

## Article

# Aboveground Biomass and Endogenous Hormones in Sub-Tropical Forest Fragments

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**Abstract:** Associated endogenous hormones were affected by forest fragmentation and significantly correlated with aboveground biomass storage. Forest fragmentation threatens aboveground biomass (AGB) and affects biodiversity and ecosystem functioning in multiple ways. We ask whether and how forest fragmentation influences AGB in forest fragments. We investigated differences in AGB between forest edges and interiors, and how plant community characteristics and endogenous hormones influenced AGB. In six 40 m × 40 m plots spread across three forest fragments, AGB was significantly higher in plots in the forest interior than in those at the edge of forests. The proportion of individuals with a large diameter at breast height (DBH > 40 cm) in the forest edges is higher than that in the forest interiors. Further, trees within a 15–40 cm DBH range had the highest contribution to AGB in all plots. Trees in interior plots had higher abscisic acid (ABA) and lower indole-3-acetic acid (IAA) concentrations than those in edge plots. In addition, AGB was significantly positively and negatively correlated with ABA and IAA concentrations at the community scale. In this study, we provide an account of endogenous hormones' role as an integrator of environmental signals and, in particular, we highlight the correlation of these endogenous hormone levels with vegetation patterns. Edge effects strongly influenced AGB. In the future, more endogenous hormones and complex interactions should be better explored and understood to support consistent forest conservation and management actions.

**Keywords:** forest fragmentation; endogenous hormones; edge effects; high-performance liquid chromatography; aboveground biomass



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## 1. Introduction

Forests play an important role in responding to global climate change, especially the carbon cycle. Forests contributed more than half of the organic carbon to terrestrial ecosystems according to previous studies [1,2]. Therefore, accurate estimation of forest carbon storage is crucial to our response to global climate change and other unknown factors [3,4]. Intact evergreen forests store much more living carbon per unit area than fragmented forests do, most of it in AGB and soil [4]. Further, forest fragmentation is globally pervasive and increasing in extent, with forest fragments now accounting for 46% of all remaining forested areas [5,6]. Fragmentation has been a major driver of declining forest biomass and altered carbon fluxes, contributing 6%–17% of global anthropogenic CO<sub>2</sub> emissions to the atmosphere [7]. However, forest fragmentation likely alters forests' potential for carbon storage in ways that are not yet completely understood.

Fragmentation can result from various types of human disturbances, such as selective logging, understory fires, fragmentation, and overhunting [8–10]. Most ecological research on carbon storage of forests has either focused on monitoring change in relatively undisturbed primary forests or on quantifying deforestation and the effects of forest fragmentation on AGB [11–13]. In addition, forest fragmentation creates isolated forest patches and degrades forest edges [14]. The discontinuities fashioned between forest patches by open, deforestation habitats induce a transition zone at the border where a suite of edge effects occur [15,16].

Forest edges are ubiquitous in many fragmented landscapes, and they strongly influence biodiversity [17]. Indeed, edge effects have been reported as one of the most significant patterns structuring both flora and environmental conditions [18], making it crucial to understand how vegetation, ecological processes, and ecosystem services are affected by edges [19,20]. Edge effects can influence species composition, community structure, AGB, and nutrient cycling [21]. Bueno and Liambi [22] reported that both facilitation and edge effects influence the effectiveness of vegetation regeneration within old-field communities in the high tropical Andes. De Paula [23] suggested that fragmented forests and the consequent establishment of forest edges drastically limit forest capacity for carbon storage across human-modified landscapes, since the loss of carbon due to the reduced abundance of large trees is not compensated for by either canopy or understory trees. Forest edges also have different microclimates than interiors do, often with more light, wind, warmer temperatures, and drier air and soil than forest interiors [19]. However, higher rates of tree mortality caused by microclimatic changes in forest edges lead soil carbon stocks to increase in central Amazon Forest fragments [20].

Plants face environmental challenges including competition with neighbors for sunlight, as well as acclimation to ambient temperature fluctuations and to prevailing moisture and nutrient conditions [24]. To complete their life cycle under abiotic and biotic environmental stresses, plants have developed sophisticated mechanisms to sense and adapt to ever-changing and often adverse environmental conditions [25]. It is well known that plant hormones, such as ABA and IAA, are involved in plant adaptation to adverse environments [26]. ABA has been widely reported for its role in adaptation to different kinds of abiotic stress responses, such as high salinity, drought, high temperature, and freezing [27]. ABA has been extensively studied for its importance in the regulation of plant growth and development [28].

Auxin is also a key integrator of environmental signals, and emerging evidence implicates auxin biosynthesis as an essential component of the overall mechanisms of plants' tolerance to stress [29]. Auxin is involved in numerous biological processes ranging from control of cell expansion and cell division to tissue specification, embryogenesis, and organ development [30]. As the main auxin in higher plants, IAA plays a central role in developmental programming and environmental responses such as gravitropism, phototropism, and plastic root development [31,32]. Dinis [33] reported that environmental signals stimulate variations in IAA levels and/or their redistribution and transport in order to regulate plant growth and development. Our standing of how endogenous hormone levels shift in response to fragmentation, and how these hormone affects translate to changes in AGB potential of tree communities remains incomplete. More research is needed to understand how endogenous hormones limit the capacity of AGB in fragmented forests. Furthermore, there is a lack of estimation of the role of endogenous hormones on AGB within forest fragments.

In the interest of filling the knowledge gap, we evaluate the relationships between AGB and hormone concentrations within fragmented forests in South China. We addressed the following three questions: (1) How do edge effects influence AGB distribution within these forest fragments? (2) How are the concentrations of hormones of seven dominant tree species affected by forest edges within these fragments? (3) How do endogenous hormones influence AGB in these forest fragments? The results of this study provide new knowledge on the relationship between endogenous plant hormone levels and vegetation distributions,

and its underlying mechanism. Our study could help elucidate the underlying mechanism of fragment structure and provide a basis for the development of planning strategies for the conservation of these forest fragments.

