International Journal of Life Science and Agriculture Research
ISSN (Print): 2833-2091, ISSN (Online): 2833-2105
Volume 03 Issue 09 September 2024
DOI: https://doi.org/10.55677/ijlsar/V03I9Y2024-08
Impact Factor: 6.774 , Page No : 782-788

Responses to Defoliation of *Voacanga africana* Are Dependent on Light Availability

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ABSTRACT: Understorey plants are often subjected to damage by branches falling from forest canopies. *Voacanga africana* is an understorey tree that is native to tropical Africa. To investigate the combined effects of light availability and defoliation on growth of the species, seedlings were subjected to three defoliation levels (0 %, 25 %, 50 %) and two light regimes (50 % sunlight, full sunlight) in a greenhouse. The experiment followed a split-plot design with light availability as the whole plot and defoliation level as the sub-plot. Morphology, biomass, and leaf chlorophyll content were measured three months after the initiation of treatments. The lower light regime increased height while it decreased root mass and leaf chlorophyll content. No significant main effect of defoliation was detected for any parameter. There were, however, significant light × defoliation interactions for height, root-collar diameter, leaf mass, stem mass, and total mass. While the effect of the lower light regime on height was limited to the 25 % defoliation level, the treatment resulted in a decline of root-collar diameter and leaf mass only at 0 % defoliation. The 25 % defoliation level increased stem mass and total mass under the 50 % sunlight but not full sunlight treatment where differences between defoliation levels were not statistically significant. The mass ratios of leaf, stem, root, and leaf area ratio were unresponsive to light availability and defoliation either individually or in combination. The findings indicate that growth compensatory responses of *Voacanga africana* to defoliation are controlled by light availability.

Published Online:
September 26, 2024

KEYWORDS: defoliation, biomass, compensatory growth, light availability, morphology, *Voacanga africana*.

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1. INTRODUCTION

Defoliation is a common phenomenon affecting the physiology and growth of forest plants (Quentin *et al.,* 2010; Ambebe *et al.,* 2020). It may be caused by abiotic factors such as storms and winds or human and non-human biotic agents like wildlife, insects and fungi whose interaction with plants result in partial or complete loss of foliage and individual leaves (Candy and Zalucki, 2013). Plants respond to defoliation by a mobilization of stored non-structural carbohydrates to maintain metabolism (Jacquet et al. 2014), leading to carbon limitation. The net photosynthetic rate may be upregulated in the remaining leaves so that the carbohydrate pool is replenished and new tissues and organs are produced. The photosynthetic enhancement may be explained by greater amounts of light reaching shaded leaves or belowground resources for the remaining leaves. The carbon limitation disappears after a period of regrowth and growth rates or total biomass may attain or even surpass levels for undefoliated plants. However, the actual magnitude and direction of the response to defoliation is dependent on plant physiological state, degree of defoliation, and environmental conditions (Quentin *et al.,* 2012; Lambers *et al.,* 2013; Jacquet *et al.,* 2014). The literature differentiates overcompensation when growth rates are increased from partial compensation or damage when they are decreased by defoliation (Belsky, 1986; Galvez and Cohen-Fernandez, 2006; Landhäusser and Lieffers, 2012). On the other hand, when defoliated plants exhibit growth rates similar to undefoliated plants the response is known as full compensation (Ferraro and Oesterheld, 2002).

Complex interactions between light availability and defoliation treatments have been reported. Although there was a compensatory growth after defoliation of *Robinia pseudoacacia* and *Amorpha fruticosa*, for instance, the response of total biomass in high light markedly superseded that in low light conditions (Wang *et al.,* 2022) as was also the case for leaf area of *Brosimum alicastrum*

(Ballina-Gómez *et al.*, 2010). A similar trend was observed in *Quercus rubra* where defoliation additionally resulted in twice more mortality under shade than full sun (Mcgraw *et al.*, 1990). As for *Abies alba* trees, there was defoliation-induced compensatory growth under high but not low light availability (Yang *et al.*, 2021). Thus, the nature of response to defoliation × light interaction varies with plant species.

