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Solar radiation effects on leaf nitrogen and phosphorus stoichiometry of Chinese fir across subtropical China

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Abstract

Background: Solar radiation (SR) plays critical roles in plant physiological processes and ecosystems functions. However, the exploration of SR influences on the biogeochemical cycles of forest ecosystems is still in a slow progress, and has important implications for the understanding of plant adaption strategy under future environmental changes. Herein, this research was aimed to explore the influences of SR on plant nutrient characteristics, and provided theoretical basis for introducing SR into the establishment of biochemical models of forest ecosystems in the future researches.

Methods: We measured leaf nitrogen (N) and phosphorus (P) stoichiometry in 19 Chinese fir plantations across subtropical China by a field investigation. The direct and indirect effects of SR, including global radiation (Global R), direct radiation (Direct R) and diffuse radiation (Diffuse R) on the leaf N and P stoichiometry were investigated.

Results: The linear regression analysis showed that leaf N concentration had no association with SR, while leaf P concentration and N:P ratio were negatively and positively related to SR, respectively. Partial least squares path model (PLS-PM) demonstrated that SR (e.g. Direct R and Diffuse R), as a latent variable, exhibited direct correlations with leaf N and P stoichiometry as well as the indirect correlation mediated by soil P content. The direct associations (path coefficient = − 0.518) were markedly greater than indirect associations (path coefficient = − 0.087). The covariance-based structural equation modeling (CB-SEM) indicated that SR had direct effects on leaf P concentration (path coefficient = − 0.481), and weak effects on leaf N concentration. The high SR level elevated two temperature indexes (mean annual temperature, MAT; ≥ 10 °C annual accumulated temperature, ≥ 10 °C AAT) and one hydrological index (mean annual evapotranspiration, MAE), but lowered the soil P content. MAT, MAE and soil P content could affect the leaf P concentration, which cause the indirect effect of SR on leaf P concentration (path coefficient = 0.004). Soil N content had positive effect on the leaf N concentration, which was positively and negatively regulated by MAP and ≥ 10 °C AAT, respectively.

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Conclusions: These results confirmed that SR had negatively direct and indirect impacts on plant nutrient status of Chinese fir based on a regional investigation, and the direct associations were greater than the indirect associations. Such findings shed light on the guideline of taking SR into account for the establishment of global biogeochemical models of forest ecosystems in the future studies.

Keywords: Solar radiation, Leaf, Soil, Nitrogen and phosphorus, Stoichiometry, Chinese fir

Background

Solar radiation (SR) is the main source of energy for organisms in the forest ecosystems, affecting the plant physiological processes and regulating the ecosystem functions (Urban et al. 2007; Díaz-Guerra et al. 2018; Tomes 2020). Generally, SR could significantly affect the plant growth and development via the photosynthetic, thermal and morphological effects (Li et al. 2018; Zhou et al. 2019; Punia et al. 2020). Therefore, SR is a predominant indicator controlling the forest primary productivity, and influences the stability and sustainability of forest ecosystems (Yu et al. 2008; Fyllas et al. 2017).

Ecological stoichiometry is usually used to explore the balance of energy and multiple nutrient elements (mainly N and P) under the circumstance of numerous ecological processes, such as community succession, invasion and coexistence of plant species (González et al. 2010; Zheng et al. 2020; Zhu et al. 2020). The characteristics of N and P contents in plant tissues (especially leaf) could be regarded as the result of long-term adaptation to the climate or environment changes, reflecting the plant growth status as well as the survival strategy (Li et al. 2014; Luo et al. 2021). Several hypotheses have been proposed to describe the potential stoichiometry patterns of leaf element, which is generally regulated by temperature and soil nutrient availability, e.g. temperature-biogeochemical hypothesis (TBH), temperature-plant physiology hypothesis (TPPH) and substrate-age hypothesis (SAH) (Reich and Oleksyn 2004). Recently, two studies investigated the effects of SR on the leaf N and P stoichiometry. It should be point that one was conducted across the meadows of the Tibetan Plateau with high level of SR, and the other one was studied with the meta-analysis method at the continental scale (Sun et al. 2019; Ji et al. 2020). The main conclusions of the two studies appear consonant, i.e. the effects of SR on ecosystems should be involved in the related future macroecological studies.

Fully considering the effects of SR on plant nutrient characteristics and ecological stoichiometry applications at the regional, national and global scales, the simulation models were established to evaluate the direct and indirect effects of SR on leaf N and P stoichiometry (Fig. 1). The fourth pathway in the model suggested that SR could directly affect the leaf elements concentrations by changing plant physiology processes such as photosynthesis and transpiration (Ji et al. 2020). In addition, the other five pathways all showed the indirect effects of SR on leaf N and P stoichiometry (Reich and Oleksyn 2004; Wang et al. 2015; Comola et al. 2015; Dagon and Schrag 2016; Xu et al. 2020). It should be noted that SR had significant effects on various soil biogeochemistry and nutrient cycling, which was mainly achieved by influencing the microbes and enzymes activities (Wang et al. 2015).

