Allometric models for the estimation of foliage area and biomass from stem metrics in black locust

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Allometric equations relating trees’ vascular system and other stem metrics with foliage area and mass are important to estimate their growth, carbon stocks and interactions with abiotic environment in terms of carbon and water balance. In this study we focused on Robinia pseudoacacia restoration plantations in Greece and aimed at establishing species-specific models to predict foliage leaf area and biomass based on stem traits. In particular, we evaluated stem cross-sectional areas of sapwood, current sapwood and total stem (sapwood and heartwood), measured at different tree heights, as predictors of leaf area and mass, based on the pipe model theory. Furthermore, we assessed the variation in the ratios of leaf area to different stem cross-sectional areas across the tree profile and we examined the relationships of diameter at breast height (DBH) with diameter at the base of the live crown and with leaf area. Taking into account the trees’ DBH distribution according to the plantations’ inventory, 25 black locust individuals were destructively sampled and the relationships among the studied traits were analyzed by means of multiple and simple linear regression at p<0.001. Foliage dry mass and area were best predicted by total stem cross-sectional area at mid-bole and stump height ($R^2=0.81$), followed by current sapwood area at stump height ($R^2=0.74$), which outperformed the most often used sapwood area ($R^2=0.70$). DBH was also reliably estimating tree leaf area ($R^2=0.72$) but was less precise, compared to total cross-sectional area, while it was a useful proxy of diameter at the base of the live crown ($R^2=0.80$). In line with the pipe model theory, the ratio of leaf area to total cross-sectional area declined across the canopy basipetally, but only when total cross-sectional area was considered. Deviations from the sapwood-foliation functions described by the pipe model theory may be due to the small sample size and the variability in tree size in such developing restoration plantations. The produced species-specific relationships between stem and foliage metrics may be a useful tool to predict the carbon sequestration and climate change adaptation potential of black locust restoration plantations, which are often characterized by harsh site conditions.

Keywords: Sapwood Area, Current Sapwood Area, Total Cross-sectional Area, Diameter at Breast Height, Diameter at Live Crown Base, Leaf Area, Foliage Dry Weight, Robinia pseudoacacia

Introduction

In a broad sense, allometry describes how the characteristics of living organisms change with size (Singleton 2010) and it refers to the analysis of logarithmic-transformed size data by means of linear regression (Pretzsch & Dieler 2012). Allometric models are widely needed in forestry for the estimation of tree dimensions that are difficult to measure directly, such as crown leaf area and mass, above-ground biomass and others, based on easily assessed traits like diameter at breast height. These allometric equations are typically built through the destructive sampling of trees that have been felled to measure the desired parameters. Allometric relationships to estimate wood and foliage biomass are of high priority for reliable ground-based monitoring of carbon storage in forest ecosystems, for assessing their climate change mitigation potential and applying forest management resilient to climate change (Chave et al. 2014, Chojnacky et al. 2014, Duncanson et al. 2017, Cunliffe et al. 2020).

In addition, allometric models for estimating canopy leaf area are vital, given the direct connection of leaf area to photosynthesis, transpiration and respiration and, thus, to the productivity and water balance of forest stands (Baldocchi et al. 2002). Relationships between trees’ hydraulic architecture and their physiological processes are based on the principle that water flow within the tree takes place through an assembly of pipes and is controlled by physical processes (Tyree & Ewers 1991). The...
conductive tissue of a tree has been coupled to its photosynthetic area and biomass by the Pipe Model Theory (PMT – Shinozaki et al. 1964a, 1964b) supporting that a given amount of leaves is associated with a constant amount of downward continuation of pipes that supply the leaves with water and nutrients. As it has been comprehensively reviewed by Lehnebach et al. (2018), PMT has offered a conceptual framework to explain biomass allocation to the foliar versus stem compartments and to estimate a plant’s or stand’s foliar area or mass. Several allometric relationships between foliar and root dimensions and sapwood area are based on PMT (Vertessy et al. 1995, McDowell et al. 2002, Gienciala et al. 2006, Chojnacky et al. 2014, Cruickshank et al. 2015, Caldwell & O’Hara 2017). However, many variations from the theory’s basic properties were revealed when tested for a range of species under varying growth regimes. Therefore, the ratio of foliage area to sapwood area has been found to change within a forest tree species with developmental stage, site microclimate and quality, species-mixture, stand density and applied silviculture (Ogawa 2015, Lehnebach et al. 2018 and literature therein). Although allometric models relating forest trees’ leaf area and dry weight to their vascular system are essential for forest management, carbon stocks monitoring and forest ecosystems ecological research, they are scarce as their development and testing depends on destructively sampled data, which are laborious and time-consuming to acquire. Thus, studies that develop allometric functions to estimate foliage area and mass by tree diameter or sapwood area which can be measured with non-destructive measures are valuable. In this context, we focused on the calibration of such relationships for Robinia pseudoacacia L. (black locust), a forest tree extensively used for restoration purposes.