## 2. Materials and Methods

This study was carried out in Guangzhou City, South China (22°26′–23°56′ N, 112°57′–114°03′ E) within the most threatened region of the fengshui forests. The region is influenced by a typical sub-tropical monsoon climate. The annual mean temperature is 21.8 °C, and the annual precipitation is 1690 mm. Typhoons and thunderstorms occasionally damage trees and the mild climate permits continuous vegetation growth throughout the year. In rural areas of South China, sub-tropical forest fragments can be found near local villages. These remnants are called fengshui forests and have been protected by local residents. As a result, these fragmented forests have retained features of the original vegetation and provide a basis for testing the various theories of fragmentation in sub-tropical forests. Although these fengshui forests occur near local villages, human disturbance has had no significant effect on most of the community characteristics [34]. Certainly, such human-modified landscapes offer an interesting opportunity to examine the potential effects of habitat loss and fragmentation on AGB.

This study was carried out from September to December 2017. Three forest patches were selected in this study. These three forest fragments share similar climatic and soil conditions due to being very close in space (they are less than 10 km away from each other), leading to relatively similar soil and plant community characteristics. Previous research has shown that species turnover among these fragments is limited [34]. In the present study, we established two 40 m × 40 m plots within each forest fragment. The two plots are located in the forest core area and near the forest edge. All trees with DBH greater than 1 cm were identified and DBH was recorded within all plots. Tree species were identified by an experienced field botanist. Plant community characteristics (species richness, abundance, number of individuals within different DBH ranges, and basal area) were estimated according to the data from field censuses.

The forest floor biomass includes woody debris and surface litter in this study. Three randomly distributed 2 m × 2 m subplots were established within every plot. The fresh weight of debris and litter was obtained by using an electronic balance. In order to calculate the ratio between fresh and dry mass, subsamples of the debris and litter were then transported back to the lab and oven dried at 80 °C until constant weight.

Tree AGB was estimated using the allometric equation developed by Wen [35] for sub-tropical mixed forests in Dinghushan Nature Reserve not far away from these forest fragments:

$$\text{TAGB} = a \times \text{DBH}^b \quad (1)$$

where  $a$  and  $b$  are statistical parameters (see Table S1 for equations and summary statistics). TAGB was the sum of the dry weight of trunks, branches, leaves, and roots. This model has been successfully applied to estimate tree biomass in sub-tropical forests located in Dinghushan Nature Reserve [36]. Finally, AGB of each plot was calculated by summing forest floor biomass and TAGB.

Wood samples were collected from randomly chosen individuals of seven tree species within each plot (two or three replicates dependent on the abundance of per tree species; Table 1). In order to obtain a 1 mm diameter core, an increment borer was applied at about 1.5 m high on the main stem of each individual. In addition, the litter of seven tree species was collected within each plot with the assistance of an experienced field botanist. All these samples were immediately placed into a liquid nitrogen tank (−80 °C) and then transported to the laboratory and stored to minimize damage to the live tissue and changes to ion concentrations. We determined endogenous hormone concentrations of IAA in wood samples and ABA in litter using high-performance liquid chromatography (HPLC). IAA and ABA content in these seven tree species within each plot represent the endogenous hormone levels of each plot.

**Table 1.** Seven common tree species were selected in each plot within three forest patches.

No.	Species	Shade Tolerance
1	<i>Castanopsis chinensis</i> Hance	Light-demanding
2	<i>Aleurites moluccanus</i> (L.) Willd.	Light-demanding
3	<i>Cryptocarya concinna</i> Hance	Mid-tolerant
4	<i>Syzygium rehderianum</i> Merr. et Perry	Light-demanding
5	<i>Schima superba</i> Gardn. et Champ	Mid-tolerant
6	<i>Carallia brachiata</i> (Lour.) Merr.	Shade-tolerant
7	<i>Girardinia subaequalis</i> Planch	Mid-tolerant

Statistical analysis was performed using SPSS 20.0. Before statistical analysis, all data were tested for normality using the Shapiro–Wilk test and for homoscedasticity using the Levene test. Results were represented as the mean  $\pm$  standard error. Differences among means of IAA and ABA concentration between forest edges and interiors were analyzed with one-way ANOVA tests. The statistical significance of the difference between means was determined with Duncan’s new multiple range test. Pearson correlation analysis was also conducted in this study.

### 3. Results

#### 3.1. Vegetation Distribution in Fragments

Both basal area and stem density were significantly lower ( $p < 0.05$ ) near forest edges than in interior plots, respectively (Table 2). In addition, the number of stems within two DBH ranges (DBH < 15 cm; 15–40 cm) was significantly lower in forest edge plots than in forest interior plots. Smaller trees (individuals within 1–15 cm DBH range) had the highest proportion in all forest fragments. However, both the number of individuals and the percentage of larger trees (DBH > 40 cm) were higher near forest edges (191; 8.2%) than in interior plots (153; 6.4%). Aboveground biomass (AGB) was significantly lower near forest edges (80.6 Mg ha<sup>−1</sup>) than in the forest core area (143.2 Mg ha<sup>−1</sup>). In addition, AGB of smaller trees and medium trees (DBH: 15–40 cm) were significantly lower in forest edges than in forest interiors ( $p < 0.05$ ). Although smaller trees had the largest stems, AGB was highest in medium trees (38.5 Mg ha<sup>−1</sup>; 77.9 Mg ha<sup>−1</sup>) and larger trees (33.2 Mg ha<sup>−1</sup>; 36.4 Mg ha<sup>−1</sup>) both in forest edges and interior within these studied plots ( $p < 0.05$ ). In addition, medium trees had the highest contribution to AGB storage in the studied plots due to their relatively higher mean DBH and abundance.