Chinese fir is the tree species widely distributed and mainly cultivated across subtropical China. Despite many previous studies have focused on the effects of geography, climate, stand chronosequence and nitrogen deposition on leaf elements stoichiometry of Chinese fir (Chen et al. 2015; Chen et al. 2018; Tong et al. 2019), little information is available on the correlations between these parameters and SR. Here, we investigated the leaf nutrient concentrations and collected the related SR and climate data, aiming to explore the direct and indirect effects of SR on leaf N and P stoichiometry. Our study could shed new lights on the potential effects of SR on the plant physiological traits of Chinese fir at a regional scale, and also help evaluate whether SR should be taken into account in the future macroecological studies.

Methods

Study area

The leaf and soil samples were collected from 19 Chinese fir plantations across 12 provinces of subtropical China. According to the division by Cooperation Group of Chinese fir, the sampling sites covered the traditional and representative production area including northern, middle and southern cultivated regions (Wu 1984) (Fig. 2). The study area was geographically located 103.30°–119.32° E, 22.25°–33.55° N, and its elevation varied from 60 to 1150 m above the sea level. The SR was at the mediate level in this study area with a global radiation (Global R) ranging from 3534 to 5029 $MJ\cdot m^{-2}\cdot year^{-1}$ and a diffuse radiation (Diffuse R) ranging from 1162 to 2258 $MJ\cdot m^{-2}\cdot year^{-1}$. The Global R exhibited a decreasing trend and then increasing along the latitude, whereas had no associations with longitude and altitude (Fig. S1). Temperature and precipitation generally exhibited decreasing trends along the latitude, with a mean annual temperature (MAT) ranging from 10.7 to 22.4 °C and a mean annual precipitation (MAP) ranging from 773 to 1782 mm. According to the 1-km soil type diagram of China by the American Soil Taxonomy from

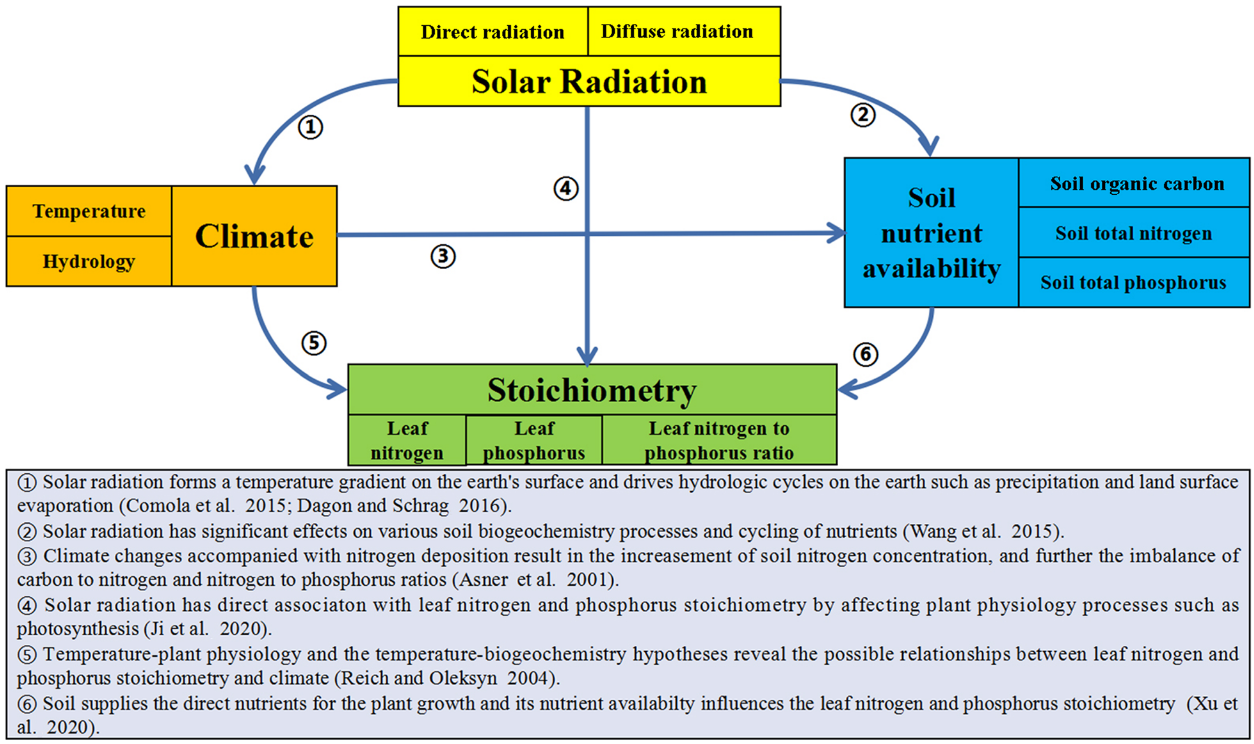

Fig. 1 Simulation models for evaluating the direct and indirect effects of SR on leaf N and P stoichiometry

the Soil Science Database of China (http://www.soilinfo.cn/map/index.aspx), the study area is dominated by the ferrosols and ferralosols. Chinese fir is the absolutely dominant tree species of arbor layer, and the undergrowth vegetation is relatively sparse, mainly including ferns, greenbriers and Miscanthus.