Black locust is a hardy tree species, native to North America, which appeared in Europe in the beginning of the 17th century where is considered as alien and invasive (Vítková et al. 2017). However, it is naturalized in several Mediterranean and temperate regions (Vítková et al. 2017, Nicolescu et al. 2020). Black locust has wood of high natural strength, used for several purposes such as fuel, mine timbers, fence posts, railroad poles, boards, timber (De-Gomez & Wagner 2001). Most importantly, black locust is extensively used for carbon sequestration and restoration of heavily degraded lands (Annighöfer et al. 2012) in several countries, such as China (Kou et al. 2016), Germany (Böhm et al. 2011), Greece (Spyroglou et al. 2021), Italy (Mercurio et al. 2018) and others, due to its beneficial traits. *R. pseudoacacia* has low nutrient requirements as it is an N-fixing woody legume (Liu et al. 2020, Annighöfer et al. 2012), it is fast-growing and drought-tolerant (Carl et al. 2017, Vítková et al. 2017, Nicolescu et al. 2020, Nola et al. 2020) and it spreads rapidly by root-suckers (Cierjacks et al. 2013). Black locust grows intensively in height for the first 10-15 years and can reach mean or dominant heights of over 20 m at 20 years (Nicolescu et al. 2020). The species also exhibits rapid diameter growth of 3-4 cm in the first years under optimal conditions, while the peak of diameter growth may be observed sooner than 20 years even at poor sites (Nicolescu et al. 2020). For example, at a rehabilitated former lignite mining area in Germany, the biomass of black locust peaked at the age of 14 years (Grünewald et al. 2009).

Within the present study we aimed to establish and evaluate different relationships of tree foliage area and dry mass with xylem, sapwood and other stem metrics in *R. pseudoacacia*. Specifically, our objectives were to: (i) establish and evaluate species-specific allometric equations for *R. pseudoacacia* for the estimation of foliage leaf area and dry biomass based on the cross-sectional areas of sapwood, current sapwood and total stem (sapwood and heartwood) measured at different tree heights; (ii) assess the variability of the ratio of foliage area to stem cross-sectional areas across the tree profile; (iii) test whether diameter at breast height could be a reliable predictor of the leaf area and diameter at the base of the tree’s live crown.

**Materials and methods**

**Study area**

The study took place at the restoration plantations of *R. pseudoacacia* established for the rehabilitation of open-cast lignite mines of the Hellenic Public Power Corporation (HPPC) in NW Greece, which cover a total area of about 2,570 ha. The lignite center comprises two restoration sites, Amyntaio (788 ha; 40°33’36” – 40°36’36” N, 21°37’12” – 21°41’24” E) and Ptolemaida (1780 ha; 40°23’24” – 40°30’36” N, 21°41’60” – 21°53’24” E) with a distance of approximately 15 km among them (Fig. 1). The altitude of the two sites ranges from 530 to 950 m a.s.l. (Spyroglou et al. 2021) and they both grow on depositions produced by the lignite mining activities of

![Fig. 1 - Location of the study area (lignite center of the Hellenic Public Power Corporation) in NW Greece, comprising the two black locust restoration plantations in Amyntaio and Ptolemaida (inner plots).](image-url)
Fig. 2 - Tree diameter at breast height (DBH – a) and height (b) distribution of the black locust plantations inventory for Amyntaio (left), Ptolemaida (center) and both sites together (right). Data are obtained from 214 inventory plots. The dashed blue lines indicate the mean DBH and height of the trees.