Voacanga africana (Apocynaceae) is an understorey tree of the African tropics. It is native to Angola, Benin, Burkina, Burundi, Cabinda, Cameroon, Central African Republic, Congo, Democratic Republic of Congo, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Gulf of Guinea Is., Ivory Coast, Kenya, Liberia, Malawi, Mali, Mozambique, Nigeria, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Uganda, Zambia, and Zimbabwe (POWO, 2024). The multipurpose tree is found in forests and savannah woodlands which, like other complex ecosystems, are characterized by variable light conditions. The roots, stems, leaves and seeds are loaded with alkaloids that are exploited for pharmacological purposes. Some tannins and flavonoids have also been identified in the plant (Burkill, 1985-2004). A seed oil bi-product from the extraction of medicinal compounds by the pharmaceutical industry is valued for its cosmetic and nutritional attributes (Fern, 2024). The wood is used locally as building material, fuel and for making musical instruments, arrow and knife sheaths. Branches falling from forests canopy often inflict damage on understorey plants (Chazdon, 1991). This study was aimed at investigating the effect of light availability on the growth response of *Voacanga africana* to defoliation.

2. MATERIALS AND METHODS

2.1. Study site

The experiment was conducted in a greenhouse at The University of Bamenda (1444 m asl; 5.983° N, 10.250° E), Bambili, North West Region, Cameroon. The structure was not equipped with a system for an automated regulation of it environmental conditions. Bambili is characterized by a rainy season that extends from March to September and a dry season that starts in September and ends in March. Under a changing global climate, however, there have been variations in the timing and duration of the seasons in recent years. Bambili has as mean annual rainfall 2095 mm, temperature 22.51 °C, and relative humidity 75.96 %. With over 350 mm of rainfall each, the wettest months are July, August, and September while the driest is January with 6 mm of precipitation. The warmest month is February with an average temperature of 29.8/16.1 °C (high/low) while August is the coldest with 21.6/15.6 °C (Weather Atlas, 2024).

2.2. Plant material

The experiment made use of five-month old *Voacanga africana* seedlings. They were obtained in polythene bags from the Reforestation Task Force (RETAFO) nursery located in Bamenda III Sub-Division of the North West Region. The seedlings were of uniform size and had no visual signs of developmental abnormality and damage. Upon arrival at the experimental site, they were transplanted into larger volume polythene bags filled with soil that was immediately saturated with normal tap water thereafter.

2.3. Experimental design

Treatments were comprised of two light (50 % sunlight, 100 % sunlight) and three defoliation (0 %, 25 %, 50 %) levels. They were laid out in a split-plot design with light as the whole plot, the defoliation treatments as the sub-plots, and the greenhouse as the field. There were two replications of each treatment combination. The lower light availability treatment was imposed by covering the seedlings with a well ventilated shade cloth for the entire duration of the experiment. The 25 % and 50 % defoliation treatments were achieved by a onetime removal of one-quarter and one-half, respectively, of each leaf on the seedling with a pair of scissors. There were ten randomly assigned seedlings in each light and defoliation treatment. Irrigation was administered as needed with normal tap water using a watering can. Any weed emerging from the growing medium was immediately removed by hand. The treatments were commenced on 5 March 2024 and terminated on 5 June 2024.

2.4. Data collection

At the end of the experiment, three plants were randomly selected from each treatment and replication for data collection. Height was measured as the distance from the soil surface to the shoot tip with the use of a ruler while diameter at the root-collar was obtained with a Vernier caliper. Number of new leaves was recorded after which the most fully expanded leaf was chosen for measurements of chlorophyll content and leaf area. The chlorophyll content was the average of three measurements taken at the upper third, middle and lower third of the leaf with a SPAD meter (Konica Minolta) while leaf area was determined with a graph paper. The graph paper was made up of 1 cm^2 cells which were each comprised of twenty-five 0.04 cm^2 cells. The leaf was fully spread out on the graph sheet and its margin traced. The leaf area was determined from the number of 1 cm^2 and 0.04 cm^2 cells that fell within the boundary of the traced region. The soil was rinsed off the root system and the plant was divided into leaf, stem, and root. Each of the fragments was oven-dried to constant weight and then weighed with a digital balance. The masses of the plant fragments and leaf area were then expressed as ratios of the total mass.

2.5. Statistical analysis

The data were checked graphically for normality and homoscedasticity before being subjected to split-plot ANOVA. When the outcome of the ANOVA was significant for a given parameter, Scheffe's test was used for pairwise comparison of means. The statistical tests were performed in Data Desk 6.01 at $p = 0.1$.