Sampling design and database creation

In order to represent the most vigorous period of forests or plantations throughout the year, the tree summer fast-growing season was generally chosen. In late July and early August 2018, 19 middle-aged Chinese fir plantations were investigated in main production area of subtropical China (Fig. 2). Field sampling was conducted from the south to north to weaken the effects of phenological differences between the northern and southern China. Those plantations were averaged 16- years old, ranging from 12- to 22- years old, and were all in the first rotation, without fertilization in recent 10 years.

The sampling stands in the planted land with relative consistency of slope degree (20°–35°) and slope direction (southward) were set up. Three 20 m × 20 m plots were established, and the horizontal distance of neighbouring plots was more than 20 m. Five or six trees with uniform and good growth were randomly selected, and were also measured the diameter at breast height in each plot. The details of 19 plantations information were shown in Appendix Table S1, and the division of the distribution zone was according to Wu (1984).

In each plot, the 1- and 2- year old matured leaves were randomly sampled in the middle of the sun-exposed crown, with the leaves from the selected trees mixed to form a single sample. Recently (natural) senesced leaves under each selected tree were collected, and then mixed them to form a leaf litter sample. We picked roughly ten pieces of compound leaf and leaf litter in each sampling site, respectively. In the laboratory, we removed the leaflets from each sample and weighed (more than 10 g in mass) for measurement. Moreover, after removing the understory plant and surface litter, the 0–20 cm depth topsoil was collected using soil auger by the five-point sampling method. All above processes were repeated in triplicate to obtain a total of 57 samples for leaf, leaf litter and soil (3 samples per site).

The geographical locations (latitude, longitude, and altitude) of the sampling sites were also recorded to explore the plant long-term adaption ability to the climate changes. It was widely accepted that the values of climatic variables during a certain period had better implications for the plant nutrient characteristics than these at a certain time point. Thus, 30 years (1981–2010) annual mean global radiation (Global R) and diffuse radiation (Diffuse R) were extracted following the methods in Ji et al. (2020) for each site. The direct radiation