Tree harvest and biometric traits determination

Given the similar characteristics of the two restoration plantations of HPPC (climate, vegetation, planting history, substrate, tree height and DBH distribution), black locust trees from both sites were destructively sampled (10 from Amyntaio and 15 from Ptolemaida, considering the larger area of the latter) and pooled together. In total 25 R. pseudoacacia trees were destructively sampled during the growing period of 2019 and 2020. The DBH distribution of the plantations (Fig. 2, Fig. S2 in Supplementary material) was taken into account for the selection of the trees to be harvested. However, although the mean arithmetic DBH was within the 5-10 cm class, trees with DBH of the next class (10-15 cm) were also included to avoid building an allometric model that would underestimate above-ground biomass by depending solely on the smallest DBH class. The number of harvested trees with DBH > 15 cm was small, as these were less frequent (Fig. 2) and in most cases not easily accessible. The selected trees were healthy, not suppressed individuals, without apparent tree defects, such as being forked, cracked, bent or crooked.

For each selected tree, measurements of DBH (with a diameter measuring tape) and length/height (with Spencer loggers tape) were performed. After harvest, the determined biometrical traits comprised diameter at stump height (at 0.3 m height), length and diameter at the middle of the stem (mid-bole), the base of the live crown, at 1/3 and 2/3 of the crown. Stem disks, about 10 cm thick, were sampled at all above-mentioned stem sections for the estimation of cross-sectional areas (see below). The fresh weight of the whole crown, separated into thirds was determined in the field using an electronic balance with 100 g accuracy. Dead and epicormic branches were weighed separately from the live crown. The whole crown was taken to the laboratory, foliage was separated from branches and pods and all parts’ dry weight was determined after they were oven-dried at 80 °C until constant weight was reached. In order to estimate foliage leaf area, 30 leaves from the upper, middle and lower crown (90 leaves in total) were collected in the field, put in plastic bags in a cool box and transferred to the lab for leaf area and dry weight determination. Based on the collected leaves’ ratio of dry weight to leaf area, the respective area of foliage at the three parts of the crown, as well as of the total crown, were calculated.

Leaf area and area of stem compartments

The collected leaves and stem discs were scanned (Epson 11000XL, resolution 200 dpi) to calculate the leaf area (LA), the area of sapwood (SAPA), current sapwood (CSA) and total cross-sectional area (STA) of the stem. The current sapwood area was defined as the cross-sectional area of the penultimate growth ring and the early wood portion of the current year’s growth ring, according to Meadows & Hodges (2002). After digitizing the leaves, the im-
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age files were used to calculate the area of each leaf with the software LAFORE (Leaf Area FOR Everyone – Lehsten 2005). The image files of stem discs were used to calculate their above-mentioned cross-sectional areas with ImageJ (Schneider et al. 2012).

**Data analysis**

For all variables, the Levene test was used to confirm the homogeneity of variances and the suitability of parametric tests to identify the homogeneous groups between the different height sections along the stem profile. An ANOVA was performed to check for statistically significant differences between the height sections along the stem profile for each of the independent variables (sapwood area, current sapwood area, total cross-sectional area of the stem). Tukey’s HSD test was used to investigate homogeneous groups. Simple linear regression was applied to identify the relationships between either leaf area (LA) or foliage dry weight (FDW) and the independent variables. Multiple linear regression analyses were also run to test whether the inclusion of additional variables, such as age at the breast height, total tree height, crown length (CrLen) and crown ratio (CR) in the linear models increased the accuracy of estimation of LA and FDW. Statistical analysis was conducted with R programming language (R Development Core Team 2014).

**Results**

**Descriptive characteristics of felled trees**

Mean age of the harvested trees was 14 years, ranging from 4 to 25 years, reflecting the tree age variation of the restoration plantations of HPPC. Mean height and DBH of the trees were 11.93 m (range: 6.10-17.80) and 11.33 cm (range: 4.30-22.10), respectively. The distribution of the DBH and height classes of the felled trees is shown in Fig. S2 (Supplementary material).

