Jurnal Kultivasi Vol. 24(3) December 2025
ISSN: 1412-4718, eISSN: 2581-138x

Rahma SA · Budiarto R · Mubarok S

Analysis of source–sink organ dynamics in kaffir lime (*Citrus hystrix* DC.) at different plant ages

Abstract. Kaffir lime (*Citrus hystrix* DC.) is a leafy spice commodity widely used as a culinary ingredient, in bio-pharmaceuticals, and as a raw material for essential oil production. Despite its high demand, leaf productivity remains relatively low, highlighting the need for improved cultivation practices. A better understanding of source–sink dynamics is essential, as leaf production is strongly influenced by the balance between assimilate-producing and assimilate-consuming organs. Therefore, this study aimed to evaluate the source-sink capacity of kaffir lime plants of different ages as a preliminary step toward identifying cultivation strategies to enhance leaf production. The experiment was conducted at Bale Tatanen experimental field, Universitas Padjadjaran, Sumedang. This work used a randomized complete block design with five replications and three age treatments: A = 1 year, B = 2 years, and C = 3 years. The results showed the source-to-sink ratio in 1-, 2-, and 3-year-old plants were 53:47, 50:50, and 48:52, respectively. As kaffir lime plants grow older, their source–sink balance shifts because older plants allocate assimilates more efficiently to developing organs. In this study, increasing plant age was associated with a greater capacity to develop sink organs, which in turn supports leaf expansion and overall leaf productivity. This study offers baseline information on the source–sink proportions of kaffir lime plants at different ages, providing a foundation for improving cultivation practices. The findings support better harvest timing and more accurate yield estimation to enhance planning efficiency.

Keywords: Citrus · Roots · Shoots · Source-capacity · Sink-capacity

Submitted: 28 August 2025, Accepted: 15 December 2025, Published: 31 December 2025
DOI: https://doi.org/10.24198/kultivasi.v24i3.66455

Rahma SA[1] · Budiarto R[2]* · Mubarok S[2]
[1] Graduate student in Master of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang Km. 21, Jatinangor, Sumedang 45363, Indonesia
[2] Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang Km. 21, Jatinangor, Sumedang 45363, Indonesia
*Correspondence: rahmat.budiarto@unpad.ac.id

Rahma SA, Budiarto R, Mubarok S. 2025. Analysis of source–sink organ dynamics in kaffir lime (*Citrus hystrix* DC.) at different plant ages. Jurnal Kultivasi, 24(3): 298-308.

Introduction

Kaffir lime (*Citrus hystrix* DC.) is a high-value horticultural commodity, primarily due to its leaves, which serve as a key ingredient in culinary preparations and as a raw material in the food, beverage, and cosmetics industries (Budiarto et al., 2024). The increasing demand for both fresh and dried kaffir lime leaves, driven by the growth of the culinary and herbal industries (Abidin et al., 2020), underscores the need for cultivation strategies that sustainably optimize leaf production.

As a perennial species, the growth and leaf yield of kaffir lime are strongly influenced by the balance between the source system (photosynthate-producing organs such as mature leaves) and the sink system (photosynthate-utilizing organs such as shoots and young leaves) (Goldschmidt & Koch, 2017; Li et al., 2024). Variations in plant age and size can lead to differences in source capacity and sink strength (Sunmonu & Kudo, 2014) , thereby shaping vegetative growth patterns (Smith et al., 2018). A comprehensive understanding of source–sink dynamics is therefore essential as a foundation for developing targeted cultivation strategies, particularly those aimed at manipulating plant physiological processes to maximize leaf production.

The source–sink relationship plays a crucial role in determining plant growth and productivity, as it governs the allocation of photosynthates between producing organs (sources, e.g., mature leaves) and utilizing organs (*sinks*, e.g., shoots, young leaves, stems, and roots) (Amarullah, 2021). Managing this allocation effectively is key to sustaining vegetative growth and optimizing productivity (White et al., 2016; Yu et al., 2015). In perennial crops such as kaffir lime (*Citrus hystrix* DC.), insights into these physiological processes provide a foundation for designing cultivation practices that enhance leaf production (Li et al., 2024; Budiarto et al, 2023).

Plant age strongly influences source and sink capacities. Younger plants typically exhibit higher sink demand due to rapid vegetative development, whereas older plants tend to have greater source capacity from mature leaves, often exceeding sink requirements (Chen et al., 2021). In leaf-oriented cultivation systems, strategies such as close planting spacing can suppress reproductive development and promote continuous leaf production (Haque & Sakimin, 2022).

This study investigates source and sink capacities in 1-, 2-, and 3-year-old kaffir lime plants under a close-planting system designed to maintain vegetative growth. The analysis focuses on vegetative sinks (young leaves, young stems, and roots) while excluding reproductive organs, aiming to clarify age-related differences in photosynthate allocation patterns and their implications for sustainable leaf yield optimization.

Materials and Methods

This research was conducted at the open field of Bale Tatanen garden, Universitas Padjadjaran, Jatinangor District, Sumedang Regency, West Java Province. Present experiment used kaffir lime (*Citrus hystrix* DC. cv. Puri Agrihorti) seedling as plant materials. The plant materials were produced through vegetative method, i.e., grafting, combining kaffir lime scion into Rangpur lime (*Citrus limonia* Osbeck) rootstock, produced by local seedling producer in Majalengka. There were three tested-plant age in present experiment, i.e., 1, 2, and 3 years after grafting. All plant were raised in Inceptisol soil growing bed supplemented with goat manure.

