Manipulation of Source-Sink Relationship in Pertinence to Better Fruit Quality and Yield in Fruit Crops: A Review

Ravina Pawar1*, Vishal S. Rana2

ABSTRACT

Profuse flowering and fruiting create high demand for a limited source of carbohydrates, which affects fruit set and development. These plenty number of flowers and fruits must be reduced to allow the trees to produce fruit that meets market expectations for size, color, and quality. The concept of source-sink relationship and the regulation of carbon partitioning in plants is useful for better understanding of crop physiology and the influence of yield-limiting factors on crop production. This relationship between source leaves and the various sink organs affects fruit production in not only the current season, but also the long-term performance due to the perennial nature of fruit trees. Modeling early-season whole-tree carbohydrate supply and demand have greatly improved the understanding of the response of trees to manipulation strategies relating source-sink alliance. Various strategies have been adopted to manipulate source-sink relationship like flower bud inhibition, flower thinning, fruitlet thinning, defoliation, girdling, pruning, application of hormones and nutrients, etc. Thus, a balance between vegetative and reproductive growth is an important aspect for improvement in yield and quality of fruit crops.

Keywords: Fruit quality, Manipulation strategies, Source-sink alliance, Yield.

Agricultural Reviews (2019)

INTRODUCTION

In higher plants, carbon fixed during photosynthesis is either directly metabolized to provide energy and carbon skeletons for the cell’s respiration and growth or it is exported, mainly in the form of sucrose, to other organs to support their growth and development to provide assimilates for the synthesis of storage compounds. Therefore, the organs in higher plants can be generally divided into the source and sink organs. Photosynthetically active source organs are defined as net exporters of photoassimilates, represented mainly by mature leaves and sink organs that are photosynthetically inactive are referred as net importers of fixed carbon like root, seed, fruit, root tuber, etc. Crop physiology and the influence of yield-limiting factors on crop production can be better understood through source-sink relationship and the regulation of carbon partitioning among sinks in plants. Fruit production and quality depend on the adequate source-sink relationship. The source-sink relationship is a process involved in translocation of photosynthetic products in plants. The carbohydrates translocated from leaves or reserve organs are the most important for growth and development of sink organs i.e. fruits. Sinks import and use assimilates in respiration, growth and storage material (Wareing and Patreek, 1975). Within a tree, reproductive organs such as fruits compete for assimilate with each other, especially in trees with heavy crop loads (Dejong et al., 1987).

Manipulation of the fruit load has been applied as a measure to improve fruit quality and as a research tool to gain insight in the competition between shoot growth versus flowering and fruit growth. Balance maintenance between vegetative and generative growth of a tree is of great importance for growth and production of fruit plants (Park, 2011). The relationship between photosynthetic and non-photosynthetic tissues is less pronounced in fruit trees than in herbaceous plants due to the structure of the tree, which implies high energy costs to maintain a notable quantity of non-photosynthetic tissue (Coleto, 1995). DeJong and Ryugo (1998) described fruit trees as solar energy collection systems whose efficiency depends on the capture and conversion of light energy into chemical energy (photosynthesis) and later the translocation, storage and utilization of that chemical energy. The translocation of organic materials throughout the plant in the phloem is a complex operation, and therefore, this process does not have a full scientific explanation. The concepts of source and sink strength have appeared in the literature for decades, but there remains a lack of consensus regarding their role in the process of carbon allocation because of the complex quantitative interactions between ‘sources’ and ‘sinks’ in a whole-plant system (Farrar, 1993).
Characteristics of Source and Sink

A sink is defined as a plant organ which is net importer, while a source is defined as plant organ which is a net exporter (Warren Wilson, 1972). Sinks are reproductive structures (flowers and fruits) and storage organs (eg. tubers, rhizomes), usually form the yield forming parts of plants and are economically as well as physiologically important. Leaves are the most important sources in a plant which photosynthetically fix carbohydrate to become a net exporter of stored assimilates. The most important source-sink relationships are the interactions between leaves and the variety of sinks present on a plant competing for exported assimilates.

Once produced by source organs (mainly leaves), carbohydrates may be initially partitioned between use by the source leaf and transport as to other plant organs. Carbohydrates available for transport must then be allocated between the many competing sinks on the plant. Competing sinks include roots, expanding shoot tips, expanding leaves, buds, flowers, fruits, and stems. Although productivity is likely to be improved by increasing the allocation of photo-assimilate to harvestable sinks (Turner, 1986), net accumulation of carbohydrate will be either source or sink limited depending on the type of sink and stage of development (Patrick, 1988).

The ability of individual sink to accumulate assimilates is determined by an intrinsic property of the sink, and this has been defined as sink strength. Sink strength was initially defined by (Warren Wilson, 1972):

\[ \text{Sink strength} = \text{sink size} \times \text{sink activity} \]

where sink size is the dry weight of the sink and sink activity is the relative growth rate. However, sink strength defined in this way has several shortfalls. Firstly, dry matter values do not account for respiratory losses which may be as high as 50% of the total accumulated carbohydrates (Wareing and Patrick, 1975). Secondly, the equation formulated in this way does not consider the availability of carbohydrate, which may be limited and therefore, competition with other sinks will occur. Thus, sink strength estimated from dry matter data is more aptly considered as competitive ability relative to other sinks (Wareing and Patrick, 1975), or apparent sink strength (Ho, 1988).

