

## Elucidation of Source - Sink Relationship in Mulberry (*Morus* spp.)

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### ABSTRACT

*Sericulture is essentially an agro-based industry, and it has been practiced for ages, particularly in China and India. However, the industry has taken a back seat due to stiff competition with other agricultural crops. In order to make sericulture more remunerative and withstand this competition, value addition through fruit processing is a viable option. The fruit-bearing cultivars of mulberry can be effectively manipulated to sustain silkworm rearing while being simultaneously used to yield quality mulberry fruit. This will be a key factor in boosting the income of silkworm rearers and will transform sericulture from a household occupation to a vibrant commercial activity, opening a new vista of opportunities to the farmer community. The first step towards achieving this crop diversification is to understand the phenology and interaction between sources and sink in mulberry. By elucidating the flow of assimilates between sources (photosynthetic tissues) and sinks (non-photosynthetic tissues), the present article is an attempt to illuminate how this phenomenon can be harnessed to make sericulture a profitable practice.*

**Keywords:** Mulberry; diversification; phenology; source; sink.

### INTRODUCTION

Mulberry is a fast growing woody perennial plant belonging to the Genus *Morus* and family *Moraceae*. The major species include *M. alba*, *M. indica*, *M. nigra*, *M. rubra*, *M. australis*, *M. atropurpurea*, *M. cathayana*, *M. notabilis* and *M. mesozygia*. Displaying remarkable adaptability, mulberry thrives well in diverse climatic, topographic and soil conditions. It is widely distributed across the tropical, sub-

tropical and temperate zones of Asia, Europe, North and South America (Ozgen et al., 2009).

Mulberry foliage is the only food and primary source of nourishment for silkworms (*Bombyx mori* L.). The intricate relationship between mulberry leaves and silkworms has sustained the silk industry for centuries, producing high-quality silk yarn in the form of cocoons.

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Besides this, a few species of mulberry are also valued for their edible fruit (Vijayan, 2004). In the temperate region of India, the amount of fruits from *M. multicaulis* and *M. nigra* is high per tree (Khan & Singhal, 2006).

Botanically, the mulberry fruit is not a berry but a collective fruit, "sorosis". Recently, the demand for mulberry fruits has been mounting as a healthy natural product because of their delectable taste, dietetic value and constructive biological activities. These fruits harbor a significant repository of biologically active constituents, potentially contributing to various pharmacological activities that promote human well-being. They are known to possess diverse biological activities including anti-diabetic (Ahn et al., 2017 & Choi et al., 2016), anti-hyperlipidemia (Tenda et al., 2021; & Pel et al., 2017), anti-inflammatory (Wang et al., 2016), anti-cancer (Chen et al., 2016 & Eo et al., 2014), neuroprotective (Xu et al., 2020), macrophage activating activity (Kim et al., 2013) and anti-atherogenic (Chen et al., 2005). Beyond their biological activities, fresh mulberry fruits are replete with essential amino acids, vitamin and minerals such as zinc, manganese, iron and calcium, all indispensable for human health. Additionally, mulberry fruits possess significant amounts of pectin and fibrin content (Kumar et al., 2020; & Imran et al., 2010) which are beneficial for human health. The fruit is taken either as such or can also be processed into mulberry juices, paste, jam, pulp or jelly (Maskan & Gogus, 1998) besides their use as natural, economic and ecofriendly coloring and flavoring agents.

### **Phenology of mulberry**

Successful mulberry cultivation necessitates a comprehensive understanding of periodic phenological events, including bud sprouting, leaf flushing, flowering and fruit development, particularly in diverse climatic conditions.