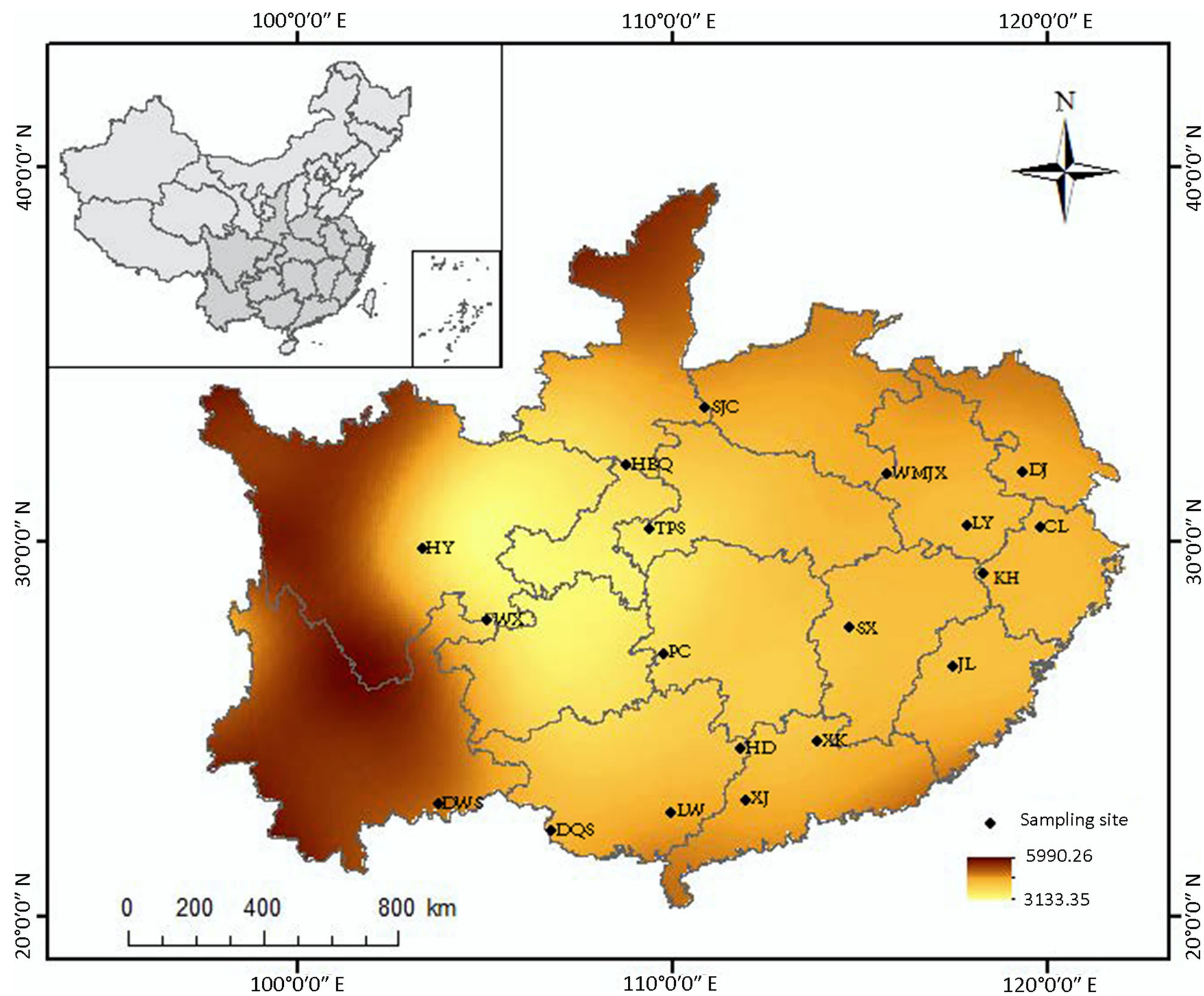

Fig. 2 Map of the sampling sites of Chinese fir plantations and the variation of solar radiation across subtropical China (The full name of each sampling site and values of solar radiation can be found in the Table S1)

(Direct R) was equal to the differences between Global R and Diffuse R (Wang et al. 2020). Moreover, we also derived the MAT, MAP, MAE (mean annual evapotranspiration) and ≥ 10 °C AAT (≥ 10 °C annual accumulated temperature) during 30 years (1981–2010) from the WorldClimate web site (www.wordclim.org) with a resolution of 1 km × 1 km.

Chemical measurements

All leaf and leaf litter samples were ground with ball mill (Retsch MM400, Germany) after over drying for 72 h at 70 °C. The organic carbon concentration was determining for each sample using potassium dichromate oxidation external heating method. The N and P concentrations were determining for each sample using the wet digestion with sulphuric and perchloric acid method.

Soil samples were air-dried after being sieved (2-mm mesh). Soil organic carbon was determined by the potassium dichromate oxidation external heating method. Soil N content was determined by Kjeldahl method, continuous flow analyzer and element analyzer. Soil P content was determined by alkali melting method and acid dissolving method. Soil pH value was determined by potentiometric method.

Data analysis

The data on leaf N concentration exhibited normal distribution, and the leaf P concentration and N:P ratio exhibited left and right skewed distribution, respectively (Fig. S2), which was tested by the K-S method using SPSS 22.0 software (SPSS, Inc., Chicago, IL, USA). All the data (except for the soil pH) of leaf N and P stoichiometry, SR (including Global R, Direct R and Diffuse R), the climatic and edaphic variables were log 10-transformed to improve the data normality.

General linear model (GLM) was used to explore the relationships between the leaf N or P stoichiometry and SR by R software 4.0.1 (R Core Team 2020).

According to the simulation models (Fig. 1) and the variables features, partial least square path modeling (PLS-PM) and covariance-based structural equation modeling (CB-SEM) were used to test the direct and indirect effects of SR on leaf N and P stoichiometry, as well as their correlations among the other variables included in this study. The PLS-PM was considered more as an exploratory approach than as a confirmatory one, while the CB-SEM was a statistical method for establishing, estimating and verifying causality models. The PLS-PM was conducted using "plspm" function from the package (Henseler and Chin 2010) based on R software 4.0.1 (R Core Team 2020). The CB-SEM was conducted in the AMOS statistical module of the SPSS 22.0 software (SPSS, Inc., Chicago, IL, USA).

Results

Leaf N and P concentrations, and N:P ratio in relation to SR

Leaf N concentration showed no significant correlation with the Global R, Direct R and Diffuse R (Fig. 3a, d and g). The leaf P concentration decreased with the increasing Global R, Direct R and Diffuse R, whereas N:P ratios displayed an opposite trend (Fig. 2b, c, e, f, h and i).

