Physiological adaptations of the Japanese plum tree for agricultural productivity: A promising crop for high altitude tropics

Adaptaciones fisiológicas del ciruelo japonés para productividad agrícola: un cultivo promisorio para el trópico alto

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ABSTRACT

The Japanese plum tree is of great importance in the productive development of Colombian fruit growers due to its nutritional contribution to human health, its great adaptability in the tropical highlands, and its good yields. This review presents the current investigative state of physiology of this plant and its management in tropical highlands, including aspects such as its ecophysiology, forced production, gas exchange, flowering, pollination, and fruit development. In Colombia, Japanese plum production systems are adapted between 1,670 and 2,900 m a.s.l., average solar brightness of 1,400 h per year, 12 h photoperiods, temperatures between 14 and 20°C during the day and 6 and 8°C during the night, and rainfall between 700 and 1,600 mm per year. Under these conditions, management can be implemented to produce cyclical crops of the Japanese plum. This management consists of the selection of varieties with low chilling requirement, chemical defoliation, proper fertilization, fruit and green pruning, and the application of chemical substances that promote the breaking of flower buds. Flowering and pollination require a high specificity so that they do not present incompatibility. The growth and development of the fruit requires 1,538 degree days until harvest. This review indicates the great adaptability, management, and production of Japanese plum in the Colombian high tropics.

Key words: *Prunus salicina* Lindl., ecophysiology, stone fruit, dormancy, flowering, harvest.

RESUMEN

El ciruelo japonés es de gran importancia en el desarrollo productivo de los fruticultores colombianos, debido a su aporte nutricional a la salud humana, su gran adaptabilidad a la altitud tropical y sus buenos rendimientos. Esta revisión presenta el estado investigativo actual de la fisiología de esta planta y su manejo en tierras altas tropicales, incluyendo aspectos como su ecofisiología, producción forzada, intercambio gaseoso, floración, polinización y desarrollo de frutos. En Colombia, los sistemas de producción de ciruela japonesa están adaptados entre 1.670 y 2.900 m s.n.m., brillo solar promedio de 1.400 h anuales, fotoperiodos de 12 h, temperaturas entre 14 y 20°C durante el día y 6 y 8°C durante la noche, y precipitaciones entre 700 y 1.600 mm anuales. Debido a estas condiciones, se puede implementar un manejo para producir cultivos cíclicos de ciruela japonesa. Este manejo consiste en la selección de variedades con bajo requerimiento de frío, defoliación química, adecuada fertilización, poda de fructificación y poda en verde, y la aplicación de sustancias químicas que favorezcan la brotación de las yemas florales. La floración y polinización requieren una alta especificidad para que no presenten incompatibilidad. El crecimiento y desarrollo del fruto requiere 1.538 grados día hasta la cosecha. Esta revisión indica la gran adaptabilidad, manejo y producción de la ciruela japonesa en el trópico alto colombiano.

Palabras clave: *Prunus salicina* Lindl., ecofisiología, fruta de hueso, dormancia, floración, cosecha.

Introduction

The Japanese plum is a deciduous tree belonging to the family Rosaceae, genus *Prunus*. Ancestral plum plants have been domesticated independently on three continents, mainly in temperate zones, with three large centers of domestication: (1) Europe for *P. domestica*, (2) China for *P. salicina*, and (3) North America for the species of section *P. americana* (Ramming & Cociu, 1991; Topp *et al.*, 2012). *P. salicina* originated in China and was introduced to Japan approximately 200 to 400 years ago, where the domestication and diversification of the crop began and most of the varieties that are grown worldwide today were obtained (Okie & Ramming, 1999; Ruiz *et al.*, 2018). Modern Japanese plum cultivars are from *P. salicina*, but they also include other species resulting from genetic improvement and later use of their cultivars as parents, namely

P. simonii Carr., *P. cerasifera* Ehrh., and *P. angustifolia* Marsh. (Fanning *et al*., 2014).

In 2021, the production of plums and sloe (*P. spinosa*) in the world reached 12,014,482 t; China was the main producer with 55.15% participation (6,626,317.1 t), Colombia contributed with 0.15% participation (18,460 t) (FAO, 2023). In Colombia, the production of deciduous fruit trees in the high-altitude tropics began in the 1980s with the introduction of varieties from Germany and Brazil, via alliances between private producers and government entities (Patiño & Miranda, 2013). In the case of the plum tree, a drupaceous plant, planting and production has focused on the Japanese plum tree of the species *P. salicina* (Fischer, 2013). This is because the cultivation of some genotypes of plum trees of Japanese heritage, unlike European plums (*Prunus domestica* L.), is favored in tropical and subtropical areas due to their warmer summers and less accumulation of chilling hours (Looney & Jackson, 2010). The production and consumption of this plum tree have been increasing in recent years, promoting employment and productive development in rural Colombian communities. Between 2012 and 2021, the quantity of plums harvested in Colombia increased by 66.7%, reaching a production of 18,459 t in 1,387 ha (13.30 t ha⁻¹) for 2021 (FAO, 2023). Boyacá is the department with the largest production, contributing 78% of the total (Agronet, 2021), since it has comparative advantages in the planting of deciduous crops, including its climate, soils, regimes of rainfall, favorable accumulation of cold hours in some varieties and the fruit vocation of the producers (Puentes Montañéz, 2006). This was due to two key factors: (1) the organoleptic and nutritional quality it possesses compared to other imported varieties (Puentes *et al*., 2008) and (2) the agronomic management that allows the producer to obtain two harvests in one year according to the ecophysiology (Castro & Puentes, 2012).

The physiological behavior of deciduous trees in the high tropics is affected by climatic conditions since, due to their origin and adaptation in temperate zones (Erez, 2000; Fischer, 2013), the ecophysiological requirements of the species and the agronomic management of the crop must be fulfilled in a differential way (Gutiérrez-Villamil *et al*., 2022). In addition, climate change is a current risk for the production of deciduous fruit trees, including plum, as changes in temperature can affect their physiology, phenology and production (Egea *et al*., 2022). Considering

the great importance and the productive and nutritious potential of the plum tree for growing and adaptation in the tropical highlands, the objective of this review was to present the current state of research in physiology adaptation and management, including aspects such as variety selection, ecophysiology, forced production management, gas exchange, flowering, pollination and fruit development of the Japanese plum. This information serves as a basis for maximizing the productive potential of this deciduous fruit tree under tropical altitudinal conditions.