3. RESULTS

3.1. Morphology

In addition to a marginally significant effect of light availability on height, the effect of light × defoliation was marginally significant for height and significant for root-collar diameter. In contrast, number of new leaves and leaf area were unaffected by treatments (Table 1).

Values of height were highest in the 25 % defoliation treatment under shade and lowest in the 0 % defoliation in this same light regime. Similarly, the 25 % and 50 % defoliation treatments under full sunlight showed significantly lower responses of height than the 25 % defoliation treatment in shade (Figure 1). Aside from the above, no other significant differences were observed between treatments for this trait.

Root-collar diameter increased from shade to full sunlight only at 0 % defoliation. There were no significant differences in root-collar diameter between defoliation treatments under any of the light intensities. Irrespective of whether shade or full sunlight was considered, differences between the 0 % defoliation treatment and any other treatment were not statistically significant (Figure 1).

Table 1. ANOVA *p*-values for the effects of light, defoliation, and their interaction on morphology, biomass and leaf chlorophyll content

Source	Light	Defoliation	Light × Defoliation
Height	0.11	0.3895	0.1212
Root-collar diameter	0.4938	0.6188	0.0444
Leaves	0.7048	0.5968	0.3776
Leaf area	0.9792	0.5273	0.3988
Leaf mass	0.6873	0.3737	0.0711
Stem mass	0.5608	0.316	0.114
Root mass	0.0452	0.4197	0.2283
Total mass	0.3452	0.4353	0.1301
Leaf mass ratio	0.3096	0.2855	0.2762
Stem mass ratio	0.4898	0.6355	0.6749
Root mass ratio	0.3752	0.3931	0.3266
Leaf area ratio	0.7825	0.3448	0.9576
Leaf chlorophyll	0.1414	0.495	0.1925