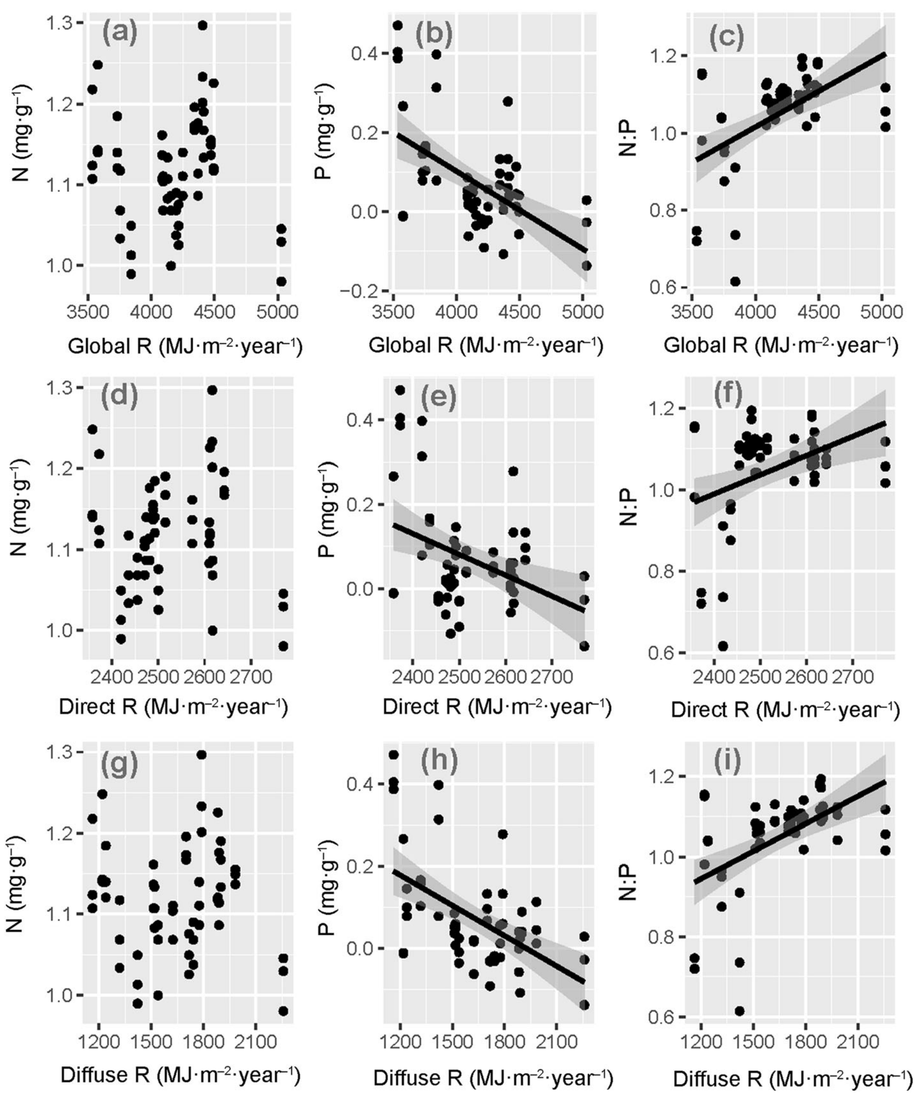

Fig. 3 Leaf N and P concentrations, and N:P ratio in relation to Global R, Direct R and Diffuse R. Each point showed a log-transformed observation of Leaf N and P concentrations, and N:P ratio ($n = 57$). Significant linear regressions were shown for (**b**) Global R and leaf P concentration ($R^2 = 0.2995$, $p < 0.001$); (**c**) Global R and leaf N:P ratio ($R^2 = 0.2835$, $p < 0.001$); (**e**) Direct R and leaf P concentration ($R^2 = 0.1537$, $p < 0.01$); (**f**) Direct R and leaf N:P ratio ($R^2 = 0.1514$, $p < 0.01$); (**h**) Diffuse R and leaf P concentration ($R^2 = 0.2979$, $p < 0.001$); (**i**) Diffuse R and leaf N:P ratio ($R^2 = 0.2790$, $p < 0.001$)

Direct and indirect associations between SR and leaf N and P stoichiometry based on the partial least square path modeling (PLS-PM)

The PLS-PM showed that SR (finally including Direct R and Diffuse R) had a significantly negative association (path coefficient = – 0.518, $p < 0.01$) with Stoichiometry (finally including leaf P concentration and N:P ratio), a significantly positive association (path coefficient = 0.730, $p < 0.001$) with Climate (finally including MAT, MAE and ≥ 10 °C AAT), and a significantly negative association (path coefficient = – 0.308, $p = 0.08$) with Soil (Finally including soil P content). Climate had no association (path coefficient = 0.136, $p > 0.1$), with Stoichiometry, but Soil had a positive association (path coefficient = – 0.284, $p < 0.05$) with Stoichiometry. The variance of Stoichiometry was explained by 36.5% with SR, Climate and Soil in the model. The variance of Climate explained by SR in the model was 53.3%. The variance of Soil explained by SR and Climate in the model was 21.6%. The direct associations (path coefficient = – 0.518) were greater than the indirect associations (path coefficient = – 0.087) for the significant paths, and the total association was 0.605 (Fig. 4).

Direct and indirect associations between SR and leaf N and P stoichiometry based on covariance-based structural equation modeling (CB-SEM)

The final CB-SEM explained 31.1% of the variation in leaf P and 18.2% of the variation in the leaf N. Figure 5 showed the direct and indirect effects of SR on leaf N and P stoichiometry ($R^2 = 0.311$). SR exhibited directly negative (path coefficient = – 0.481) and indirectly mutual offset effects (path coefficient = 0.004) on leaf P. Meanwhile, leaf N had received no direct effect from SR, positive indirect effect from SR through soil P content (path coefficient = – 0.093), and negative indirect effect from SR through ≥10 °C AAT and SN in order (path coefficient = – 0.101). Thus, the path coefficient for the total indirect effect of SR on leaf N was – 0.194. In addition, it was also evident that leaf N could be predicted from SN that regulated by MAP (path coefficient = 0.187).

