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Reviewed work(s):
Source: *Biotropica*, Vol. 27, No. 1 (Mar., 1995), pp. 71-77
Published by: The Association for Tropical Biology and Conservation
Stable URL: http://www.jstor.org/stable/2388904

BIOTROPICA 27(1): 71–77 1995

Shoot Damage Effects on Starch Reserves of *Cedrela odorata*

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ABSTRACT

The effects of shoot damage on starch concentrations in large roots and lower boles of the tropical timber tree, *Cedrela odorata,* were measured over a 30-day period following mechanical shoot removal. The degree of damage was based on amounts typically destroyed by *Hypsipyla grandella,* a serious lepidopteran pest of *C. odorata.* From 14-month-old plantations at La Selva Biological Station, Costa Rica, three treatments were established based on the length of shoot and number of leaves removed: controls (no tissue removed), moderate damage, and severe damage. Initial starch concentrations were compared with concentrations observed 18 to 30 days following shoot removal using enzymatic starch hydrolysis and colorimetry. Root starch concentrations increased in undamaged trees, decreased slightly in the moderately damaged trees, and decreased markedly in severely damaged trees during the sampling period. Starch concentrations in lower boles did not decrease following shoot damage, suggesting a specific role of root starch reserves in responding to aboveground carbon requirements. The dry weights of regrown shoots were similar for the moderately and severely damaged trees, but severely damaged trees produced numerous basal shoots while moderately damaged trees produced only one or two terminal shoots near the point of excision. Decreases in root starch concentrations following shoot damage and rapid shoot regrowth suggest that starch remobilization in roots of *C. odorata* might provide a survival mechanism after attack by *H. grandella.*

Key words: *allocation;* Cedrela odorata; *Costa Rica; herbivory;* Hypsipyla grandella; *resprouting; roots; starch.*

Reserve carbohydrates in trees serve as a resource for many carbon requirements, especially early season shoot growth (Eifert & Eifert 1963, Priestley 1970), winter survival (Bonicel *et al.* 1987, Sauter 1988, Nguyen *et al.* 1990), regrowth after pruning and defoliation (Parker & Houston 1971, Wargo *et al.* 1972, Gregory & Wargo 1986, Mika 1986, Bory *et al.* 1991), and resprouting after fire (Ahrens 1989, Pate *et al.* 1990). Although the role of reserve carbohydrates in plant-pest interactions has not been studied extensively, the results of some studies indicate that the relationship can be important. For example, Dunn and Potter (1990) found that vulnerability of trees to wood borers increases with decreased root starch content, and Wargo (1972) showed that the severity of fungal attack increases in trees with high levels of carbohydrates. Starch reserves may also enable some tree species to respond to herbivory, as we hypothesized would be the case with *Cedrela odorata.*

The neotropical hardwood *Cedrela odorata* L. (Meliaceae) is a relatively fast-growing species that is native to moist deciduous forests of Latin America. This species is valued for its high quality cabinet wood, but problems with pests and its exacting site requirements have minimized its use in large-scale plantations. Most failures of plantations of this species can be attributed to attacks by a shoot-boring lepidopteran larvae, *Hypsipyla grandella* Zeller, to excessive soil moisture, or to attacks by the fungus *Armillaria mellea* Kummer (Whitmore 1981).

Attack by *H. grandella* begins when the mature moth oviposits on the host, typically on a leaflet or young shoot (Holsten 1976). The emerging larvae migrate to the succulent tissues of the shoot apex and bore into the parenchymatous pith. During their development, the larvae consume the inner stem tissue, forming a pupation chamber. Further expansion of the chamber by the larva typically results in damage to vascular tissues which subsequently kills the shoot. The extent of shoot damage varies, yet almost always results in the loss of some shoot tissue, often including large compound leaves. *Cedrela odorata* normally responds to *Hypsipyla* attack with rapid regrowth of new shoots, but repeated attacks may result in death of the tree. Mortality rates decline if trees survive more than five years without suffering repeated attacks (Whitmore 1981). The improved survivorship of older trees is probably due to escape from herbivory since *H. grandella* reportedly oviposits only near terminal shoots and usually flies no higher than 2 m above the ground (Grijpma & Gara 1970).