Competitive Potential of a Sink

A competitive situation exists between the sinks present on a plant. In a fruiting plant, there will be both inter-fruit competitions, as well as competition between fruit and other sink organs such as shoot apices, expanding leaves and the root system. The availability of mobile assimilates to a particular sink, will be determined by the competitive ability of individual sink organs (Ho, 1988). The competitive ability of various organs is consistent throughout a plant but may change as a plant grows and develops (Ho and Hewitt, 1986). Based on the relative effect of defoliation on individual components of kiwifruit vine, Buwahla and Smith (1990h) suggested the ranking of the competitive strength of sink organs present on a kiwifruit vine during the growing season is shoot > fruit > roots > return bloom.

Proximity to the source of carbohydrate is important in determining competitive ability. Sinks which are close to a source appear to have an advantage in obtaining carbohydrate from source (Patrick, 1988; Wardlaw, 1990). However, the actual distance that assimilate must be transported between source and sink is not usually the factor which limits sink accumulation, rather the presence of closer and/or stronger sinks which are able to divert assimilate (Wardlaw, 1990). Thus, the competitive ability of sinks is particularly important for sinks distant from the carbohydrate source (Cook and Evan, 1978). For example, kiwifruit are able to obtain carbohydrate from relatively distant sources on a vine. Lai et al. (1987) found that fruit on lateral shoots with few leaves were able to obtain carbohydrate from neighboring laterals easily. When Buwalda and Smith (1990) severely defoliated the replacement canes of kiwifruit vines, fruit weight was reduced in all parts of the vine, but to a greater extent within the region of defoliation. When defoliation was carried out in the fruiting canes, the growth of fruit vine was severely inhibited, while fruit weight in the replacement cane zone which has a high leaf:fruit ratio, was not affected. The apparent contrast between the results of Lai et al. (1987) and Buwalda and Smith (1990) demonstrate the importance of proximity to the source of carbohydrate when competing sources are present and carbohydrate is very limited.

Dominance or Correlative Inhibition

Competition between sinks may be amplified when assimilate apply is limited (Ho, 1988). However, competition for assimilates does not explain all of the observations associated with dry matter accumulation by competing sinks. For example, the dominance of one sink over another can be observed very early in fruit development when assimilate supply is unlikely to be limiting (Bohner and Bangerth, 1988). Dominance phenomena are widespread, the most well known being the inhibition of growth of lateral buds by the presence of the apical bud, which is known as apical dominance (Tamas et al., 1981). Dominance is also common between fruit and may occur between fruit and vegetative sinks (Garcia-Martinez and Beltran, 1992) although a distinction between dominance and competition is often difficult to make (Bangerth, 1989). However, some form of sink priority occurs in many situations, often related to the time of initiation of development with earlier initiated fruit often dominant over later initiated ones (Ho, 1992). For example in tomato, proximal fruit normally grows to a larger size than the distal fruits, which normally set several days later unless pollination is synchronized (Bohner and Bangerth, 1988). However, if distal tomato fruit on a truss are induced to set prior to proximal fruit the dominance is reversed such that distal fruit are larger (Bangerth and Ho, 1984). The dominance of the earlier formed ovaries over later formed ones has been termed primigenic dominance to identify the dissimilarity to
apical dominance which is dependent on the morphological position on the plant (Bangerth, 1989).

In addition to the timing of fruit set, the number of seeds formed may influence dominance relationships. In many fruit species, fruit with high seed numbers are often dominant over fruit which is poorly pollinated. For example, the growth of zucchini fruit with low seed numbers is inhibited by nearby fruit with high seed numbers (Stephenson et al., 1988). The presence of seeded persimmon fruit on the same tree increased the proportion of seedless fruit which abscised (Kitajima et al., 1992). Similarly, removal of seeds from older dominant bean pods was found to release both lateral buds (Tamas et al., 1981) and young fruits from dominance (Tamas et al., 1986).

Basipetal transport of auxin appears to be involved in inter-sink dominance relationships. Apical dominance can be maintained by replacing the apex with a source of auxin (Thimann and Skoog, 1934), while the application of auxin transport inhibitors below the apex releases lateral buds from dominance (Tucker, 1978).

**Mechanism of Source-Sink Relationship**

**Phloem loading and long-distance transport of sucrose**

The evolution of source and sink tissue systems generated a need for long-distance transport between the specialized tissues, which is carried out by the phloem cells of the plant’s vascular system. To accomplish long-distance transport from source to sink, sucrose has to be loaded into the phloem in source tissues. In most plant species such as *Arabidopsis*, tobacco and potato, compelling evidence suggest sucrose to be loaded into the phloem via an apoplastic route. In the apoplastic phloem loading route, sucrose is released into the extracellular space somewhere in the proximity of the plasmalemma, where it diffuses through the cell wall. After reaching the sieve element and companion cell (SE/CC) complex, sucrose is then loaded against a concentration gradient into the phloem via the well-characterized plasma membrane-bound sucrose/proton symporter. In symplastic phloem loaders, sucrose is supposed to be transported from cell to cell via plasmodesmata-nanopores lined by a plasma membrane that bridge the cytoplasm of most plant cells to their neighbors, and eventually released into the SE/CC. In both loading routes, once sucrose is loaded into sieve tubes in the source organs, water is drawn in osmotically across the cell membranes, leading to a building up of physical pressure. The hydrostatic pressure then drives mass flow transport to less pressurized regions of the plant (sink organs) following the sieve tubes.

