Crop load – physiology, modelling and relationships to root growth in grapevines

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Abstract

In grape growing it is important to optimise vine yield and fruit quality. Probably the most important goal is to optimise 'crop load' to balance vine growth and capacity to the crop demand and the quality desired. Although the term crop load is often used incorrectly as tons per hectare, crop load entails the relative balance of both vine supply and crop demand. One central aspect of crop load is the balance of carbohydrate (CHO) supply to the CHO demand of the fruit and the other organs of the vine. If this is out of balance there are many undesirable responses to vine growth as well as fruit and wine quality. To quantify and integrate the components of crop load, we have begun to develop a simplified grapevine CHO balance model. This model calculates vine capacity and the relative requirements of the vine organs as affected by sunlight and temperature, growth stage and cultural practices to begin estimate physiological expressions of crop load at times over the season. Gaps in our knowledge identified while modelling, especially regarding root growth and function, have led us to supporting studies of vine growth and function. Integration of supply and demand with the model has been useful to examine the seasonal CHO dynamics of conventional versus minimal pruning.

Introduction

A commonly observed relationship in viticulture and oenology is that grape and wine quality is inversely related to yield. Wine producers attempt to optimise the yield to produce a desired grape and wine quality at a given price point. A key to achieving this is to understand the relationship between yield and quality, which has unfortunately not been well documented nor quantified in the myriad of climates and cultural systems. This lack of knowledge limits the ability to optimise the balance of increasing yields versus decreasing quality and return cropping for any given system, climate or cultivar.

Although many use the term vaguely to mean crop level (i.e. tonnes/ha), the concept of crop load is the *balance* of vine capacity to the demand of the fruit and the other organs of the vine (generally thought of as carbohydrate (CHO) supply versus demand). If this is out of balance there are many undesirable responses. If the crop load is too low, yields will be low, but vegetative growth is often excessive leading to dense canopies, excessive pruning, leaf pulling or other canopy management, and often a lack of achievement of the potentially high fruit quality. If the crop load is too high, fruit will have low quality and late maturation, vegetative growth might be stunted, the vine might be extra sensitive to other stresses, and return cropping might be inhibited.

Definition of crop load

The word 'load' refers to a weight, or something analogous, to be supported. In common usage it expresses some relative aspect (e.g. a 1 kg weight is a huge 'load' for an ant to carry, but a tiny 'load' for an elephant). So how can we express crop load? The most commonly used are indirect expressions of crop load (see also the excellent reviews of this topic by Dry in these proceedings, and Clingeleffer et al. 2001; Kliewer and Dokoozlian 2001; Intrieri and Filipetti 2001; Reynolds 2001):

- yield (tonnes/ha) - many say use yield/hectare to mean crop load, but this ignores the relative ability of the vineyard (i.e. supply) to grow the vine and mature the crop as many vineyards clearly have different capacities (e.g. a Lyre vineyard can support more crop than a widely spaced VSP).

- crop weight per weight of cane prunings from the previous winter uses pruning weight to estimate supply. This estimate assumes that a given pruning weight will actually attain the predicted amount of leaf area or light interception or canopy photosynthesis in the following summer. The original concept was developed and is often called the 'Ravaz Index.' This might be reasonably good to estimate relative fruit demand if shoot numbers and cluster numbers are controlled primarily by the numbers of buds retained. However, shoot or cluster thinning disrupts this relationship. This relationship is also not linear once the canopy is fully filled (Figure 1). For small- to moderate-sized vines, pruning weights do correlate with the ability of the vines to provide the appropriate amount of adequately exposed leaf area to ripen the crop. However, for large vines, leaving higher numbers of buds or shoots only leads to excessively dense canopies. Since once the trellis is filled, additional buds lead to more leaf area and additional crop, but no more vine capacity.

  If bud and shoot numbers are not too high and if there are no stresses that limit canopy development and leaf function, this method can be quite useful. However, such estimates do not address: variations in the seasonal weather (sunny versus cloudy years or climates); factors that affect leaf function (such as water stress or foliar pest stresses) or shoot thinning, or summer pruning; all of which can disrupt the relationship of pruning weight to summer canopy or amount of crop that affects the vine capacity or CHO supply. Of course, this crop load index cannot be used for minimal pruning, especially if the minimal pruning is combined with mechanical thinning. In reality, this index might be viewed more properly as a kind of production efficiency (see paper by Dokoozlian in these proceedings).