**Table 2.** Community characteristics of fragmented forests from edge to interior plots.

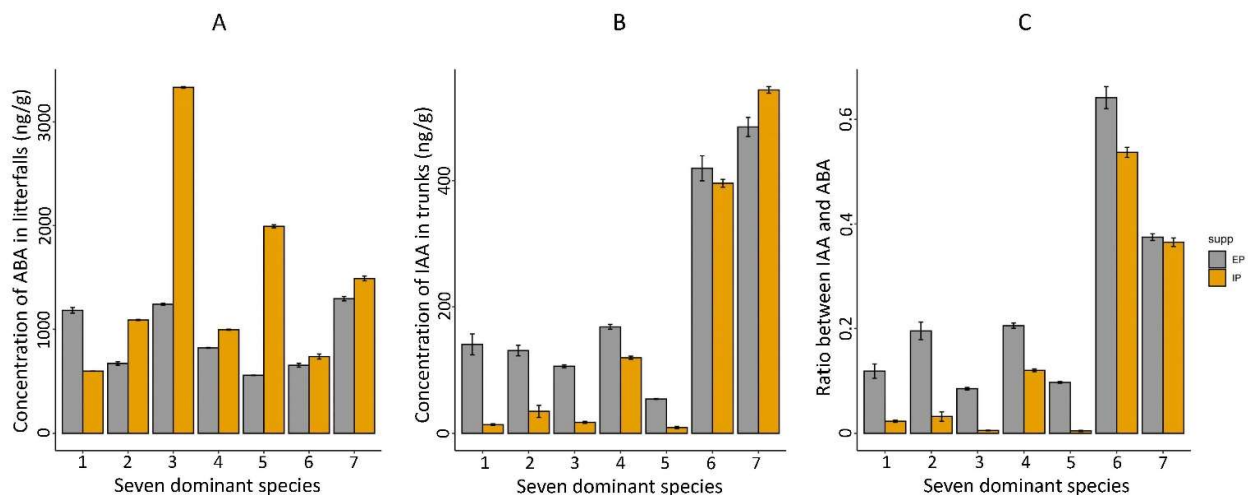
Classification	Edge Plots	Interior Plots
Aboveground biomass (Mg ha <sup>−1</sup> )	80.6 $\pm$ 12.2 <sup>a</sup>	143.2 $\pm$ 11.9 <sup>b</sup>
Stem density	1735 $\pm$ 215 <sup>a</sup>	2969 $\pm$ 308 <sup>b</sup>
Basal area (m <sup>2</sup> ha <sup>−1</sup> )	30.0 $\pm$ 2.6 <sup>a</sup>	52.5 $\pm$ 1.4 <sup>b</sup>
Stems N (DBH < 15 cm)	1421 $\pm$ 125 <sup>a</sup>	2292 $\pm$ 168 <sup>b</sup>
Stems N (DBH: 15–40 cm)	161 $\pm$ 69 <sup>a</sup>	486 $\pm$ 112 <sup>b</sup>
Stems N (DBH > 40 cm)	153 $\pm$ 21 <sup>a</sup>	191 $\pm$ 28 <sup>a</sup>
Stems AGB (DBH < 15 cm)	8.9 $\pm$ 1.7 <sup>a</sup>	28.9 $\pm$ 2.3 <sup>b</sup>
Stems AGB (DBH: 15–40 cm)	38.5 $\pm$ 5.2 <sup>a</sup>	77.9 $\pm$ 5.4 <sup>b</sup>
Stems AGB (DBH > 40 cm)	33.2 $\pm$ 5.3 <sup>a</sup>	36.4 $\pm$ 4.2 <sup>a</sup>

Lowercase letters stand for significance between each row.

#### 3.2. Endogenous Hormones Contents of IAA and ABA

ABA concentrations in the leaf litter and IAA concentrations in the trunks of seven tree species within six plots are shown in Figure 1. ABA and IAA concentrations of three tree species differed within the studied plots. ABA concentrations in all these seven tree species (Table 1), except for *Castanopsis chinensis*, were significantly lower in edge plots than in interior plots. Mid-tolerant tree species had the highest ABA concentration in

interior plots (Figure 1A). IAA concentrations of all these tree species, except for *Girronniera subaequalis*, were significantly higher in edge plots than in interior plots. In addition, both *Girronniera subaequalis* and *Carallia brachiata* had the highest IAA concentration in the studied plots (Figure 1B). Further, IAA concentration differences were even larger between the tree species (*Castanopsis chinensis*, *Aleurites moluccanus*, *Cryptocarya concinna*, and *Schima superba*) than between the residual species. The ratios between IAA and ABA of these seven tree species present a similar trend: values in edge plots were higher than those in interiors plots (Figure 1C). Further, the ratios of two tree species (*Girronniera subaequalis* and *Carallia brachiata*) were the largest both in forest edge and interior in the present study.