Equally important is the ability to recognize and delineate the distinct phenological stages within a crop species. The term "phenology" signifies the manifestation or appearance of events (Schwartz, 2013) and encompasses the timing of cyclic or recurrent biological events in plants, along with the causes and consequences of that timing (Lieth, 1974). Thus, plant phenology emerges as a complex interplay of biotic factors involving morphological and physiological adaptations in plants (Borchert, 1983), and climatic factors such as photoperiod, temperature, and rainfall (Wright & Schaik, 1994; & Opler et al., 1976). These factors collaboratively influence the optimal timing for growth and reproduction in plant species (Schaik et al., 1993). The Biologische Bundesanstalt, Bundessortenamt, and Chemische Industrie (BBCH) scale have found extensive application in elucidating growth stages of various plants (Hernández et al., 2015; Martínez et al., 2019; Guan et al., 2021; Caranqui-Aldaz et al., 2022; Chu & Chang, 2022; Ferrer-Blanco et al., 2022; & Paradinas et al., 2022), especially in northern latitudes. The extended BBCH scale (Meier, 2001) provides uniform coding of phenologically similar growth stages of all mono- and dicotyledonous plant species, which is extremely useful for studying plant phenological behaviour under different climatic and experimental conditions (Leather, 2010). In general, the BBCH scale employs a two-digit code to define life events within plant species. The initial digit denotes the principal growth stage ranging from 0 to 9 while the second digit signifies secondary life phases. Using this consistent framework, different phenological growth stages of mulberry have been successfully characterized within sub-tropical climatic conditions (as depicted in Table-2).

**Table 2: Eight of the ten principal developmental stages from BBCH scale described for *Morus* spp. under sub-tropical conditions (Sánchez-Salcedo et al., 2017)**

Principal growth stage	Description
0	Bud development
1	Leaf development
3	Shoot development
5	Inflorescence emergence
6	Flowering
7	Fruit development
8	Ripening or maturity of fruit
9	Senescence and beginning of the rest period

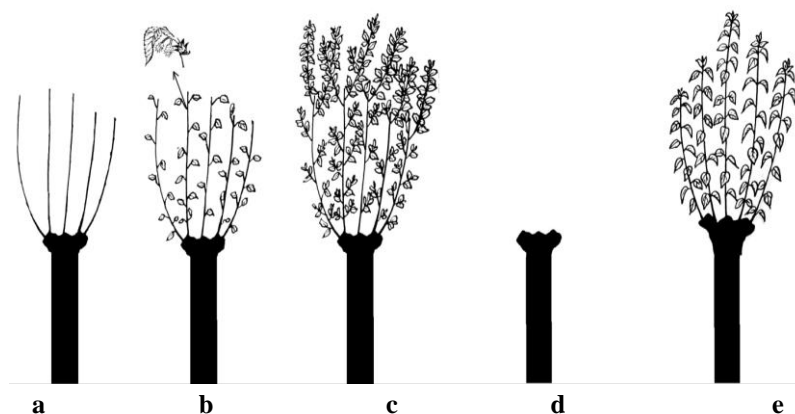
Mulberry tree has typically two phases of its growth- vegetative phase and reproductive phase which overlap under temperate conditions. The phases in case of the shoots developing after the bottom pruning are periodic. Bottom pruning involves cutting all the branches right from the crown base and is done during June every year, coinciding with the 5<sup>th</sup> stage of silkworm rearing when the leaf requirement for silkworm rearing is too high to be collected through individual plucking. A brief description of the two stages is given below:

#### **Vegetative phase of mulberry**

Like any other plant, the mulberry plant must go through sufficient vegetative growth from juvenility to maturity. However, perennial woody plants had significantly longer vegetative growth times than annual plants. Leaf emergence is almost complete in late March and this growth phase is accomplished in 7 months. Late March to early October witnesses' vegetative tremendous growth resulting in two flushes of leaf. The emergence

of reproductive bud development occurs in late March and the first flowers open in spring in early April

The practice of shoot pruning constitutes an integral aspect of advanced sericulture techniques as it stimulates regenerative growth. In temperate conditions, mulberry trees undergo shoot pruning in June coinciding with the 5<sup>th</sup> stage of silkworm rearing. This practice helps in leaf harvesting at reduced labour besides enhancing its keeping quality. The plants yield a fresh second flush of leaf which after 45 days can be used for taking another cocoon crop during late summer/ autumn. Carbohydrate reserves stored in the woody tissues of perennial plants play a vital role in sustainable crop production by contributing to nutrient uptake, assimilation and leaf area development (White et al., 2016). The plant's structural components contribute stored photosynthates to support this regrowth (Tazaki, 1959) subsequently advancing the plant toward senescence.