**Phloem unloading and metabolism in sink organs**

After reaching the sink tissues, water and sucrose move out from the phloem to the surrounding cells, where sucrose is utilized. Shreds of evidence from the use of transport inhibitors anoxia treatment feeding experiments and the analysis of plasmodesmal “size exclusion limit” in sink leaves suggest that symplastic unloading of sucrose from the phloem to heterotrophic sink tissues through plasmodesmata connections constitutes the principal unloading route. Although the symplastic unloading route is predominant, the apoplastic route is inevitably required in some cases e.g. unloading to the filial tissue in developing seeds that has no symplastic connection with the maternal tissue. In the apoplastic unloading pathway, sucrose released into the apoplast can either directly enter the heterotrophic cells via a plasma membrane-bound sucrose transporter or be hydrolyzed into glucose and fructose by cell wall-bound invertase (cw-inv) that are subsequently imported into the cells via a hexose transporter located in the plasma membrane. In some organs, sucrose phloem unloading mode is also under developmental control.

**Strategies to Manipulate Source-Sink Relationship**

**Flower and Fruitlet thinning**

Thinning controls crop load by removing the smallest fruits, usually increases the size of the remaining fruit (Goffinet et al., 1995). It improves fruit yield and quality and returns bloom for the following year. Mainly, thinning is followed in temperate fruits which produce an excessive number of flowers. It is required to set an acceptable yield of large fruit and maximize returns. There are three types of thinning, namely: hand, mechanical and chemical. Chemical thinning is the most common type of thinning. The primary impetus of chemical thinning is to reduce the labor cost of hand thinning. Bloom thinners set the advantage of diverting photosynthates to fewer sinks and, subsequently, increase fruit size. Although chemical bloom thinning may cause over thinning if it coincides with inclement weather during or shortly after bloom. The time of application to phenological stage of flower or fruit development, the temperature at and after application and cultivar sensitivity all appear to be important factors influencing the blossom thinning response in apple and peach (Westwood, 1993). The performance of the blossom thinners is therefore likely to vary by growing region and by cultivar (Fallahi, 1997).

**Girdling**

Girdling is a selective wounding process that removes strips of bark and the cambial tissue from the trunk or scaffold branches. Due to this process, reduction in shoot development, improvement in fruit quality and early ripening is noticed. Girdling breaking off the phloem flow causes a store of elaborated sap in the portion of shoot over the girdling that inhibits the photosynthetic activity of the leaves. In spite of increasing the fruit quality, the presence of fruits on the girdled shoot, also promotes transpiration. Transpiration and the store of mineral elements [nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg)] appeared to be closely connected in the leaves. A reduction in the transpiration rate of the leaves of girdled shoots, there was a decrease in store of all the...
mineral elements (Di Vaio et al., 2001). Differing transpiration between girdled and non-girdled shoots appeared to affect the global transport of mineral elements. For non-girdled shoots, the N, P, K and Ca leaf content was higher due to increased transpiration. So, girdling alters the distribution of nutrients, favoring the fruits that show higher total soluble solids content and the leaves that display more significant development concerning the linear growth of the shoot.

But, there is a number of problems associated with girdling. The most significant potential problem is tree death. Girdles that are too deep, wide or heal too slowly can severely damage or kill trees. It also resulted in a reduction of net photosynthesis.

Training and Pruning
Training and pruning alter the balance between vegetative growth and reproductive fruiting by the allocation of resources, such as carbohydrates, water, and growth regulators (Myers, 2003). Pruning has its physiological effects due to changes in the partitioning of the reserves. It changes sink preference for allocation of photosynthates. Though, pruning delayed the emergence of buds but hastened the post-flowering phenophases due to increased source and reduced sink and efficient translocation of photosynthates in the pruned shoots to the potential sinks (fruitlets). Depending upon the time of the year, the extent and frequency of pruning, some sites of accumulation will disappear and others will be created. As a result, changes in seasonal fluctuations of reserves can appear as well (Clair et al., 1999). In this way, pruning helps in both ways, firstly to regulate crop (Kindo, 2005) and secondly to manage high density (Kaur and Dhaliwal, 2001).

Factors Affecting Manipulation of Source-Sink Relationship
Carbohydrate: Nitrogen ratio
A relationship between carbohydrates and nitrogenous compounds maintains a balance between tree growth and fruitfulness within a tree. Carbohydrates are manufactured and stored in the leaves; heavy pruning which removes a large portion of the leaf area can result in a tree low in carbohydrates and high in nitrogen tends to produce vigorous vegetative growth at the expense of its fruit production capacity. Efforts should therefore be made so that the C:N ratio is not disturbed due to excessive pruning and the nitrogen applications should be adjusted according to the severity of pruning as too much nitrogen after severe pruning can aggravate the problem by causing thick and puffy fruit peel. Reducing nitrogen application avoids an imbalance when heavy pruning is done. Omitting a nitrogen application before heavy pruning and possibly after will reduce both costs and excessive vegetative growth.

