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Review article

La copa como indicador fotosintético relevante en el manejo forestal de bosques templados

The crown as a relevant photosynthetic agent over forest management in temperate forests

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Abstract

Tree crown or canopy characteristics in a stand are influenced by light exposure, nutrient competition, tree density, vegetation structure and species. The canopy is a determining photosynthetic indicator in forest productivity and guideline in forestry. The objective of this review is to document in a general way in a first version the effect of physiological processes on crown architecture and its importance for forestry management of temperate forests. The dynamics of crown growth and development is a function of the interaction between individuals in the stand, tree age, phenological stage, climatic conditions, humidity and temperature, in addition to topographic and soil characteristics. The values of the leaf area index, aerial net primary productivity, growth and increment rates and the response in yield expressed in volume, biomass or carbon are indirect parameters that measure the efficiency of the physiological processes in the species. Knowing and understanding these processes in the architecture and dynamics of the crown contributes to planning and applying forestry activities according to the particular needs of each species or stand. The application of this knowledge is focused on improving the growth rates and increase of forests.
Key words: forest exploitation, aboveground biomass, forest physiology, tree-soil-atmosphere interaction, forest management, coniferous forest.

Resumen

Las características de copa de árbol o del dosel en un rodal están influenciadas por la exposición a la luz, la competencia por nutrimentos, la densidad de árboles, la estructura de la vegetación y por la especie. El dosel es un indicador fotosintético determinante en la productividad forestal y pauta en la silvicultura. El objetivo de esta revisión fue documentar de manera general, en una primera versión, el efecto de los procesos fisiológicos en la arquitectura de copa y su importancia para el manejo silvícola de los bosques templados. La dinámica de crecimiento y desarrollo de la copa están en función de la interacción entre los individuos en el rodal, la edad del arbolado, la etapa fenológica, las condiciones climáticas, la humedad y la temperatura; además de las características topográficas y de suelo. Los valores del Índice de Área Foliar, la productividad primaria neta aérea, las tasas de crecimiento e incremento y la respuesta en el rendimiento expresado en volumen, biomasa o carbono son parámetros indirectos que miden la eficiencia de los procesos fisiológicos en las especies. Conocer y comprenderlos en la arquitectura y dinámica de copa contribuyen a planear y ejecutar actividades silvícolas acordes a las necesidades particulares de cada especie o rodal. La aplicación de estos conocimientos se enfoca en el mejoramiento de las tasas de crecimiento e incremento de los bosques.

Palabras clave: aprovechamiento forestal, biomasa aérea, fisiología forestal, interacción árbol-suelo-atmosfera, manejo forestal, bosque de coníferas.

Introduction

The projection area of a tree canopy or stand canopy is the ground cover of foliage expressed in m^2 or percentage per unit area (Nakamura *et al.*, 2017). Coverage is determined by the growth habits of the species (tolerant and intolerant), the type of foliage (coniferous and broadleaved), and the position of each individual in regard to light exposure (north, east, south, and west), the shape of the crown (circular, symmetrical, asymmetrical, sparse, degraded, suppressed or damaged) and the density of individuals within the stand (underpopulated, without competition or overpopulated), or the structure of the vegetation with one or several strata (Gomez, 2010; Vogel, 2018; Givnish, 2020).

