagram of the potential and realised growth of an organ. Solid lines indicate mechanisms, dotted lines indicate information transfer.
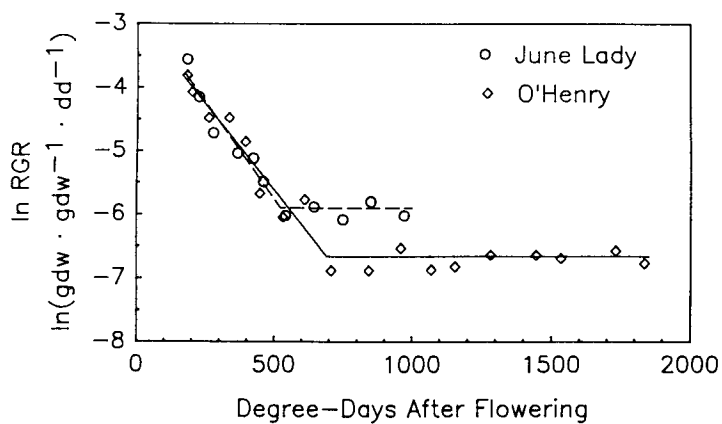
Figure 3. Log-transformed 1984 fruit relative growth rate (RGR) for June Lady and O'Henry peaches plotted against degree-days after flowering. (Figure taken from DeJong and Goudriaan, 1989a.)