- Crop weight per metre of row or canopy. In this index, the row or canopy is the estimate of supply. It can account for the greater potential supply from divided canopies – more effectively than pruning weight – but it still has many of the same limitations in that it does not relate to variations in canopy density (i.e. light interception) or photosynthetic efficiency.

- Leaf area per crop weight. This is a more direct expression of crop load used by grape physiologists over many years to express vine supply to demand balance (see Kliewer and Dokoozlian 2001). It is a conceptual improvement over the pruning weight method since it focuses on leaves, the functional organs that produce the carbohydrate supply. The general relationship seen is diagrammed in Figure 2 and shows the response that levels off once there is adequate supply to satisfy the demand. A key point is that the positive responses to increased supply will not continue with higher and higher supply abundance (i.e. reducing crop to very low levels will not necessarily improve ripening over crop levels that can be fully ripened by the vine). If no significant shading occurs, then total leaf area can be used. If shading is significant, then exposed leaf area should be used, though it is not always easy to measure exposed leaf area. In either case, there is the assumption that the leaf area is consistently functional in photosynthetic production of CHOs. Under reasonably consistent climatic and production conditions with healthy foliage, this index relates very well to crop development and berry ripening. Clearly though, stresses such as nutrient deficiency, drought stress or foliar pest injury will disrupt this assumption, and weather variations are not taken into account. Nonetheless, a general threshold of approximately 10-15 cm^2 exposed healthy leaf area per g fruit weight at harvest has been found in a variety of studies indicating that this index is widely useful.

Reductions in leaf function or vine supply, for example by foliar pest injury, can be viewed essentially the same as an increase in crop load. In a study of European Red Mite injury in apple, we have found that the final effects on fruit parameters at harvest and postharvest were indistinguishable from heavier cropping (Francesconi et al. 1996 a and b).

- Light interception per crop weight. Although leaves are the organs that produce CHOs to support the crop and might have full function, the variability in actual CHO production is mostly controlled by light energy captured. This is a function of light interception by the vineyard which might vary greatly depending on spacing, training system and canopy fill. For example, divided canopies such as the Lyre system might have similar leaf areas to undivided canopies, but considerably more light interception. This index assumes healthy leaves, but does take into account the variations due to different training systems that might have varying relations of leaf area to light interception. Although direct measures of light interception are somewhat difficult technically, some methods can be quite simple, such as the point grid method that uses estimates of shade area (Wunsche et al. 1995).

- Canopy photosynthesis per crop weight. The integration of light interception and the canopy photosynthetic conversion of energy to a carbon supply to crop demand should be a much more fundamental expression of crop load than any component by itself as it integrates the leaf area function and light interception. This directly measures the gross supply/demand nature of crop load. Although technically difficult, this ratio has been shown to explain well the interactions of apple tree variability, crop level, injury due to European Red Mite, and weather on apple growth, postharvest storage and return cropping (Francesconi et al. 1996 a and b; Lakso et al. 1996). Measurement of whole canopy gas exchange with flexible "balloon" chambers is feasible for research purposes (for example: Lakso et al. 1997; Poni et al. 2000; Pena and Tarara 2004).

- Crop weight per photosynthesis available to the fruit. The total canopy photosynthesis is used for both vegetative and reproductive growth, so not all will be available to the fruit at all times. Competition of shoot growth especially must be considered. Consequently, it is theoretically best to express supply as the amount of carbon specifically available to the fruit. This is not easy to do as we have insufficient understanding of competition amongst the organs, but can be initially estimated by modelling as discussed below.

Variability in crop load

An often neglected consideration is that of vine-to-vine or spatial variability in crop load that might be caused by soil or water variability across the vineyard. The most obvious example is that of missing vines or gaps in the vine canopies. Too many times only tons/ha are considered; but it is clear that a vineyard with 15 tons/ha carried by a full trellis of healthy vines will ripen and produce better wine than a vineyard that is missing 25% of the vines, yet carrying the same 15 tons/ha. With the missing vines, the vineyard capacity is reduced so the actual crop load would be equivalent to almost 19 tons/ha on a full vineyard. Another factor is that even with uniform vines, there might be substantial variation in the crop loads of individual vines. In an apparently uniform group of experimental Concord balance-pruned vines, that averaged 19 tons/ha, this had a range of individual vine yields from 9 to 30 tons/ha equivalent. Although the vines with the equivalent of 9 tons/ha yield might produce better quality than the average, the fruit from the 30 tons/ha vines will likely be quite unripe, yet would be mixed into the total.

