Modeling Concord Grapes with “VitiSim”, a Simplified Carbon Balance Model: Understanding Pruning Effects

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Abstract

A simplified grape carbon balance model, called VitiSim, was adapted from the simplified apple carbon balance model developed earlier. The model uses a daily time step, a big-leaf daily canopy photosynthesis light response and respiration of organs based on mass and specific respiration rates. Weather inputs are only daily max and min temperatures and radiation. Partitioning is based on the balance of total supply to total demand with relative sink strength partitioning coefficients if the carbon supply is less than total demand. Root growth and respiration and berry set submodel have been initially developed and are being tested. Validation studies indicate that simulated total dry matter production and seasonal dry matter patterns are very realistic in behavior and amount. Seasonal dynamics of simulated carbon supply to demand suggests that the period of greatest carbon deficit is around or shortly after bloom. The period of greatest positive carbon balance appears to be just before veraison when the canopy is complete, but the crop growth is slow. The model is used to simulate the seasonal variation of carbon supply to demand in minimally and balance pruned Concord vines. In field experiments minimally-pruned vines had more stable year-to-year yields, yet could not ripen any more crop than balance-pruned vines. Simulations suggest that earlier and more rapid completion of canopy development of the minimally-pruned vines gave more positive carbon supply during the early fruit set and flower bud development period. However, later during ripening, the carbon supply was no better.

1. INTRODUCTION

Modeling plant performance can be a useful tool to integrate single spot measurements, to help researchers identify areas of knowledge where more research is needed, to identify patterns of behavior over time, and to derive quantitative hypothesis. Our modeling effort is guided by two quotes: “All models are wrong; some models are useful.” - Professor George Box, and “Make it as simple as possible, but no simpler” - Albert Einstein. Consequently, the challenge is to find the proper balance of components and factors to include the essential mechanisms that control model to give realistic and useful behavior, while not becoming too complex for the modellers and interested others.

With this aim in mind, we are currently improving a carbon balance model for Concord grapes based on the previous version presented in Lakso and Poni (2005). This
earlier model was able to successfully simulate the dry matter produced by a vine over a growing season. We are now incorporating to the model: 1) a routine to partition the dry matter between organs, 2) a root sub-model component, 3) the carbohydrate reserve component, and 4) a fruit set component based on a berry drop versus berry growth relationship. Results presented in this paper describe the model itself and its use to compare the seasonal variation of supply and demand in minimally and conventionally pruned Concord vines.

Today Concord grape juice growers are trying to increase yield reducing production costs by reducing pruning, with minimal pruning (essentially no pruning except for low trimming) being used to reduce costs by eliminating pruning and increasing yields. Fruit ripening may be inadequate because of the high crop demand, particularly in poor weather conditions. Also minimal can negatively affect the long term vineyard productivity if other stresses are present. In this context the vine balance and vine performance over years is crucial. In long-term field studies we have found that minimal pruning has normally been less able to ripen crops, suggesting overcropping, yet it has also given more stable yields. Modeling is then applied as a tool to take into account the supply and demand and the effect of variable environmental conditions to evaluate such observations.

MATERIALS AND METHODS
General description of the model
The grape model (named ‘VitiSim’) described here is a seasonal dry matter production model with a daily time step and “big-leaf” type of model that was developed originally for apple (Lakso and Johnson 1990) and modified over time (see Lakso et al. 2001). The grape adaptation has been briefly described recently (Lakso and Poni, 2005; Lakso, 2006). The daily time step was chosen to simplify the complexities of diurnal radiation/canopy geometry, avoid working at multiple time scales, reduce the requirements for weather data, and to better match growth data. The validity of the big-leaf approach is also supported by recent research where we showed that crop level effects on fruit development can be considered on a whole vine basis (Intrigliolo et al. unpublished). The model is based on a “standard vine” which is a mature ‘Concord’ (Vitis labruscana Bailey) grown on a 1.8 m high cordon with Hudson River Umbrella pendant growth habit. The spacing is 2.4 x 2.7 m which is typical for the Northeast US production. Previous sub-models details about canopy photosynthesis and tissues respiration can be found in Lakso and Poni (2005) and in Poni et al. (2006) for the Vitis vinifera version of the model. Here we explain more in detail the new developments and address the observation of yield stability and ripening discussed above from a seasonal carbon balance approach.