The relationship between source and sink in kaffir lime plants of different ages was analyzed through destructive sampling. Classification of plant organs into source or sink categories was conducted using a morphometric approach. The experimental design employed was a Randomized Block Design (RBD) consisting of 3 treatments with 5 replications. The treatments were based on plant age, 1-, 2-, and 3-years-old kaffir lime plants. Observations were carried out by measuring and weighing plant components according to the defined parameters. All measurements were performed on the same day as the destructive sampling to ensure that the plant materials remained fresh.

The observation parameters consisted of plant height (cm), leaf length (cm), number of young and mature leaves, fresh weight of young and mature leaves (g), fresh weight of young and mature stems (g), fresh weight of shoots and roots (g), dry weight of shoots and roots (g), and source-sink capacity. Young leaves—characterized by pale light-green color, thin and soft texture, glossy surface, and small size

(Budiarto et al., 2022)—were classified as sink organs, whereas mature leaves—dark-green, thicker and firmer in texture, with a rough or dull surface and fully expanded size (Budiarto et al., 2022)—were classified as source organs. Young stems—identified by their bright green color, smooth surface, soft and flexible texture, and small diameter—were classified as sink organs, whereas mature stems—brownish green to dark brown in color indicating lignification, with a rough, hard, and rigid texture and larger diameter—were classified as source organs.

Data Analysis. Data were analyzed using analysis of variance (ANOVA) based on a randomized complete block design (RCBD) at a 5% significance level, followed by Tukey's Honestly Significant Difference (HSD) test (5%) for post hoc comparisons.

Result and Discussion

Plant height and leaf length. According to the results (Table 1), plant height exhibited a gradual increase with advancing plant age. This increment in height indicates the cumulative effect of progressive and continuous vegetative growth, which is strongly associated with the dynamic balance between source capacity and sink demand within the plant. As plants age, photosynthetic organs such as leaves expand in size and increase in number, thereby enhancing the source capacity of the plant to produce assimilates through photosynthesis (Leng et al., 2025). On the other hand, young organs such as apical meristems, roots, and lateral branches that function as sinks also develop more actively in older plants (Cheng et al., 2022), thus increasing the demand for assimilates and supporting overall plant growth (Doidy et al., 2024).

A balanced relationship between source capacity and sink demand is crucial to ensure efficient carbon distribution, particularly to meristematic tissues that determine plant height (Amarullah, 2021). In addition, older plants tend to have a more developed vascular system (xylem and phloem) (Swidrak et al., 2014; Yang & Wang, 2016). This allows for greater efficiency in the transport of water, nutrients, and photosynthates, thereby supporting a higher growth rate (Vadera et al., 2025).

Leaf length serves as a key indicator of morphological growth and biomass accumulation in kaffir lime. Longer leaves are closely associated with greater surface area, which enhances light absorption and photosynthetic capacity (Telaumbanua et al., 2024). As plants age, leaf development becomes more optimal in both number and size, thereby increasing carbon productivity and assimilate supply (Poorter et al., 2015; Weraduwage et al., 2015). This improvement is supported by a more developed vascular system that facilitates efficient distribution of water and nutrients, promoting cell expansion and leaf elongation (Yang & Wang, 2016).

Table 1. Plant height and leaf length of kaffir lime at different ages

Treatment	Plant height (cm)	Leaf length (cm)
A: 1 year old	68.00 a	4.58 a
B: 2 years old	93.80 b	6.70 b
C: 3 years old	187.80 c	8.64 c

Note: Mean values followed by the same letter in the same column are not significantly different according to Tukey's HSD test at the 0.05 significance level.

Within the source–sink framework, longer leaves contribute significantly to source capacity due to their higher photosynthetic potential (Nuranisa et al., 2020). In three-year-old kaffir lime plants, the presence of longer leaves suggests enhanced assimilate production to sustain the growth of sink organs such as young leaves, stems, roots, and shoots (Lambers et al., 2019). This reflects a transition toward greater physiological stability, allowing more efficient assimilate production and allocation (Chang & Zu, 2017).

Number and weight of young and mature leaves. An increase in leaf number directly influences the source–sink relationship in kaffir lime. Mature leaves serve as the primary source by producing assimilates through photosynthesis, while young leaves act as sinks due to their active growth and limited photosynthetic ability (Zhang et al., 2023). With advancing plant age, the rise in mature leaf number significantly enhances source capacity (Table 2), thereby providing sufficient energy and carbon to sustain the growth of sink organs such as young leaves, shoots, and meristematic tissues (Bielczynski et al., 2017; Durand et al., 2018). The coexistence of more mature and young leaves in older plants indicates a more efficient and balanced source–sink system (White et al., 2016).

A higher sink capacity, reflected in the increased number of young leaves, creates strong demand for assimilates, which physiologically stimulates metabolic activity in source organs (Fernie et al., 2020). The abundance of mature leaves also contributes to an eltevated overall photosynthetic rate, ensuring a continuous assimilate supply to support vegetative growth and leaf regeneration (Wu et al., 2018). As a result, older kaffir lime plants tend to accumulate greater biomass and exhibit faster canopy development (Sunmonu & Kudo, 2014).

The increase in leaf biomass not only reflects the quantitative rise in leaf number but also indicates an enhanced physiological capacity of the plant to produce, store, and distribute photosynthates more efficiently (Weraduwage et al., 2015). This is closely related to the concept of source–sink dynamics, in which mature leaves, functioning as the primary photosynthetic organs, act as sources, while young leaves undergoing cell expansion and tissue development act as active sinks (Yu et al., 2015; Jansson et al., 2015; Koley et al., 2019).