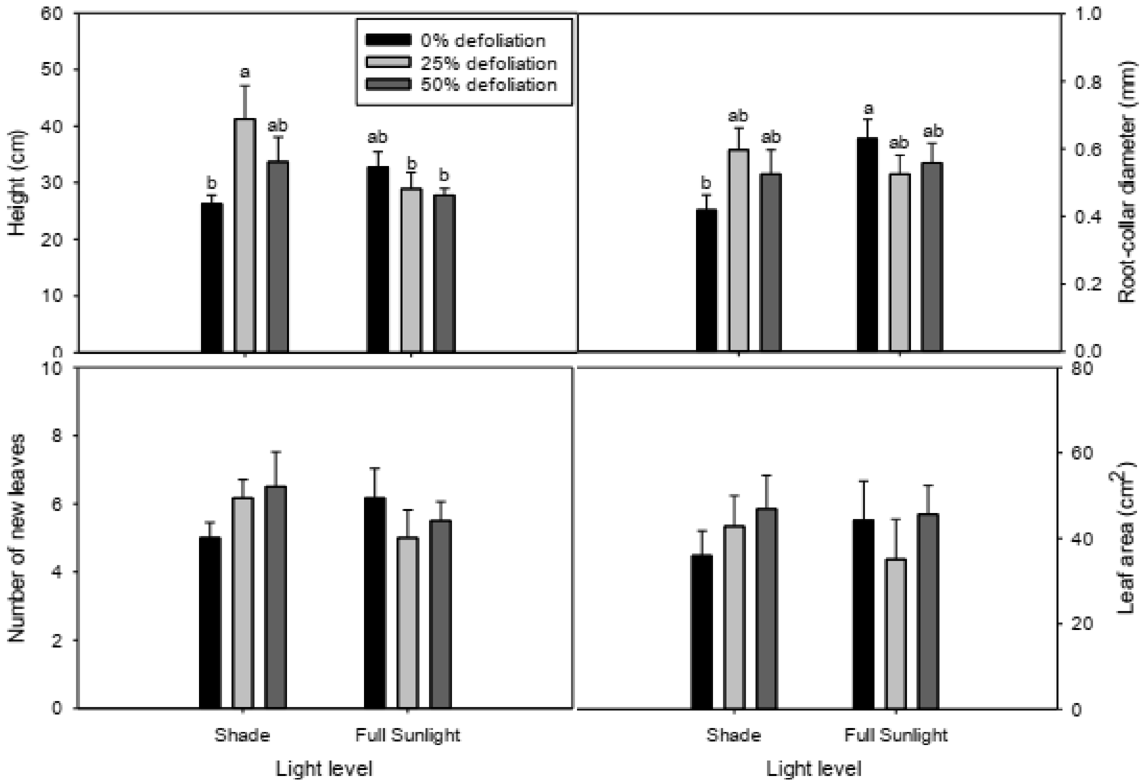

Figure 1. Effects of light and defoliation on morphology. The upper- and lower-case letters indicate the effect of light and light × defoliation, respectively, while absence of letter labels indicates non-significant. Means without a common letter differ significantly.

3.2. Biomass production

There was a significant effect of light on root mass with the parameter increasing from shade to full sunlight (Table 1, Figure 2). In addition, the effect of light × defoliation was significant for stem mass and marginally so for total mass (Table 1).

Shade suppressed leaf mass at 0 % but not at the other two defoliation treatments which did not differ between the light regimes (Figure 2). Similarly, the 50 % defoliation treatment in shade resulted in significantly lower values than the 0 % defoliation level in full sunlight. Differences between the aforementioned and any of the other remaining treatments were insignificant (Figure 2).

Stem mass declined from 25 % to 0 % defoliation under shade. In contrast, there were no significant differences between defoliation treatments under full sunlight (Figure 2). Neither the 25 % nor 0 % defoliation treatment under shade differed with any other treatment combination for stem biomass. Total biomass responded to treatments in a similar manner to stem biomass (Figure 2).

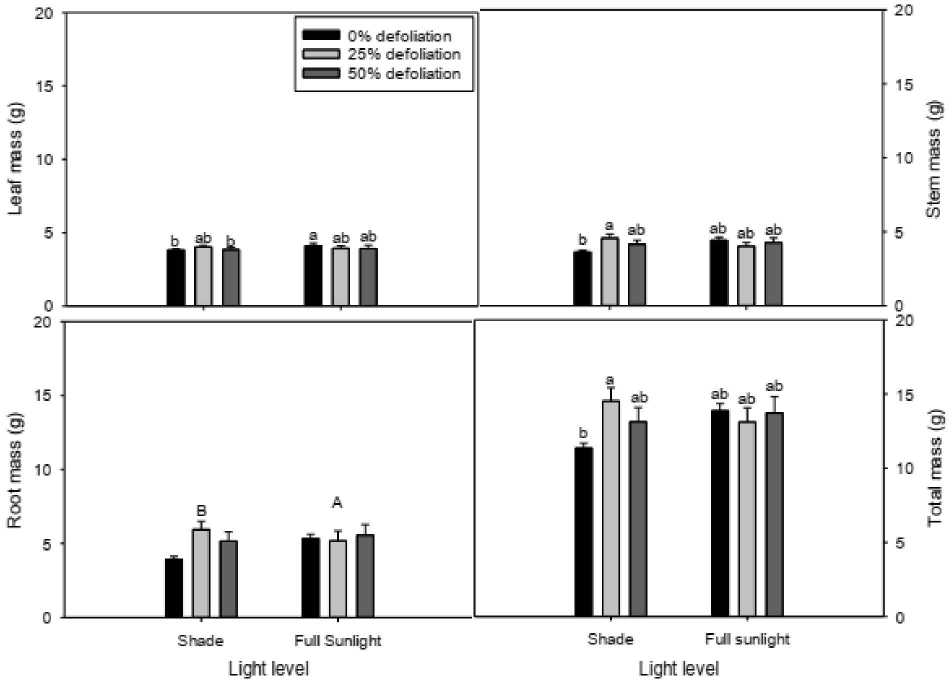

Figure 2. Effects of light and defoliation on biomass production. See caption of Figure 1 for other explanations.

3.3. Biomass allocation

Unlike biomass production, the mass ratios of leaf, stem, root, and leaf area were not influenced by either light, defoliation or their combinations (Table 1, Figure 3).