Crown characteristics are particular to each species, as they vary with age and social position of the individual within the stand, in addition to being influenced by the growth and expansion space of samples within the site (Parker, 1995). For example, Hess *et al.* (2016) estimated densities of 124, 177 and 500 individuals ha^{-1} by using mean values of crown projection area of 80.6, 56.4 and 20.2 m^2, respectively, for three growing sites with different conditions in Brazil for *Araucaria angustifolia* (Bertol.) Kuntze. Costa *et al.* (2016) determined percentages of differentiated crown proportion (Pc, %) for *Prosopis alba* Griseb. in Argentina of 74 and 65 % for dominant and suppressed trees by their position within the stand, respectively. When evaluating the health condition of forests in Mexico, Alvarado-Rosales *et al.* (2021) calculated for *Pinus* and *Quercus* genera -which are the most abundant within temperate forests- live crown percentages (Pcv, %), crown density (DenC, %), foliage transparency (TraF, %) and crown regressive death (Mreg, %) of 47.52, 46.27, 51.19 and 1.24 %, respectively, for the first genus; for *Quercus* they estimated 32.75, 44.29, 50.51 and 2.73 %, respectively, since the numbers change by genus and species, as well as by the geographic region where the trees grow (Vogel, 2018).

In addition, the dynamic interaction of the topographic conditions where the trees develop and the percentage of diffuse light that enters the site, the availability of nutrients in the soil and the litter, as well as the changing rate of regeneration under the canopy (Saldaña and Lusk, 2003). In a similar way, the morphology of the crown tends to flatten as the individual becomes longer-lived, has an average light demand or the status of the species in plant succession is persistent in the ecosystem (Vargas-Silva, 2019).

In intolerant gymnosperms, the branches of the lower parts are more likely to die because they are exposed to shade and present a loss of photosynthetic efficiency; thus, the tree tries to eliminate these branches and increase its growth in height, which favors its slenderness and conical shape at high densities (Nakamura *et al.*, 2017). This dynamic explains why the trees intercept around 98 % of the light inside the forest and maintain the foliage of the lower parts to capture the remaining percentage (2 %), which is not economically viable for the individual and favors self-pruning; this energy is used for other physiological functions (Vogel, 2018).

In this sense, the heterogeneous light and shade conditions within the stands tend to maximize photosynthetic rates, transpiration processes and improve the water balance of the trees (Pearcy *et al.*, 2005), however, these invariably decrease with their longevity (Thomas and Winner, 2002). For example, the maximum photosynthetic assimilation (A_{max} μmol m^{-2} s^{-1}) of *Alnus acuminata* Kunth decreases 2.89 μmol m^{-2} s^{-1} in an adult tree with dimensions between 6-15 m in total height (*At*) and 20-30 cm in normal diameter (*d*) (14.04 μmol m^{-2} s^{-1}) at a young individual between 10-12 m *At* and between 20-25 cm *d* (11.15 μmol m^{-2} s^{-1}), a situation that causes the elimination of lower branches, even when the species is tolerant to shade (González *et al.*, 2017).

The crown allows characterizing and quantifying the growth conditions of each individual, stand, forest or plantation (Allen, 2009; Aguirre-Salado *et al*., 2011; Castaño *et al.*, 2013; Givnish, 2020). It affects the understanding of forest dynamics (density dependence) and the influence of environmental factors such as water stress, architectural plasticity and genetic variation (Barthélémy and Caraglio, 2007; Vargas-Silva, 2019). The tree canopy is a dynamic interface between vegetation and atmospheric conditions, it is responsible for regulating the thermal variability and the available levels of CO_2 that create optimal habitats with specific microclimates for the proper development of the species (Penman *et al*., 2003; Schomaker *et al*., 2007).

The aforementioned dynamics positively or negatively influence the speed of physiological processes and ecosystem services, since it determines the percentage of photosynthetically active radiation that reaches or falls on a particular point under the canopy, temperature intervals within the ecosystem and water vapor pressure, which together influence the biochemical processes of trees and the biogeographic processes of the soil (Parker, 1995; Anhuf and Rollenbeck, 2001; Fauset *et al*., 2017; Nakamura *et al*., 2017).

In this context, under drought conditions, water stress is produced in the trees, which negatively alters the various eco-physiological and functional processes of the canopy; consequently, the growth of the species decreases (Valladares, 2004), or else, in stands with light intensities less than 2 %, the net yield is inactivated and competition in the undergrowth is suppressed, which also negatively affects the site (Vogel, 2018).