The increase in mature leaf biomass signifies an expansion of active surface area for photosynthesis, which directly enhances the plant's capacity to produce soluble carbohydrates such as sucrose and glucose through carbon fixation (Liu et al., 2022). In older plants, particularly at three years of age, the accumulation of biomass in mature leaves indicates that the plant has reached a vegetative phase with a more developed phloem transport system, enabling efficient translocation of photosynthates from sources to sink tissues (Milne et al., 2015; Nam et al., 2022). This activity is critical, as young leaves, functioning as sinks, not only require energy for cell expansion but also for the construction of internal structures such as chloroplasts and incompletely developed vascular tissues (Van Campen, 2016).

In young plants, source limitation leads to higher competition among sink organs, thereby slowing leaf growth (White et al., 2016). Conversely, older plants exhibit a more stable source–sink ratio, allowing a more proportional allocation of photosynthates to support extensive sink growth (Burnett et al., 2016), such as the sharp increase in the number and weight of young leaves. This condition demonstrates that enhanced source capacity accelerates sink expansion, while stronger sink growth also stimulates greater source activity (Fatichi et al., 2014). Moreover, the increase in young leaf biomass in three-year-old plants indicates greater potential for continued growth (Table 2). Active sinks such as young leaves will remain a primary target for carbon allocation, facilitating the formation of a larger canopy (Fatichi et al., 2019). This is particularly important in kaffir lime, where canopy development is directly correlated with the productivity of vegetative organs (Feng et al., 2016).

Young and mature stems weight. A greater biomass of young stems in older plants indicates that meristematic growth activity remains high in the stem, which functions as part of the active sink system (Rademacher et al., 2022). Young stems continue to grow through cell division and elongation, thus requiring large amounts of carbon and energy supplied by source tissues, particularly mature leaves (Czedik-Eysenberg et al., 2016; Kocurek et al., 2020). Meanwhile, mature stems that have undergone lignification and secondary tissue formation serve as supporting and more efficient conducting organs (Asaoka et al., 2024). The significant increase in mature stem biomass in three-year-old plants (Table 3) demonstrates that cambial thickening is actively taking place, contributing substantially to the accumulation of vegetative organ mass (Guada et al., 2018).

Table 2. Number and weight of young and mature leaves of kaffir lime at different ages

Treatment	Number of young leaves	Number of mature leaves	Young leaves weight (g)	Mature leaves weight (g)
A: 1 year old	49.00 a	86.00 a	17.00 a	33.00 a
B: 2 years old	64.00 a	180.40 a	21.00 a	87.00 a
C: 3 years old	319.60 b	574.00 b	144.00 b	263.00 b

Note: Mean values followed by the same letter in the same column are not significantly different according to Tukey's HSD test at the 0.05 significance level.

ISSN: 1412-4718, eISSN: 2581-138x

Table 3. Young and mature stems weight of kaffir lime at different ages

Treatment	Young stems weight (g)	Mature stems weight (g)
A: 1 year old	38.14 a	57.21 a
B: 2 years old	86.40 a	129.60 a
C: 3 years old	306.00 b	459.00 b

Note: Mean values followed by the same letter in the same column are not significantly different according to Tukey's HSD test at the 0.05 significance level.

Table 4. Fresh and dry weight of shoots and roots of kaffir lime at different ages

Treatment	Shoots fresh weight (g)	Roots fresh weight (g)	Shoots dry weight (g)	Roots dry weight (g)
A: 1 year old	149.36 a	24.64 a	44.81 a	7.39 a
B: 2 years old	320.00 a	109.00 a	96.00 a	32.70 a
C: 3 years old	1,172.00 b	332.00 b	351.60 b	99.60 b

Note: Mean values followed by the same letter in the same column are not significantly different according to Tukey's HSD test at the 0.05 significance level.

The relationship between stem biomass and the source–sink system can also be understood from the perspective of long-term carbon allocation. In older plants, carbon distribution is not only directed toward young organs but also allocated to permanent tissues such as mature stems (Hartmann et al., 2018). Mature stems play a role in storing energy reserves in the form of starch and in maintaining the integrity of the vascular system (Plavcova & Jansen, 2015). Therefore, greater biomass of mature stems can be considered an indicator of long-term carbon allocation efficiency (Hartmann et al., 2018), whereas young stem biomass reflects the ongoing potential for vertical and lateral growth (Speck & Burgert, 2011). The coexistence of both young and mature stems with significant biomass in three-year-old plants illustrates a balance between active growth and the differentiation of functionally mature tissues.

Fresh and dry weight of shoots and roots. The shoot system, comprising leaves, stems, and branches, is the center of source activity where photosynthesis and assimilate production occur. The greater the shoot biomass, the larger the photosynthetic surface area of the plant (Chen et al., 2020; Zhang et al., 2020), thereby increasing carbon production capacity through CO_2 fixation (Dhami & Cazzonelli, 2021). Table 4 showed that three-year-old plants have the highest shoot dry weight (Table 4), implying that the tissues formed are more structural and durable, such as lignin and sclerenchyma, which are essential for supporting continued growth and facilitating assimilate transport to sink organs (Putra et al., 2023).