Carbon partitioning submodel
The partitioning of the accumulated fixed carbon is adapted from Buwalda’s kiwifruit vine model (Buwalda, 1991) and it is similar to the routine used in the apple model (Lakso et al. 2001). Carbon available for partitioning is first estimated by calculating the net CO₂ exchange from canopy photosynthesis. After that, total organ respiration is subtracted to give the available CO₂/dry matter pool. The total demand for shoots and cluster is estimated from its numbers, and estimated maximum growth rates
obtained in vines with high source-demand ratio in a field trial conducted in 2006 (Intrigliolo and Lakso, unpublished results). Seasonal pattern of root demand are estimated from recent findings (Comas et al. 2005) where it was found that most of the root growth appears to occurs during approximately 60 days from flowering to veraison. Based on a detailed soil core study (Eissenstat et al. unpublished) root growth demand is calculated considering a fine root length density over a whole soil volume of 0.1 cm cm⁻³. We assumed that the primary root zone (assumes grass cover crops) is about 2.4 long x 1 wide x 1m deep. Considering that for own rooted Concord vines 1.5 cm of root length corresponds to 1 mg of dry weight, we estimate a need of about 167 g of dry weight per vine for Concords as a demand for fine new root growth.

The total demand for an organ is calculated considering the maximum growth demand (adjusted for temperature) times the number of active organs of that type. If adequate carbon is available to fully support all organs, the carbon is partitioned equal to the demands and maximum growth occurs for all organs. However, if the carbon supply is less than the total demand, a prioritization was used. A “relative sink strength” (RSS) factor was estimated for each type of organ, and the total of the RSS factors equal 1.0. Based on review of the literature, and our unpublished studies of shoot and berry growth responses to different crop and shading levels, the relative sink strengths were chosen to be in the following order: shoots>>fruits>roots=wood. After veraison however fruits have priority over shoots and the rest of the organs. Overall this gave priority to shoots so that early in the season when shoots are active, they receive a greater proportion of their demand. Later, as shoots terminate growth and their relative sink strength decreased, the partitioning shifts to fruits. This is consistent with studies that indicated that shoot tips were very strong competitors for carbon in the early season (Hale and Weaver 1962). However by veraison the berry undertakes dramatic physical and metabolic changes and most of the dry matter is allocated to the fruit (Coombe 1992). Based on this organs such as roots and woods.. The actual amount partitioned to each organ type depends on the individual demands, the number of actively-growing organs (e.g. number of active shoots), and whether carbon is adequate or limiting. The relative partitioning to a given organ (RPᵢ) is estimated by: \( RPᵢ = \frac{\text{Demand}ᵢ - (\text{Demand}ᵢ \times (1 - \text{RSS}ᵢ)) \times (1 - \text{Carbon avail} / \text{Demand total})}{\Sigma RPᵢ} \). The actual carbon partitioned then to each organ is: \( \text{Carbon}ᵢ = \frac{\text{Carbon avail}}{\Sigma RPᵢ} \).

**Root respiration submodel**

In the present version of the model root respiration was also taken into account. Roots were treated differently than the other organs and we could not just assume a big root organ, as it was done for fruit or leaves. For root respiration then we divided roots structure in two sections: 1) thick roots and root shank, and 2) new thin roots production. Due to lack of data in literature about respiration of structural roots we assume that its respiration rate would be similar to the aerial wood respiration. Based on some carbon partitioning studies (Mullin et al. 1992; Williams 1997; Lakso et al unpublished data) in a mature vine the amount of structural roots was estimated to be half of the aerial wood. For new fine root production the seasonal amount was derived from the carbon partitioning sub-model. Respiration rate equations used were those reported for Concord (Huang et al. 2005). Root temperature was simply estimated as soil temperature that equalled air temperature since over a day, then means were similar.
Inputs required by the model