Crown architecture and canopy structure are the visible morphological response of trees to the dynamic interaction with the biogeographic characteristics of the site and the genetic load of each species (Rodríguez *et al*., 2008; Givnish, 2020). The morphological design of the crown and the distribution of the canopy define the different speeds in the processes of growth and stand yield, biomass production and carbon sequestration (Vidal *et al.*, 2004; Ruiz-Díaz *et al.*, 2014), acclimatization to thermal variation or extreme conditions of water deficit and adaptability to hydrometeorological phenomena (Castelli I Puig, 2002; Nunes *et al*., 2019).

In terms of forestry management in forests of temperate climate species, the dimensions of diameter and crown length must be taken into account, in addition to characteristics such as projection surface, extension, shape, proportion and indices of growth amplitude and projection (Costa *et al.*, 2016; Hess *et al*., 2016). This is explained because age and environmental factors influence tree morphometry and nutrient assimilation rates (productive capacity) (da Cunha and Finger, 2013). Therefore, understanding the interaction of the physiological processes within the trees, favors a better application of the activities of monitoring, technical management and use of the forest resources, since the silvicultural practices would be programmed according to the needs of the forest mass (Leite *et al*., 2012; Hess *et al.*, 2016).

In this sense, understanding that the vegetative activity (AVeg) of a tree is determined by the amount of Nitrogen (N) in the soil and the production of sap (PS) by the carbohydrates produced in the foliage, leads to pruning apply when PS<Aveg, if growth is vigorous and the individual is young (2-7 years, or 2-3 m) (Basantes, 2016). In temperate climate forests, the opening of stand spaces should be carried

out to ensure that the light intensity that enters the site is greater than 1 % for the most tolerant species, since it is the minimum value necessary for the species to photosynthesize and soil dynamics does not stop (Basantes, 2016; Vogel, 2018). In monitoring activities, the indirect evaluation of the physiological response of the foliage can be observed through digital images, which allows an early detection of trees damaged by pests or diseases, to plan a control and to give timely management to the affected forest (Leautaud and López-García, 2017).

The length, extent, diameter, and crown volume in a tree are indirect indicators of photosynthetic respiration rate and transpiration capacity (Sprinz and Burkhart, 1987; Hess *et al*., 2016; Givnish, 2020). For example, in species with monolayer crown architecture such as *Pinus*, *Cupressus* or *Abies*, they have a photosynthetic yield per unit area for optimal carbon consumption of less than <0.75 μmol CO_2 s^{-1}, while multilayer species such as those of the *Quercus*, *Alnus* or *Tilia* genera present yields between 1-2 μmol CO_2 s^{-1}, but the former with a higher carbon absorption rate (>0.5-<0.8 μmol CO_2 s^{-1} cost of foliage^{-1}) than multilayer species (<0.35 μmol CO_2 s^{-1} foliage cost^{-1}) (Givnish, 2020).

The incidence and speed of light assimilation that translates into the photosynthetic capacity of the trees vary between species, site conditions or growth habits (Vogel, 2018; Givnish, 2020); can be estimated indirectly through the leaf area index (*LAI*), which largely expresses the growth and productivity of forest masses (Lang *et al.*, 2010; Leite *et al*., 2012; McIntosh *et al.*, 2012); additionally, these indicators help to program the forestry activities that must be contained in a forest management program (Hess *et al*., 2016).

From the importance of the crown in the regulation of the biological mechanisms and interactions of the forest masses, the objective of this contribution is to document, in a general way and in a first approach, the effect of the physiological processes of photosynthesis, respiration and transpiration of the tree in the crown architecture and its relevance for the management of temperate forests.

Development and Discussion

Allometry is the functional relationship between the size of parts of organisms or that of these parts with the speed of biochemical processes, which can be represented mathematically between parts or be referred to an individual or complete physiological process (Niklas, 1994; Gutiérrez and Sánchez, 2017).