The mean sapwood area, current sapwood area and total cross-sectional area were 30 cm$^2$ (10.28-81.64), 9.07 cm$^2$ (2.71-24.20) and 83.81 cm$^2$ (10.28-272.68), respectively. The analysis of the crown showed that mean LA was 25.20 m$^2$ (7.8-101) and mean FDW was 1.87 Kg (0.6-8.1). The average CrLen was 5.15 m (3.35-8.10), while the mean CR was 0.45 (0.30-0.76).

**Relationships between crown traits and cross-sectional areas of the stem**

The multiple linear regression analyses for the estimation of foliage area and mass, based on the combination of several independent factors, resulted in models of lower accuracy than the simple linear regression ones (data not shown). Thus, we focused on simple linear regression analyses.

The regression models predicting LA and FDW from the different stem cross-sectional areas along the tree profile are presented in Tab. S2 (Supplementary material). Among these, the strongest models, having the higher $R^2$ coefficients and smaller MSE values, are depicted in Fig. 3 and Fig. 4 for LA and FDW, respectively. STA at middle bole was the best estimator of both LA and FDW, as indicated by the lowest standard errors and the highest $R^2$ coefficients (Fig. 3A, Fig. 4A) among all tested models. The next best estimator of LA and FDW was the CSA at stump height (Fig. 3B, Fig. 4B), followed by SAPA at stump height (Fig. 3C) and at 1/3 of the crown height (Fig. 4C).

**Fig. 3** - Linear relationships between leaf area (LA) with STA at mid bole (A), CSA at stump height (B) and SAPA at stump height (C). The regression models, their coefficients (adjusted $R^2$) and standard errors (RMSE) are presented (n=25).

**Fig. 4** - Linear relationships between foliage dry weight (FDW) and STA at mid bole (A), CSA at stump height (B) and SAPA at 1/3 of crown height (C). The regression models, their coefficients ($R^2$) and standard errors (RMSE) are presented (n=25).
Ratios of leaf area to cross-sectional areas of the stem

LA/STA differed significantly among the different section heights across the tree profile (F = 7.39, p<0.001) and it presented a constant decreasing pattern from the crown to stump height (Fig. 5A). LA/CSA also differed significantly among section heights (F = 3.6, p<0.01 – Fig. 5B) and it was the highest at the base of the crown and at middle bole. Finally, there were no statistically significant differences in the LA/SAPA ratio between the section heights (F = 1.91, p = 0.095). The ratio only tended to be higher at the base of the live crown and at stump height (Fig. 5C).

Relationships between leaf area, DBH and diameter at the base of the live crown

The square of DBH was the best estimator of LA having the highest R² (0.72) and the lowest SE (11.7 – Fig. 6A) among all tested diameters at different heights (see Tab. S3 in Supplementary material). Moreover, Dhlc² could be reliably determined by DBH², as indicated by the strong relationship shown in Fig. 6B.

Discussion

The estimation of forest trees’ leaf area is important for the assessment of their productivity and interaction with the environment, as foliage is actively involved in tree and ecosystem carbon and water balance (Baldocchi et al. 2002). Furthermore, foliage reflects the amount of trees’ assimilatory tissue and is the main driver of C storage in forests. Thus, assessing foliage dry weight is crucial for the calculation of carbon stocks in this pool. However, the accurate determination of these foliage traits in the canopy of tall forest trees is often difficult and rather laborious. Therefore, the estimation of tree foliage leaf area and dry weight based on different stem dimensions is a helpful tool for forest management and ecosystem research. In this study, we evaluated various linear allometric models relating stem’s cross-sectional areas (total sapwood and heartwood area, sapwood area, current sapwood area) at different heights across the tree profile (stump height, DBH, middle bole, base of crown, 1/3 and 2/3 of crown), with the foliage area and dry mass of black locust (Robinia pseudoacacia L.). In addition, we tested the relationships of diameter at breast height with diameter at the base of the live crown, as well as with leaf area. We focused on this species, as it is extensively planted in several countries for the restoration and enhancement of carbon sequestration at heavily degraded sites (Liu et al. 2020).