Leaf area index (LAI)
The LAI in conjunction with sunlight interception is useful as a basis for analyzing canopy productivity. Minimum quantities of leaf area and shoot structure are required for setting large fruit crops (Lakso and Flore, 2003). Compared to annual crops (e.g., cereals), little information about the LAI (the relationship between leaf area and occupied soil area) is known about fruit species. The LAI in conjunction with sunlight interception is useful as a basis for analyzing canopy productivity. The rapid LAI development at 2300 m above sea level allowed early and higher fruit production throughout the culture compared to the higher site. The leaves close to developing fruits exhibit increased photosynthetic capacity as compared to the remaining leaves of the tree. Apart from cultural practices, agro-ecological conditions and age of plants can influence LAI development (Fischer, 2011).

Jackson (1980) reported that the LAI in the apple lies between 1.5 and 5 depending on the variety, rootstock, pruning, trellising, fertilization and other cultural practices. The index in the peach is higher, between 7 and 10 (Faust, 1989). Moreover, height and type of training define light penetration to the foliage (Faust, 1989). The leaf area index in the orange can be as high as 9 or 11 (Dussi, 2007). Rajan et al. (2001) found that mango (Mangifera indica) cultivars well adapted to subtropical conditions develop large crowns with dense foliage, measuring an average LAI of 2.94 (1.18-4.48). The varieties with a low LAI (‘Fernandin’, ‘Malihabadsaefa’ and ‘Ratal’) were better exposed to solar radiation and produced more reproductive stems and good color fruits than varieties with denser foliage.

Harvest index (HI)
The harvest index (HI) is used in crop physiology as the percentage of total DM partitioned to the harvested portion (sink). The HI increases with the age of the fruit tree and depends on various factors viz. variety, rootstock, agro-ecological conditions and crop management. For apple trees in production, the HI (including root system) can be between 30 and 50%, which can go up to 65 and 80 percent in very favorable conditions. In peach trees, it can reach 70% (Lakso and Flore, 2003).

Leaf: fruit ratio
Leaf: fruit ratio means how much leaves should be retained for better results in terms of quality and yield. The optimal leaf-to-fruit ratio varies according to the species and variety and orchard geographic location (Schumacher, 1989). Moreover, the capacity of leaf photosynthesis depends on the incidence of light, whereas, the shaded parts of the canopy assimilate less and need more leaves than the well-illuminated part for optimal fruit development.

Hansen (1978) stated that decreasing the leaf-fruit ratio increases the photosynthetic efficiency of the leaves resulting in a raised sink-effect. The increase in the leaf-fruit ratio may facilitate the accumulation of starch reserves, favoring vegetative growth, and fruiting in the following season (Chacko et al., 1982). Tree fruits with a high leaf-to-fruit ratio, as in young plants or those with a low fruit load, often form large fruits with a “spongy” tissue which reduces postharvest
life and increases susceptibility to diseases (Friedrich and Fischer, 2000). The optimum exposure of the maximum number of leaves to light normally results in the greatest yield of DM (DeJong and Ryugo, 1998). Grapes doubled the root starch concentration from 12–25 percent DW when the leaf-fruit ratio increased from 0.5 to 2.0 m² of light-exposed leaf area per kg fruit (Zufferey et al., 2012).

The optimal leaf area in several fruit species is 200 cm² per 100 g of fresh fruit mass for favorable growth and quality (Fischer, 2011). Furthermore, grapes require 2000 cm² per 100 g of fresh fruit mass for optimum growth and quality (Sauer and Baumann, 2007). Cannel (1976) studied the partitioning of assimilates between leaves and fruits and concluded that a leaf area of 20 cm² is required to fulfill the requirements of each coffee fruit growth. The rate of sucrose accumulation for the Satsuma mandarin in the fruit was higher at an average load (25 leaves/fruit), as compared to trees with 50 leaves per fruit in which thinning practiced at 70 days after anthesis (Kubo et al., 2001). When thinning performed in the mango ‘Lirfa’ (grafted on ‘Maison Rouge’) resulted in the highest fresh weight of fruit at 100 leaves, while flesh DW increased 11% when the number of leaves increased from 10–100 (Lechaudel et al., 2004). The increased TSS content and pulp/stone ratio in the ‘Rubioux’ peach was observed when optimal leaf:fruit ratio maintained at 40–50 leaves/fruit with thinning (Casierra-Posada et al., 2007).

The leaf-fruit ratio changes with the production area latitude in which, the temperature and light have a great influence, with lower ratios at sites nearer to the equator (Fischer, 2011). Schumacher (1989) considered that the leaf-fruit ratio is not reliable as it alters with the fluctuating conditions. So, growers can rely on several methods which directly or indirectly influence photosynthesis and sink activity. Among them, tree height, distance, fruit thinning, pruning, fertilization, application of growth regulators, irrigation and phytosanitary control are the most important methods (Fischer, 2005).