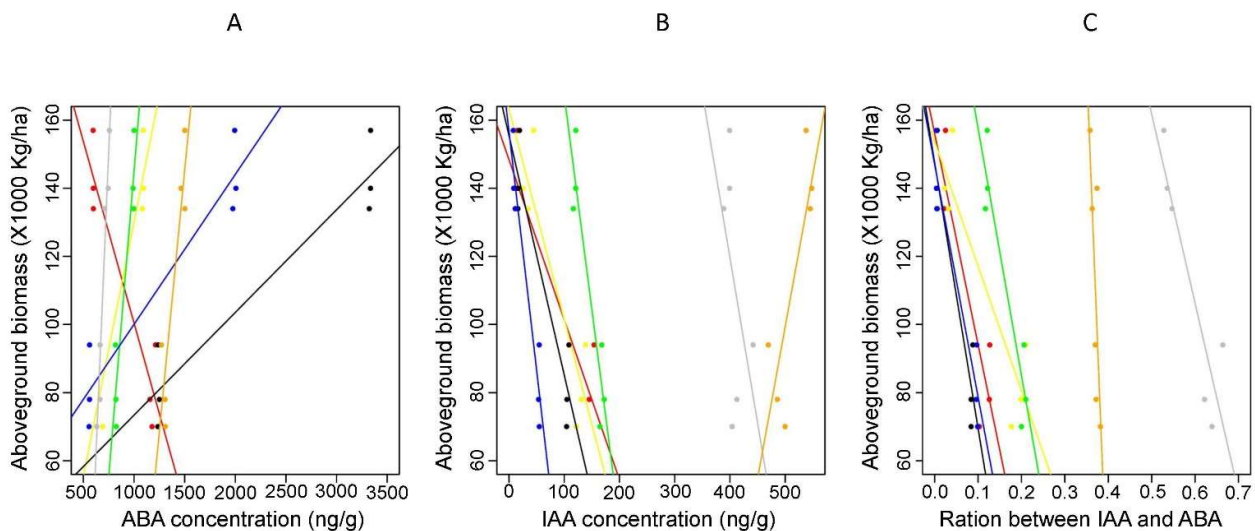


**Figure 1.** The concentration of endogenous hormones and their ratios in seven common species in edge (EP) and interior plots (IP). (A) The concentration of ABA in litter falls; (B) The concentration of IAA in tree trunks; (C) The ratios of IAA to ABA in 7 common tree species. Number 1 stands for *Castanopsis chinensis* Hance; 2 stands for *Aleurites moluccanus* (L.) Willd.; 3 stands for *Cryptocarya concinna* Hance; 4 stands for *Syzygium rehderianum* Merr. et Perry; 5 stands for *Schima superba* Gardn. et Champ; 6 stands for *Carallia brachiata* (Lour.) Merr.; 7 stands for *Girronniera subaequalis* Planch.

### 3.3. Relationships between AGB and Endogenous Hormones Level

The relationships between AGB and endogenous hormones are shown in Figure 2. In the present study, AGB was significantly positively correlated with mean ABA concentration among six dominant tree species (except *Castanopsis chinensis*). In addition, the gradients of four tree species (*Aleurites moluccanus*, *Syzygium rehderianum*, *Carallia brachiata*, *Girronniera subaequalis*) were even higher than the last two species, which indicated that slight changes in ABA may cause large fluctuations in AGB (Figure 2A). Mean IAA concentrations of six tree species (except *Girronniera subaequalis*) had significant negative relationships with AGB regardless of plot type (edge or interior) (Figure 2B). In addition, higher IAA:ABA ratios were significantly correlated with lower AGB in these forest fragments (Figure 2C).





**Figure 2.** The relationships between aboveground biomass and the concentration of endogenous hormones. (A) Relationship between aboveground biomass and the concentration of ABA; (B) relationship between aboveground biomass and the concentration of IAA; (C) relationship between aboveground biomass and the IAA:ABA ratio. Red stands for *Castanopsis chinensis* Hance; yellow stands for *Aleurites moluccanus* (L.) Willd.; Black stands for *Cryptocarya concinna* Hance; Green stands for *Syzygium rehderianum* Merr. et Perry; Blue stands for *Schima superba* Gardn. et Champ; Grey stands for *Carallia brachiata* (Lour.) Merr.; Orange stands for *Gironniera subaequalis* Planch.

#### 4. Discussion

In this study, the patterns of aboveground biomass storage and endogenous hormone concentrations of seven dominant tree species were studied. Three fragmented forests were significantly affected by edge effects, and their AGB ranges were 80.6–143.2 Mg ha<sup>−1</sup> (Table 2). In addition, endogenous hormone concentrations were also significantly affected by forest edges (Figure 2). Compared with intact forests, fragmented forests showed a higher proportion of habitat edges exposed to other habitats, resulting in a higher probability of edge effects according to previous studies [21,33]. Furthermore, the forest edge can be regarded as a buffer zone, and the ecological conditions gradually change within a certain distance, which has a significant impact on AGB. Edge effects are among the primary mechanisms by which forest fragmentation can influence the link between biodiversity and ecosystem processes [21,29].

Habitat fragmentation and the consequent establishment of permanent forest edges reduce forest capacity for AGB because forest edges retain only one-third as much biomass as forest interior habitat according to former studies [37]. In the present study, AGB storage near forest edges contributes about 36.0% to the total AGB (Table 2). Our study fragments are consistent in size with previous studies, and we also found that the changes in community structure along fragment transects were consistent with knowledge of forest edge effects. The higher basal areas in the forest interior suggest that AGB in the forest interior could contain more biomass, were it not for the edge effects [38]. In this study, the AGB storage within different DBH ranges was also significantly affected by forest edge. In addition, AGB storage within different DBH ranges differed within different types of plots (edge plots and interior plots). Larger trees (DBH > 40 cm) accounted for a greater proportion of all trees at the forest edge than in the interior (Table 2), where the mean basal area of individual trees was lower than at the forest edge habitat. However, in contrast to our results, other studies have reported that tree density at forest edges generally exceeds that in the interior [39]. Our results suggested that AGB reduction in edge-affected habitats results from reduced larger tree individuals together with insufficiency of biomass make up by residual trees (Table 2). Furthermore, larger trees are likely particularly important for maintaining AGB at the forest edge, as we observed little changes in the amount of

AGB held in smaller trees at forest edges in these fragments. Therefore, any impacts on larger trees, either by global change or other disturbances that affect the abundance and persistence of these large stems, are therefore likely to have a major impact on forest AGB [40]. Our results agreed with other tropical forest studies, wherein the lower number of large and medium emergent trees near the forest edges is a major contributor to the loss of AGB [41,42].