Conversely, roots function as active sinks that require carbon supply from sources for growth, elongation, and lateral root formation (Waheed et al., 2025). The sharp increase in root biomass at three years of age suggests extensive root system development to support greater water and nutrient demands (Carvalho & Foulkes, 2019). The balance between shoot and root biomass reflects that the plant has achieved an optimal shoot–root ratio (Punyasu et al., 2024). This ratio is important because roots are not only passive sinks but also long-term carbon storage sites in the form of starch (Irving, 2015), and they influence stability and efficiency of nutrient uptake from the soil (Lopez et al., 2023).

The increase in both shoot and root biomass indicates synchronization between production (source) activity and the distribution and utilization of photosynthetic products (sink). In young plants, source capacity remains limited, leading to lower root dry weight as sinks. However, in three-year-old plants, the more developed vascular and hormonal systems enable more efficient communication between organs (Savage et al., 2016), thus allowing assimilate allocation to be more effective in generating large and balanced biomass growth (Wang & Ruan, 2016).

In addition, the increase in dry weight compared to fresh weight reflects greater tissue density and structural compounds (cellulose and lignin) accumulation (Afzal et al., 2022). This indicates that the plant has reached an advanced vegetative phase and physiological stability. Plants in this condition have stronger adaptability to environmental stresses, supported by a well-developed root system and a broad canopy that sustain photosynthesis and transpiration (Koevoets et al., 2016).

Source-sink capacity. The results indicated that plant age influenced the distribution of source and sink capacities. Mature leaves and mature stems were classified as source organs, whereas young leaves, young stems, and roots represented sink organs. The relative contribution of each organ changed progressively with increasing plant age. The 1-year-old plant display a total source capacity for about 53%, while the sink capacity was 47% (Figure 1). The dominance of source capacity indicates that the plants were still in the early growth phase, focusing on the development of photosynthetic tissues (Körner, 2015). The proportion of source and sink capacities became balanced in 2-year-old plants, each accounting for 50% (Figure 2). This indicates that the plant's metabolic system began to stabilize, with an increased distribution of photosynthates toward actively growing sink organs, particularly the roots, which showed a significant increase from 15% to 25%. The decrease in the proportion of young leaves from 10% to 5% suggests that most leaves had matured and functionally served as source organs. Later on, sink capacity increased to 52% in 3-year-old plants, while source capacity decreased to 48% (Figure 3). This indicates that the plants had entered an active vegetative growth phase with a higher demand for photosynthates to support the development of new tissues such as young stems and roots (Burnett, 2019). Roots remained the dominant sink organs, followed by young stems and young leaves. The relative proportion of mature leaves declined, not because their number decreased, but due to the increasing activity and demand of sink organs (Brant & Chen, 2015).