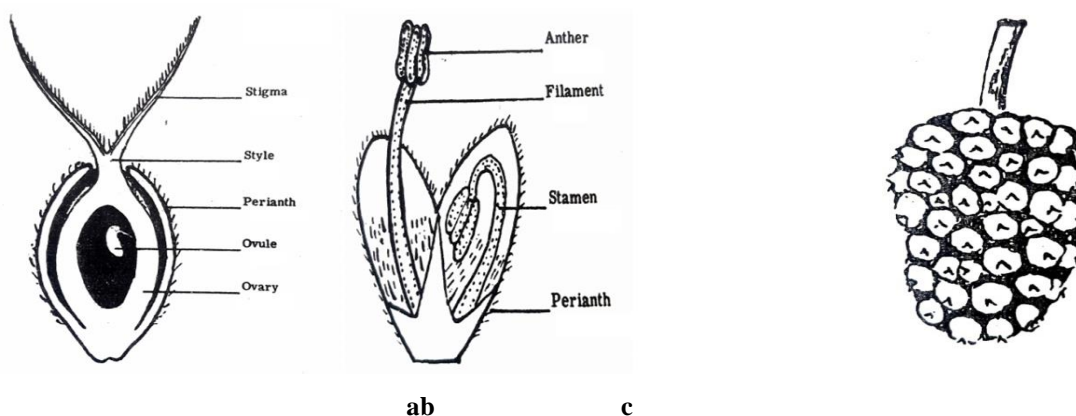
**Figure 1: Scientific management of annual shoot growth stages of mulberry under temperate climatic conditions**

- a : Plant in dormancy
  - b : Sprouting of dormant winter buds
  - c : First flush of mulberry leaves
  - d : Mulberry plant after leaf harvesting/bottom pruning
  - e : Second flush of mulberry leaves after the annual pruning
- Source: (Mir et al., 2024)

**Reproductive phase of mulberry**

The vegetative phase transition is a prerequisite for flowering in angiosperm plants. In temperate conditions, flowering occurs during first fortnight of April. Mulberry

fruits are available during the spring season. From April to early May, fruit growth takes place and fruit maturation completes until early June.



**Figure 2: Structure of reproductive parts of a plant**  
 a: Female reproductive part      b: Male reproductive part  
 c: Mulberry fruit (Sorososis)

**Photosynthetic source and assimilate partitioning**

Leaves in higher plants play a central role in acquiring resources, harnessing the captured light energy through photosynthesis for the reductive assimilation of oxidized forms of carbon and nitrogen into carbohydrates and amino acids (Anuradha et al., 2017). Therefore, photosynthesis stands as a crucial biological process wherein plants capture light energy and convert it into chemical energy

stored within organic compounds. This energy conversion serves as the primary carbon and energy source for plant growth, development and reproduction. The products of carbon assimilation or photosynthesis such as hexoses, sucroses and starch (referred to as fixed carbon) are known as photosynthates, photo assimilates or simply assimilates. These assimilates are generated in the green leaves of higher plants which constitute the source. In simpler terms, a source is a region in which

organic materials are synthesized. The assimilates are then either metabolically utilized, stored or transformed into transport sugars, primarily sucrose, for export to various parts of the plant like young leaves, roots, tubers, stems, fruits and seeds, which collectively form the sink. Thus, any organ that is not involved in photosynthesis or does not generate sufficient photosynthates to fulfill its own requirements is referred to as a sink.

The interactions between organs responsible for assimilating production and those involved in assimilate consumption plays a crucial role in the targeted movement and distribution of photosynthates within plants (Chanishvil et al., 2005). The assimilates received by the sink are subsequently metabolically utilized and/or stored within the recipient cells of the sink. The differential distribution of these assimilates among different sinks is determined by their nature and specific needs. Within this framework of resource allocation, sucrose takes on a pivotal role as the primary metabolite as it is the major end product of photosynthetic carbon metabolism. This systematic distribution of photosynthates is commonly known as “assimilate partitioning”. The distribution of photo assimilates plays a crucial role in the agricultural physiology of crops influencing overall productivity (Ravishankar, 2014). Usually, the assimilates transported to harvest organs is much more than other organs.