AGB is an important ecosystem function altered by edge effects, with implications for the management of micro-environmental conditions in forest fragments [22]. The establishment of forest edges during fragmentation and the ensuing alteration in microclimate affect plant populations [4]. We observed a significant increase in the proportion of larger trees with proximity to fragment edges, likely a consequence of increased temperature and light availability. Higher biomass storage is predicted at the edge compared to the interior as a result of increased productivity resulting from increased sunlight and temperature at the forest edge. Edges expose organisms to dry, windy, high-light conditions that differ considerably from the dark, humid forest interior [43]. Elevated wind stress in fragmented forests is widely reported and has been proposed as a likely factor in reducing AGB in fragmented forests. In addition, the relaxing of competition for light as a result of lower stem density, more open canopies, and increased lateral light penetration from habitat edges might further reduce AGB in fragments [44]. Moreover, forest edges were dominated by shade-intolerant, fast-growing pioneer species, as compared to the more shade-tolerant maple, ironwood, and elm species that dominated the fragment interiors according to former studies [45]. Barros [17] reported that fragment edges had greater exposure to harsh winds compared to the forest interior, directly increasing tree mortality. As a result, there is increased biomass loss due to the mortality of large trees [27,35]. This might be an explanation for our result that plants in edge plots experience a relaxing of competition for light and have decreased biomass density.

The present study has focused specifically on the ways in which edge effects can alter the link between endogenous hormones and ecosystem functions occurring within subtropical forest fragments. As sessile organisms, plants have evolved mechanisms allowing them to control their growth and development in response to environmental changes [46]. As a primary source of energy, light is one of the most important environmental factors for plant growth [17]. The number of stems within interior plots was significantly higher than that in edge plots in the present study (Table 2). Distances between two adjacent plants are reduced, creating changes in environmental factors [47]. Moreover, the distance and size of neighboring plants determine the type of stress the plant will suffer. If a plant is exposed to intense neighboring shade, it will receive limited light input, but in open areas, it is more likely to be exposed to heat and oxidative stress caused by the high radiation load [20]. Competition for light determines the success of individual plants in dense vegetation, and the presence of neighbors is an important environmental factor inhibiting plant growth [45]. It is well known that ABA is an essential mediator in triggering the plant responses to many environmental stresses including shade [46]. Such analysis was already reported in competition among *Arabidopsis* plants, suggesting the involvement of plant hormones in responses to the presence of neighbors [47,48]. In the present study, higher stem density was accompanied by higher ABA concentration in leaves in the interior areas of forest patches, probably due to competition for light. Moreover, the inhibition of lettuce plant growth under increased planting density was accompanied by the accumulation of ABA in the shoots of competing plants [49]. These results confirm the important role of ABA in the growth-inhibiting effect of increased planting density.

ABA concentration is closely related to IAA concentration according to former studies [15]. Vysotskaya et al. [49] suggested that ABA is involved in the allocation of IAA in competing plants. Shkolnik-Inbar [50] reported the role of ABA accumulation in the reduction of polar auxin transport and a resulting decrease in root auxin. Our results are in accordance with theirs: concentration of ABA increased in leaves within interior plots, accompanied by a decline in the concentration of IAA in trunks. Moreover, higher stem

density leads to shade avoidance syndrome, which decreased the IAA content and auxin polar transport [51,52]. The same results were observed in this study: the decline in the proportion of larger trees (DBH > 40 cm) and simultaneous increase in stem density was accompanied by a decrease in the concentration of IAA in leaves within interior plots.

It is thus not surprising that auxin has emerged as an important regulator of adaptive growth responses to environmental stresses [53]. It was discovered that local auxin biosynthesis maintains optimal plant growth in response to environmental signals, including light, temperature, and humidity [54]. Auxin is one of the most important plant hormones mediating endogenous developmental signals and exogenous environmental cues to control various plant growth and developmental responses [55]. Strong evidence for induced auxin production are indications that auxin sensitivity is also increased in response to stress [56]. Light and temperature are arguably two of the most important signals regulating the growth and development of plants [57]. Meanwhile, light and temperature patterns are often correlated under natural plant growth conditions [58]. Islam [59] reported that light quality is sensed by different photoreceptors in plants, which are involved in a wide range of developmental processes, and IAA is an important determinant of shoot elongation in poinsettia, as shown for a wide range of species. Earlier, it was generally believed that drought results in a decrease in IAA content. At present, however, it became gradually clear that the adaptation to drought is accompanied by an increase in the IAA content [60,61]. In our results, the higher concentration of IAA in plants at edge plots might result from decreased soil moisture at the forest edges compared to the forest interior. Our results are in accordance with the reports that higher auxin content in *Arabidopsis* might create positive regulation of drought stress resistance [62]. However, the present study focuses only on the AGB storage, endogenous hormones concentration, and its relationships within the edge and interior plots in forest fragments. In the future, research will be carried out on how endogenous hormones regulate the growth of trees to affect biomass storage under the influence of forest fragmentation.

## 5. Conclusions

The distribution of AGB and its associated plant endogenous hormones were analyzed in three sub-tropical forest fragments in the present study. AGB and the number of individuals were considerably reduced at forest edges, however, the proportion of larger trees (DBH > 40 cm) increased near forest edges. In addition, it is evident from our work that community characteristics change from forest edges to interiors. Plant endogenous hormone concentrations were likely affected by edge effects due to micro-environmental conditions. IAA and ABA decreased and increased from the forest edge to the interior, respectively. Higher stem density was accompanied by higher ABA concentration in leaves in the core areas of forest patches while IAA concentrations of woody species were higher at edge plots. This study shows that the fragmentation of forests and thus the spread of marginal habitats drastically reduces aboveground biomass storage, resulting from the regulation of plant growth by endogenous hormones. The present study also provided key data for the development and validation of AGB conditions in subtropical forests in southern China.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14040661/s1>, Table S1: Allometric regression equations and summary statistics.