Based on the high proportion of total biomass allocated to large-diameter roots in *C. odorata* (Haggar & Ewel, in press); preliminary tests indicating high levels of starch in these roots (J. P. Haggar,

[1] Received 2 June 1993; revision accepted 1 April 1994.

pers. comm.); and the prevalence of starch as the primary reserve carbohydrate in roots and boles of trees (Keller & Loescher 1989), it was hypothesized that the starch reserves in lower boles and roots of *C. odorata* facilitate rapid regrowth in response to attack by *H. grandella*. The objectives of this study were to determine the effect of shoot damage on starch concentrations in large roots and lower boles of *C. odorata* and to determine if the change in starch concentrations in roots and lower boles was closely related to shoot regrowth following shoot damage.

METHODS

The study was conducted at the Organization for Tropical Studies' La Selva Biological Station in the humid tropical lowlands of northeastern Costa Rica (10°26'N, 84°00'W). The average temperature is 26°C and the mean annual rainfall is 3841 mm (Clark & Clark 1991). Data were gathered on 14-month-old trees growing in three plantations (0.12 ha each) located on an 8-ha research site. All trees showed signs of having been attacked at least once by *H. grandella*. Forty-five trees were randomly selected from the subset of trees that met the following criteria: not currently under attack by *H. grandella*; 1.3 to 2.2 m tall; 14 to 31 leaves; and 3.9 to 7.9 cm basal diameter.

The 45 selected trees were randomly assigned in groups of 15 to each of three treatments: controls (no tissue removed); moderate damage (removal of 0.2 to 0.3 m of terminal shoot, including 4 to 7 leaves); and severe damage (removal of 0.5 to 0.6 m of terminal shoot, including 10 to 14 leaves). These treatments were based on observations of the degree of stem and leaf damage by *H. grandella* on other trees in the plantations.

Post-treatment tree heights and number of remaining leaves were recorded and dry weights of excised stems, leaflets, and rachises were determined after oven-drying (70°C) for 48 hours. To protect the experimental plants from attack by *H. grandella*, the bases of rachises of all leaves were encircled with a sticky insect barrier (*Tanglefoot*®) to inhibit larval movement from the leaflets (the site of most oviposition) to shoots.

On the day of treatment application, the soil around the base of each plant was removed until a large (2–6 cm diameter) secondary root was located. A 7 mm diameter cork borer was used to remove two cores from one root and two cores from the lower bole (10 to 15 cm above the ground) of each tree. The samples were immediately rinsed with water, patted dry, sealed in plastic bags, placed on ice, and returned to the laboratory within two hours.

Eighteen days after administering the treatments, resampling of root and bole tissues was initiated. In an attempt to determine if tissue samples were obtained during the period of maximum depletion of starch reserves, a different set of three trees from each treatment was randomly sampled every three days during the 12-day period from 18 to 30 days after shoot damage. This post-excision delay of 18 days was incorporated into the sampling schedule because starch is not immediately utilized following pruning (Eissenstat & Duncan 1992). All new shoot growth was excised (including basal shoots) at the time tissues were sampled and dry weights were determined after oven-drying (70°C) for 48 hours. To determine stem growth during the same period, terminal shoots of control plants were removed at the shoot height recorded at day 0.

EXTRACTION AND ANALYSIS OF STARCH.—Starch concentrations were determined using the enzyme digestion and colorimetric method (Allen *et al.* 1988 modification of Carter *et al.* 1973). On returning to the lab, the samples were immediately dried at 70°C for 40 hours. The two cores from each part (root or bole) of each tree were then ground together using a Wiley mill with a 40 mesh screen. To isolate starch from sugars and other soluble carbohydrates, a subsample of the ground tissue (0.05 to 0.12 g) was refluxed in 30 ml of 90 percent ethanol for 1 hour, the supernatants were removed, and the extraction was repeated. The remaining residue (containing starch) was then air-dried overnight. After adding 5 ml of deionized water and autoclaving the mixture for 30 minutes, each subsample received 5 ml of acetate buffer and 1 ml of amyloglucosidase solution before being incubated for approximately 48 hours at 46°C to 50°C.