Varieties in Colombia

Temperate deciduous fruit crops, such as Japanese plum, are limited in tropical zones mainly by the lack of sufficient low temperatures to meet chilling hour (CH) requirements and overcome bud dormancy (Erez, 2000). Therefore, varieties with low chilling requirements are favored. Additionally, global warming has become a new challenge for the physiology of deciduous species (Luedeling, 2012), since an increase of 3.2°C in the global average temperature is expected by the end of the 21st century, compared to the year 1960 (IPCC, 2021). This could decrease the accumulation of CH in deciduous species, affect bud break and reduce pollinator activity (Egea *et al*., 2022), as has been observed in cultivated apple trees in the subtropical highlands of India (Nautiyal *et al*., 2020). Added to this, the highland areas of the tropical Andes will be more affected by climate change than the low-lying valley areas (Fischer, Parra-Coronado *et al*., 2022b). Therefore, implementing varieties with a low CH requirement could meet the physiological requirements of deciduous fruit trees and reduce the negative effects of the increase in temperature (Gutiérrez-Villamil *et al*., 2022).

In Colombia, the varieties of Japanese plum that are used for the production of fresh fruit are characterized by having a low CH requirement, which is why they adapt and are planted in high-altitude areas (Tab. 1). This allows good dormancy behavior and high yields. The 'Horvin' variety is a plum tree with skin and red pulp that is widely accepted in markets due to its excellent organoleptic and nutritional characteristics (Álvarez-Herrera *et al*., 2021). In addition, it is the most cultivated variety in the main Colombian producing regions (Miranda & Carranza, 2013), since it has an early harvest and two harvests a year can be obtained due to its low chilling requirement (Castro & Puentes, 2012; Fischer, 2013).

TABLE 1. Physiological characteristics of Japanese plum (*P. salicina*) varieties cultivated in the Colombian high tropics.

Variety	Adaptation altitude (m a.s.l.)	Rootstock	CH accumulation <7.2°C	Heat accumulation (GDD)	Pollinating varieties	Reference
'Horvin'	2,400 – 2,800	'DBC' y 'Ecuatoriano'	300 – 400	1528 between fruit set and fruit harvest	Self-compatible	Fischer (2000); Campos (2013)
'Amarillo Japonés' or 'Ogden'	2,400 – 2,700	'DBC'	650 – 100	-	'Santa Rosa', 'Horvin', and 'Methley'	Campos (2013)
'Santa Rosa'	2,200 – 2,600	'DBC' y 'Ecuatoriano'	600 – 700	6591–9099	Self-compatible, 'Beauty', 'Horvin', and 'Mirabolano'	Ormistas (1993); Agustí (2010); Ruiz *et al*. (2018)
'Beauty'	2,500 – 2,900	'Ecuatoriano'	750 – 800	6727–7183	'Santa Rosa'	Campos (2013); Agustí (2010); Ruiz *et al*. (2018)
'Ecuatoriano'	2,200 – 2,700	'DBC'	400 – 450	-	'Santa Rosa', 'Horvin' and 'Beauty'	Ormistas (1993)
'Methley'	2,200 – 2,800	'DBC', 'Mirabolano' and 'Ecuatoriano'	235 – 700	-	'Santa Rosa', 'Satsuma' and 'Golden Japan'	Ormistas (1993); Campos (2013); González-Pérez *et al*. (2018)

DBC: 'Durazno blanco común'; CH: Chilling hours; GDD: Growing degree days.

Ecophysiology

Altitude, light, and solar radiation

The producing areas of the tropics are characterized by constant photoperiod conditions throughout the year and do not present marked temperature seasons (Fischer, 2013). However, altitude is one of the key factors in the production of fruit trees in the tropics, since it determines most climatic parameters, such as temperature, radiation, pressure, atmospheric CO_2, and their effect on the different phenological stages of fruit trees (Fischer, Parra-Coronado *et al*., 2022). In the tropics, especially in the Cundinamarca and Boyaca departments of Colombia, Japanese plums adapt to high altitudes, between 1,800 and 2,800 m a.s.l. (Tab. 1), which are characterized by low temperatures, increased radiation (UV, visible and infrared light), a lower concentration of CO_2 and O_2, and more intense winds (Fischer, Parra-Coronado *et al*., 2022). However, commercial peach and Japanese plum crops have been established in the mountains of Norte de Santander (Colombia), specifically in the Catatumbo River basin at an altitude of 1,670 m a.s.l. (Quevedo-García *et al*., 2017). The varieties of Japanese plum trees grown there have not been reported. Fruit plants at higher tropical altitudes, as in the case of cape gooseberry, have been shown to increase the number of stomata to compensate for the lesser concentration of O_2 and CO_2 at these high elevations (Fischer *et al*., 2023). Also, at these elevations, humidity is typically low and diurnal temperature variation is large, even at the equator (George & Erez, 2000).

Solar radiation is the source of energy for photosynthesis and therefore for the growth and development of all fruit trees and is determined by intensity, quality and duration. In general, deciduous fruit trees grow in tropical areas with an average of 1,400 h of direct sunlight per year (Fischer, 2013). In addition, the tropics have a constant photoperiod throughout the year (about 12 h), so deciduous fruit trees have photosynthetically active leaves that last for more than 11 months a year, unlike in subtropical and temperate areas where leaves are only active for 8 to 9 months and 6 to 7 months, respectively (George & Erez, 2000). Likewise, the high UV radiation to which deciduous fruit trees are subjected can influence the physiology of the plant. Positively, visible and UV light regulate anthocyanin synthesis in Japanese plums in the photosynthesis-respiration interaction by controlling malate metabolism through malate dehydrogenase and the ethylene ATP signaling pathway (Zhang *et al*., 2021). Adversely, the high UV radiation in the tropical highlands causes sunburn on the fruits, which greatly affects the marketability of the fruit and, therefore, the productivity of the crop (Fischer, Orduz-Rodríguez *et al*., 2022). In plum and peach trees, open vase formation is commonly used, which allows a higher radiation level and encourages sunbursts (Fischer, 1992a). In this regard, Makeredza *et al*. (2018) reported that excess radiation causes an increase in fruits affected by sunburn in Japanese plums, mainly those located in the upper part of the canopy.