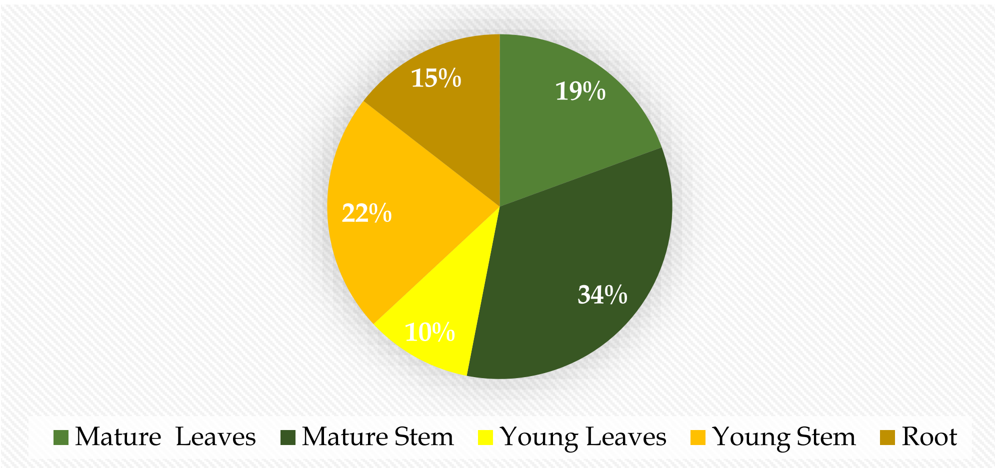

Figure 1. Source and sink capacity diagram for 1-year-old kaffir lime plants

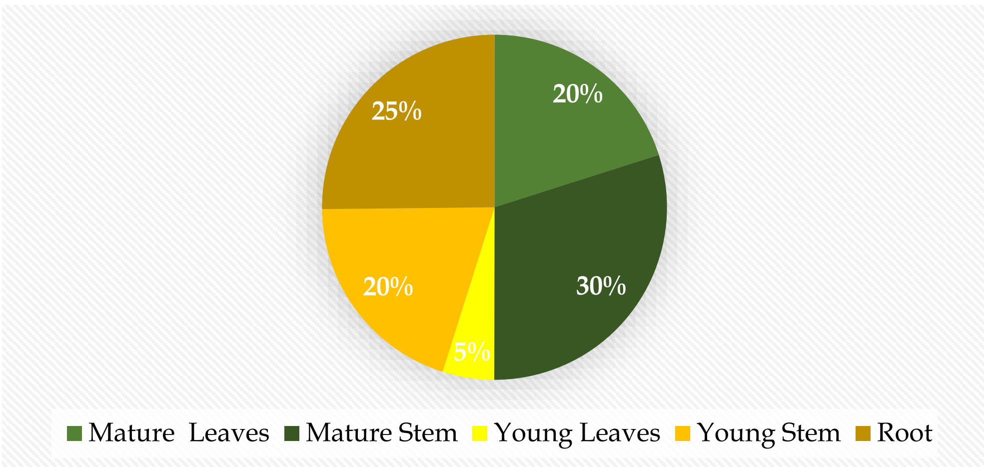

Figure 2. Source and sink capacity diagram for 2-year-old kaffir lime plants

Jurnal Kultivasi Vol. 24(3) December 2025
ISSN: 1412-4718, eISSN: 2581-138x

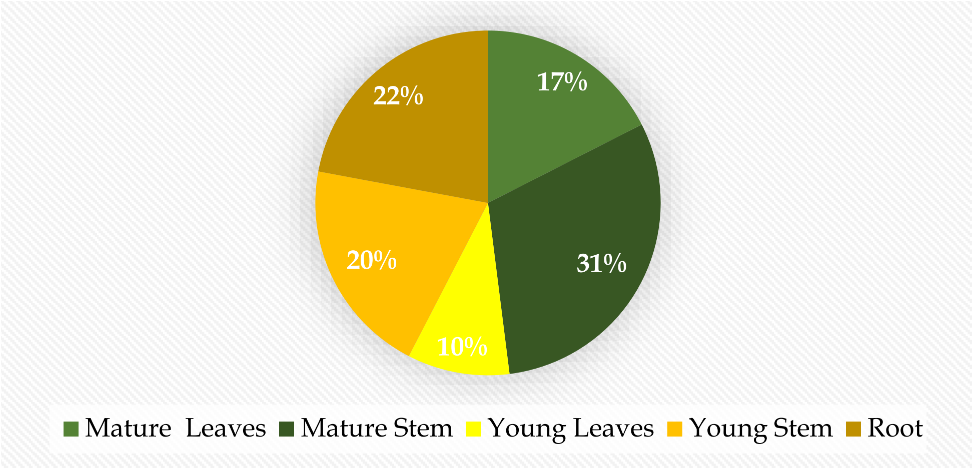

Figure 3. Source and sink capacity diagram for 3-year-old kaffir lime plants

In young plants, growth is constrained by source capacity because developing shoots have relatively low photosynthetic ability compared to the energy required for growth (Trugman & Anderegg, 2024). Conversely, in older plants, growth is more often limited by sink capacity, as growth rates slow while photosynthetic activity remains high (Burnett et al., 2018; Campany et al., 2017). The transition from source-limited to sink-limited growth typically occurs as plants begin entering the reproductive phase, when metabolism shifts toward seed or fruit production (Lv et al., 2020; White et al., 2016). This shift aligns with plant physiology theory, which states that with increasing age, sink capacity rises due to the enlargement, increased number, and complexity of source organs (Burnett, 2019). Young organs and roots continue to grow as major consumers of photosynthates, thereby influencing assimilate distribution patterns within the plant (Anuradha et al., 2017).

Plant age showed a positive correlation with the increasing number of mature leaves, which serve as the primary organs of photosynthesis. Mature leaves have greater photosynthetic capacity compared to young leaves (Budiarto et al., 2022) because their anatomical structure and chlorophyll content are more fully developed (Wu et al., 2018). As the number of mature leaves increases, overall photosynthetic capacity also rises, producing more assimilates available for distribution to various plant organs. This enhanced photosynthetic capacity directly contributes to increased sink capacity, as sink organs such as shoots, roots, and buds gain greater access to photosynthates (Pawar & Rana, 2019; Singh et al., 2017). Thus, plant aging not only strengthens the source system through a higher number of mature leaves but also enhances the efficiency and capacity of sink organs, which are critical for supporting plant growth and productivity (Sonnewald & Fernie, 2018).

Older plants also exhibit a greater ability to store carbon in permanent structures such as stems, branches, and roots (Plavcová et al., 2016). This activity can be categorized as carbon trading, a process of capturing and storing carbon from the atmosphere into plant biomass (Nath et al., 2015; Shen et al., 2020). This process holds important ecological value as it helps reduce atmospheric carbon dioxide (CO_2) concentrations (Kukah et al., 2024) and highlights the role of aging plants in climate change mitigation through enhanced carbon storage capacity (Nunes et al., 2020).

Overall, the combined increase in mature leaf biomass, stem thickening, and root development with plant age reflects a coordinated shift in source–sink balance. Older plants accumulate greater source capacity through expanded mature leaf area, while simultaneously supporting stronger sink activity in developing shoots and roots. This integrated response demonstrates that the progression of plant age does not enhance individual organs in isolation but reshapes the entire assimilate allocation system, ultimately strengthening both the source and sink components of kaffir lime's growth physiology.

ISSN: 1412-4718, eISSN: 2581-138x

Conclusion

The study demonstrates that plant age significantly influences the source–sink dynamics in kaffir lime. As the age of the kaffir lime plant increases, the plant's ability to form sink organs also increases. Younger plants tend to be source-dominated, relying on limited photosynthetic tissues to support growth, while older plants show a gradual increase in sink capacity through the development of young leaves, stems, and roots. By the third year, sink demand exceeds source supply, reflecting active vegetative growth and greater assimilate allocation to developing organs. These findings highlight the importance of managing age-related source–sink balance as a foundation for optimizing cultivation practices aimed at maximizing leaf production in kaffir lime.

Acknowledgment

The authors express their gratitude to Ministry of Research, Technology, and Higher Education, Republic of Indonesia, for providing support and finding through the grant of Master Thesis Research fiscal year 2025 number 093/C3/DT.05.00/PL/2025, sub number 1636/UN6.3.1/PT.00/2025.