**Author Contributions:** Conceptualization, L.M.; methodology, C.S.; software, H.C.; validation, C.L.; formal analysis, W.D.; investigation, L.M.; resources, L.M.; data curation, H.C.; writing—original draft preparation, C.L.; writing—review and editing, C.S. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** If there are legitimate reasons, you can contact the corresponding author to request data.

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**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Fauset, S.; Johnson, M.O.; Gloor, M.; Baker, T.R.; Monteagudo, A.M.; Brien, R.J.; Feldpausch, T.R.; Lopez-Gonzalez, G.; Malhi, Y.; ter Steege, H.; et al. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **2015**, *6*, 6857. [\[CrossRef\]](#)
2. Haddad, N.M.; Brudvig, L.A.; Clobert, J.; Davies, K.F.; Gonzalez, A.; Holt, R.D.; Lovejoy, T.E.; Sexton, J.O.; Austin, M.P.; Collins, C.D.; et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **2015**, *1*, e1500052. [\[CrossRef\]](#) [\[PubMed\]](#)
3. Pütz, S.; Groeneveld, J.; Henle, K.; Knogge, C.; Martensen, A.C.; Metz, M.; Metzger, J.P.; Ribeiro, M.C.; de Paula, M.D.; Huth, A. Long-term carbon loss in fragmented Neotropical forests. *Nat. Commun.* **2014**, *5*, 5037. [\[CrossRef\]](#) [\[PubMed\]](#)
4. Schmidt, M.; Jochheim, H.; Kersebaum, K.C.; Lischeid, G.; Nendel, C. Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes—A review. *Agr. Forest Meteorol.* **2017**, *232*, 659–671. [\[CrossRef\]](#)
5. Asner, G.P.; Powell, G.V.N.; Mascaró, J.; Knapp, D.E.; Clark, J.K.; Jacobson, J.; Kennedy-Bowdoin, T.; Balaji, A.; Paez-Acosta, G.; Victoria, E.; et al. High-resolution forest carbon stocks and emissions in the Amazon. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 16738–16742. [\[CrossRef\]](#) [\[PubMed\]](#)
6. Baccini, A.; Goetz, S.J.; Walker, W.S.; Laporte, N.T.; Sun, M.; Sulla-Menashe, D.; Hackler, J.; Beck, P.S.A.; Dubayah, R.; Friedl, M.A.; et al. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim. Chang.* **2012**, *2*, 182–185. [\[CrossRef\]](#)
7. Osuri, A.M.; Kumar, V.S.; Sankaran, M. Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats. *Forest Ecol. Manag.* **2014**, *329*, 375–383. [\[CrossRef\]](#)
8. Carvalho, F.D.G.D.; Costa, K.; Romitelli, I.; Barbosa, J.M.; Vieira, S.A.; Metzger, J.P. Lack of evidence of edge age and additive edge effects on carbon stocks in a tropical forest. *Forest Ecol. Manag.* **2018**, *407*, 57–65.
9. Numata, I.; Silva, S.S.; Cochrane, M.A.; d'Oliveira, M.V.N. Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *Forest Ecol. Manag.* **2017**, *401*, 135–146. [\[CrossRef\]](#)
10. Bregman, T.P.; Lees, A.C.; Seddon, N.; MacGregor, H.E.A.; Darski, B.; Aleixo, A.; Bonsall, M.B.; Tobias, J.A. Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology* **2015**, *96*, 2692–2704. [\[CrossRef\]](#)
11. Baker, T.P.; Jordan, G.J.; Baker, S.C. Microclimatic edge effects in a recently harvested forest: Do remnant forest patches create the same impact as large forest areas? *Forest Ecol. Manag.* **2016**, *365*, 128–136. [\[CrossRef\]](#)
12. Baker, T.P.; Jordan, G.J.; Steel, E.A.; Fountain-Jones, N.M.; Wardlaw, T.J.; Baker, S.C. Microclimate through space and time: Microclimatic variation at the edge of regeneration forests over daily, yearly and decadal time scales. *Forest Ecol. Manag.* **2014**, *334*, 174–184. [\[CrossRef\]](#)
13. Arroyo-Rodríguez, V.; Cavender-Bares, J.; Escobar, F.; Melo, F.P.L.; Tabarell, M.; Santos, B.A. Maintenance of tree phylogenetic diversity in a highly fragmented rain forest. *J. Ecol.* **2012**, *100*, 702–711. [\[CrossRef\]](#)
14. Wekesa, C.; Maranga, E.K.; Kirui, B.K.; Muturi, G.M.; Gathara, M. Interactions between native tree species and environmental variables along forest edge-interior gradient in fragmented forest patches of Taita Hills, Kenya. *Forest Ecol. Manag.* **2018**, *409*, 789–798. [\[CrossRef\]](#)
15. Cutler, S.R.; Rodriguez, P.L.; Finkelstein, R.R.; Abrams, S. Absciscic acid: Emergence of a core signaling network. *Annu. Rev. Plant Biol.* **2010**, *61*, 651–679. [\[CrossRef\]](#)
16. Goosem, M.; Paz, C.; Fensham, R.; Preece, N.; Goosem, S.; Laurance, S.G.W. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. *J. Veg. Sci.* **2016**, *27*, 504–514. [\[CrossRef\]](#)
17. Barros, H.S.; Fearnside, P.M. Soil carbon stock changes due to edge effects in central Amazon forest fragments. *Forest Ecol. Manag.* **2016**, *379*, 30–36. [\[CrossRef\]](#)
18. Chen, D.; Fu, Y.; Liu, G.; Liu, H. Low light intensity effects on the growth, photosynthetic characteristics, antioxidant capacity, yield and quality of wheat (*Triticum aestivum*, L.) at different growth stages in BLSS. *Adv. Space Res.* **2014**, *53*, 1557–1566.
19. Ma, L.; Shen, C.; Lou, D.; Fu, S.; Guan, D. Patterns of ecosystem carbon density in edge-affected fengshui forests. *Ecol. Eng.* **2017**, *107*, 216–223. [\[CrossRef\]](#)
20. Mroue, S.; Simeunovic, A.; Robert, H.S. Auxin production as an integrator of environmental cues for developmental growth regulation. *J. Exp. Bot.* **2017**, *69*, 201. [\[CrossRef\]](#)
21. Bueno, A.; Llambi, L.D. Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest line. *Appl. Veg. Sci.* **2015**, *18*, 613–623. [\[CrossRef\]](#)
22. Yang, D.L.; Yang, Y.; He, Z. Roles of Plant Hormones and Their Interplay in Rice Immunity. *Mol. Plant* **2013**, *6*, 675–685. [\[CrossRef\]](#)
23. de Paula, M.D.; Costa, C.P.A.; Tabarelli, M. Carbon storage in a fragmented landscape of Atlantic forest: The role played by edge-affected habitats and emergent trees. *Trop. Conserv. Sci.* **2011**, *4*, 349–358. [\[CrossRef\]](#)