For example, large, dense crowns and high leaf area indices are an indirect indicator of efficient photosynthesis rates and accelerated growth (Salas and Infante, 2006), while, in general, small crowns with little foliage indicate low productivity, higher susceptibility to damage by storms, winds, temperature variations due to its low mechanical resistance and up to a certain level to tolerate the attack of pests or diseases for developing in an unfavorable condition for the species (Zaragoza *et al*., 2014), in both cases as consequence of climatic and soil conditions (Li *et al*., 2015).

The allometric relationship between the normal diameter, the diameter of the stump or the total height of a tree with the amount of aerial biomass of the tree (stem, branches and foliage), productivity and carbon absorption capacity (C), allows estimating yield in forests (Castañeda-Mendoza *et al.*, 2012; Hernández-Ramos *et al.*, 2017). For this purpose, the biomass (B) that the trees incorporate and fix over time is evaluated, considering the energy losses due to respiration estimated as aerial net primary productivity (PPNA), without taking into account the capture of CO_2 and the production of oxygen or gross primary productivity (GPP) (Clark *et al*., 2001; Li *et al.*, 2014).

The PPB and PPNA are the product of the physiological activities of the crown, they present changes due to variations in the foliage and are modified by the effect of the climate (Li *et al*., 2014; Hernández-Ramos *et al.*, 2017). In this sense, young stands have higher aerial net primary productivity, which tends to decrease with age (Tuner *et al.*, 2009). In temperate regions, foliage production is stimulated by temperature (leaf production in warm seasons and foliage drop in cool seasons). In fact, both dynamics are influenced by age, the availability of water in the soil, the photoperiod and the amount of solar radiation (Manzo-Delgado and Meave, 2003).

The responses of the architecture and dimension of the crown are the result of metabolic processes that involve the plant-soil-atmosphere relationship (*e.g.* photosynthesis and transpiration), phenological state of the vegetation, soil moisture content and cover density that, in an integral way with the age of each individual, determine the growth rates and performance of the ecosystem (Manzo-Delgado and Meave, 2003). The relationships between biophysical parameters and vegetation indices, for example, the Normalized Difference Vegetation Index (*NDVI*) or the photochemical reflectance index (*PRI*), are physiologically sensitive to the chlorophyll content and the epoxidation state of the cycle pigments of xanthophylls and photosynthetic efficiency (Hernández-Clemente *et al.*, 2011). For this reason, they can be used to evaluate the structure of native forests or plantations through the spectral behavior in different plant communities and climatic regions or determine the level of productivity in a forest stand or plantation (Manzo-Delgado and Meave, 2003; Garrido *et al*., 2017; Hernández-Ramos *et al.*, 2017), as well as its process of forest decline (Granados-Sánchez and López-Ríos, 2001; Allen, 2009).

Forest decline is the gradual deterioration of trees manifested by the loss of vigor, color, malformation and reduction of foliage (Granados-Sánchez and López-Ríos, 2001), which negatively impacts the water, C and nutrient cycles, it directly affects the ecophysiological dynamics and the regulation of the biochemical processes of the forest masses (Nakamura *et al.*, 2017). This physiological phenomenon can be avoided, to a certain extent, through appropriate and differentiated silvicultural practices for each species, growth condition or climatic region of the plant community, as well as through the execution of monitoring activities to continuously evaluate the state of the plant tree health and timely mitigate the presence of pests, diseases or fire outbreaks. The foregoing under the premise that climate is the engine of growth and the main responsible for mortality in forests (Allen, 2009).