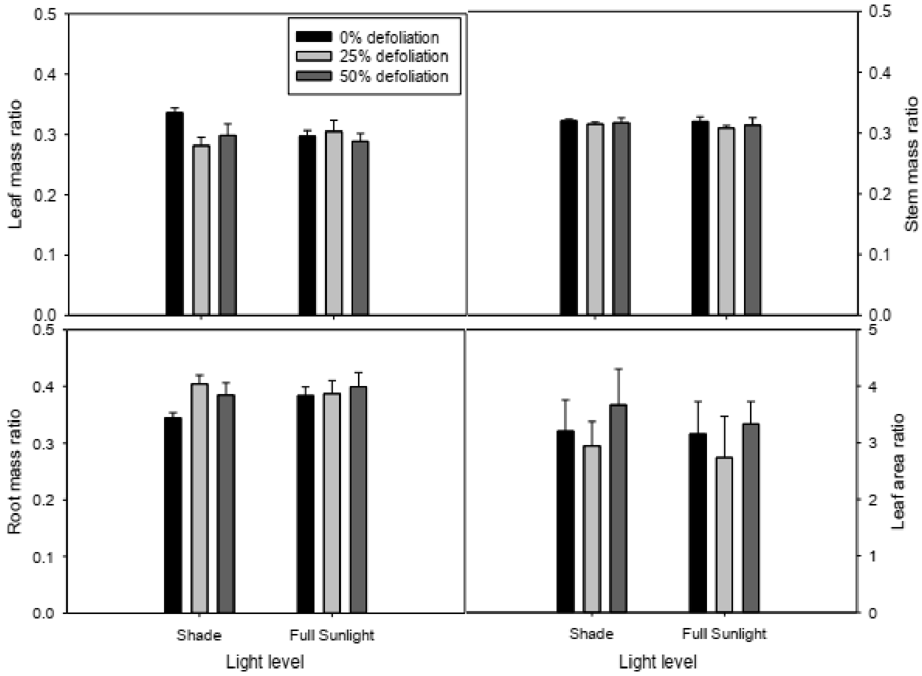

Figure 3. Effects of light and defoliation on biomass ratios. See caption of Figure 1 for other explanations.

3.4. Leaf chlorophyll content

Leaf chlorophyll content responded to light but not defoliation alone or the combination of the two factors (Table 1). The full sunlight treatment resulted in an augmentation of the parameter (Figure 4).

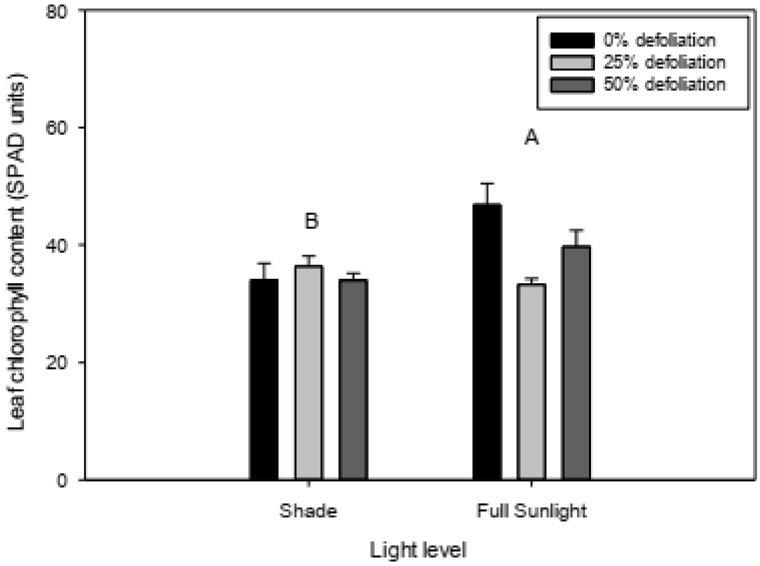

Figure 4. Effects of light and defoliation on leaf chlorophyll content. See caption of Figure 1 for other explanations.