Following incubation, the samples were filtered through glass fiber filters, and aliquots of the filtrate were transferred to test tubes. Water (1 ml) and alkaline reagent (1 ml) were added to each sample as well as to a tube containing a known amount of glucose (to permit determination of the fraction of glucose recovered in the analysis). The solutions were then heated in a water bath (100°C) for 22 minutes and allowed to cool. Arsenomolybdate reagent (1 ml) and water (7 ml) were added to each sample solution and to standards containing known concentrations of glucose. The optical densities of the solutions were read on a spectrophotometer at 540 nm and converted to glucose concentrations, which were then converted to starch concentrations

TABLE 1. *Relative changes in starch concentrations (percent of initial level) of roots and lower boles of* Cedrela odorata *on five sampling dates following varying degrees of terminal shoot damage (removal). Values are means ± SE (N = 3).*

Shoot damage	Relative change in starch (%)				
	Days after treatment				
	18	21	24	27	30
Roots					
None	11.9 ± 13.6	37.1 ± 6.1	−0.5 ± 8.8	−1.1 ± 6.3	19.0 ± [1]
Moderate	−1.7 ± 3.8	−25.8 ± 3.5	1.0 ± 18.9	9.1 ± 14.5	9.9 ± 8.6
Severe	−12.9 ± 3.0	−18.7 ± 15.4	−16.6 ± 11.1	−40.6 ± 10.0	−43.1 ± 7.3
Boles					
None	−22.3 ± 19.9	−3.4 ± 8.1	−0.6 ± 11.0	3.6 ± 5.0	59.6 ± 15.1
Moderate	26.3 ± 7.9	2.5 ± 10.5	−12.0 ± [1]	14.9 ± 11.7	14.3 ± 12.1
Severe	−6.7 ± 3.4	28.8 ± 13.1	2.6 ± 4.5	−16.9 ± 4.6	6.1 ± 14.2

[1] N = 2.

as percent dry weight of tissue, after correcting for percent recovery. As an overall check on the methodology, cores of cassava root (starch concentrations of about 30%, Kawano *et al.* 1987) were processed and analyzed in the same way as the *C. odorata* samples.

DATA ANALYSIS.—The relative change in starch concentration of roots and boles was calculated as $((s_n - s_{initial})/s_{initial})100$, where s_n = starch concentration (% dry wt) on day n after shoot damage and $s_{initial}$ = starch concentration (% dry wt) immediately prior to shoot damage. Treatment differences in the relative change in starch concentration in roots and the amount of shoot regrowth were analyzed using analysis of covariance with date of sampling as the covariate. When the interaction between the treatment effect and the covariate precluded analysis of covariance, treatment differences in the linear regression relation between relative change in starch concentration in boles and sampling date were tested for heterogeneity of slopes using a general linear model (SAS 1991). Comparisons of the slopes of the absolute change in root starch concentration ($s_{initial} - s_n$) over amount of shoot regrowth were made in the same manner.

RESULTS

Mean initial starch concentrations (percent dry-weight) in roots of *C. odorata* for the three damage treatments ranged from 16.9 percent to 18.4 percent, which are similar to values reported for *Acer saccharum,* (12 to 14%, Wargo *et al.* 1972), *Prunus avium* 'Bing', (16 to 27%, Keller & Loescher 1989), and *Mangifera indica* (13.5% in boles and 25.5% in roots, Whiley *et al.* 1989), and lie within the range of values reported for *Populus* (5.1 to 31.5%, Nguyen *et al.* 1990). Although the effect of time after treatment on the relative change in root-starch concentration was not significant ($P = 0.48$), starch concentrations tended to increase in undamaged trees, fluctuated in moderately damaged trees, and consistently decreased in severely damaged trees over the 12-day sampling period (Table 1). Severely damaged trees were still losing stored root starch 30 days after shoot damage.

Mean values (±SE) of relative change in starch concentration in roots averaged over time showed that trees in the control group accumulated starch during the study period and were 13.1 ± 5.4 percent higher than initial starch levels, while moderately damaged trees lost 3.7 ± 5.7 percent and severely damaged trees lost 26.4 ± 7.3 percent of their initial root starch (Fig. 1). Analysis of covariance detected significant differences in treatment adjusted means (effect of time removed) between the control and severe damage treatment (P = 0.0002), and the moderate and severe treatments (P = 0.01), but not between the control and moderate treatments (P = 0.14).

Mean initial starch concentrations in the lower boles were similar to those in the roots and ranged from 17.5 percent to 18.1 percent for the three treatments. The relative change in starch concentrations in lower boles of control plants increased steadily during the sampling period, but did not change consistently over time in the moderately and severely damaged plants (Table 1).