Temperature
Temperature plays an important role in carbohydrate partitioning. The optimum temperature for transporting carbohydrate in most species is between 20 and 30 ºC. Translocation diminishes with decreasing temperatures due to the increased viscosity of the phloem solution which lowers down the movement of photosynthates (Guardiola and Garcia-Luis, 1993). However, some species are not sensitive to low-temperature conditions as their sieve tubes are functional at freezing point and even lower temperatures. Night temperature is also of considerable significance for carbohydrate translocation because the movement of carbohydrates takes place during night hours. It has been reported that the majority of growth in members of the Rosaceae family occurs during the night period as compared to day time (Fischer, 2011).

Water stress
Water stressed plants delay carbohydrate transport due to an increase in the viscosity of the solution translocated. Prolonged water deficits cause the accumulation of abscisic acid that inhibits phloem loading in leaves (Guardiola and Garcia Luis, 1993). The distribution of assimilates may be affected by a deficiency or imbalance of mineral nutrients and by the initiation and development of sink organs.

Nutrients
The distribution of assimilates may be affected by a deficiency or imbalance of mineral nutrients and, furthermore, by the initiation and development of sink organs and for source functioning, the plant requires an adequate supply of nutrients (Taiz and Zeiger, 2006).

Due to high concentrations of K in companion cells of sieve elements, they are claimed to be essential in the process of loading and unloading the phloem (Taiz and Zeiger, 2006). Its deficiency affects vegetative growth because the plant alters the distribution of K to improve the growth of the fruit (Ho, 1996). Lechaudel and Joas (2007) found higher K and Mg concentrations in the flesh of mango fruit with higher leaf:fruit ratios. In contrast, boron does not facilitate sugar transport via the formation of borate–sugar complexes, because sucrose builds only weak complexes with B and, additionally, B is not involved in sucrose phloem loading (Marschner, 2012).

Advanced Strategies Implied to Manipulate Source-Sink Relationship in the Eyes of Various Researchers

L-PEACH Model (Allen et al., 2005)
The integration of physiological and architectural aspects of plant function is the essential concept of functional–structural plant modeling (Sievanen et al., 2000). Functional–structural plant models simulate the development of plant structure. They include physiological and environmental factors. The L-PEACH model is based on the development of peach trees. L-PEACH uses L-systems to modeling source–sink interactions, architecture, physiology of growing trees and to solve differential equations for carbohydrate flow and allocation. It incorporates a carbon-allocation model driven by source–sink interactions between tree components. It accounts for storage and mobilization of carbohydrates during the annual life cycle of a tree. Carbohydrate production in the leaves is simulated based on the availability of water and light. This model outputs an animated three-dimensional visual representation of the growing tree and user-specified statistics that characterize selected stages of plant development. The model is applied to simulate a tree’s response to fruit thinning and changes in water stress.

Cane stringing: SupaVine cane control system in Kiwifruit
Supa Vine is a unique, patented stringing system for growing kiwifruit developed by engineer Andrew McIsaac in Paengaroa, New Zealand. It provides substantial benefits to
the orchard owner. It is smart, easy, affordable and effective. SupaVine offers a string of grower benefits, including massive reductions in labor as well as increased fruit volumes of superior quality. In this, the new season replacement canes are grown in the sunlight above the canopy. There is a top wire along with the canes and above the female rows. The new canes are grown up to the string, above the existing fruiting canopy. As the fruits have been picked and canes are pruned, the replacement canes from year old wood which will fruit are now retied and ready for the new season growth. It also improves air circulation throughout the canopy. It also improves the dry matter and maximizes production. Other benefits are as follows:

- Create easy and stress-free winter pruning with reduced labor costs.
- Eliminate specialized pruning.
- Increase efficiency by re-using string, year after year.
- Promote bigger, stronger, healthier new canes, growing up to nine meters.
- Reduce shading because leaders are evenly spaced.
- Increase bud growth.
- Reduce risk of fungal disease as leaders are kept clean.
- Minimize wind damage, preventing blowouts.
- Make laying of new canes effortless as there is no bending.

Shading: Effective means for crop load management and fruit quality enhancement in apple (Aliev et al., 2012)

Aliev et al. (2012) observed that shade cloth (80% shade/ PAR reduction, 90% UV reduction) applied for either 3, 6 or 9 days either at the end of bloom (EB) or 23 days after full bloom (DAFB) improve the increased fruit sugar content by improving tree source: sink relationships and fruit mass with better (75–100% red surface) colouration of 85-96% in Gala and Elstar cultivars. The shading treatment also induced the desired stronger return bloom viz., less alternate bearing, with the least flowers in the un-shaded control. Thus, shading has proven itself as an environment-friendly technology having effects on source-sink relationships and tree carbon starvation. It may affect the fruit of the desired quality in terms of firmness, size, color, and sugar content and prevent biennial bearing of fruit trees.

Foliar application of urea to “Sauvignon Blanc” and “Merlot” vines (Lasa et al., 2012)

Management of nitrogen fertilization may allow wine parameters to be modified and improves the quality in grapevines. The nitrogen fertilization enhances the grape juice parameters. During veraison, the assimilable yeast nitrogen was found higher with foliar application of urea, resulting in increased amino acid and proline content. The isotopic analysis also showed that the urea applied to leaves was transferred to the berries, with the maximum translocation. Thus, foliar application of urea modifies grape juice quality and can be used as an effective tool for obtaining quality wines.