There are two general types of inputs: vine descriptions and weather data. To describe the vine, initial inputs are required of numbers of shoots, numbers of clusters, berries/cluster and row x vine spacing. Many values of light-saturated photosynthesis rates, quantum yield, extinction coefficient, and temperature responses of organ respiration, leaf area development or photosynthesis, or cultivar specific growth data may be entered from measurement data or default values averaged from experimental and literature data can be accepted. The required weather data are limited to the commonly available values of daily maximum and minimum temperatures and daily total radiation to allow the model to be used with common weather data sets.

RESULTS AND DISCUSSION
Simulations of total dry matter production and carbon partitioning

The simulated values (model version 7-07) of total dry matter as well as its partitioning between shoots and clusters was compared with data obtained in the seasonal vine growth analysis study above mentioned (Lakso et al. unpublished). The simulated pattern of total dry matter production fit the data in pattern and totals giving confidence that the central dry matter production component behaves realistically (Figure 1). The apple model from which this model was adapted similarly has shown good validation for dry matter production (Lakso et al. 2001). The carbon partitioning between shoots and fruits was also in general close agreement with the measured values (Figures 2 and 3). This suggests that despite its simplicity and the fact that very little is known about the mechanisms of partitioning, the model is able to simulate reasonably well the partitioning of dry matter between shoots and fruit.

Using the weather data from the year and location of the seasonal growth analysis studied we summarized some of the output obtained in the model (Table 1). At the end of the growing season plant respiration was estimated to be 30% of the CO₂ fixed via photosynthesis, which is the range of values for plant respiration reported in Lambers (1993). It is felt that due to the high proportion of simple, energetically inexpensive carbohydrates accumulated by grapes, the total respiration may be an overestimate. More respiration data is needed. Relative respiration totals amongst the different organ respirations were: leaves 61% of the total plant respiration while woody structure, roots and fruit accounted for 20, 13 and 6% respectively.

The vines that are simulated produced slightly more than 4 kg of dry matter over the season (Table 1), very close to that measured. Again similar to the measured values the relative partitioning to shoots, crop, woody structure (both above and below ground), and fine roots was 45, 53, 2 and 1% respectively. The mature vine growth analysis gave 39, 59, 2 and 0 respectively. Total dry matter allocated for new fine root production was estimated to be only 40 g or about 1% of the seasonal total dry matter production of about 4 kg. In the seasonal growth study with old vines, there was essentially no net gain in root system dry matter over the season. In addition, a recent soil coring study with similar mature Concord vines (Eissenstat et al. unpublished) it was estimated that fine roots amounts was equivalent to about 60 g of dry matter per vine, difficult to measure. Certainly more effort needed to better estimate the root respiration rate and to validate the
simulation data with actual data. However, initial results of the model are quite realistic and promising.

**Seasonal variation supply vs demand of minimally and conventionally-pruned vines**

A seasonal pattern of daily net fixed CO2 (Figure 4) showed patterns for normally and minimally pruned vines that are similar to those seen in gas exchange studies with Concord vines (Lakso, et al., 1997). Canopy photosynthesis is higher for the minimally-pruned vines at the beginning of the season because of the much rapid canopy development and thus larger light interception early in the season. However later in the season minimally and balanced pruned vines have similar canopy photosynthesis because both systems gave a similar final light interception values, and exposed leaves had the same photosynthesis rates (Lakso, unpublished).