References

Abidin MRZ, Ishak FAC, Ismail IA, Juhari NH. 2020. Issues and Challenges of Malaysian Local Herbs toward the Development of Local Herbs-Based Culinary Products. Food Studies, 10(3): 13–30. https://doi.org/10.18848/2160-1933/CGP/v10i03/13-30

Afzal RA, Pennells J, Yamauchi Y, Annamalai PK, Nanjundan AK, Martin DJ. 2022. Lignocellulosic plant cell wall variation influences the structure and properties of hard carbon derived from sorghum biomass. Carbon Trends, 7(1): 1–12.

Amarullah. 2021. Sink source relationship dalam tanaman. Banda Aceh: Syiah Kuala University Press.

Anuradha, Goyal R, Bishnoi C. 2017. Assimilate partitioning and distribution in fruit crops: A review. Journal of Pharmacognosy and Phytochemistry, 6(3): 479–484.

Asaoka M, Badel E, Ferjani A, Nishitani K, Hamant O. 2024. Contributions of lignification, tissue arrangement patterns, and cross-sectional area to whole-stem mechanical properties in Arabidopsis thaliana. Journal of Plant Research, 137(5): 773–783.

Bielczynski LW, Łaçki MK, Hoefnagels I, Gambin A, Croce R. 2017. Leaf and plant age affects photosynthetic performance and photoprotective capacity. Plant Physiology, 175(4): 1634–1648.

Brant AN, Chen HYH. 2015. Patterns and mechanisms of nutrient resorption in plants. Critical Reviews in Plant Sciences, 34(5): 471–486.

Budiarto R, Mubarok S, Nanda MA, Nabiyyu M, Haris M, Jaya IS. 2023. The increase in kaffir lime leaf production due to gibberellin is diminished by pruning. Horticulturae, 9(9):1018.

Budiarto R, Poerwanto R, Santosa E, Efendi D, Agusta A. 2022. Comparative and correlation analysis of young and mature kaffir lime (Citrus hystrix DC) leaf characteristics. International Journal of Plant Biology, 13(3): 270–280.

Budiarto R, Wathoni N, Mubarok S, Sauman J. (2024). Recent overview of kaffir lime (*Citrus hystrix* DC) dual functionality in food and nutraceuticals. Journal of Agriculture and Food Research, 18(1): 101384.

Burnett AC. 2019. Source–sink relationships. eLS, 1(1): 1–27.

Burnett AC, Rogers A, Rees M, Osborne CP. 2018. Nutrient sink limitation constrains growth in two barley species with contrasting growth strategies. Plant Direct, 2(1): 1–13.

Burnett AC, Rogers A, Rees M, Osborne CP. 2016. Carbon source–sink limitations differ between two species with contrasting growth strategies. Plant Cell and Environment, 39(11): 2460–2472.

Campany CE, Medlyn BE, Duursma RA. 2017. Reduced growth due to belowground sink limitation is not fully explained by reduced photosynthesis. Tree Physiology, 37(1): 1042–1054.

Carvalho P, Foulkes MJ. 2019. Roots and uptake of water and nutrients. In: Crop Science. Springer Science+Business Media New York. p. 107–130.

Chang, T. G., & Zhu, X. G. (2017). Source–sink interaction: a century old concept under the light of modern molecular systems biology. Journal of Experimental Botany, 68(16) : 4417-4431.

Chen J, Liu L, Wang Z, Zhang Y, Sun H, Song S, Li C. 2020. Nitrogen fertilization increases root growth and coordinates the root–shoot relationship in cotton. Frontiers in Plant Science, 11: 880.

Chen Q, Lu X, Guo X, Xu M, Tang Z. 2021. A source-sink model explains the difference in the metabolic mechanism of mechanical damage to young and senescing leaves in *Catharanthus roseus*. BMC Plant Biology, 21: 154.

Cheng S, Wang Q, Manghwar H, Liu F. 2022. Autophagy-mediated regulation of different meristems in plants. International Journal of Molecular Sciences, 23(11): 1–15.

Czedik-Eysenberg A, Arrivault S, Lohse MA, Feil R, Krohn N, Encke B, Stitt M. 2016. The interplay between carbon availability and growth in different zones of the growing maize leaf. Plant Physiology, 172(2): 943–967.

Dhami N, Cazzonelli CI. 2021. Short photoperiod attenuates CO2 fertilization effect on shoot biomass in Arabidopsis thaliana. Physiology and Molecular Biology of Plants, 27(4): 825-834.

Doidy J, Wang Y, Gouaille L, Goma-Louamba I, Jiang Z, Pourtau N, Le Gourrierec J, Sakr S. 2024. Sugar transport and signaling in shoot branching. International Journal of Molecular Sciences, 25(23).

Durand M, Mainson D, Porcheron B, Maurousset L, Lemoine R, Pourtau N. 2018. Carbon source–sink relationship in Arabidopsis thaliana: the role of sucrose transporters. Planta, 247(3): 587–611.

Fatichi S, Leuzinger S, Körner C. 2014. Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. New Phytologist, 201(4): 1086–1095.

Fatichi S, Pappas C, Zscheischler J, Leuzinger S. 2019. Modelling carbon sources and sinks in terrestrial vegetation. New Phytologist, 221(2): 652–668.

Feng G, Luo H, Zhang Y, Gou L, Yao Y, Lin Y, Zhang W. 2016. Relationship between plant canopy characteristics and photosynthetic productivity in diverse cultivars of cotton (Gossypium hirsutum L.). Crop Journal, 4(6): 499–508.