When should we measure crop load?

Many times crop demand is expressed as 'per g of fruit' at harvest. This might be fairly robust, but it might also be confounded by changes over time. During the season, there are changing supply/demand balances so that the supply might be deficient or in excess at varying times. For example, if there is a carbon supply deficit to the fruit due to poor weather early postbloom, there might be less cell division and, therefore, a smaller size potential. This might then reduce crop demand later in the season. At harvest this would lead to the conclusion that the crop load was light even though a carbon limitation earlier was clear. Also, the light interception and leaf areas of many winegrape canopies are modified by mid-season shoot positioning into catch wires, or summer pruning to varying severities. So when during the season is the crop load most critical?

The answer seems to depend on what processes we are examining. For example, in a 12-year study comparing balance-pruned (BP) versus minimally-pruned (MP) Concord grapes in New York (see below), we found that the MP vines had much quicker leaf area development and light interception before bloom than the BP vines. This led to a higher apparent vine capacity through bloom. Post-bloom, however, the differences declined and were minor after about fruit set. We found that over 12 years the MP vines produced about 35% more yield (averaging about 27 t/ha versus 20 t/ha). However, the Brix/Yield relationship was the same for both systems indicating that the MP vines could not ripen fruit any better than BP vines. This suggests that the early supply/demand advantage of MP vines primarily affected bud fruitfulness and return crop, but the similar supply for the rest of the season meant that the MP vines could not ripen any more of the crop. Consequently, we feel that it is important to consider the dynamics of crop load over the season in relation to the desired vine behaviour. Therefore, we have begun to develop a dynamic seasonal model of carbohydrate supply and demand as discussed below.

The key is to understand all these concepts and their limitations, so that we can use the simplest one that is accurate under the conditions, but also to know when it is not appropriate. A more physiologically sound and dynamic approach is needed that takes into account at least the major components of supply (leaf area development, photosynthesis rates, light availability, light interception, availability of carbohydrate reserves, and cultural and stress factors that affect these) and of demand (growth and respiration of the crop, the shoots, the roots, the wood structure and the accumulation of carbohydrate reserves). Due to the complexity of these factors and their interactions, a dynamic model is needed to overcome the limitations of simple indices discussed earlier. A more quantitative model is needed to elucidate the behaviour of a complex system. Eventually, the understanding from the more complex model should help in the development of simpler models that are more appropriate to apply in practice.

Before the model is described, some results from several studies of carbohydrate supply and demand and root growth dynamics that relate to the model will be reviewed.

Studies of carbohydrate supply of minimally- versus normally-pruned vines

Using clear plastic whole canopy chambers, we have measured seasonal whole canopy photosynthesis and respiration in MP versus normally-pruned (32 buds/m canopy or 32-bud) Concord grapevines (Lakso et al. 1997). We found that, as expected, the more rapid early season canopy development of the MP vines led to more light interception and a higher rate of mid-day canopy photosynthesis in the early season (Figure 3). Mid and late-season gas exchange was similar. The higher number of shoots (350 versus 90) also led to higher respiration rates in the MP vines, but the overall net effect was still about a 20% increase in vine supply over the season, even though the final leaf areas and leaf photosynthesis rates were similar. These direct measurements of early season advantage, but mid-late season similarities lend support to the conclusions discussed above regarding supply-demand balances in relation to bud fruitfulness for continued cropping versus ripening of the current crop.

Root studies of minimally- versus balance-pruned vines

Root growth is generally found to be poor competition for fruit growth in most fruit crops and in grapes (Rodriguez-Lovelle and Gaudiller 2002). Clingeleffer and Krake (1992) reported that minimal pruning led to a reduction in the size of the root system compared to normal spur pruning. Also, Ruhl and Clingeleffer (1993) found that minimally-pruned vines stored relatively less of the total reserves in the root system than spur-pruned vines. Since some Concord grape growers had seen erratic bearing with minimal pruning in New York, there was concern that minimal pruning (with no crop thinning in this study) might overcrop the vines and debilitate the root system. Therefore, we studied fine root growth dynamics over the season for four years (the eighth to the eleventh years) in a 13-year study of minimal- (MP) versus balanced-pruning (BP) with and without supplemental irrigation on each pruning system. We used the method called the 'minirhizotron' technique in which clear 5-cm diameter plastic tubes are inserted in the soil under vines. After some months to allow the soil to settle around the tubes and allow roots to re-establish, video recordings of root activity were taken at the same locations in each tube at two-weekly intervals with a remote video camera. Observations began in March and continued into December.