Translocation of organic solutes such as sucrose occurs through the sieve tube elements of the phloem from supply end (source) to consumption end (sink). Before translocation can begin, however, photo assimilates must first be transferred from mesophyll cells to the sieve tube elements of the corresponding leaves. This movement of sugars from mesophyll cells to sieve tube elements is referred to as phloem loading. Conversely, the transfer of sugars from sieve tube elements to the recipient cells of the consumption end (sink) is known as phloem unloading. Phloem loading is a specific and selective process for transport sugars. Phloem unloading, on the

other hand, occurs in the sink tissue (consumption end). It involves the departure of sugars from the sieve elements of the sink tissue, followed by short-distance transport to cells within the sink tissue, referred to as post-sieve element transport. It is important to highlight that the direction and quantity of transportation are dependent upon the location of sink and relative attraction strength. Notably, around 90 percent of solute molecules in the sap are carbohydrates which move at a velocity of approximately 50-100 cm/h (Friedrich & Fischer, 2000).

### **Source-sink interactions and its manipulations in Horticultural trees**

Source-sink relationship refers to the integration of sugar and amino acid production in photosynthesis with sugar and amino acid utilization in growth, storage, maintenance and production (Foyer & Paul, 2001). Carbohydrate partitioning within a tree is not a genetically programmed process, but a result of the unique combination of competing organs and their relative abilities to compete for limited carbohydrates (Lakso & Flore, 2003). A sink hierarchy exists among organs or tissues of perennial species, and the priority rank ordering from high to low can be summarized as seeds > fleshy fruit part > shoot apices > mature leaves > cambium > roots > storage (Lauri et al., 2010). However, the source (supply of photosynthates) - sink (utilization of photosynthates) limitations are strongly affected by interactions between genotype and environment (Marschner, 2012). However, dominance or correlative phenomena are widespread in the plant kingdom (Goodwin et al., 1978) and are particularly common among fruits and between fruits and vegetative sinks. In species and cultivars with an indeterminate growth habit in which the vegetative phase overlaps with the reproductive phase, balance their supply to both sink types (vegetative and reproductive) (Fischer, 2005), there is maintenance of a balance between vegetative and generative growth of a tree is of great importance for growth and production of fruit species (Park, 2011).

In horticultural trees, fruits demand large quantities of photosynthates and the growth of branches and the root system decrease as the fruit load increases (Lakso & Flore, 2003). In young olive trees, almost a 1:1 trade-off between annual production of biomass in reproductive tissue and vegetative growth has been reported whereby it was indicated that as the fruit production increased, vegetative growth reduces proportionately (Rosati et al., 2018). Fruit-growing trees build more dry matter per unit leaf area than plants without fruit. The seasonal changes in photosynthesis of apple trees (*Malus domestica*) indicate that the first period of increased photosynthetic rates is during the bloom period, when the spur leaves exhibit up to 25 per cent higher photosynthetic rates than vegetative spur leaves on a leaf area basis (Fujii & Kennedy, 1985). In comparison to the fruit bearing trees, the non-fruiting ones develop much more foliage *i.e.*, leaf area per tree (Lenz, 2009). Another research indicated that fruitless strawberries produced 61.1 per cent assimilates in leaves, but there was only 39.2 per cent and 21.1 per cent of assimilates respectively in plants with 6 and 12 fruit (Friedrich & Fischer, 2000). Studies suggest that fruit load adjustment improves fruit quality in the same year and ensures the accumulation of reserves which can positively influence tree development during the subsequent years (George et al., 1995). Further, artificial removal of fruits increase leaf number and total plant photosynthesis as compared to plants with unrestricted fruit load as reported in Charentais melons (Valantin et al., 1998). Cai et al. (2021) reported that source-sink manipulations differentially affect carbon and nitrogen dynamics, fruit metabolites and yield of SachaInchi plants. Leaf photosynthetic rate and specific leaf area largely remained unchanged in response to defoliation or defloration. However, compared with control, higher nitrogen contents were recorded in both remaining leaves and branches of the defoliated plants which indicates that N-mobilization was mainly due to the enhanced N-uptake from soil.