4. DISCUSSION

As expected, morphology, biomass and chlorophyll content of *Voacanga africana* seedlings were modified by the alteration of light availability. Depending on the trait, both the trend and underpinning explanations are variable. The greater height under shade than full sunlight at 25 % defoliation is a typical plant shade avoidance response (Lambers *et al.,* 2013). Plant reactions to shading are two-fold. Firstly, there is shade avoidance where plants elongate more in response to the rich far-red light and lowered red/far-red ratio that is characteristic of a shaded environment (Iglesias *et al.,* 2018). As was the case with seedlings under the zero defoliation treatment, leaf biomass may decrease as plants invest the biomass in stem elongation rather than the leaf (Su et al., 2014; Wu et al., 2017). Under a shade tolerance scenario, in contrast, the far-red light triggers leaf expansion leading to an increased interception of radiation for photosynthetic carbon gain (Meng *et al.,* 2024). The latter hypothesis could not, however, explain the light-related difference in height in the present study since leaf area was unaffected by light availability. On the other hand, the higher root-collar diameter in full sunlight at 0 % defoliation aligned with the findings of other investigators that shaded conditions favor the upward growth of stem while reducing the stem diameter and breaking strength (Gommers *et al.,* 2013). Consistent with the work of Khalid *et al.* (2019), seedlings under the shade treatment would have attained greater heights if the light availability was lower.

Sunlight stimulates plant growth and development through the photosynthesis process in which chlorophyll plays an important role in converting the solar to chemical energy. In changing light conditions, measurements of Chlorophyll a, Chlorophyll b, and Chlorophyll a + b confer important information on the plant's ability to capture irradiance (Fan *et al.,* 2018). The results of the present study are consistent with the conclusion of Li *et al.* (2014 a, b) that chlorophyll contents decrease with reduction in light availability. Given that leaf area was unaffected by light availability, it is evident that the leaf chlorophyll content was more important than leaf size for attenuation of photosynthetic active radiation. Khalid et al. (2019) found lowering chlorophyll contents to be the reason for declines in photosynthetic rates under progressive shading conditions. The overall decline in root biomass, but not other biomass characteristics, due to the shading treatment in the present study supports the view of Caldwell *et al.* (1981) that a reduction in growth of the root system is the first response to a decrease in carbon assimilation. Plants growing in full sun require larger and more efficient root systems to meet up with higher transpiration demands Gonçalves *et al.* (2012).

The literature presents opposing responses of growth to defoliation. While the loss of functional tissue decreased growth rate and final biomass in some studies (Verkaar, 1986; Painter and Belsky, 1993), the effect was positive in others (McNaughton *et al.,* 1993; Ferraro *et al.,* 2002). In this study, a compensatory response to the tissue removal mitigated the potentially negative influence of defoliation on stem and total biomass production. Possible explanations for the response include an upregulation of photosynthetic rate (Senock *et al.,* 1991), a decrease of self-shading (McNaughton 1992), greater water-use efficiency (Varnamkhasti *et al.,* 1995), and delayed senescence (Prins and Verkaar, 1992). Among other factors, the degree of compensatory response depends on availability of nutrients (Hicks and Reader, 1995), moisture (Li *et al.,* 2022), and light (McNaughton 1992). The compensatory regrowth of the seedlings was favored more by shading than exposure to full sunlight to the extent that the lower defoliation treatment exceeded the control in terms stem and total biomass production under the former light level.

The theory of functional equilibrium predicts that plants would respond to a limited resource availability by a relative increase in flow of assimilates to the organ responsible for its acquisition (Brouwer, 1963). The findings of previous studies that leaf area ratio of *Talinum triangulare* (Alexandre *et al.,* 2018), *Mentha arvensis* (Chagas *et al.,* 2010) and other plant species increase with shade are consistent with this model. Similarly, modifications of leaf area ratio has been highlighted as a crucial morphological mechanism behind regrowth of defoliated plants (Prins and Verkaar, 1992). The general absence of a significant effect of either light or defoliation on biomass allocation in this study is an indication that the level of stress imposed by the shade and defoliated treatments on the seedlings that were growing under favorable environmental conditions was mild.

CONCLUSION

There was growth recovery of *Voacanga africana* seedlings following defoliation. However, two-factor interactions indicated that the compensatory response was dependent on light availability, being greater under shade than full sunlight. In fact, while height and biomass production under full sunlight approximated to values for undefoliated seedlings, the situation under shade was such that the undefoliated seedlings had lower responses of the traits. The findings suggest that seedlings that suffer defoliation under a forest canopy are likely to have greater growth rates and be more competitive than counterparts on open sites. Thus, canopy retention may be beneficial in areas where defoliation activity is likely to occur.

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