Interaction between treatment and date of sampling effects precluded analysis of covariance for relative change in starch concentrations of boles. The rate of change in starch concentration in boles of control trees as a function of sampling date was positive (β = 5.69) and larger than values found for either the moderate (β = −2.29) or severe (β = −0.68) damage treatments. Coefficients of the linear regression of relative change in starch concentrations in lower boles over time differed significantly between the control and moderate damage treatment (P = 0.006) and the control and the severe damage treatment (P = 0.026), but were similar for the moderate and severe damage treatments (P = 0.465). Means (±SE) of the relative change in starch concentration in lower boles over time showed modest increases of 7.4 ± 9.2, 13.4 ± 10.3 and 3.0 ± 5.7 percent for the control, moderate and severe treatments, respectively (Fig. 1).

New shoot growth in all treatments did not increase in a consistent manner during the 12-day sampling period and was not significantly influenced by time after treatment (P = 0.14). Values for new shoot growth averaged over time (mean ± SE) showed that undamaged trees produced 67.1 ± 7.4 g of new shoot tissue while moderate and severe treatments produced 14.4 ± 2.2 g and 17.5 ± 4.0 g, respectively. Analysis of covariance detected significant differences in treatment-adjusted means (effect of time removed) between the control and both the moderate (P = 0.0001) and severe (P = 0.0001) damage treatments, but not between the moderate and severe treatments (P = 0.69). Severely damaged trees produced numerous basal shoots that accounted for most of the regrowth, while regrowth from moderately damaged trees consisted primarily of 1 to 2 shoots just below the point of excision and few or no basal shoots.

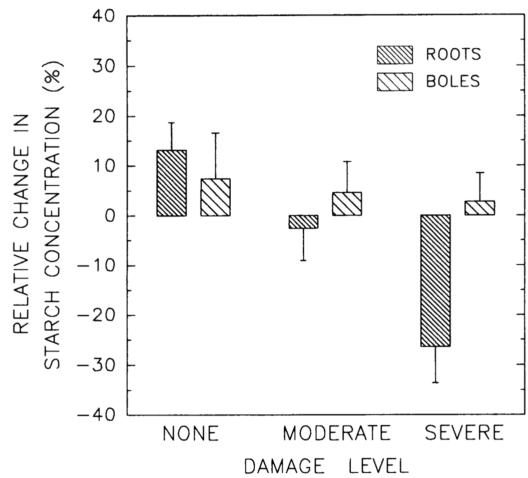

FIGURE 1. Means of relative changes in starch concentrations (percent of initial level) in roots and lower boles of *Cedrela odorata*. Trees were subjected to three levels of terminal shoot damage: control (no shoot tissue removed); moderate damage (0.2 to 0.3 cm of terminal shoot excised); severe damage (0.5 to 0.6 cm of terminal shoot excised). Values represent combined data obtained from five sampling dates over a 12-day period beginning 18 days after treatment application. Bars represent one standard error.

Linear regression of the absolute change in starch concentration (initial starch concentration − starch concentration on resampling date) in roots as a function of new shoot growth in plants with no damage was not significant (P = 0.29), whereas both the moderate and severe damage treatments had negative regression coefficients that differed significantly from zero (P = 0.0019 and 0.0108, respectively) (Fig. 2). Differences in the rate of change of starch concentration in the roots to dry weight of shoot regrowth were significant between the control and both damage treatments, but not between the moderate and severe treatments. The change in starch concentration in the lower boles was not related to biomass of regrown shoot tissue.

DISCUSSION

Evidence from this study of starch depletion in large roots of *C. odorata* subsequent to removal of portions of the shoot indicates that these reserves are remobilized and facilitate rapid shoot regrowth after damage. The marked decrease in starch in the roots of severely damaged trees supports the findings of similar work on sugar maple (Wargo *et al.* 1972),