Through the photochemical reflectance of the color of the canopy, it is possible to evaluate the water stress of the trees in forests or forest plantations with an acceptable precision (>0.40-<0.60) at low cost and in a short time; this stress is the result of stomatal closure, the reduction in the transpiration rate and the increase in leaf temperature (Hernández-Clemente *et al*., 2011). The combination of geographic information systems (GIS) with in situ visualization of the canopy can be applied in forest management for early detection and mitigation of the effects caused by forest decline, whether due to water stress (Granados-Sánchez and López-Ríos, 2001; Navarro *et al*., 2004), presence of pests and diseases (Otaya *et al*., 2006; Leautaud and López-García, 2017) or damage caused by forest fires (Madrigal *et al*., 2009).

The fall of leaves from trees is the physiological response to water stress determined by the climate (Di Stefano and Fournier, 2005), it is essential for the circulation of nutrients that maintains soil fertility in ecosystems (Marmolejo *et al*., 2013) and can cause a decrease in forest productivity (Allen, 2009). Therefore, it is essential to understand the plant-atmosphere interaction to propose forestry activities aimed at increasing the productivity of forests or forest plantations.

Managing density (number of trees per unit area) by manipulating canopy structure is critical to maintaining consistent growth and increasing yield. It can be affirmed that the fertilization of stands and the homogeneous distribution of the trees, which generates 100 % occupancy, encourages the volatilized Nitrogen (N) to remain in the site and not reduce its productivity (Penman *et al*., 2003). This basic aspect positively influences the amount of diffuse light that enters the site, the availability of nutrients in the soil and litter, as well as the regeneration of the stand (Saldaña and Lusk, 2003). While, at a young stage of vegetation, depending on the species or species within the stands, there is a greater capture and assimilation of C, which is reflected in a higher photosynthetic rate and accelerated growth (Tuner *et al.*, 2009), as long as the stand does not have an overpopulation that leads to an imminent death of the trees.

The crown architecture is fundamental in the dynamics of forest growth and productivity, since it is a response to physiological processes and interaction with the environment, so it must be taken into consideration to plan, execute and manage forestry activities in forests or forest plantations.

Hess *et al.* (2016) point out that the crown projection area is a reliable indicator of the response of trees to silvicultural interventions and that, within the stand, the small projection areas due to the architecture of the length, width and breadth of the canopy in the trees that make up the canopy as a result of self-thinning, are a characteristic of lower growth and a reduction in the photosynthetic rate, due to the lack of light , expansion space and competition for nutrients.

The biotic and abiotic factors of the site are determining factors in the width and length of the crown; its morphometry is dynamic with age and is constantly changing with density (Condé *et al.*, 2013). In young trees, growth in height is greater than lateral growth, which induces the conical shape of the canopy, which translates into lower photosynthetic assimilation and productivity (Lang *et al.*, 2010; Condé *et al*., 2013). For this reason, the control of the number of trees per surface unit through thinning is essential in technical management activities and in yield projections (Basantes, 2016).

Crown morphometry is flexible to growth conditions (Lang *et al.*, 2010). For example, in *Alnus acuminata* the ratio between the light energy transmitted to a depth of the canopy and the light energy at the top of the canopy decreases exponentially from 0.7 lumen (lm) to 0.3 lm as the value of *IAF* increases; furthermore, leaf insertion angles change from a lower stratum (39.6°) to a tree growing in a middle stratum (37.8°) as a result of intraspecific site competition (Castaño *et al.*, 2013). Castelli i Puig (2002) describes how in *Quercus ilex* L. the percentage of dry crown ($\%C_{dry}$) increases as the volume per hectare increases within the oak forest, going from a $\%C_{dry}$<40 with 51 m^3 ha^{-1} in the stand at 70 % C_{dry} when there are about 160 m^3 ha^{-1} due to the effect of drought and a water deficit of the trees. Whereas, Costa *et al.* (2016) describe how the height of the clean stem (*Afl*) and the average dimension of the crown change in *Araucaria angustifolia* with respect to the vertical dominance that the tree has within the site, when passing from an *Afl* from 19.1 m in dominant individuals to 15.9 m in suppressed trees, while the average crown dimension for the former is 22.3 m and for dominated trees 13.0 m. In any of the cases described, it has been consistently observed that the diameter is the first dendrometric variable that is affected by competition and the one that indirectly influences its dimensions, the decrease in foliage photosynthetic efficiency, the rate of current increase, growth rate and productivity level (Sanquetta *et al.*, 2014; Rodríguez-Catón and Villalba, 2018).