We detected significant relationships between foliage area and sapwood area at breast height (Tab. S2 in Supplementary material), in line with literature. Foliage area has been commonly expressed as a function of sapwood area at breast height for several broadleaf forest trees, like cher-
ry bark and green ash (Meadows & Hodges 2002), eucalypts (Medhurst & Beadle 2002), European beech (Bartelink 1997) and Coigue or Dombey's beech (Gajardo-Caviedes et al. 2005). Foliage biomass, on the other hand, has been estimated by sapwood area at different heights across the tree trunk in various forest species (Marchand 1984, Morataya et al. 1999, Schneider et al. 2011). However, in our study the best predictor of trees' leaf area and dry mass was the total cross-sectional area at middle bole (Fig. 3, Fig. 4), in line with the findings of Spyroglou et al. (2019) for Quercus frainetto.

Total cross-sectional area was strongly related to leaf area and dry mass also at the stump height (Fig. 3, Fig. 4; Tab. S2 in Supplementary material). The increase in xylem and sapwood area at the trees' base, as indicated by the lowest ratios of leaf area to stem cross-sectional areas at stump height (Fig. 5A, Fig. 5C), may be attributed to a strong increase in ring area at the trunk base consistent to several studies reviewed by Lehnebach et al. (2018). Across a European gradient, Petit et al. (2018) also found that trees have a lower leaf area to sapwood area at the stem base compared to distal branches. Leaf area and dry biomass were closely coupled with total cross-sectional area at the trees' base. The increase in STA at stump height can be attributed to the basal widening of xylem conduits (Anfodillo et al. 2013), to ensure better mechanical support and resistance against bending (Larjavaara & Muller-Landaau 2010) and higher water conductance and storage (McDowell et al. 2002).

Following total cross-sectional area, current sapwood at stump height was also a reliable indicator of foliage area and dry mass (Fig. 3, Fig. 4; Tab. S2 in Supplementary material), indicating that the youngest vessels of black locust are more actively transferring water to the leaves, as similarly reported for the current sapwood area of Quercus robur L. (White 1993) and Nothofagus dombyei (Mirb.) Oerst. (Gajar- do-Caviedes et al. 2005). In addition, legume species are reported to conduct water mostly in the outermost rings of sapwood (Reyes-García et al. 2012); a response that may apply for the studied black locust which is also a legume. On the other hand, we found all cross-sectional areas at the base of the crown to be less appropriate for the prediction of leaf area, contrary to the findings of Gajardo-Caviedes et al. (2005).

The well-established relationships between sapwood area and crown dimensions were the least strong in our study, compared to total stem cross-sectional area and current sapwood area. Several studies reviewed by Lehnebach et al. (2018) concluded that sapwood area and its relation to leaf area varies with tree ontogenetic stage and size, site quality and other factors. Hence, it cannot be excluded that the different size of the sampled trees, due to the variation in age and size of the plantations because of the ongoing rehabilitation with black locust planting, may have influenced the strength of the relationship between sapwood area and foliage area or biomass. Furthermore, the deviations from PMT observed in our study, could be at least partially attributed to the relatively small number of sampled trees. Across six forested sites in the USA, Duncanson et al. (2015) have shown that allometric parameters are sensitive to sample size and that small sample sizes affect the model's ability to predict. In regard to the potential role of edaphic traits on the relationship between sapwood area and foliage metrics, we believe this is of minor importance. Although all studied plantations were established on depositional created by the residuals of lignite excavation, some differences in substrate traits were, indeed, detected (CaCO₃, organic matter, ammonium and nitrate content – Tab. S1 in Supplementary material). However, at least in regard to ammonium and nitrate contents, their effect on the relationship between the trees' vascular system and their foliage area and mass is less probable, since black locust is N₂-fixing and depends mostly on symbiotically fixed nitrogen, and less on other N sources (Liu et al. 2020).

The Pipe Model Theory predicts an increasing sapwood area downwards following the increase in foliage biomass/area towards the crown base and, subsequently, a constant sapwood area between crown and stem base (Lehnebach et al. 2018). Selin & Kupper (2006) observed a similar variation of leaf to sapwood area within the crown of silver birch. However, in our study the change of the ratio of leaf area to sapwood area across the tree profile (Fig. 5C) was not in line with PMT. A clear decreasing pattern of the ratio from the top to the bottom of the crown was observed only when the total cross-sectional area of the trees was considered, but even in this case the ratio further decreased across the tree trunk basipetally (Fig. 5A). These deviations from PMT may be attributed to the young age of the studied black locust plantations or be site-and species-specific. Variations in the ratio of leaf area to sapwood area have been assessed by several studies, as this parameter is related to the strategy that different tree species adopt to couple leaf transpiration and carbon gain with xylem water transport (Petit et al. 2018). An increasing ratio of leaf area to sapwood area with tree height was reported by Phillips et al. (2003) in Oregon white oak, while the opposite was observed in conifers (McDowell et al. 2002, Delzon et al. 2004).