Seasonal pattern

The seasonal pattern of root growth showed little root growth in the early Spring or postharvest (there is a very early Autumn so little good postharvest weather in New York) (Comas et al., 2005). Root growth generally began after budbreak and generally peaked first around bloom, and then again just before veraison (often pre-veraison was the greatest period of root growth) (Figure 4).

Yearly root production

A reduction in fine root production was observed, over a four year period, due to lack of moisture in the soil during two dry years. The strongest effect in root production occurred in the pre-veraison peak of root growth during drought stress (Figure 5). Total root production varied year by year. This variation appeared to be an interaction of crop level and soil water status (Figure 6). In 1997 and 2000, the moderate crops and wet seasons led to moderate root production in all vines. The greatest root production occurred in 1998 with irrigated vines, as the crop level was relatively low and water stress was avoided. The reduction in the root growth in non-irrigated vines indicates the dry soil effect. In 1999, a heavier crop occurred and seemed to reduce root production in irrigated vines; combined heavy crops and drought in 1999 reduced root production even more, yielding only about 30% as many roots as in the lightly-cropped irrigated vines in 1998. Although this trial did not directly adjust crop loads, the results are consistent with crop load and drought stresses as major limiting factors for grape root production.

Surprisingly, pruning regime had no significant effect on patterns or amounts of root production. This lack of effect appears to be due to the increased early-season supply of carbohydrates in MP vines compared to normally-pruned vines, balancing the increase demand of a larger crop. The greatest difference in crop demand is post-veraison, yet almost all root production occurred preveraison in this study in a cool, short-season climate.

The seasonal periodicity of root growth did show two general peaks although in some other years they merged to become a general growth period between budbreak and veraison. The Spring flush of new root production beginning around or just after budbreak, and peaking around bloom, has been documented in other climates (Freeman and Smart 1976; Richards 1983; van Zyl 1988; Ibacache and Lobato 1995). This synchrony amongst climates is due, most likely, to the vine development responding to the same temperature thresholds in the Spring regardless of date or day length. Also, in a seasonal growth analysis of mature Concord vines we found that much of the budbreak-bloom fine root growth corresponded with a decline in weight of the larger roots suggesting a redistribution of dry matter from coarse to fine roots then. The main difference was that we see little new root growth after veraison or harvest while in longer seasons (and probably hotter and more stressful during the mid-season) the second peak occurs later when the crop demand diminishes and conditions are milder.

So, how do we combine all of these useful but limited measurements over many different years or vineyards into a more integrated understanding of the many effects of crop load? Mathematical modelling must be considered.

Modelling and measuring – pros and cons

There are pros and cons for any research approach. Measuring provides 'real' data under real conditions, and can allow presumably true comparisons of treatment effects. Additionally, direct measurements can determine the variability as well as an average value. Gathering actual data is indispensable to effective research. However, since any measurement is taken under a unique set of conditions of time, stage of plant development and environment, the values cannot be assumed to be the same under different conditions. For example, the leaf photosynthesis of a vine early in the growing season with no water stress cannot be used to predict behaviour of leaves late in the season under drought stress. Consequently, 'real' data cannot be generalised directly to predict behaviour under different conditions.

Modelling is a tool which potentially can estimate what will happen under any given set of circumstances if we understand the principles controlling vine behaviour. We all use models constantly to plan our lives. Knowing that it is 10 km to a desired location and that we can expect to average 40 km/hour, we model that it will take 15 minutes to drive. In crop modelling there are several major uses. One is to quantitatively integrate spot readings over time so that we can have estimates over longer time periods. Models can integrate over time the 'snapshot' measurements that we take. It is equivalent to trying to make a movie from still photos by estimating what happens in between the stills. Another important value of modelling is to elucidate patterns of behaviour over time which are not obvious without such models. An example we will discuss later is to look for periods over the season of carbohydrate supply excesses or deficits that might relate to key process of vine growth or productivity.

It is important to acknowledge that crop models are gross simplifications of very complex biological and environmental systems. So they inherently are very limited. Yet if they address key principles that generally control our systems, they can be helpful in understanding system behaviour. Good reality checks for modelling are to acknowledge that: "all models are wrong; some models are useful" (attributed to Professor G. Box), and "models should be as simple as possible, but no simpler" (attributed to Albert Einstein). Thus, a key problem for modelling is finding the right balance: too simple and it does not behave realistically; too complex and it becomes incomprehensible. We believe in beginning with the simplest set of central physiological principles, testing the model, and only adding complexity if it is needed to attain realistic behaviour.