From the importance of crown morphometry in the biology of forest growth, it is proposed that in forestry management, characteristics of shape (*e.g.* circular, symmetric, asymmetric, sparse, degraded, suppressed or damaged), dimension (diameter, length, projection area, proportion of crown and cover) and indexes (protrusion or amplitude) to establish the first forestry interventions such as thinning (Basantes, 2016; Costa *et al.*, 2016; Hess *et al*., 2016).

The shape-dimension relationship expressed as the crown proportion in percentage ($pc\%$); $pc\% = \left({}^{ec}/_{At}\right)100$, where ec refers to the crown extension determined by the difference of the $At - crown\ insertion\ height\ (Aic)$, it is an indicator that reflects the load capacity of the site and the intra and interspecific competition for light, space and nutrients, aspects that can suggest guidelines in the management of the forest mass to establish forestry treatments that regulate the density or evaluate the response of the applied silvicultural activities (Lang *et al.*, 2010; Hess *et al.,* 2016). However, even today, the aforementioned crown characteristics remain little explored and used for forestry management of natural forests (Hess *et al*., 2016), forest plantations (Leite *et al.*, 2012) and urban parks (Zaragoza *et al.*, 2014).

To apply knowledge about the attributes of the crown in terms of technical management to stands, it is essential to understand the dynamics of its dimensions, such as radius (*rd*), diameter (dc), projection area (*Apc*) and crown extension (*ec*), in addition to its form expressed with the amplitude index: $ia = dc/At$ or outgoing index: $is = \frac{dc}{d}$, as well as the characteristics that correlate with its foliar functionality by stratum, represented by Pc%. All these are criteria that define the architecture of the crown, and also contribute to understanding the influence on the processes of absorption of solar radiation, temperature in the tree and the concentration of water vapor and CO_2 in the sub-stomatal chamber of the leaves (Ross, 1981; Castaño *et al.*, 2013).

However, the application of the aforementioned attributes is still difficult and impractical, since for most forest managers the understanding of how the physiology of the tree and the interactions with the environment determine the transpiration rates in the forest is irrelevant or complex, trees, the cellular elongation of plant structures in foliage, branches, stem and root. Consequently, they have little clarity on how they impact the dynamics of growth and increment with respect to age and tree competition.

Quantitative forestry support tools have been generated for the technical management of natural stands or plantations of some forest species. For example, morphometric indices are proposed that quantify the significant effect between age and the stratum where *Alnus acuminata* trees grow with the leaf insertion angle, which indicates that as the insertions become more horizontal, the rate of growth is reduced (Castaño *et al*., 2013), which can be considered as a reference in the application of thinnings. Another example is the equations proposed to quantify the relationship height to the base of the crown as a function of the normal diameter, or the expressions to estimate the maximum width of the crown and the height above the stem of the maximum width point of the diameter of the crown, depending on the total height and the crown ratio (crown length/total height) for *Pinus sylvestris* L., relations that can be used to develop structural and competition indices for individual trees (Domínguez *et al.*, 2006).

In a similar way, models have been proposed that quantify through the dimensions of the crown, the influence of the planting location, the age of the stand and the meteorological elements in the dimension of the normal diameter for *Acacia mearnsii* De Wild. in order to evaluate the capture of C (Sanquetta *et al*., 2014), as well as to select optimal places for the establishment of forest plantations. Expressions have also been developed that simulate competition between individuals in *Araucaria angustifolia* in which the dimensions of the crown can be the guideline for the application of thinnings (Costa *et al.*, 2016).