Discussion

Direct effects of solar radiation on leaf N and P stoichiometry

SR is a major source of energy on the Earth's surface, and is also the primary driver of water, heat and nutrient

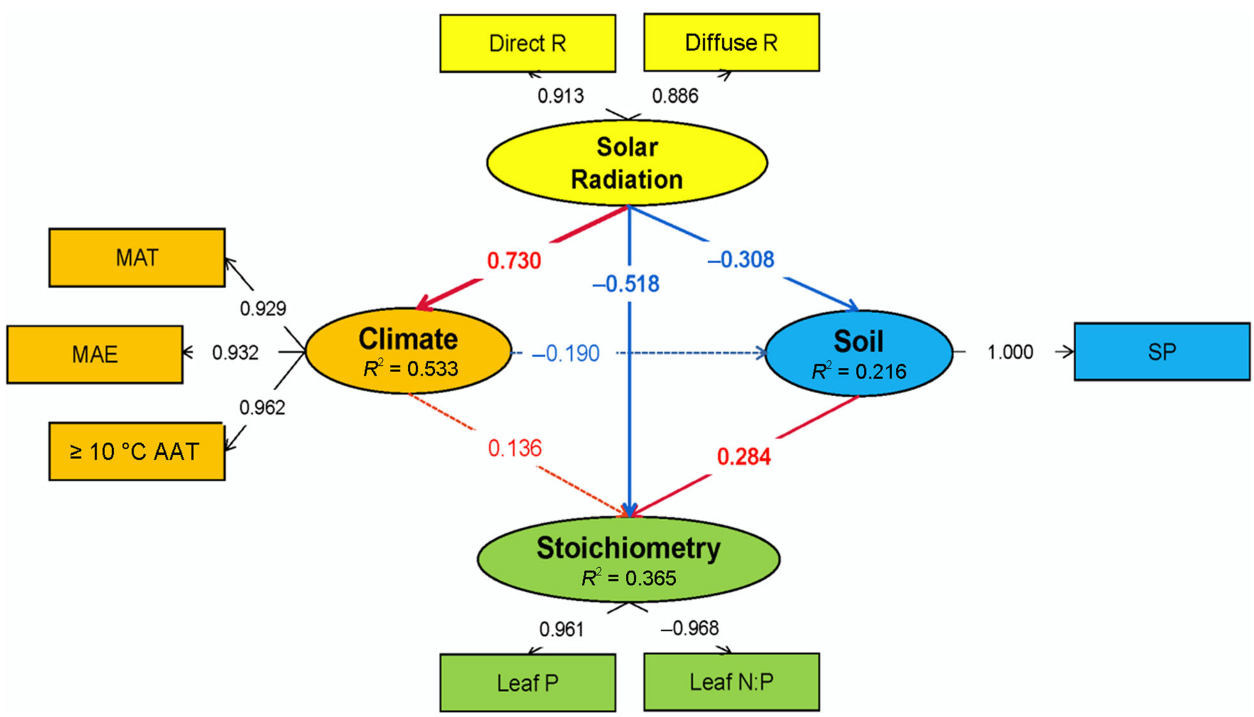

Fig. 4 Predicted partial least squares path modeling (PLS-PM) for the direct and indirect associations between SR and leaf stoichiometry. Ellipse represents the structural model, and box represents corresponding measurement models. In the structural model, the lines indicated paths, and the values adjacent to the lines denote the magnitude of the path coefficients calculated by PLS regression. R^2 values are shown for all endogenous latent variables in the ellipse. Values in the measurement model represent the loadings between a latent variable and its indicators. The figure is showing the final models after model diagnosis processes. MAP, leaf N concentration, soil pH, SOC (soil organic carbon) and SN (soil N content) were removed because of low loadings (|loading| < 0.70). Pseudo Goodness-of-Fit (GoF) of the model is 0.570. All paths are significant except the paths from Climate to Soil, and Climate to Stoichiometry ($p < 0.05$)