24. Vanstraelen, M.; Benková, E. Hormonal interactions in the regulation of plant development. *Annu. Rev. Cell Dev. Biol.* **2012**, *28*, 463–487. [\[CrossRef\]](#)
25. Zörb, C.; Geilfus, C.M.; Mühling, K.H.; Ludwig-Müller, J. The influence of salt stress on ABA and auxin concentrations in two maize cultivars differing in salt resistance. *J. Plant Physiol.* **2013**, *170*, 220–224. [\[CrossRef\]](#) [\[PubMed\]](#)
26. ÁlvarezFlórez, F.; Lópezcristoffanini, C.; Jáuregui, O.; Melgarejo, L.M.; López-Carbonell, M. Changes in ABA, IAA and JA levels during calyx, fruit and leaves development in cape gooseberry plants (*Physalis peruviana* L.). *Plant Physiol. Biochem.* **2017**, *115*, 174–182. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Li, X.; Wang, L.; Wang, S.; Yang, Q.; Zhou, Q.; Huang, X. A preliminary analysis of the effects of bisphenol A on the plant root growth via changes in endogenous plant hormones. *Ecotox. Environ. Saf.* **2018**, *150*, 152–158. [\[CrossRef\]](#)
28. Seki, M.; Umezawa, T.; Urano, K.; Shinozaki, K. Regulatory metabolic networks in drought stress responses. *Curr. Opin. Plant Biol.* **2007**, *10*, 296–302. [\[CrossRef\]](#)
29. Suh, J.H.; Han, S.B.; Wang, Y. Development of an improved sample preparation platform for acidic endogenous hormones in plant tissues using electromembrane extraction. *J. Chromatogr. A* **2007**, *1535*, 1–8. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Kumar, R.; Khurana, A.; Sharma, A.K. Role of plant hormones and their interplay in development and ripening of fleshy fruits. *J. Exp. Bot.* **2014**, *65*, 4561–4575. [\[CrossRef\]](#)
31. Peer, W.A. From perception to attenuation: Auxin signalling and responses. *Curr. Opin. Plant Biol.* **2013**, *16*, 561–568. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Zhao, Y. Auxin Biosynthesis and Its Role in Plant Development. *Annu Rev. Plant Biol.* **2010**, *61*, 49–64. [\[CrossRef\]](#)
33. Dinis, L.T.; Bernardo, S.; Luzio, A.; Pintó, G.; Meijon, M.; Pintó-Marijuan, M.; Cotado, A.; Correia, C.; Moutinho-Pereira, J. Kaolin modulates ABA and IAA dynamics and physiology of grapevine under Mediterranean summer stress. *J. Plant Physiol.* **2017**, *220*, 181–192. [\[CrossRef\]](#) [\[PubMed\]](#)
34. Ma, L.; Huang, M.; Shen, Y.; Cao, H.; Wu, L.; Ye, H.; Lin, G.; Wang, Z. Species diversity and community structure in forest fragments of Guangzhou, South China. *J. Trop. Forest Sci.* **2015**, *27*, 148–157.
35. Wen, D.; Wei, P.; Kong, G. Biomass study of the community of *Castanopsis chinensis* + *Cryptocarya concinna* + *Schima supura* in a Southern China reserve. *Acta Ecol. Sin.* **1997**, *17*, 497–504, (In Chinese, English Summary).
36. Liu, S.; Luo, Y.; Huang, Y. Studies on the community biomass and its allocations of five forest types in Dinghushan Nature Reserve. *Ecol. Sci.* **2007**, *26*, 387–393, (In Chinese, English Summary).
37. Ziter, C.; Bennett, E.M.; Gonzalez, A. Temperate forest fragments maintain aboveground carbon stocks out to the forest edge despite changes in community composition. *Oecologia* **2014**, *176*, 893–902. [\[CrossRef\]](#)
38. Wilson, M.C.; Chen, X.Y.; Corlett, R.T.; Didham, R.K.; Ding, P.; Holt, R.D.; Holyoak, M.; Hu, G.; Hughes, A.C.; Jiang, L.; et al. Habitat fragmentation and biodiversity conservation: Key findings and future challenges. *Landsc. Ecol.* **2016**, *31*, 219–227. [\[CrossRef\]](#)
39. Slik, J.W.F.; Paoli, G.; McGuire, K.; Amaral, I.; Barroso, J.; Bastian, M.; Blanc, L.; Bongers, F.; Boundja, P.; Clark, C. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob. Ecol. Biogeogr.* **2013**, *22*, 1261–1271. [\[CrossRef\]](#)
40. Barlow, J.; Peres, C.A.; Lagan, B.O.; Haugaasen, T. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* **2003**, *6*, 6–8. [\[CrossRef\]](#)
41. Lindenmayer, D.B.; Laurance, W.F.; Franklin, J.F. Global decline in large old trees. *Science* **2012**, *338*, 1305–1306. [\[CrossRef\]](#)
42. Hallinger, M.; Johansson, V.; Schmalholz, M.; Sjöberg, S.; Ranius, T. Factors driving tree mortality in retained forest fragments. *For. Ecol. Manag.* **2016**, *368*, 163–172. [\[CrossRef\]](#)
43. Pütz, S.; Groeneveld, J.; Alves, L.F.; Metzger, J.P.; Huth, A. Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. *Ecol. Model.* **2011**, *222*, 1986–1997. [\[CrossRef\]](#)
44. Liu, J.; Wilson, M.; Hu, G.; Liu, J.; Wu, J.; Yu, M. How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? *Landsc. Ecol.* **2018**, *33*, 341–352. [\[CrossRef\]](#)
45. Legris, M.; Nieto, C.; Sellaro, R.; Prat, S.; Casal, J. Perception and signalling of light and temperature cues in plants. *Plant J.* **2017**, *90*, 683. [\[CrossRef\]](#)
46. Reinmann, A.B.; Hutyra, L.R. Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 107. [\[CrossRef\]](#)
47. Malmivaara-Lämsä, M.; Hamberg, L.; Haapamäki, E.; Liski, J.; Kotze, D.; Lehtvähä, S.; Fritze, H. Edge effects and trampling in boreal urban forest fragments—Impacts on the soil microbial community. *Soil Biol. Biochem.* **2008**, *40*, 1612–1621. [\[CrossRef\]](#)
48. Cagnola, J.L.; Ploschuk, E.; Benech-Arnold, T.; Finlayson, S.A.; Casal, J.J. Stem Transcriptome Reveals Mechanisms to Reduce the Energetic Cost of Shade-Avoidance Responses in Tomato. *Plant Physiol.* **2012**, *160*, 1110–1119. [\[CrossRef\]](#)
49. Vysotskaya, L.B.; Arkhipova, T.N.; Kudoyarova, G.R.; Veselov, S.Y. Dependence of growth inhibiting action of increased planting density on capacity of lettuce plants to synthesize ABA. *J. Plant Physiol.* **2018**, *220*, 69–73. [\[CrossRef\]](#)
50. Shkolnik-Inbar, D.; Bar-Zvi, D. ABI4 Mediates Absciscic Acid and Cytokinin Inhibition of Lateral Root Formation by Reducing Polar Auxin Transport in Arabidopsis. *Plant Cell.* **2010**, *22*, 3560–3573. [\[CrossRef\]](#)
51. Li, Y.; Zhao, H.; Duan, B.; Korpelainen, H.; Li, C. Effect of drought and ABA on growth, photosynthesis and antioxidant system of *Cotinus coggygria*, seedlings under two different light conditions. *Environ. Exp. Bot.* **2011**, *71*, 107–113. [\[CrossRef\]](#)