In other approaches, the dimensions of the crown have been taken as a reference for the selection of genetic material for the purpose of ecosystem restoration or for the establishment of plantations, according to its growth and adaptability, of provenances in *Pinus greggii* Engelm. ex Parl. (Rodriguez *et al.*, 2008), or to evaluate fragmented stands in *Araucaria angustifolia*, where a differentiated technical management can be proposed based on the specific morphometric characteristics of the trees (Hess *et al.*, 2016).

The projections of leaf area index and tree cover can be used to estimate the timber stock per hectare and classify the managed stands by productivity level. Aguirre-Salado *et al.* (2011) worked with *Pinus patula* Schltdl. & Cham., as well McIntosh *et al.* (2012) with *Acer macrophyllum* Pursh, *Alnus rubra* Bong., *Fraxinus latifolia* Benth., *Pinus contorta* Douglas ex Loudon, *P. ponderosa* P. Lawson & C. Lawson., *P. monticola* Douglas ex D. Don, *Populus* spp., *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus* spp., *Sequoia sempervirens* (D. Don) Endl. y *Tsuga heterophylla* (Raf.) Sarg., in order to assess applied forestry treatments and adapt forest management programs according to the particular response of each stand.

With another approach, crown profile models have been developed and adjusted (Poudel *et al*., 2021) that can be used as competition indices dependent on the size of the crown, as well as taken as a reference in the application of thinnings with the purpose of optimize the occupation of the stand and increase the growth of each individual. This is proposed by Crecente-Campo *et al.* (2007) for *Pinus radiata* D. Don and Soto-Cervantes *et al.* (2016) for *Pinus cooperi* C. E. Blanco.

In Mexico and Latin America, the development of this type of tools is still partial. In addition, professionals in charge of the management and use of forest resources have a chance to achieve a full understanding of the dynamics of the crown for its practical application in the technical management of stands.

To understand the dynamic and integral aspect of plant growth and the forms of its structures in temperate climate forests, it is essential to know: i) the types of stem growth by species (*e.g.* indefinite, defined, monopod or sympodium), ii) the type of branching of the crown when they are mixed forests or broadleaf species, (*e.g.* sylleptic or cataleptic), and iii) the direction of growth of the stem and branches as a whole as the response of each plant structure to unfavorable conditions and development habits (*e.g.* orthotrophs or plagiotrophs), and types of phyllotaxy of each species (*e.g.* alternate, opposite, whorled or fasciculated) (Perreta and Vegetti, 2005).

The control of the light intensity in the stands by manipulating the crowns through pruning or thinning must be carried out in the early stages of formation and aggregation of the basal tissue of the stem (Corvalán, 2017). For example, for intolerant conifers such as *Pinus*, applying these silvicultural treatments at these stages (*e.g*. thicket, *vardascal* or pole), will have a positive effect on the quality of the wood and on the basimetric area of the stand, consequently, it will be reflected in a higher economic income at the time of the timber harvest (Larson *et al*., 2001).

Schoelzke (2003) demonstrated how plantations of *Pinus elliottii* Engelm. with an age of five years in which thinning and pruning were applied, they had 30 % more increase in the normal diameter with respect to plantations that were not thinned or pruned. In addition, he indicated that the tree should not be pruned in more than 30 % of the total height, since the increase decreases.

Ferrere *et al.* (2015) recorded for 13-year-old *Pinus radiata* plantations, which were thinned with a 50 % cutting intensity and without pruning, that the volume is greater (74.4 m^3) than when applying the same cutting intensity, but with pruning (64.6 m^3); however, for the first case, only 46 % of this volume was in dominant trees. López and Caballero (2018) showed that the programming of a thinning cut in *Pinus patula* plantations, based on the net primary productivity (PPN), was fundamental for the opening of growth spaces in order to obtain a yield in volume of 120.14 m^3 ha^{-1} and with this an increase in volume of 38.9 m^3 ha^{-1} $year^{-1}$ was propitiated. However, the response to these factors may vary depending on the altitudinal gradient, ontogeny of the species and topographic and edaphic characteristics of the site (Puntieri *et al*., 2013) or the adequate application of the treatments.