Apart from the reliability of stem cross-sectional areas for the estimation of foliage mass and area, we also evaluated the easily determined DBH as a predictor of the leaf area of black locust. A strong regression model was built to predict leaf area based on DBH (Fig. 6A), consistent to the reports for other broadleaves (Sumida et al. 2009, Sirri et al. 2019) and conifers (Petersen et al. 2008, Goude et al. 2019).

However, it is worth noticing that for the prediction of the leaf area of black locust, the model based on STA at middle bole (Fig. 4A) outperformed the one based on DBH (Fig. 6A) and should, thus, be preferred although it requires more laborious sampling.

Another important relationship between stem and crown dimensions is the one connecting DBH and diameter at the base of the live crown. According to the Pipe Model Theory (Shinozaki et al. 1964a, 1964b), Dhlc is a good predictor of total foliage area, as it is an index of the amount of leaves of the tree. Thus, diameter at the base of the crown can be an alternative indicator for the estimation of a tree’s foliage weight and area. However, as the direct measurement of Dhlc in high forest trees may also be difficult, it could be calibrated mostly on the relationship to STA. Indeed, Sumida et al. (2013) supported that DBH is related to the diameter at the base of the live crown, based on 20-year data from Hinoki cypress (Chamaecyparis obtusa) stands. However, DHlc has been related mostly to other crown traits, such as crown diameter and width, crown projected area and height of live crown base, in different forest species (Grote 2003, Blanchard et al. 2016), as well as in black locust (Moser et al. 2015, Carl et al. 2017, Rédei et al. 2018). To our knowledge, the relationship between DBH and the diameter at the base of the live crown received little attention (Lockhart et al. 2005), but it has been verified also by our findings (Fig. 6B) and it may be a useful tool to predict Dhlc based on the easily measured DBH.

**Conclusions**

The estimation of trees’ foliage area and biomass is laborious, but crucial to assess forest ecosystems productivity and potential for climate change mitigation. A range of stem metrics have been evaluated for their strength in the prediction of foliage area and dry mass in black locust restoration plantations in Greece. Contrary to the often-used sapwood area, the total cross-sectional area and current sapwood area produced more accurate models for the estimation of these foliage traits. Diameter at breast height was also proven to be a reliable predictor of leaf area and diameter at the base of the live crown. The calibrated allometric models are species-specific and their replicability may be restricted by the particular edaphic conditions of the former lignite mines where the restoration plantations are established. In addition, the accuracy of the functions would benefit from a larger sample size which, on the other hand, is rather time and effort demanding. Future research should focus on the evaluation of the calibrated allometric relationships to other black locust plantations which are commonly established for the re-
habilitation of regions that are heavily degraded by anthropogenic activities.

List of abbreviations
PMT: Pipe Model Theory; LA: Foliage Leaf Area (m²); FDW: Foliage Dry Weight (Kg); SAPA: Sapwood cross-sectional area (cm²); CSA: Current sapwood cross-sectional area (cm²); STA: Total stem (sapwood and heartwood) cross-sectional area (cm²); LA/STAPA: ratio of LA to SAPA; LA/CSA: ratio of LA to CSA; LA/STA: ratio of LA to STA; DBH: Diameter at breast height; Dihc: Diameter at the base of the live crown; CRelen: Crown length; CR: Crown ratio.

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Supplementary Material

Tab. S1 - Substrate characteristics at the two restoration plantations.

Tab. S2 - Characteristics of simple linear regression models of LA and FDW to SAPA, CSA and STA.

Tab. S3 - Characteristics of simple linear regression models of LA and FDW with DBH' and Dhlc', as well as of Dhlc' with DBH'.

Fig. S1 - Ombrothermic diagrams of the two restoration plantations for the period 2008-2018.

Fig. S2 - Distribution of the diameter at breast height (DBH) and height classes of the 25 felled black locust trees.

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