52. Masclaux, F.G.; Bruessow, F.; Schweizer, F.; Gouhier-Darimont, C.; Keller, L.; Reymond, P. Transcriptome analysis of intraspecific competition in *Arabidopsis thaliana* reveals organ-specific signatures related to nutrient acquisition and general stress response pathways. *BMC Plant Biol.* **2012**, *12*, 227. [[CrossRef](#)]
53. Wit, M.D.; Lorrain, S.; Fankhauser, C. Auxin-mediated plant architectural changes in response to shade and high temperature. *Physiol. Plantarum.* **2014**, *151*, 13–24. [[CrossRef](#)]
54. Lv, B.; Yan, Z.; Tian, H.; Zhang, X.; Ding, Z. Local Auxin Biosynthesis Mediates Plant Growth and Development. *Trends Plant Sci.* **2019**, *24*, 6–9. [[CrossRef](#)] [[PubMed](#)]
55. Franklin, K.A.; Toledo-Ortiz, G.; Pyott, D.E.; Halliday, K.J. Interaction of light and temperature signalling. *J. Exp. Bot.* **2014**, *65*, 2859–2871. [[CrossRef](#)] [[PubMed](#)]
56. Pustovoitova, T.N.; Zhdanova, N.E.; Zholkevich, V.N. Changes in the Levels of IAA and ABA in Cucumber Leaves under Progressive Soil Drought. *Russ. J. Plant Physiol.* **2004**, *51*, 513–517. [[CrossRef](#)]
57. Wang, T. Exogenous abscisic acid reduces water loss and improves antioxidant defense, desiccation tolerance and transpiration efficiency in two spring wheat cultivars subjected to a soil water deficit. *Funct. Plant Biol.* **2013**, *40*, 494–506.
58. Crockatt, M.E.; Bebb, D.P. Edge effects on moisture reduce wood decomposition rate in a temperate forest. *Glob. Chang. Biol.* **2014**, *21*, 698–707. [[CrossRef](#)] [[PubMed](#)]
59. Islam, M.A.; Tarkowská, D.; Clarke, J.L.; Blystad, D.; Gislerod, H.R.; Torre, S.; Olsen, J.E. Impact of end-of-day red and far-red light on plant morphology and hormone physiology of poinsettia. *Sci. Hortic.* **2014**, *174*, 77–86. [[CrossRef](#)]
60. Karageorgou, P.; Levizou, E.F.I.; Manetas, Y. The influence of drought, shade and availability of mineral nutrients on exudate phenolics of *Dittrichia viscosa*. *Flora* **2002**, *197*, 285–289. [[CrossRef](#)]
61. Vanneste, S.; Friml, J. Auxin: A trigger for change in plant development. *Cell* **2009**, *136*, 1005–1016. [[CrossRef](#)] [[PubMed](#)]
62. Shi, H.; Chen, L.; Ye, T.; Liu, X.; Ding, K.; Chan, Z. Modulation of auxin content in *Arabidopsis* confers improved drought stress resistance. *Plant Physiol. Biochem.* **2014**, *82*, 209–217. [[CrossRef](#)] [[PubMed](#)]

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