The natural elimination of branches reduces the dimensions of the canopy, generally forms clean stems (which is a variable characteristic in each species), favors the entry of light for plants from lower strata and allows to reduce costs in the application of cultural tasks (Mäkelä and Valentine, 2006). This mechanism is the result of branches being support structures and hydraulic conductivity between root, stem and active foliage, but when the latter reduces the photosynthetic rate, the tree tends to shed leaves and branches together, which has an impact on timber yield, which is limited by the size, insertion angle and ontogenetic age of branches and foliage according to their vertical position within the crown (Garber and Maguire, 2005; Lowell *et al.*, 2014; Corvalán, 2017).

In shade-intolerant species, such as most pine trees (Gil and Aránzazu, 1993; Smith *et al.*, 1993; Rubio-Camacho *et al.*, 2017), in the seedling to pole stage, the canopy is narrower that in a stage of stem development, the orientation of the first-order branches with respect to the stem is ascending at angles less than 45°, which causes a rapid growth in height to subsequently expand the crown and dissipate the excess heat that is absorbed by direct exposure to solar radiation (Roeh and Maguire, 1997; Castaño *et al.*, 2013; Nelson *et al*., 2014; Vogel, 2018). In medium strata, the crown has branches with angles greater than 45° to improve light capture and make foliage photosynthetic processes more efficient (Poorter *et al.*, 2006; Interián-Ku *et al.*, 2009).

According to the previous concepts, by virtue of the fact that the dynamics and architecture of the crown are a reflection of the genetic constitution and the physiological processes in the species over time, and indirectly of the environmental, edaphic, topographic and competition factors of each growth condition, the characteristics of the crown such as diameter, length, shape, leaf density, angle of insertion of the branches or the ontogenetic age of each level in the foliage, should be taken into consideration for the choice of species, planning forestry establishment and management of forests, plantations, agroforestry or silvopastoral systems, as well as to promote greater efficiency of forestry activities.

In addition, it would be desirable not to lose sight of the fact that the constant updating of this knowledge and its applicability within technical forest management are essential, since the paradigms continue to be redesigned with the discoveries about the dynamics of the canopy and the intra and interspecific interactions in ecosystems (Givnish, 2020).

Conclusions

The dynamics and architecture of the crown with respect to age in temperate forests are complex phenomena that vary depending on the species, climate of each region, soil conditions, humidity and characteristics of the site where the forest masses develop. However, their understanding is vital for forestry management because they determine photosynthetic rates, CO_2 assimilation speed, growth dynamics and, in general, productivity in forest species or ecosystems.

It is essential to understand the role of physiological processes in the architecture and dynamics of the crown in order to correctly plan and apply technical management activities according to the particular needs of each species, stage of development or growth condition, whether in natural or protected forests or forest plantations. This represents an essential component of the biological basis for assessing and quantifying increased growth and productivity of stands.

Even when there is particular information to understand the interactions of the canopy with the atmosphere and soil, there is a need to quantify the soil-plant-atmosphere interaction through allometric relationships, generation of equations or process descriptions. Based on the results that are generated, propose guidelines, intervals or intensities to apply specific forestry practices such as pruning, thinning or harvesting by taxon of commercial interest. This may contribute to improving the efficiency of the physiological processes of the species managed in temperate forests, as well as reducing susceptibility to pests and diseases, all of this to help increase forest productivity and generate greater financial returns with the reduction of rotation times in forest exploitation of natural stands or plantations, as well as agroforestry or silvopastoral systems.

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Conflict of interests

The authors declare that they have no conflicts of interest.

Contribution by author

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