Temperature and chilling requirement

Deciduous fruit trees need to accumulate a specific amount of cold during winter to overcome dormancy and then experience warm temperatures to finally flower in spring (Erez, 2000). This factor conditions the adaptation of species and cultivars in the regions and is the main drawback for its extension to lower altitudes. In the tropics, there are

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fewer seasonal temperature fluctuations than in temperate regions, with a relatively constant temperature throughout the year (Fischer, 2000). Temperatures, where highly productive crops of Japanese plum are found (high-altitude tropical climate), range between 14 and 20°C during the day, and 6 and 8°C at night (Fischer, 2013). In the tropical mountains of Morocco, the Japanese plum tree 'Angelino' grown under heat stress (+2.5°C in average daily temperature) had a decrease in leaf area, number of leaves per fruit, stomatal area index, conductance stomata, chlorophyll concentration, and the yield and fresh weight of the fruits (Hamdani *et al.*, 2023). Therefore, the Japanese plum tree is a species with considerable risk due to the temperature that will be caused by climate change in tropical areas.

Bud dormancy is a physiological period within the development cycle of deciduous fruit trees that, through genetic control, allows the tree to accumulate reserves, mainly carbohydrates, to eliminate sensitive organs (leaves), develop organs to protect the meristems and resist excessively chilling conditions during the winter season (Falavigna *et al.*, 2019). Low temperatures are the most important factor that induces dormancy and requires the plant accumulate the necessary amount of chilling, which is known as endodormancy. In the tropics, most deciduous fruit trees, such as Japanese plum, exhibit symptoms of chilling failure, commonly leading to poor and patchy bud break, reduced and delayed foliage development, poor flowering, abnormal flower development, deficient fruit set and/or early cessation of growth (Dennis Jr., 2000; Ramírez & Kallarackal, 2014), so special management must be implemented to compensate for chilling hours (CH). Each species and variety of deciduous fruit tree has some specificity to the requirements of CH to break dormancy. In the Japanese plum grown in tropical areas, the accumulation of CH depends on the variety (Tab. 1), with the variety 'Horvin' requiring the least CH, which means it adapts well to the high tropics. In temperate zones, 1 CH is described, in many cases, as 1 h <7.2°C. However, for the tropics, the best way to quantify CH is with the Utah model of Richardson *et al.* (1974) because it also includes the effect of hours that exceed 7.2°C; thus, in the Utah model, a temperature between 2.5 and 9.1°C for 1 h is 1 chilling unit, and a temperature between 9.2 and 12.4°C for 1 h is 0.5 chilling units. These are temperatures that often occur in the tropical highlands and greatly influence the reproductive physiology of deciduous trees. Likewise, this model includes negative weights for temperatures above 15.9°C. In addition, it has been shown that the dormancy of *P. salicina* buds is controlled by the Dormancy Associated MADS-box (*PsDAM6*) genes, and their expression is lower in varieties with low CH requirements than in those with high CH requirements (Fang *et al.*, 2022).

Although it is true that plants require a certain amount of chilling during endodormancy, exposure to and accumulation of warm temperatures are needed to grow after the release of dormancy (accumulation of heat), so it is necessary to quantify the thermal time through the growing degree days (GDD) (Fadón *et al.*, 2020). In the tropics, depending on management, deciduous fruit trees can suppress or evade endodormancy (Fischer *et al.*, 2011), so GDD accumulation has not been studied much in varieties planted during dormancy (Tab. 1). However, Orjuela-Angulo, Parra-Coronado *et al.* (2022) reported that the 'Horvin' variety planted in Colombia has a base temperature of 2.9°C and requires 1,528 GDD between fruit set and fruit harvest. Further studies are required to report on the warm temperature requirements of tropical varieties when endodormancy is not suppressed. In addition, as reported by Erez (1986), in continuous production systems in the tropics, in order to suppress deciduous trees that are not the intended crop, soil temperatures should not drop below 10°C, as this prevents the cultivated crop roots from reducing their activity and facilitating the entrance of roots from other trees.

Water and soil

The absorption of water is an essential process for plants, derived from their need to lose water to the atmosphere through the stomata and thus regulate their temperature. Deciduous fruit trees in Colombia receive rainfall between 1,000 and 2,000 mm per year (Fischer, 2013). To manage the production of two harvests per year in some plum varieties, it is recommended to carry it out in areas with rainfall between 1,400 and 1,600 mm per year (Gutiérrez-Villamil *et al.*, 2022). However, it is important to have a good water resource and drip irrigation systems (Castro & Puentes, 2012). For the 'Methley' variety grafted on 'Mirabolano', the combination of a flow rate of 0.85 L h⁻¹ (daily irrigation) and the implementation of manure cover maintained soil moisture and improved the yield and quality of the fruits (Eduardo del Angel *et al.*, 2001). In subtropical semi-arid regions, it is recommended to manage two drippers per tree with flow rates of 4 L h⁻¹ and not to implement controlled deficit irrigation during the year, since this reduces gas exchange, tree water status, growth, yield and quality of fruits in Japanese plum varieties (Hajlaoui *et al.*, 2022). In addition, there are modeling reports on the redistribution of soil water in *P. salicina* crops through the HYDRUS-2D model, which provides information on the amount of water required according to seasonality, cultivar, and soil water

balance (Jovanovic *et al*., 2023). A 50% deficit irrigation regime based on the daily water requirements of the crop (ETc) in different varieties of *P. salicina* (including 'Santa Rosa') caused a decrease in the yield and fresh weight of the fruit, leaf area, stomatal density, chlorophyll concentration, and stomatal conductance (Hamdani *et al*., 2022; Hamdani, Hssaini, Bouda, Charafi *et al*., 2023).