Modified BBCH scale: source-sink relationships (Rajan et al., 2011 and Singh et al., 2015)

The crop presents well defined phenological stages during growth and flowering, depending upon climatic conditions which of course is amenable to manipulate through cultural interventions, especially irrigation. Tree management strategy to increase shoot numbers (fruited units) and induce profuse flowering for crop manipulation is essential for profitable fruit cultivation.

The modifications done in existing extended BBCH-scale are suggested to make it more useful for phenological studies. The modified BBCH scale is further a step forward in achieving uniformity of growth stage descriptions and can be adopted widely. Refinement of the modified scale may further pave the way for the development of more robust scale. Intensive data collection from diverse ecologies and its analysis will lead to further refinement. However, in the absence of such advancements, the present endeavor will help in harmonious phenological data recording at various location and data analysis.

Under the changing climatic scenario and adoption of hi-tech horticultural practices, there is an urgent need to modify BBCH scale vis a vis phenophases under location specific climatic, soil condition, pruning intensity and time (Singh et al., 2015). Pruning operations impact the normal BBCH scale rating. This method is basically a decimal system that identifies different developmental stages by a two-digit code. While, the first digit refers to its major stages using values between zero and nine, the second digit, also scaled from zero to nine, relates to its secondary stages. Once the phenological stages of crops are clearly identified, it will be easier to assess the best timing for its canopy architecture management through pruning for enhanced quality yield.

Water versus sink-source relationships in a semiarid tempranillo vineyard: vine performance and fruit composition (Miras-Avalos et al., 2016)

Grapevine yield and fruit composition largely depend on vine water status, which can be manipulated by irrigation strategies and training systems. They suggested that vine performance is more influenced by water availability than by the amount of sunlight intercepted by the vineyard. They reported higher berry anthocyanins concentration with an early deficit irrigation strategy.

IMapple: a source-sink developmental model for ‘Golden Delicious’ apple trees (Fisher et al., 2017)

Functional, structural botanical tree models are one of the most difficult models in biology. IMapple, a model for ‘Golden Delicious’ apple (Malus × domestica) trees based on source-sink descriptions of plant resources. The model uses precise geometrical representations with high-quality polygonal meshes and geometric details. It gives a novel simulation algorithm that provides detailed information about leaf irradiance by simulating direct illumination and self-shadowing. This provides information about incoming
light and energy that is distributed by a source-sink mathematical model.

**Conclusion**

Therefore, considering the positive aspect of manipulation of source-sink relationship, a balance has to be maintained between vegetative and reproductive growth for improvement in yield and quality of fruit crops. It can be achieved by various manipulations in either source or sink strength or the translocation paths. But, care should be taken that manipulations should not lead to drastic yield reductions.

**References**

Aliev, T., Solomakhin, A., Blanke, M., Kunz, A., Klad, A. (2012). Shading as an effective means for crop load management and fruit quality enhancement in apple trees. Acta Horticulturae, 10: 956-963.

Allen, M.T., Prusinkiewicz, P., Dejong, T.M. (2005). Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-Peach model. New Phytologist, 166: 869-880.

Bangerth, F. and Ho, L.C. (1984). Fruit position and fruit set sequence in a truss as factors determining final size of tomato fruits. Annals of Botany, 53: 315-319.

Bangerth, F. (1989). Dominance among fruit sinks and the search for a correlative signal. Physiologia Plantarum, 76: 608-614.

Bohner, J. and Bangerth, F. (1988). Effects of fruit set sequence and defoliation on cell number, cell size and hormone levels of tomato fruits (Lycopersicon esculentum Mill.) within a truss. Plant Growth Regulation, 7: 141-55.

Buwalda, J.G. and Smith, G.S. (1990). Effects of partial defoliation at various stages of the growing season on fruit yields, root growth and return bloom of kiwifruit vines. Scientia Horticulenta, 29: 29-44.

Casierra-Posada, F., Rodriguez, P.J.I., Cardenas, H.J. (2007). Leaf to fruit ratio affects yield, fruit growth and fruit quality of peach (Prunus persica L. Batsch, cv. ‘Rubidoux’). Revista Facultad Nacional de Agronomía Medellin, 60(1): 3657-3669.

Chacko, E.K., Reddy, Y.T.N., Ananthanarayanan, T.V. (1982). Studies on the relationship between leaf number and area and development in mango (Mangifera indica L.). Journal of Horticultural Sciences, 57(4): 483-492.

Clair, M.D., Le, D.I., Bory, G. (1999). Pruning stress: changes in the tree physiology and their effects on the tree health. Acta Horticulenta, 496: 317-324.

J.M. 1995. Crecimiento y desarrollo de las especies frutales. Ed. Mundi-Prensa, Madrid.

Cook, M.G. and Evans, L.T. (1978). Effect of relative size and distance of competing sinks on distribution of photosynthetic assimilates in wheat. Australian Journal of Plant Physiology, 5: 495-509.

Dejong, T., Doyle, J.F., Day, K.R. (1987). Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (Prunus persica) cultivars. Physiologia Plantarum, 71: 83-88.