Fernie AR, Bachem CW, Helariutta Y, Neuhaus HE, Prat S, Ruan YL, Sonnewald U. 2020. Synchronization of developmental, molecular and metabolic aspects of source–sink interactions. Nature Plants, 6(2): 55-66.

Goldschmidt EE, Koch KE. 2017. Citrus. In: Photoassimilate distribution in plants and crops: source-sink relationships. Routledge. p. 797-824.

Guada G, García-González I, Pérez-de-Lis G, Vázquez-Ruiz RA, Montserrat-Martí G. 2018. Dry matter content during extension of twigs, buds and leaves reflects hydraulic status related to earlywood vessel development in Quercus pyrenaica Willd. European Journal of Forest Research, 137(1): 307–319.

Haque MA, Sakimin SZ. 2022. Planting arrangement and effects of planting density on tropical fruit crops—A review. Horticulturae, 8(6): 1–17.

Hartmann H, Adams HD, Hammond WM, Hoch G, Landhäusser SM, Wiley E, Zaehle S. 2018. Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests. Environmental and Experimental Botany, 152(1): 7–18.

Irving LJ. 2015. Carbon assimilation, biomass partitioning and productivity in grasses. Agriculture, 5(4): 1116-1134.

Jansson C, Vogel J, Hazen S, Brutnell T, Mockler T. 2018. Climate-smart crops with enhanced photosynthesis. Journal of Experimental Botany, 69(16): 3801-3809.

Kocurek M, Kornas A, Wierzchnicki R, Lüttge U, Miszalski Z. 2020. Importance of stem photosynthesis in plant carbon allocation of Clusia minor. Trees, 34(4): 1009-1020.

Koevoets IT, Venema JH, Elzenga JTM, Testerink C. 2016. Roots withstanding their environment: Exploiting root system architecture responses to abiotic stress to improve crop tolerance. Frontiers in Plant Science, 7(1): 1–19.

Koley S, Raorane ML, Junker BH. 2019. Shoot tip culture: a step towards 13C metabolite flux analysis of sink leaf metabolism. Plant Methods, 15(1): 48.

Körner C. 2015. Paradigm shift in plant growth control. Current Opinion in Plant Biology, 25: 107–114.

Kukah ASK, Xiaohua J, Osei-Kyei R, Perera S. 2024. How carbon trading contributes to reduction in emission of greenhouse gases: a narrative literature review. Journal of Facilities Management, 23(3): 463–479.

Lambers H, Oliveira RS, Pons TL. 2019. Growth and allocation. In Plant Physiological Ecology. Cham: Springer International Publishing, p. 385–449.

Leng H, Zhou L, Yan W. 2025. Variations in leaf photosynthesis and its limitations at different canopy positions in mature camphor trees. Forests, 16(4).

Li SY, Hussain SB, Vincent C. 2024. Response of carbon fixation, allocation, and growth to source–sink manipulation by defoliation in vegetative citrus trees. Physiologia Plantarum, 176(3): e14304.

Liu L, Hao L, Zhang Y, Zhou H, Ma B, Cheng Y, Tian Y, Chang Z, Zheng Y. 2022. The CO2 fertilization effect on leaf photosynthesis of maize (*Zea mays* L.) depends on growth temperatures with changes in leaf anatomy and soluble sugars. Frontiers in Plant Science, 13: 1–15.

Lopez G, Ahmadi SH, Amelung W, Athmann M, Ewert F, Gaiser T, Seidel SJ. 2023. Nutrient deficiency effects on root architecture and root-to-shoot ratio in arable crops. Frontiers in Plant Science, 13: 1067498.

Lv X, Zhang Y, Zhang Y, Fan S, Kong L. 2020. Source-sink modifications affect leaf senescence and grain mass in wheat as revealed by proteomic analysis. BMC Plant Biology, 20(257): 1–17.

Milne RJ, Offler CE, Patrick JW, Grof CP. 2015. Cellular pathways of source leaf phloem loading and phloem unloading in developing stems of Sorghum bicolor in relation to stem sucrose storage. Functional Plant Biology, 42(10): 957–970.

Nam H, Gupta A, Nam H, Lee S, Cho HS, Park C, Hwang I. 2022. JULGI-mediated increment in phloem transport capacity relates to fruit yield in tomato. Plant Biotechnology Journal, 20(8): 1533–1545.

Nath AJ, Lal R, Das AK. 2015. Managing woody bamboos for carbon farming and carbon trading. Global Ecology and Conservation, 3: 654–663.

Nunes LJR, Meireles CIR, Gomes CJP, Ribeiro NMCA. 2020. Forest contribution to climate change mitigation: Management oriented to carbon capture and storage. Climate, 8(21): 1–20.

Nuranisa S, Sudiana E, Yani E. 2020. Hubungan umur dengan stok karbon pohon duku (*Lansium parasiticum*) di Desa Kalijajar Kecamatan Kaligondang Kabupaten Purbalingga. BioEksakta: Jurnal Ilmiah Biologi Unsoed, 2(1): 146–151.

Pawar R, Rana VS. 2019. Manipulation of source-sink relationship in pertinence to better fruit quality and yield in fruit crops: A review. Agricultural Reviews, 40(3): 200–207.

Plavcova L, Jansen S. 2015. The role of xylem parenchyma in the storage and utilization of nonstructural carbohydrates. In Functional and Ecological Xylem Anatomy. Springer, p. 209–234.