It is safe to say that as models do not give answers, and only give quantitative predictions, they must be used with caution. Further, models should be used only as one of many tools to address key questions. The initial questions that are addressed with this modelling effort are (1) are there periods during the season of deficits or excesses of carbohydrate supply in relation to demand? (2) does root growth primarily occur only when there is an excess of carbohydrates, since roots seem to be poor competitors for carbohydrates?

Model structure

As Einstein suggests we have begun simply. The grape model (named 'VitiSim') described here is a seasonal dry matter production model with a daily time step that was developed originally for apple (Lakso and Johnson 1990) and eventually modified further (see Lakso et al. 2001 for general equations and description). Briefly, leaf area development and light interception are estimated, then vine photosynthesis is estimated from a 'big leaf' canopy light response to intercepted light (from Charles-Edwards 1982). Net fixed carbon is estimated by subtracting estimates of respiration of fruits, leaf area, and woody structure. Demands of varying organs are estimated to compare to supply over the season.

Leaf area development

For a given pruning regime the model considers all shoots to have the same sigmoidal growth patterns adjusted for temperature, but with a range of effective rates and growth durations. All shoots were given the same amount of leaf area increase per shoot per degree day (degree-days, an integral of heat and time above a base temperature), and the total daily increase was summed over all active shoots. The fraction of shoots growing at any time was limited by a curve estimated from observations of growth durations of shoots on vines similar to the modeled vines. We have found that the leaf area development rate pattern over time of shoots varies across the extremes from heavy to minimal pruning by about 2-3 fold.

Canopy photosynthesis

Canopy photosynthesis is estimated by a daily whole canopy light response curve versus daily total intercepted light (using daily total radiation from weather stations as inputs). This is a 'big leaf' model that treats all leaves as an organ. It simply calculates the fraction of light that can be intercepted, multiplied by the incident light to estimate total light intercepted, and then puts that into the canopy light response curve. The response does not saturate as single leaves do. It increases up to full sunlight since it is estimating the full daily photosynthetic activity and, over the day, most leaves are not normal (i.e. perpendicular) to the sun (Figure 7). This response curve is very similar in shape to the canopy light response curves reported by Poni and Intrieri (2001) and Pena and Tarara (2004). The varying leaf angles and exposures of all the leaves in the canopy make the canopy response more gradual than the common leaf light response. Temperature effects are incorporated by scaling down the calculated photosynthesis if the temperature is not optimum.

Respiration components

Again, for simplicity, all organs are treated as a single big, fruit, leaf, woody structure or root. All respiration rates are based on estimates of organ respiration at a standard 20ºC (which varies over the season), then adjusted for temperature by the classical exponential respiration as a function of temperature. The total respiration of any organ depends on the specific respiration rate multiplied by the total organ weight or area. Also, currently no root respiration submodel is included due to the limited good data on root respiration and amount of root in mature vines, but that is under development.

Demands of crop and shoots

Although not an integral part of the model yet, similar seasonal estimates have been made of the amounts of dry matter or fixed CO_2 that are needed to account for measured seasonal growth of the shoots and the crop over many years. As discussed earlier, the great majority of dry matter in mature vines is in the shoots and crop, so a simple initial approach for modelling is to compare these observed requirements to the available next fixed CO_2, assuming that crop and shoots have first priority.

Testing the Model Behaviour

Seasonal dry matter production

Several simulations and tests were run of the model and its components. First, it is important to determine if the total dry matter production amounts and patterns of accumulation are realistically modelled. Two vine growth analysis studies have been done in New York on Concord grapes harvesting entire vines, including roots, at intervals. We have the weather data and reasonable estimates of the vine parameters needed. A growth analysis of third-season, cropping vines was done by Bates et al. (2002) over a season harvesting whole plants with roots at eight periods. Although not measured, we estimated a 35% maximum light interception for that vineyard based on measurements taken previously in similar vineyards. Estimates of shoot and crop growth rates and photosynthesis from adjacent trials in that location that year were used. The simulated pattern and total of dry matter production were very good (Figure 8). Another recent study, just being completed, was a similar growth analysis of 40-year old vines with standard treatments common in the Concord industry. This too was quite well simulated although there was a great amount of vine-to-vine variation.