Soil conditions for deciduous fruit trees are mainly loamy soils with a good organic matter content, good drainage, and deep soils with a low water table (1.20 m), due to their susceptibility to root asphyxiation (Castro & Puentes, 2012). In Japanese plum var. 'Horvin' cultivated in Colombia, the mass and length of the fruits highly correlated with soil chemical properties, such as pH, cation exchange capacity, total organic carbon, contents of phosphorus, calcium, magnesium, potassium, zinc, copper, boron, and sulfur, and with soil physical properties, such as bulk density, which indicates that good root development requires good oxygenation (Orjuela-Angulo, Dussán-Sarria *et al*., 2022). Managing the soil with mulches between rows in Japanese plum crops significantly improved the maximum organic carbon content and available nutrient content in soil, nutrient content of leaves, yield (Rakesh *et al*., 2020), and soil moisture content (Jovanović *et al*., 2023). The cover with mulches should not be placed below the tree, since there may be competition for nutrients from fertilization and water, affecting the optimal development of the plum tree.

Nutrition and fertilization

As in most fruit trees, mineral nutrition is one of the fundamental aspects in the production of deciduous fruit trees since it provides the necessary elements for proper growth and development. To effectively manage the fertilization of deciduous fruit trees, the effect of soil pH must be managed as a priority since the availability of nutrients for the plant depends on it, and the decisions regarding their application, whether conventionally, foliar or in fertigation, are taken based on the foliar analyses that are carried out in each season (Klein & Weinbaum, 2000). In seedlings of Japanese plum var. 'Horvin' at the nursery stage of growth, the concentrations of foliar N were highest, followed by K, and finally P and Mg (Orduz-Ríos *et al*., 2020). Likewise, the plum tree is one of the deciduous fruit species with the lowest demand for nitrogen (N), however, Japanese plum trees require a greater amount of N than European plum trees (Agustí, 2010). In tropical areas, management of forced production greatly affects fertilization, which will be discussed in a later section of this review. In general terms, it is recommended to apply N before flowering, and

K and P at the end of dormancy (Agustí, 2010). Additionally, when analyzing the relationship between the mineral elements and the severity of cracking of the *P. salicina* fruits, it was found that when the organic matter content, the total porosity, the Ca^{2+} content in the soil and leaves, and the apparent density decreased, the cracking of the Japanese plum fruits was milder; meanwhile, the higher the Mn content in the soil and leaves, the more severe the fruit cracking, possibly due to competition with Ca or Mn toxicity (Ma *et al*., 2023).

Gas exchange and leaf traits

There has been little study of the quantification of the net photosynthetic rate (A_n), stomatal conductance (g_s), transpiration (E), and dark respiration (R_d) in Japanese plum, especially in the tropics. Due to the aforementioned ecophysiological conditions in the tropical highlands, the leaves of deciduous fruit trees are photosynthetically active for longer periods and with a higher incidence of UV radiation, which could alter these variables. Ziska *et al*. (1990) reported that Japanese plum var. 'Santa Rosa' reached A_n, g_s, and R_d values of 20 to 25 µmol CO_2 m^{-2} s^{-1}, 200 to 250 mmol H_2O m^{-2} s^{-1}, and 0.5 µmol CO_2 m^{-2} s^{-1} at a saturation of 350 mg kg^{-1} of internal CO_2, respectively. However, under saline stress, stomatal and metabolic limitations in photosynthesis occurred through a decrease in g_s, RuBisCO activity, chlorophyll content and in an increase in R_d (Ziska *et al*., 1990). Similar results were obtained in a study carried out in China, where Japanese plum leaves had values of 11.8 µmol CO_2 m^{-2} s^{-1}, 0.24 mmol H_2O m^{-2} s^{-1}, and 6.7 µmol H_2O m^{-2} s^{-1} for A_n, g_s, and E, respectively, which decreased with the application of saline stress accompanied by low water use efficiency (WUE) (Wang *et al*., 2016). Likewise, under drought stress, drastic decreases in A_n, g_s, and WUE were observed in three Japanese plum cultivars (Hajlaoui *et al*., 2022). Therefore, *P. salicina* trees are very sensitive to osmotic stress due to their low WUE and limiting photosynthetic mechanisms.

Chloroplasts perform multiple biological functions within plants, such as photosynthesis and the synthesis of organic compounds. To reveal their formation and evolution, Fang *et al*. (2021) sequenced the complete chloroplast genome of *P. salicina*, identifying a circular structure of 157,921 bp, containing a large single-copy (LSC) region of 86,184 bp, a small-copy (SSC) region of 19,031 bp, and 110 unique genes. Compared to other species of the genus *Prunus*, *P. salicina* shows interesting similarities and differences in phylogenetic evolution with *P. armeniaca* and *P. mume* (Xue *et al*., 2019). In the Japanese plum trees 'Horvin' grown in tropical

highlands, the relative chlorophyll content in SPAD units had values of 23.3 and 47.7 in young and fully developed leaves, respectively (Orduz-Ríos *et al*., 2020).

In *P. salicina* cv. 'Horvin', the increase in width and length of the leaf are continuous and adjust to a potential model. These length and width parameters are very useful to estimate the leaf area through a simple or bivariate regression model (Vera Rodríguez & Pérez Chasoy, 2021), resulting in a non-destructive determination of the leaf area as a basis for a large number of physiology studies of this species. These same authors also found a positive correlation between the leaf width and length with the fruit diameter (Vera Rodríguez & Pérez Chasoy, 2021), indicating that larger leaves can perform greater photosynthesis to provide carbohydrates to the fruits as the main sinks.

González-Pérez, Quevedo-Nolasco *et al.* (2018) reported correlation between intercepted photosynthetically active radiation (iPAR) and phenological phases of *P. salicina* cv. Methley, indicating that the leaf area increased during the growth and development of fruits. The greatest leaf area was obtained during the second fruit growth stage and physiological maturity. There was a significant positive correlation of the leaf area with iPAR and the vegetative and fruit growth. These authors also reported that efficient radiation use was highest during the vegetative and reproductive stage but decreased when the fruit developed (González-Pérez, Quevedo-Nolasco *et al*., 2018). An efficient way to capture greater radiation in the plum is by training in open vase. This strategy places the main branches almost horizontally and within the center of the free tree, thus allowing the tree to capture greater PAR that it will then use in photosynthesis.