Dejong, T.M. and Ryugo, K. (1998). Carbohydrate assimilation, translocation and utilization. In: Walnut production manual. UCA NR Publication. University of California, Oakland, CA. p. 109-114.

Di, Vaiu C., Petito, A., Buccheri, M. (2001). Effect of girdling on gas exchanges and leaf mineral content in the ‘Independence’ nectarine. Journal of Plant Nutrition, 24: 1047-1060.

Dussi, M.C. (2007). Interrecepción y distribución luminica en agrosistemas frutícolas. In: Sozzi G. (ed.). Arboles frutales: ecofisiología, cultivo y aprovechamiento. Editorial Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires. p. 200-241.

Fallahi, E. (1997). Applications of endothalic acid, pelargonic acid, and hydrogen cyanamide for blossom thinning in apple and peach. Hortotechnology, 7: 395-399.

Farrar, J.F. (1993). Sink strength: what is it and how do we measure it? Plant, Cell and Environment, 16: 1015.

Faust, M. (1989). Physiology of temperate zones fruit trees. John Wiley and Sons, New York, NY.

Fischer, G., Jose, Almanza-Merchan P., Ramirez, F. (2011). Source-sink relationships in fruit species: A review. Revista Colombiana de Ciencias Horticolas, 6(2): 238-253.

Fischer, G. (2005). Aspectos de la fisiología aplicada de los frutales promisorios en cultivo y poscosecha. Rev. Comalfil, 32(1): 22-34.

Fisher, M., Ravi, J., Benes, B., Shi, B., Hirst, P. (2017). iMappe: a source-sink developmental model for ‘Golden Delicious’ apple trees. Acta Horticulenta, 1160: 51-60.

Friedrich, G. and Fischer, M. (2000). Physiologische Grundlagen des Obstbaues. Ulmer Verlag, Stuttgart, Alemania. p. 95-107.

Garcia-Martinez, J.L. and Beltran, J.P. (1992). Interaction between vegetative and reproductive organs during early fruit development in pea. In: Progress in plant growth regulation, Karssen, C.M., van, Loon L.C., Vreugdenhil, D., eds. Kluwer Academic Publishers, Dordrecht. p. 401-410.

Goffinet, M.C., Robinson, T.L., Lakso, A.N. (1995). A comparison of "Empire" apple fruit size and anatomy in unthinned and hand thinned trees. Journal of Horticulture Sciences, 70: 375-387.

Guardiola, J.L. and Garcia-Luis, A. (1993). Transporte de azucares y otros asimilados. In: Azcon-Bieto, J. and Talon, M. (eds.). Fisiología y bioquímica vegetal. McGraw-Hill Interamericana de España, Madrid. p. 149-171.

Hansen, P. (1978). Blatt/Frucht-Verhaltensze, Assimilatverteilung Fruchtentwicklung. Erwerbsobstbau, 20: 228-231.

Hansen, P. (1982). Assimilation and carbohydrate utilization in apple. In: Proceedings of 21st International Horticulture Congress. 1: 257-268.

Ho, L.C. and Hewitt, J.D. (1986). Fruit development. In: The tomato crop: A scientific basis for improvement; Atherton, J.G., Rudich, J. (eds). p 201-239.

Jackson, J.E. 1980. Light interception and utilization by orchard systems. Horticulture Revolution, 2: 208-267.

Kaur, R. and Dhalviwal, G.S. (2001). Effect of time and pruning intensity of tree canopy volume, girth and height in Sardar guava. Journal of Horticulture Sciences, 30(3-4): 154-156.

Kindo, P. (2005). Studies on various methods of crop regulation in guava (Psidium guajava L.) cv. Pant Prabhat. M.Sc. Thesis. G.
Manipulation of Source-Sink Relationship in Pertinence to Better Fruit Quality and Yield in Fruit Crops: A Review

B. Pant University of Agriculture and Technology, Pantnagar, U. S. Nagar, India. p 84.

Kitajima, A., Akuta, H., Yoshioka, T., Entani, T., Nakano, M., Ishida, T. (1992). Influence of seeded fruit on seedless fruit set in Japanese persimmon cv. Fuyu (Diospyros kaki L.). Journal of the Japanese Society for Horticultural Science, 61: 499-506.

Kubo, T., Hohjo, I., Hirat, S. (2001). Sucrose accumulation and its related enzyme activities in the juice sacs of Satsuma mandarin fruit from trees with different crop loads. Scientia Horticultriae, 91(3-4): 215-225.

Lai, R. (1987). Leaf fruit relationships in kiwifruit (Actinidia delicosa). Ph.D Thesis. Massey University, Palmerston North, New Zealand.

Lakso, A.N. and Flore, J.A. (2003). Carbohydrate partitioning and plant growth. In: Baugher, T.A., Singh, S. Concise encyclopedia of temperate tree fruit. Food Products Press, New York, NY, p 21-30.

Lasa, B., Menendez, S., Sagastizabal, K., Cervantes, M.E.C., Irigoyen, I., Muro, J., Aparicio-Tejo, P.M., Ariz, I. (2012). Foliage application of urea to "Sauvignon Blanc" and "Merlot" vines: doses and time of application. Plant Growth Regulation, 67: 73-81.