Seasonal supply-demand balances

The seasonal patterns of canopy photosynthesis of minimally-pruned versus a constant 32 buds/m of canopy (32 Bud) were simulated under New York climatic conditions (Figure 9). The general pattern was quite realistic compared to the measured canopy gas exchange shown earlier (Figure 3). It should be noted that this was not a completely appropriate test as the measured values were only mid-day rates while the model estimates total daily photosynthesis. The main differences occur in the later season when the mid-day rates could be relatively high, but the daily totals decline due to the shorter day lengths. Nonetheless, the model seasonal behaviour seemed realistic.

When the vegetative and crop development was summarised, it was clear that the greatest differences in MP versus 32 Bud vines was the much earlier shoot development due to the many shoots on the MP vines, but earlier decline in demand from shoot growth due to the slower growth and earlier termination of growth (Figure 10). Conversely, the crop development phenology is not significantly affected by the pruning regime although the amplitude of demand varies with the crop level.

If the demands of the crop and shoot growth are then combined and compared to the supply curve, the model simulation predicts that after crop and shoot demand is satisfied, there might be some excess carbohydrate supply in the period around bloom (Figure 11). This effect is greater in the minimally-pruned vines due to the early canopy development and the earlier decline in shoot demand compared to the heavier pruning that stimulates longer shoot growth periods. Possibly, this better carbohydrate balance around and after bloom might help to explain the greater sustained cropping levels in the minimally-pruned vines. In both pruning regimes, the greatest potential carbohydrate supply is just before veraison when crop and shoot demands are low and canopy supply is high. Between veraison and harvest it appears that the 32 bud/m pruning was more in balance with the crop demand while the minimal pruning was not able to meet the larger demand of the ripening crop. Again, it should be emphasised that these simulations were for quite heavy 18 and 27 tons/ha crops in the short, cool season in New York.

It would be expected that in longer, sunnier seasons, like many in Australia that start earlier, ripening would occur during warmer, longer days. Therefore, the apparent carbohydrate supply deficit noted for the minimal pruning between veraison and harvest would be expected to be less severe.

Relation of carbohydrate supply/demand to root growth

It is interesting that the two periodsof positive carbohydrate supply (around bloom and pre-veraison) coincide with the main periods of fine root production noted earlier (i.e. compare Figure 12 with Figure 3), providing some support for the concept that during the growing season, root growth might be limited by competition for carbohydrates by the shoots and crop. Although the current carbohydrate supply may be adequate, the early season root production from budbreak through bloom is likely supported also by root carbohydrate reserves. We have found in a study of the 40 year-old vines a decline in dry weight of the coarse storage roots coinciding with initial fine root production (unpublished data of Goffinet, Lakso, Bates, Cheng, and Dunst). The pre-veraison peak of root growth does appear to be related to the current season carbohydrate supply availability. The most striking effect is the rapid drop in root production after veraison when the crop demand peaks. Under limiting conditions, roots are well known to suffer compared to the crop and shoots (Buttrose 1966; Morinaga et al. 2000). This effect appears to be also aggravated by drought stress (McLean 1993). Candolfi-Vasconcelos et al. (1994) reported a drop in root growth and a movement of carbon from roots post-veraison, when the vine was defoliated, although the defoliation treatment is rather extreme. This correlation must, however, be tempered by other results, such as those of Hunter et al. (1995) who found that partial canopy defoliation could actually stimulate fine root production.

In longer seasons, there might be significant postharvest photosynthesis; little or no shoot and crop demand; and warmer soil temperatures which should allow significant root development after harvest. This has been noted in several cases for studies in warm climates (Freeman and Smart 1976; Richards 1983; Van Zyl 1988; Williams and Matthews 1990; Ibacache and Lobato 1995), but it clearly cannot be assumed to be true in cool, short seasons as in New York. Regardles of climate a peak of root growth around budbreak to bloom was seen, suggesting that early root growth may be a consistent pattern supported by redistribution of internal root reserves.   However, if mid and late-season root production is regulated by photosynthetic carbohydrate availability, then a model as described should be able to explain these patterns regardless of climate. Much more work is needed to fully understand the regulation of root growth and function, but we feel that the current research is helpful to address the carbohydrate aspect.

In summary, we feel that the integrated approach of several experimental organ-level and whole canopy measurement techniques, combined with dynamic modeling, can help focus our thinking and efforts on key questions and times, and help elucidate the physiology of crop load.

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