Agronomic management in forced production

As previously mentioned, the agroclimatic conditions of the tropics alter the physiology of dormancy in deciduous trees, and so specific cultural management is carried out to promote fruit production. Within this management, sprouting can be encouraged to the point of obtaining two harvests in a year or cyclical harvests, as has been reported in peach (Fischer, 1993; Fischer *et al*., 2011), apple (Fischer, 1992b; Gutiérrez-Villamil *et al*., 2022), and Japanese plum (Castro & Puentes, 2012). This phenomenon occurs because ecodormancy (imposed by the environment) is used to provide the preconditions for floral initiation and differentiation in predormancy (George & Erez, 2000), and, thus, suppresses deep rest. As a result, a new growth cycle can be forcibly induced by agronomic techniques, before the plants eventually enter endodormancy (Westwood, 1993).
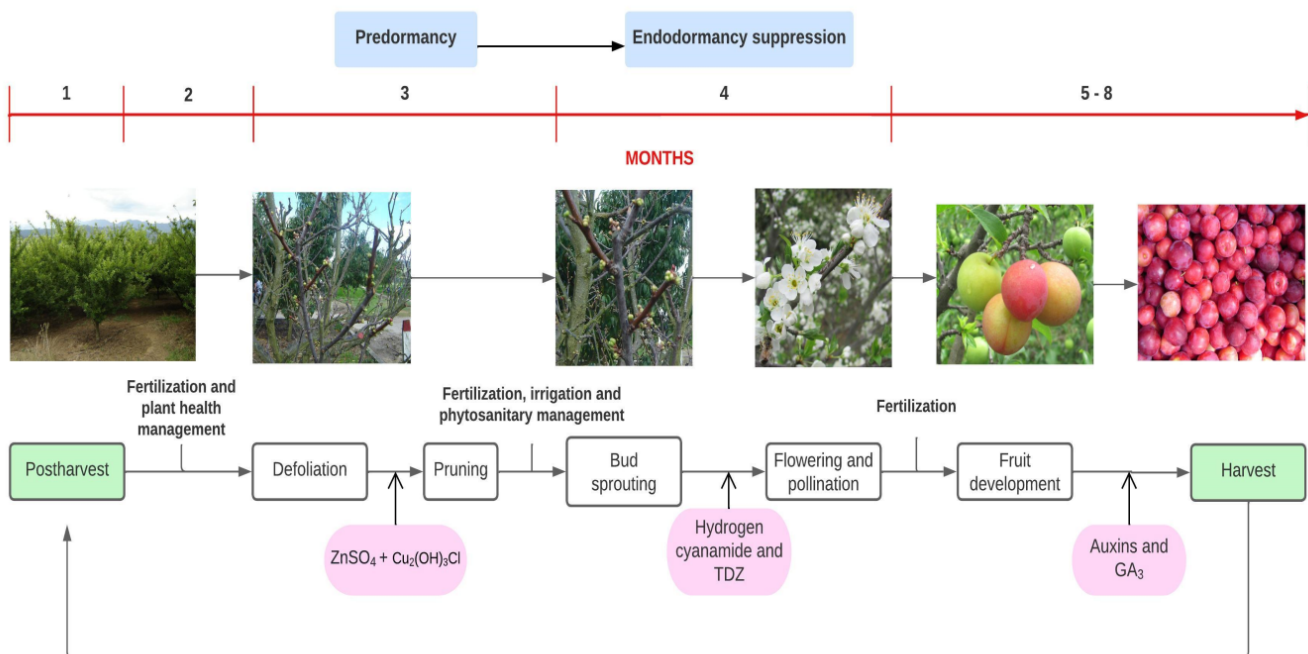

FIGURE 1. Diagram of agronomic management for obtaining two harvests per year in the Japanese plum (*P. salicina*) cultivated in tropical highlands. TDZ – thidiazuron. Adapted from Fischer *et al.* (2010) and Castro & Puentes (2012), with permissions of Revista Colombiana de Ciencias Hortícolas and Produmedios. Photos: G. Fischer.

In summary, the continuous harvest technique is based on suppressing the deep dormancy of deciduous fruit trees but not on breaking dormancy (Gutiérrez-Villamil *et al.*, 2022).

In all cases, according to the authors of this review, Japanese plum producers in the tropics should monitor their trees for normal growth and development because, in the cycle of two harvests per year, the time available to rest and accumulate a sufficient amount of reserve carbohydrates before the new flowering is highly reduced. This could cause a setback in the normal development of the tree, which would mean working with only three crops in two years.

As a first step, continuous harvests in Japanese plum should be carried out in varieties that have a low chilling requirement, since they present an early harvest and accumulate more CH in a shorter time. 'Horvin' is the variety with the lowest CH requirement in the tropics (Tab. 1) and the time between harvests is 7 to 8 months (Puentes Montañéz, 2006), which makes it a suitable variety for cycling. Once the variety has been chosen, areas with a bimodal climate (two rainy seasons a year) must be selected to avoid a long chilling season and provide a good amount of water to the plum trees for fruiting (Fischer, 1993). Examples of these zones are the municipalities of Duitama and Paipa (Boyacá, Colombia), which have bimodal rainfall during the year, unlike the municipality of Nuevo Colon (Boyacá, Colombia), which has a monomodal rainfall regime (Fischer, 2013).

After the first harvest, Japanese plum trees should be fertilized with an N-rich formula until bud swelling (Fig. 1) to increase reserve accumulation in the trunk and branches. This improves bud swelling, bud break and fruit set, altering the perception of dormancy in the plants. Subsequently, an application is made again after fruit set and during its development but not as close to harvest, as otherwise the postharvest handling could be affected (Agustí, 2010; Castro & Puentes, 2012).