Plavcová L, Hoch G, Morris H, Ghiasi S, Jansen S. 2016. The amount of parenchyma and living fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. American Journal of Botany, 103(4): 603–612.

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytologist, 208(3): 736–749.

Punyasu N, Thaiprasit J, Kalapanulak S, Saithong T, Postma JA. 2024. Modeling cassava root system architecture and the underlying dynamics in shoot–root carbon allocation during the early storage root bulking stage. Plant and Soil, 507(1): 863–880.

Putra SP, Santosa S, Salsinha YCF. 2023. Waterlogging and salinity stress affecting growth and morphological character changes of Limnocharis flava. Biodiversitas Journal of Biological Diversity, 24(1).

Rademacher T, Fonti P, LeMoine JM, Fonti MV, Bowles F, Chen Y, Richardson AD. 2022. Insights into source/sink controls on wood formation and photosynthesis from a stem chilling experiment in mature red maple. New Phytologist, 236(4): 1296–1309.

Savage JA, Clearwater MJ, Haines DF, Klein T, Mencuccini M, Sevanto S, Turgeon R, Zhang C. 2016. Allocation, stress tolerance and carbon transport in plants: How does phloem physiology affect plant ecology? Plant Cell and Environment, 39(4): 709–725.

Shen N, Zhao Y, Deng R. 2020. A review of carbon trading based on an evolutionary perspective. International Journal of

ISSN: 1412-4718, eISSN: 2581-138x

Climate Change Strategies and Management, 12(5): 739–756.

Singh SK, Nath V, Swati Sharma ESM. 2017. Source-sink relationship in litchi versus mango: A concept. International Journal of Current Microbiology and Applied Sciences, 6(3): 500–509.

Smith MR, Rao IM, Merchant A. (2018). Source-Sink Relationships in Crop Plants and Their Influence on Yield Development and Nutritional Quality. Frontiers in Plant Science, 9(1):1889.

Sonnewald U, Fernie AR. 2018. Next-generation strategies for understanding and influencing source–sink relations in crop plants. Current Opinion in Plant Biology, 43: 63–70.

Speck T, Burgert I. 2011. Plant stems: Functional design and mechanics. Annual Review of Materials Research, 41(1): 169–193.

Sunmonu N, Kudo G. 2014. How do sink and source activities influence the reproduction and vegetative growth of spring ephemeral herbs under different light conditions? Journal of Plant Research, 127(4): 503–511.

Swidrak I, Gruber A, Oberhuber W. 2014. Xylem and phloem phenology in co-occurring conifers exposed to drought. Trees - Structure and Function, 28(4): 1161–1171.

Telaumbanua PH, Nazara RV, Zebua HP, Samudin S, Monde A, Purba JH, Sulistiyowati R, Oksifa A, Harti R, Telaumbanua ED, Kartini NL, Khide P, Mendrofa T. 2024. Dasar-Dasar Agronomi. Azzia Karya Bersama.

Trugman AT, Anderegg LDL. 2024. Source vs sink limitations on tree growth: from physiological mechanisms to evolutionary constraints and terrestrial carbon cycle implications. New Phytologist, 245(1): 966–981.

Vadera H, Pandya J, Mehta S. 2025. A review: The Elucidation of Source-Sink Relationship. Life Sciences Leaflets, 179(1): 12-35.

Van Campen JC. 2016. Early leaf development in rice (*Oryza sativa* L.): structure, physiology, and gene expression (Doctoral dissertation, University of Sheffield).

Waheed A, Qiao X, Muhammad M, Yiremaikebayi Y, Yingying X, Xu H, Wahab A. 2025. Plant root-mediated carbon sequestration and nutrient cycling in grassland ecosystems under land use and climate change. Agriculture, Ecosystems & Environment, 393: 109865.

Wang L, Ruan YL. 2016. Shoot-root carbon allocation, sugar signalling and their coupling with nitrogen uptake and assimilation. Functional Plant Biology, 43(2): 105–113.

Weraduwage SM, Chen J, Anozie FC, Morales A, Weise SE, Sharkey TD. 2015. The relationship between leaf area growth and biomass accumulation in Arabidopsis thaliana. Frontiers in Plant Science, 6: 167.

White AC, Rogers A, Rees M, Osborne CP. 2016. How can we make plants grow faster? A source–sink perspective on growth rate. Journal of Experimental Botany, 67(1): 31–45.

Wu Y, Gong W, Wang Y, Yong T, Yang F, Liu W, Wu X, Du J, Shu K, Liu J, Liu C, Yang W. 2018. Leaf area and photosynthesis of newly emerged trifoliolate leaves are regulated by mature leaves in soybean. Journal of Plant Research, 131(4): 671–680.

Yang JH, Wang H. 2016. Molecular mechanisms for vascular development and secondary cell wall formation. Frontiers in Plant Science, 7(356): 1–8.

Yu SM, Lo SF, Ho THD . 2015. Source–sink communication: regulated by hormone, nutrient, and stress cross-signaling. Trends in Plant Science, 20(12): 844–857.

Zhang J, Zhang L, Wang Q, Liu J, Sun Y. 2023. Diurnal regulation of leaf photosynthesis is related to leaf-age-dependent changes in assimilate accumulation in Camellia oleifera. Plants, 12(11): 1–15.

Zhang N, Van Westreenen A, Evers JB, Anten NP, Marcelis LF. 2020. Quantifying the contribution of bent shoots to plant photosynthesis and biomass production of flower shoots in rose (*Rosa hybrida*) using a functional–structural plant model. Annals of Botany, 126(4): 587-599.