### **Source-Sink interaction in Mulberry and Future line of work**

The concept of the source-sink relationship is a fundamental cornerstone of plant physiology governing the allocation and transport of photosynthates among various plant organs. Mulberry, a highly promising woody plant of both economic and ecological significance, exhibits intricate phenology and source-sink interactions. Understanding the nuanced mechanisms of source-sink dynamics holds profound importance in elucidating the growth, yield and quality of both leaves and fruits. The processes of plant growth and reproduction entail substantial consumption of carbohydrates and nitrogen which primarily originate from photosynthate and nitrogen absorption from soils respectively and/or internal reserve remobilization (Millard & Grelet, 2010). Carbon and nitrogen sourced from the plant's source tissues serve as substrates for diverse sink metabolic activities encompassing sink formation, development and maintenance. During vegetative growth, the principal sinks are the root and shoot apices, while during the reproductive phase, fruits typically become the dominant sinks, particularly for neighboring and adjacent leaves (Taiz & Zeiger, 2006).

The leaf serves as the primary site for photosynthesis, which in turn serves as the bedrock for plant growth and productivity (Chen et al., 2020). This process forms the foundation for biological yield (Sinclair et al., 2019). In the case of mulberry, the maximum photosynthesis rate is achieved around 20 days after the leaf unfolding, followed by a subsequent decline. During the rapid growth season, mature leaves can attain an impressive photosynthesis rate of up to 40 mg CO<sub>2</sub>/100cm<sup>2</sup>/h (Sekhar et al., 2014, 2015). The rate of photosynthesis, together with factors like cumulative shoot length, leaf area and stem yield, collectively contribute to leaf yield (Singhvi et al., 2002). However, the fruit-bearing stage is relatively brief. A significant influence of annual pruning on the economic yield of high-quality mulberry fruits has been marked (Gangwar & Rai, 1997). For any plant

species, while the timing of pruning primarily affects the fruit ripening period (Morgani et al., 2023), the severity of pruning directly impacts the qualitative and quantitative attributes of the fruit.

A comprehensive grasp of physiological attributes, growth patterns and reproductive traits in response to source-sink dynamics is a pivotal stride forward. The following questions need to be raised:

- Within the plant system, which component of source and sink along with their associated physiological mechanisms, exerts a more pronounced influence on plant growth and/or fruit development
- What metabolic adaptations do occur in fruitlets in response to adjustments in source or sink activity?
- How do variations in sericulture practices influence the demand for specific qualities of mulberry leaves and how can this be integrated into optimizing fruit and leaf production?
- Does defoliation really lead to a reduction in plant growth accompanied by a depletion of plant reserves?
- How does the nutrient availability in the soil affect the growth, fruit quality and overall health of mulberry trees and how can this knowledge be applied to optimize sericulture practices?
- What role do plant hormones play in regulating the balance between vegetative growth and reproductive processes in mulberry trees?
- What is the potential economic impact of maximizing the utilization of both fruit and leaf from mulberry trees and how can this contribute to rural livelihoods and diversification?

### CONCLUSION

Mulberry trees are principally utilized for silk production since mulberry foliage is the primary food for silkworm (*Bombyx mori* L.). However, certain species of mulberry are also valued for their edible fruit. Photosynthesis, a vital process that generates energy and carbon for plant growth and development, holds

paramount importance. Yet the correlation between reproductive processes and vegetative growth in mulberry has not been explored fully. The greater interaction between sericulture and tree physiology would be fruitful for exploiting the diversification potential of fruit bearing mulberry genotypes with sufficient fruit load and optimum quality leaf to sustain silkworm rearing to make sericulture more remunerative. The insights provided in this manuscript contribute to a deeper understanding of the intricate processes underlying photosynthetic source and assimilate production.

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### Conflict of Interest

The authors declare no conflict of interest in the publication of this manuscript. All the authors read and approved the manuscript in its final form.

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**Authors' contributions:** This work was carried out in collaboration among all authors. Author ARR and OBA conceptualized the idea and wrote the manuscript. Author MRM and ILK supervised and reviewed the manuscript. Author OAH edited the manuscript. All authors read and approved the final manuscript.

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