Defoliation is a process that occurs naturally in deciduous fruit trees in temperate zones. However, in the tropics, this process does not occur in the same way, so chemical or manual treatments are needed for 100% defoliation (Fischer, 2013). Removing the leaves of the trees is the main technique used to suppress endodormancy, since it decreases the concentration of abscisic acid (which comes from the leaves) in the buds and increases the activity of gibberellins and cytokinins (Ramírez & Kallarackal, 2014). In addition, early defoliation has been shown genetically to accelerate auxin translocation from buds, which accelerates

dormancy release and promotes bud break (Wei *et al.*, 2022). Castro and Puentes (2012) recommend that, for early production of the Japanese plum, it should be defoliated with copper oxychloride (110 g 20 L^{-1}) + zinc sulfate (200 g 20 L^{-1}). In addition, these authors suggest that diseases that affect flowering, such as flower blight (*Monilia* sp.), should be controlled.

Water stress followed by a period of rain or irrigation is a technique that promotes bud breaking in apple and peach trees (Fischer, 1993). However, no effect on the suppression of dormancy has been reported in Japanese plum trees planted in the tropics of stress. Faust (2000) states that the water deficit, on occasion, is not necessary to force flowering in deciduous trees, since a good supply of N, defoliation and the application of chilling compensators can achieve sprouting. On the contrary, Samperio *et al.* (2015) found that by applying controlled deficit irrigation after harvest in the Japanese plum 'Red Beauty', the water potential of the stem decreased, which enabled not only saving of water but also control of vegetative growth (considered as total pruning), maintenance of the yield and quality of the fruits, and increase in the final profitability of the producer. However, studies are needed to evaluate the effect of water deficit on floral sprouting and yield of Japanese plums grown in tropical areas.

Fruit thinning is carried out on deciduous trees to regulate the fruit load and the balance of vegetative-reproductive branches (taking into account the angle of their position) and to enable the differentiation of flower buds and the translocation of nutrients from the leaves (Fischer, 2013). In Japanese plum trees in the tropics, the formation of shoots (productive or mixed branches) is sought cycle after cycle (Castro & Puentes, 2012); therefore, this practice must be carried out to obtain high yields. Green pruning is implemented to eliminate the "suckers" that are produced inside the tree and hinder the penetration of solar radiation; this pruning improves the differentiation of branches and generates better color development in plum fruits (Castro & Puentes, 2012).

The aforementioned techniques will cause bud swelling, which is the optimum time for the application of rest-breaking chemicals. However, these chemicals will not act as chilling compensators as the tree will not enter endodormancy and, therefore, they will not work as rest-breaking substances (Gutiérrez-Villamil *et al.*, 2022). The application of hydrogen cyanamide (Dormex®) at 1% increased the flowering percentage, fruit set, number of fruits per tree and yield, and reduced the days until

harvest in the Japanese plums 'Horvin', 'Methley', 'Santa Rosa', 'Sangre Toro', 'Santa Rosa', and 'Ogden' cultivated in the municipality of Nuevo Colón (Buitrago et al., 1992). Thidiazuron (TDZ) is a substance with cytokinin activity used to increase bud-breaking. In the Japanese plum var. 'Shiro', the application of TDZ at 50, 100, and 200 mg L^{-1} increased the flowering percentage and showed the same performance as with the application of Dormex® (5 ml L^{-1} a.i. hydrogen cyanamide); however, TDZ at 100 ml L^{-1} increased the diameter of the ovary, which can increase the size of the fruits (Alvarado-Raya et al., 2000). Similar results were obtained in the variety 'Santa Rosa' by Almaguer-Vargas et al. (2000). Contrary to these reports, the exogenous application of gibberellins ($GA_3 > 50$ mg L^{-1}) to the buds inhibited flowering but increased the fruit quality parameters such as weight, diameter, and soluble sugar contents in cultivars of *P. salicina* (González-Rossia et al., 2006), so the use of GA_3 to inhibit flowering appears to be an indirect technique to reduce fruit load and a useful method to control the cost of manual fruit thinning in Japanese plum. Thus, the application of Dormex® or TDZ promotes bud break in Japanese plums grown in the tropics, making this an essential tool for the production of two crops per year and to suppress dormancy (Fig. 1).

Flowering, pollination, and fruit development

When the technique of suppressing dormancy through defoliation and the application of chemical substances that induce flowering is used, the flower buds swell and show light brown scales (Fischer, 2013). When this method is not used, flowering depends, ultimately, on whether the bud has received enough CH to satisfy its low-temperature requirement, which can be complemented by the application of chilling compensators. Once the bud opens, the individual flowers appear separated on short stems, showing first the green sepals, then the white petals, forming a globe, where gradually the anthers become evident followed by the pistil, which is the flower. It is fully open in anthesis (Hartmann & Neumüller, 2009).

In general, the flowering of Japanese plum occurs soon and the flowering period is the shortest of all stone fruit trees. The inflorescence is an umbel that generally contains one to three flowers, which are smaller than those of other *Prunus* species, with a diameter of 5 to 25 mm and white petals that open flat on the cup-shaped corolla. The flowers are hermaphrodite, with a single pistil, and have 20 to 30 stamens that are enclosed in five petals and five sepals (Guerra & Rodrigo, 2015). It should be noted that the percentage of flowers that become fruits is much lower in the Japanese plum (5% to 14%) than in other *Prunus*

species (Guerra & Rodrigo, 2015), since a mature tree can produce up to 100,000 flowers, of which only 1% to 5% must be set for an economically profitable harvest and, in many cases, chemical or manual thinning is necessary (Fischer, 2013). The application of GA_3 (50 mg L^{-1}) 14 d after anthesis, when the buds are swelling, causes flower abortion in the Japanese plum tree, decreasing fruit yield per tree, but increasing size and fruit quality characteristics (Erogul & Sen, 2015), which is why it is considered an effective technique to control the thinning of flowers and fruits in this species.

Pollination in the Japanese plum tree must be managed very carefully, since fertility is cultivar-specific and, in most cases, there is incompatibility between varieties (Looney & Jackson, 2010). Most Japanese plums, like other *Prunus* fruit tree species, are self-incompatible and require cross-pollination to ensure fruit set, *i.e.*, the plant rejects its pollen. Pollen recognition or rejection is determined by the genotype and the incompatibility reaction is genetically controlled by a polymorphic (S) locus, which encodes two linked genes that establish the alleles of the pistil and pollen (Guerra & Rodrigo, 2015). Therefore, knowledge of the pollination requirements of the cultivars is essential for solving low-yield problems related to the lack of pollination and for the planting design of new orchards with an adequate proportion of pollinating agents. In the tropics, there is recognition of some varieties that are self-compatible with each other or that require specific cross-pollination of other genotypes (Tab. 1). It is important to recognize pollen compatibility for each variety within the Japanese plum crop since the pollen source directly affects fruit set, growth, gene expression, and fruit quality (Deng et al., 2022).