Mature Concord vines were found to allocate over 90% of the seasonal dry matter to the current shoots and crop (Table 1). So, if the demands of the crop and shoot growth are combined and compared to the supply curve, the model suggests that (a) in general the supply and demand are in reasonable balance for the proven conventional system; (b) the supply/demand balances are not constant over the season, and (c) after crop and shoot demand is satisfied, there are varying patterns carbohydrate supply/demand balance over the season (Figure 4). The early-season period shortly after bloom of relatively positive carbon balance around and after bloom is greater in the minimally-pruned vines due to the early canopy development for supply combined with the earlier decline in shoot demand compared to the heavier pruning that stimulates longer shoot growth duration. This better carbohydrate balance around bloom might help to explain the greater sustained cropping levels we have seen in non-stressed minimally-pruned vines as this is the period of fruit set and basal flower bud development. Balance-pruned vines normally set 3,000 to 5,000 berries per vine while minimally-pruned vines set about 7,000-8,000.

It might also explains an earlier flush of root growth observed in the minimally pruned vines leading that over various years minimally pruned vines produced at least as many roots as the conventionally pruned (Comas et al. 2005). In both pruning regimes, the greatest potential carbohydrate supply for growth processes other than shoot and crop growth is just before veraison when crop and shoot demands are low and canopy supply is high. Between veraison and harvest it appears that the normal pruning was in balance with the crop demand while the minimal pruning was not able to meet the larger demand of the ripening crop. These analyses provide a plausible explanation of why minimally-pruned vines had higher but more stable year-to-year yields, yet could not ripen those larger crops compared to the balance-pruned vines.

**CONCLUSIONS**

Despite its relative simplicity the model presented quite realistically and quantitatively estimates the dry matter production and its partitioning amongst the different organs. The model appears to be a useful tool to estimate the vine capacity as a function of the vine and the climate, providing a more physiologically-based estimate of actual crop load. Its simplicity allows the model to be shared with other researchers (see Poni et al. 2006) and to be applied to different crops. It is clear that much work is needed to emphasize the role of the reserves in the carbon supply and demand and validate the model under different conditions. Currently the model assumes a healthy vine with
optimal water and nutrient status, so the effects of drought stress, nutrient imbalances or pest stresses are not simulated although the structure of the model allows these components to be added.

ACKNOWLEDGEMENTS
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Literature cited
Table 1. Summary of some output values of the model simulating the growth of 41-year-old ‘Concord’ vines from a growth analysis using 2003 Fredonia, NY weather. Data reported are accumulated seasonal values.

<table>
<thead>
<tr>
<th></th>
<th>G CO2/vine</th>
<th>% of Total</th>
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</thead>
<tbody>
<tr>
<td>Total Photosynthesis</td>
<td>10 543</td>
<td>100</td>
</tr>
<tr>
<td>Total Respiration</td>
<td>3 147</td>
<td>30</td>
</tr>
<tr>
<td>Leaf Respiration</td>
<td>1 916</td>
<td>18</td>
</tr>
<tr>
<td>Fruit Respiration</td>
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<td>2</td>
</tr>
<tr>
<td>Wood Respiration</td>
<td>595</td>
<td>6</td>
</tr>
<tr>
<td>Fine Root Respiration</td>
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<td>4</td>
</tr>
<tr>
<td>Total Seasonal Vine Dry Matter Production (kg)</td>
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<td>100</td>
</tr>
<tr>
<td>Shoot DM (kg)</td>
<td>1.83</td>
<td>45</td>
</tr>
<tr>
<td>Crop DM (kg)</td>
<td>2.18</td>
<td>53</td>
</tr>
<tr>
<td>Wood (woody structures of the top and roots) DM (kg)</td>
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<td>2</td>
</tr>
<tr>
<td>Fine Root DM (kg)</td>
<td>0.04</td>
<td>1</td>
</tr>
</tbody>
</table>

Fig. 1. Actual versus simulated dry matter trends for 41-year-old Concord vines.
Fig. 2. Actual versus simulated trends for 41-year-old Concord vines of dry matter allocated into shoots.

Fig. 3. Actual versus simulated trends for 41-year-old Concord vines of dry matter allocated into the crop (equivalent to 29 t/ha yield).

Fig. 4. Simulation of the seasonal daily canopy CO2 fixation for normally and minimally-pruned Concord vines using NY weather.

Fig. 5. Simulations of seasonal requirement for fixed carbon for shoots and crop for minimally and normally-pruned vines.