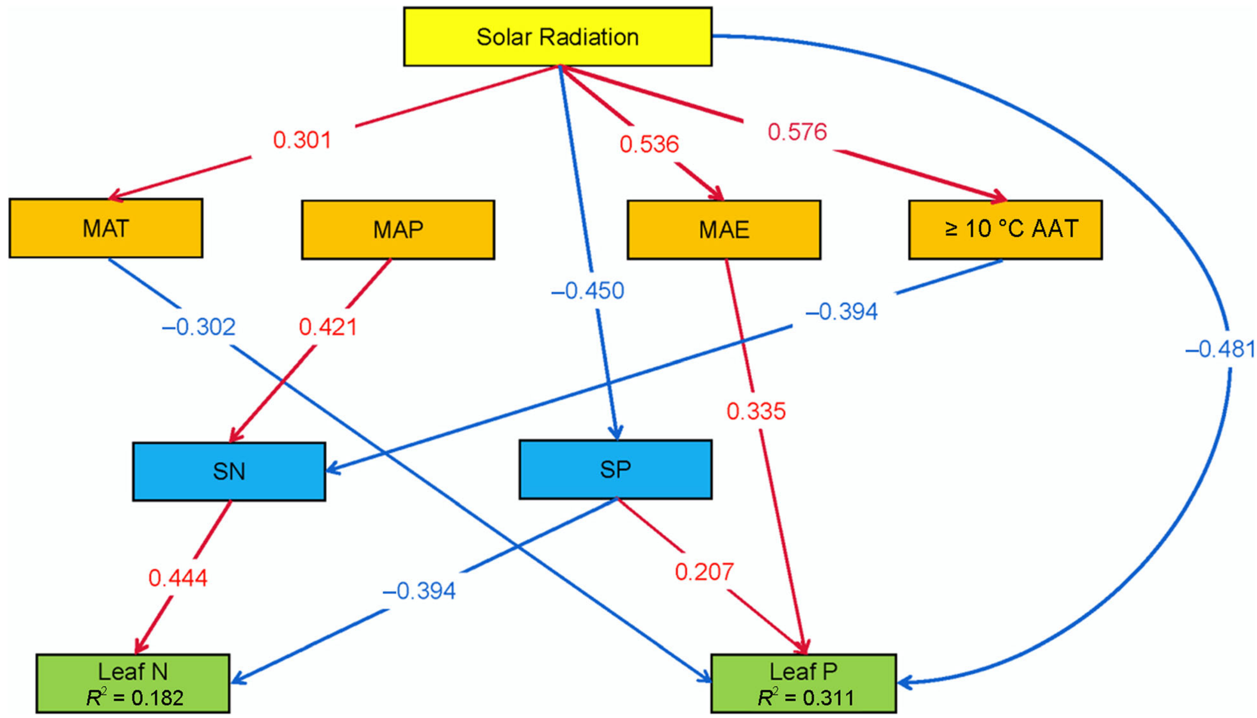

Fig. 5 Covariance-based structural equation modeling (CB-SEM) analysis of the direct and indirect effects among variables. Results of model fitting: $\chi^2 = 15.324$; Probability level = 0.501; df = 16; GFI = 0.943; RMSEA = 0.000; AIC = 73.32. All the paths in the model were significant, and the standardized coefficients were listed on them. The thickness of the solid arrows reflected the magnitude of the standardized SEM coefficients, the red solid line represented the positive effect while the blue solid line represented the negative effect

fluxes, influencing climate changes, plant growth and evolution, vegetation distribution and succession, and the productivity of forest ecosystems (Jordan et al. 2005; Li et al. 2011; Fyllas et al. 2017). However, most of the previous studies have overlooked the influences of SR on numerous ecological communities and processes in forest ecosystems, especially at regional or national scales. N and P were the most essential elements involved in the leaf photosynthesis, which was generally considered as the most common association between SR and green plants (Dubey et al. 2017; Martini et al. 2019). Thus, it was essential to explore the large-scale biogeographical patterns of leaf N and P stoichiometry in relation to SR, and widely distributed tree species provided an ideal experiment object for this purpose.

Recently, the potential relationships between SR and leaf N and P stoichiometry had drawn some attentions due to their close associations to nutrient fluxes of terrestrial ecosystems (Sun et al. 2019; Ji et al. 2020). In the current study, leaf N concentration showed no significant associations with Global R, Direct R and Diffuse R (Fig. 3a, d and g, Figs. 4 and 5), which was different from the two mentioned studies across the meadows of the Tibetan Plateau and Chinese mainland (Sun et al. 2019; Ji et al. 2020). A possible explanation could be that N was the limited element for the plant growth and usually kept relatively stable even at a regional scale ($CV_{leaf\ N}$ = 0.156, N:P ratio = 11.49, Figs. S2a and S2c) (Han et al. 2013; Tong et al. 2020). It was well known that leaf N concentration could be used for the estimation of the leaf photosynthetic rate, which was critically important in models of plant, ecosystem, and biosphere responses to global changes (Peterson et al. 1999). This indicated that the stable leaf N concentration might imply that the variation of leaf photosynthesis was little for Chinese fir across subtropical China. Thus, it could be speculated that plant respiration influenced mostly by temperature might cause the plant growth performance differences of Chinese fir among northern, middle and southern cultivation areas.

According to our result, leaf P concentration had negative associations with SR (Global R interval: 3500–5000 $MJ \cdot m^{-2} \cdot year^{-1}$) (Figs. 3b, e, h, 4 and 5), which was in line with Sun et al. (2019) for alpine meadows of the Tibetan Plateau. They reported that the leaf P concentration decreased with increasing SR, especially at the high SR level (5475–6294 $MJ \cdot m^{-2} \cdot year^{-1}$). Notably, it was generally accepted that high level of leaf P concentration might be a positive indicator of high leaf photosynthesis, and leaf photosynthesis increased with increasing SR in specific light intensity interval. In addition, under normal circumstances, the light intensity was still higher than the leaf photosynthetic saturation point even if the amount of SR was reduced by 50% during the day in the upper part of plant community. Thus, in natural situations, the thermal effect of SR could lead to the overheating of leaf surface due to the prolongation of strong SR maintenance time. That will further affect the photosynthetic processes and eventually result in the no obvious increase or decrease of leaf photosynthesis induced by the excess SR.

Divergent from our observations, Ji et al. (2020) demonstrated that leaf P concentration had significantly positive correlation with SR (Global R interval: 3000–7000 MJ·m^{-2}·year^{-1}), but with a low explanatory power ($R^2 = 0.057$) for the 2176 species at a continental scale. One explanation for this result is the continental study contained a high proportion of sun plants or light-requiring plants with higher leaf photosynthetic saturation point. In addition, it should be noted that leaf P concentration decreased with increasing Diffuse R in this study (1150–2200 MJ·m^{-2}·year^{-1}) and the study of Chinese mainland (2000–2700 MJ·m^{-2}·year^{-1}) (Ji et al. 2020), implying that the Diffuse R might be an important driving factor for the leaf nutrient traits, and this was still needed more evidence (Gu et al. 2002).