The identification of pollinating agents is important in order to increase their presence and occurrence during the flowering stage and thus increase the percentage of fruit set in deciduous fruit trees. Vaca-Uribe et al. (2021) observed in four orchards (apple, pear, peach, and plum) located in the municipality of Nuevo Colon, Boyacá (Colombia) the presence of 453 flower visitors from 35 taxa, of which the Japanese plum had the highest richness of floral visitors (71.4% of the total flower visitor species) of all deciduous trees, Hymenoptera being the most abundant order of flower visitors. Also, it was found that the plum tree shares floral visitors with 44 species of plants, including weeds, other deciduous fruit trees, and native species of the area. Of these floral visitors, the *Apis mellifera* species is particularly important, so care of this species is necessary to increase the flow of pollinating agents. In addition, during the bud break and flowering

of the Japanese plum, the number of floral visitor species increased considerably compared to when it was not in the flowering stage, indicating that plum blossom events could be influencing the mobilization of the flower visitor populations in the environment (Vaca-Uribe *et al.*, 2021). Therefore, it is recommended to promote the production of these insects to increase biodiversity and fruit set. In this sense, Castro and Puentes (2012) recommend implementing three boxes of beehives per ha for good peach and plum pollination.

Stone fruit trees (*Prunus* spp.), including Japanese plums, exhibit a typical double sigmoid growth pattern during fruit development and ripening (Casierra-Posada *et al.*, 2004; González-Pérez, Becerril-Román, *et al.*, 2018). Within this period of development, four distinct stages (S1-S4) are recognized. The first stage (S1) is characterized by a rapid increase in cell division and elongation, S2 by only slightly increased fruit size but an endocarp hardened to a solid stone (stone hardening), S3 by a rapid cell division that results in a significant increase in the size of the fruit, and S4 by the ripening of the fruit or climacteric stage (Casierra-Posada *et al.*, 2004). During fruit development, the regulation of sugar transport from the source to the sink cells is a key factor in ensuring the growth, yield, and quality of the fruits. SWEET proteins (sugars will eventually be exported to transporters) are essential for the transport of sugars. The relative expression of 15 SWEET genes has been identified during the development and ripening of *P. salicina* fruits (*PsSWEET1-15*) and correlated with fructose and sucrose content, suggesting their possible functions in the transport and accumulation of these two sugars in the fruits of Japanese plums (Jiang *et al.*, 2023).

The Japanese plum 'Horvin', cultivated in the tropics, requires a period of 1,538 GDD and 81 d from fruit set to the optimum harvest point (Orjuela-Angulo, Parra-Coronado *et al.*, 2022). This information is very important in order to identify the appropriate moments to carry out good agricultural practices more effectively in tasks such as irrigation, fertilization and phytosanitary management, among others. Fruit development is the longest of the other phenological stages of the Japanese plum and one of the most important in the management of fruit load (thinning) since it can affect productivity. In varieties of *P. salicina*, the trees with a higher fruit load (without thinning) decreased the individual dry mass of the fruits in comparison with trees with a low load (thinning); this effect was associated with a limitation in the source-sink relationship, since the source presented limitations in the S1 growth stage and the sink in the S3 stage (Basile *et al.*, 2002). This shows the importance of agronomic management of Japanese plum thinning in fruit quality for market requirements.

Different preharvest treatments have been reported to increase the quality of Japanese plum fruits. The exogenous application of different sources of auxins when the fruits had a size of 22 mm caused an appreciable and significant increase in fruit size and, therefore, in yield, due to an increase in the size of fruit cells; however, auxins did not affect the quality of the fruits or the yield of the following season (Stern *et al.*, 2007), which is a promising result for agronomic management in tropical conditions (Fig. 1). Additionally, the application of GA_3 (50 mg L^{-1}) before harvest increased the weight, size, firmness, and total soluble solid contents, and reduced mass loss in the fruits of two Japanese plum varieties during storage, transportation, and commercialization (Harman & Sen, 2016).

Reducing tree fruit load by decreasing the number of fruits can improve fruit size and weight by inducing a better distribution and balance of assimilates between the vegetative and reproductive growth, as reported by Pavanello *et al.* (2018) for 'Katinka' plum. Kang *et al.* (2023) quantify the carbohydrate/nitrogen (C/N) relationship as the ratio between the non-structural carbohydrates produced by leaves and the nitrogen absorbed by the roots, which strongly depends on the growth period and phenology of the tree. Variation in the leaf/fruit ratio has an impact on the C/N ratio in the leaves of plum trees. In 'African Rose' plum trees, leaf C/N ratio and yield were increased by hand thinning compared to thinning by ethephon, naphthalene acetic acid, 6-benzyladenine, or control (Maged *et al.*, 2020).

The color of the fruits is a determining aspect of the quality of the Japanese plum and each cultivar synthesizes different pigments in the peel, which is why there are yellow ('Ogden') and red ('Horvin') Japanese plums (Fischer, 2013). As mentioned in the ecophysiology section of this review, visible light (including UV radiation) is responsible for regulating the synthesis of anthocyanins in Japanese plum (Zhang *et al.*, 2021), which is promoted by the expression of the *PsbZIP1* and *PsbZIP10* genes (Shen *et al.*, 2023), so this process can be favored by the high levels of UV radiation in the high tropics. González *et al.* (2016) mention that the color in Japanese plum trees changes from the S2 growth stage until the end of S4, due to increased expression of the leucoanthocyanidin dioxygenase (LDOX) gene, which regulates flavonoid biosynthesis in the fruits. Likewise, the significant contribution of odorants to the characteristic flavor of the fruits directly affects their quality. In this regard, in the Japanese plum 'Horvin', the analysis of

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volatile compounds led to the identification of 148 components, including 58 esters, 23 terpenoids, 14 aldehydes, 11 alcohols, 10 ketones, 9 alkanes, 7 acids, 4 lactones, 3 phenols, and another 9 compounds of different structures (Pino & Quijano, 2012). Additionally, organic acids are key components to determine the flavor of the fruits. Yu *et al.* (2023) identified malic acid as the predominant organic acid during the development and ripening of Japanese plum fruits and the potential genes involved in the synthesis of this acid, such as 11 enzyme-coding genes, 21 transporter genes, and 5 *MYB* transcription factor.