Lechaudel, M., Jannoyer, M., Genard, M. (2004). Effects of the leaf fruit ratio on growth and partitioning of water and dry matter in mango fruit. Acta Horticulturae, 645: 429-433.

Lechaudel, M. and Joas, J. (2007). An overview of pre-harvest factors influencing mango fruit growth, quality and postharvest behaviour. Brazilian Journal of Plant Physiology, 19: 287-298.

Marschner, P. (2012). Mineral nutrition of higher plants. 3th ed. Elsevier, Oxford, UK.

Miras-Avalos, Jose, Buesa, Ignacio, Llacer, Elena, Jimenez-Bello, Miguel, Risco, David, Castell Juan, Intrigliolo Diego. (2016). Water versus sink: source relationships in a semiarid tempranillo vineyard: vine performance and fruit composition. American Journal of Enology and Viticulture, 68: 16-26.

Myers, S.C. (2003). Training and pruning principles. In: Baugher, T.A., Singh, S. Concise encyclopedia of temperate tree fruit. Food Products Press, New York. p 339-345.

Park, S.J. (2011). Dry weight and carbohydrate distribution in different tree parts as affected by various fruit-loads of young persimmon and their effect on new growth in the next season. Scientia Horticulturae, 130: 732-736.

Patrick, J.W. (1988). Assimilate partitioning in relation to crop productivity. HortScience, 23: 33-40.

Rajan, S., Tiwari, D., Singh, V.K., Saxena, P., Singh, S., Reddy, Y.T.N., Upreti, K.K., Burondkar, M.M., Bhagwan, A., Kennedy, R. (2011). Application of extended BBCH scale for phenological studies in mango (Mangifera indica L.). Journal of Applied Horticulture, 13: 108-114.

Rajan, S., Kumar, R., Negi, S.S. (2001). Variation in canopy characteristics of mango (Mangifera indica L.) cultivars from diverse eco-geographical regions. Journal of Applied Horticulture. 3(2): 95-97.

Sauer, E. and Baumann, E. (2007). Qualitatsoptimierung durch Entblätterung. In: http://www.lwg.bayern.de/weinbau/berufsausbildung_qualifizierung/18385/ linkurl_0_15_0_1_.pdf; consulted: October 2011.

Schumacher, R. (1989). Die Fruchtbarkeit der Obstgehölze. Ulmer Verlag, Stuttgart, Germany.

Sievanen, R., Nikinmaa, E., Nyygren, P., Ozier-Lafontaine, H., Perttunen, J., Hakula, H. (2000). Components of functional-structural tree models. Annals of Forestry Science, 57: 399-412.

Singh, V., Ravishankar, H., Anurag, Soni M. (2015). Pruning in guava (Psidium guajava) and appraisal of consequent flowering phenology using modified BBCH scale. Indian Journal of Agricultural Sciences, 85: 1472-1476.

Stephenson, A.G., Devlin, B., Horton, J.B. (1988). The effects of seed number and prior fruit dominance on the pattern of fruit production in Cucurbita pepo (Zucchini squash). Annals of Botany, 62: 653-661.

Taiz, L. and Zeiger, E. (2006). Plant Physiology. 4th ed. Sinauer Associates, Sunderland, MA.

Tamas, I.A., Engels, C.J., Kaplan, S.L., Ozbun, J.L., Wallace, D.H. (1981). Role of indole acetic acid and abscisic acid in the correlative control by fruits of axillary bud development and leaf senescence. Plant Physiology, 68: 476-481.

Tamas, I.A, Koch, J.L., Mazur, B.K., Davies, P.J. (1986). Auxin effects on the correlative interaction among fruits in Phaseolus vulgaris L. In: Proceedings, plant growth regulator society of America (PGRSA), Cooke AR, ed. PGRSA, Lake Alfred, FL. p 208-215.

Thimann, K.V. and Skoog, F. (1934). On the inhibition of bud development and other functions of growth substance in Vicia faba. Proceedings of the Royal Society of London B Biological Sciences, 114: 317-339.

Tucker, D. (1978). Apical dominance in the tomato: the possible roles of auxin and abscisic acid. Plant Science Letters, 12: 273-278.

Turner, D.W. (1986). Plant carbon balance. Acta Horticulturae, 175: 109-114.

Wardlaw, I.F. (1990). The control of carbon partitioning in plants. New Phytologist, 116: 341-381.

Wareing, P.F. and Patrick, J. (1975). Source-sink relations in the partitioning of assimilates in the plant. In: Photosynthesis and Productivity in Different Environments (JP Cooper, ed.), p. 481-499. Cambridge University Press, Cambridge.

Warren, Wilson J. (1972). Control of crop processes. In: Rees AR, Cockshull KE, Hand DW, Hurd RG, eds. Crop processes in controlled environments. London: Academic Press. p. 7-30.

Westwood, M.N. (1993). Chemical thinning. In: Temperate zone pomology. 3rd ed. Timber Press, Inc., Portland Ore. p 267-269.

Zufferey, V., Murisier, F., Vivin, P., Belcher, S., Lorenzini, F., Spring, J.L., Viret, O. (2012). Carbohydrate reserves in grapevine (Vitis vinifera L. Chasselas): the influence of the leaf to fruit ratio. Vitis, 51: 103-110.