Leaf N:P ratio was an important indicator for the limitation of plant growth, which had been widely explored in the previous studies (Koerselman and Meuleman 1996). In this study, the average leaf N:P ratio was 11.49, indicating the middle-aged Chinese fir might suffer N-limitation across subtropical China (Fig. S2c). The leaf N:P ratio increased with increasing SR (Fig. 3c, f and i, Fig. 4), confirming that the N-limitation relieved to some extent. This appeared to be coincide with that the growth performances of Chinese fir exhibited a general downward trend from southern to northern distribution areas (Wu 1984).

Indirect effects of solar radiation on leaf N and P stoichiometry

In addition to the direct effects, PLS-PM and CB-SEM results clearly revealed that SR also exhibited some indirect effects on leaf N and P stoichiometry mediated by climatic and edaphic variables (Figs. 4 and 5). Our results demonstrated that SR was positively associated with climate (mainly including MAT, MAE and ≥ 10 °C AAT) in both two SEMs (Figs. 4 and 5), which was not in line with the studies across the alpine meadows of the Tibetan Plateau and Chinese mainland (Sun et al. 2019; Ji et al. 2020). PLS-PM suggested that climate showed no significant associations with leaf N and P stoichiometry (Fig. 4), while CB-SEM showed that MAT and MAE had negative and positive associations with leaf P concentration, respectively (Fig. 5). The negative relationship between leaf P concentration and MAT supported the TPPH, suggesting that the increase of leaf P concentration might compensate the decrease of biochemical reaction rates inducing by low temperature (Reich and Oleksyn 2004; Hou et al. 2021).

Evapotranspiration refers to the total water loss to atmosphere from a land surface, mainly including the soil evaporation and plant transpiration (Stanhill 2019). Generally, the maintenance of the land surface temperature largely depended on the heat provided by SR, which was also an influencing factor of the evapotranspiration (Olivera-Guerra et al. 2017). Moreover, plant transpiration was the main driving force for the uptake of mineral elements such as phosphorus (Cernusak et al. 2011; Pang et al. 2018). Thus, as we expected, SR was observed having a positive association with MAE, and was further positively related to leaf P concentration in this study (Fig. 5).

According to the PLS-PM and CB-SEM results, SR exhibited a negative mode of regulation for the soil P content (Figs. 4 and 5), which was also observed across the alpine meadows of the Tibetan Plateau (Sun et al. 2019). One possible reason could be that high SR, especially the strong ultraviolet ray, would weaken the activity of soil microbial enzymes, resulting in the decreases of the soil organic matter decomposition rate (Wang et al. 2017). Another possibility could be that the distribution patterns of soil P content and SR exhibited opposite alteration trends along the geographical gradients, which was consistent with the SAH that soils in low latitudes were older and less fertile than these in high latitudes (Reich and Oleksyn 2004; Hou et al. 2021). Furthermore, our study observed that soil P content was significantly positive related to leaf P concentration, which had been widely confirmed at local and regional scales (Hedin 2004; Debnath et al. 2011).

Conclusions

The present study was one of a few investigations to explore the direct and indirect effects of SR on leaf N and P stoichiometry across the Chinese fir distribution area. The leaf P concentration and N:P ratio showed significant change trends with SR, while leaf N concentration kept relatively stable at a regional scale. The SEMs suggested that SR had both direct and indirect associations mediated by climatic and edaphic variables with leaf N and P stoichiometry, and the direct associations were greater than the indirect associations. Overall, our results demonstrated that SR played a key role in regulating the leaf N and P stoichiometry of Chinese fir across subtropical China, which should be involved in the establishment for the future researches of global biogeochemical models. Furthermore, the rational utilization of SR resources would be of great benefit to the Chinese fir cultivation, e.g., the site selection for the large-diameter timber and the reasonable selection of planting density. Specifically speaking, according to the investigation results shown, e.g. positive correlation of SR and leaf N:P ratio, our study evidenced that plantation areas should be selected away from the city center or heavily industrialized regions, because the high level of atmospheric pollutants in those areas, such as anthropogenic aerosols, might weaken the SR in some places, especially the southeast coastal economically developed areas.

Abbreviations

SR: Solar radiation; Global R: Global radiation; Direct R: Direct radiation; Diffuse R: Diffuse radiation; N: Nitrogen; P: Phosphorus; PLS-PM: Partial least squares path model; CB-SEM: Covariance-based structural equation modeling; MAT: Mean annual temperature; MAP: Mean annual precipitation; MAE: Mean annual evapotranspiration; ≥ 10 °C AAT: ≥ 10 °C annual accumulated temperature.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40663-021-00344-6.

Additional file 1.

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Authors' contributions

BZZ and TGW conceived the study; BZZ provided project support; RT and YNC performed the research and analyzed the data; RT, ZHZ and CYL wrote the manuscript; BZZ and TGW contributed to editing. All authors contributed to the work and gave final approval for publication.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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