Conclusion and future perspectives

Production of Japanese plum in the tropical highlands is affected by differences and particularities in ecophysiology with respect to the temperate zone; agronomic management is required to achieve the optimal productive potential of this fruit tree (Fig. 2). In Colombia, Japanese plum production systems are adapted to altitudes ranging between 2,000 and 2,900 m a.s.l., average solar brightness of 1,400 h per year, photoperiods of 12 h, temperatures between 14 and 20°C during the day and 6 and 8°C at night, rainfall between 700 and 1,600 mm per year, and loamy soils with low apparent density and good fertility. Due to these conditions, varieties with low CH requirements, preferably less than 800 CH, should be selected to achieve good production.

When Japanese plum varieties that accumulate few CH are selected, such as the 'Horvin' variety (300 – 400 CH), in an area with bimodal rainfall distribution, two harvests a year can be obtained by applying special agronomic management and achieving endodormancy suppression (Fig. 2). This management consists of chemical defoliation (copper oxychloride + zinc sulfate), good nitrogen fertilization during plum phenology, fruit and green pruning, and the application of chemical substances that promote breaking of flower buds (Dormex® and TDZ). However, it is necessary to investigate in depth the application of a water deficit in the Japanese plum cultivated in the tropics to induce flowering.

In the tropics, Japanese plum varieties require high specificity and study to achieve fertility of the flowers with pollen that does not present incompatibility. The pollinating agents in the Japanese plum tree interact with multiple native species of the producing areas, including weeds, so it is recommended to carry out sustainable management in the control of weeds to avoid affecting the biodiversity
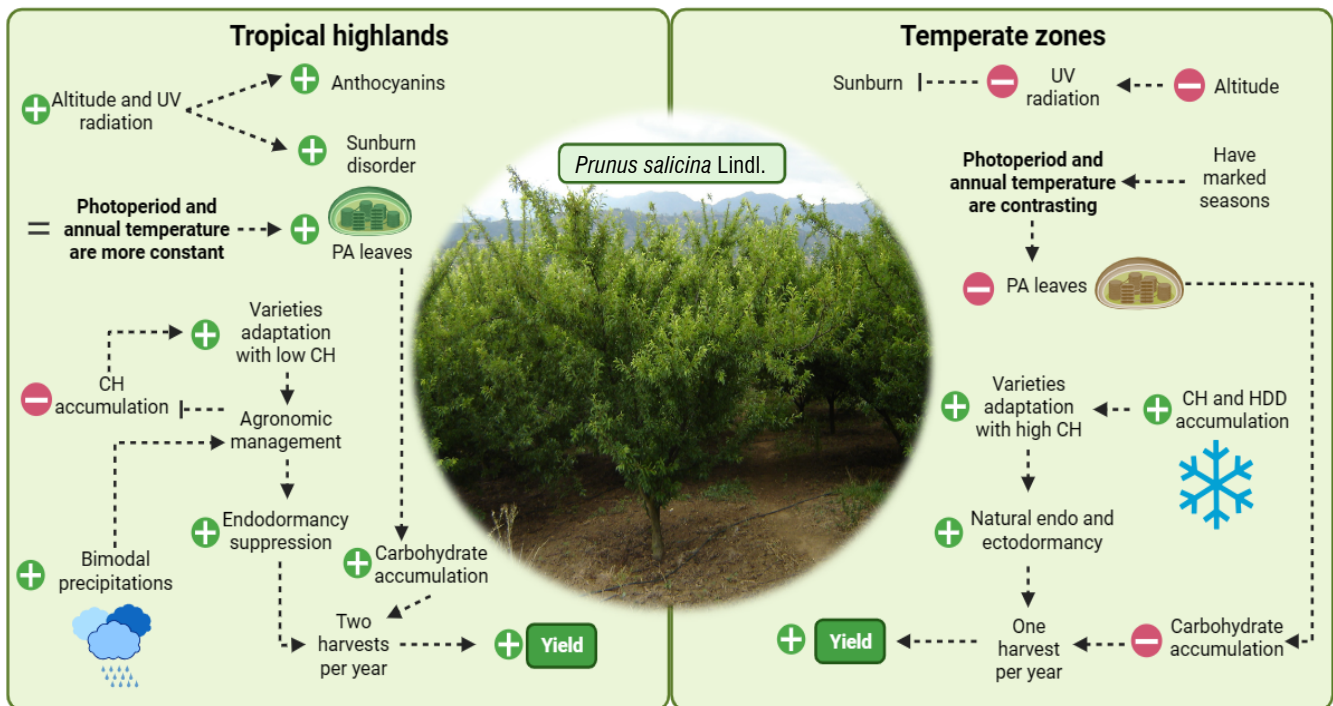

FIGURE 2. Comparison of ecophysiological and management components in the production of Japanese plum (*P. salicina*) cultivated in tropical highlands and temperate zones. PA: photosynthetically active, CH: chilling hours, HDD: heating degree day. The + (green) and - (red) symbols correspond to an increase or decrease effect, respectively. Photo: G. Fischer.

of pollinators and, therefore, reducing the fruit set. The growth and development of the Japanese plum fruits conform to a double sigmoid model, where some varieties take 3 months from fruit set to harvest. The application of growth regulators in pre-harvest seems to show good results in some varieties of *P. salicina*, but there is no information on the effect of these regulators in Colombian varieties and conditions; therefore, it is suggested this promising research topic be investigated.

Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author´s contributions

DAGV: conceptualization, research, writing - original draft, visualization, writing, and editing. JGAH: conceptualization, writing, and supervision editing. HEBL: conceptualization, visualization, writing, and editing. GF: conceptualization, writing, and editing supervision. All authors have read and approved the final version of the manuscript.

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