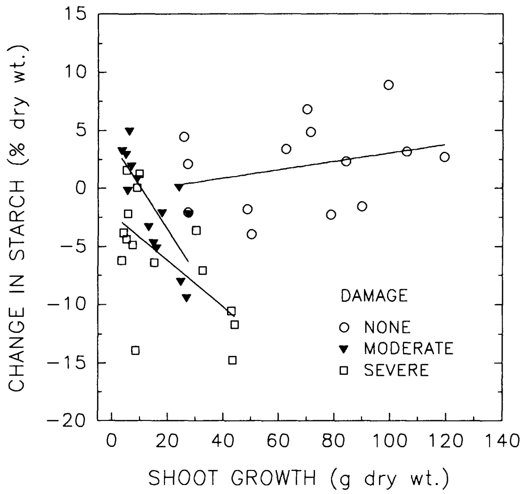

FIGURE 2. Relationship of absolute change in root starch concentration (as % dry wt) and shoot regrowth (dry wt) in *Cedrela odorata* subjected to three levels of shoot damage. Regression equations: No damage (Y = −0.50 + 0.04X, r^2 = 0.091, df = 13); Moderate damage (Y = 3.87 + −0.37X**, r^2 = 0.565, df = 13, P = 0.003); Severe damage (Y = −2.29 + −0.19X**, r^2 = 0.401, df = 14, P = 0.001). Probabilities (P) are for paired comparisons between the control group and moderate and severe groups using a t-test. Asterisks identify slopes that differed significantly ($P < 0.01$) from zero.

pecan (Worley 1979) and citrus (Eissenstat & Duncan 1992). Although the change in starch concentration in large roots of moderately damaged trees (one-fifth of the terminal shoot removed) did not differ from that of control plants, severe damage (one-third of the terminal shoot removed) resulted in a reduction of about 26 percent in the starch concentration. This suggests that carbon assimilation from leaves that remained on moderately damaged trees may have been adequate to meet carbon demands that resulted from new growth, such that reserve starch in the roots was not utilized, or that reserves utilized for new growth were simultaneously replenished.

Some investigators have argued that roots in some species do not function as storage organs since the distribution of reserve carbohydrates between roots and aboveground organs tends to remain constant, while the total reserve content may fluctuate over the season (Loescher *et al.* 1990). Such was not the case in this study where starch concentrations in the large roots and lower boles of *C. odorata* were initially similar and declined to a greater degree in the roots following severe shoot removal. This was true even in trees that produced most new growth on the lower bole. This suggests a specific role of roots as sites for reserve carbohydrates that are utilized in the regrowth of shoots. Although the net change in starch concentrations in boles did not decrease, suggesting that boles do not have the same function, information on starch turnover rates in the boles is needed to support this conclusion. Further clarification of carbohydrate sources, reallocation patterns, and rates of use would entail the use of more sophisticated techniques (Kandiah 1979) than were used in this study.

The rapid remobilization of starch reserves permitted severely damaged *C. odorata* trees to support shoot regrowth that was comparable to that of moderately damaged trees. Nevertheless, regrowth of shoots in severely damaged trees was primarily in the form of numerous basal shoots, a response that may reduce the likelihood of losing all terminal shoots to attack by *Hypsipyla grandella*. In addition to the remobilization of reserve carbohydrates, growth in severely damaged trees may have been facilitated by improved environmental conditions around the tree following shoot removal, such as increased light, nutrient, and water availability, or by increased levels of cytokinins from roots (McNaughton 1983). Changes in these factors would not be expected to be as great in trees with moderate shoot removal.

The weak relationship between the change in starch concentrations in roots and shoot regrowth in moderately and severely damaged trees probably reflects differences in the amount of time allowed for regrowth. Shoot growth in trees sampled at 30 days was likely facilitated by current assimilates from more mature regrowth, but was more dependent upon reserve carbohydrates in trees sampled at 18 days. Similar work on sweet cherry (***Prunus avium*** 'Mazzard') revealed a close relationship between starch concentrations in roots and new shoot growth (McCamant 1988). Since current carbon assimilation was the primary source of carbohydrates for growth, the absolute change in starch concentration in roots of control trees was not related to shoot growth.

It is recognized that mechanical shoot removal differs from *H. grandella* attack in its impact on hormonal activity (see review by Mika 1986). Shoot damage by *H. grandella* involves the gradual destruction of vascular tissues as the pupation chamber becomes larger in diameter. Therefore, it is likely that interruptions of apical dominance and initiation of hormonal activity in response to apical damage are delayed, and the timing of mobilization of starch reserves and resprouting would be expected to differ between our experimental plants and those subjected to *H. grandella* attacks. Nevertheless, it is the plant response in the form of new-tissue production that draws down starch reserves, and there was no obvious difference in the number and size of shoots produced in response to excision compared with those produced in response to the shoot borer.

Carbohydrate reserves are important in some species for respiration during the dry season (Janzen & Wilson 1974) and for initiation of vegetative and reproductive growth following leaf drop (Eifert & Eifert 1963, Priestley 1970). This is likely true for *C. odorata* (a dry-season-deciduous species) as well. In addition, it appears that the starch reserves in its roots facilitate rapid regrowth after attack by *H. grandella,* thus enabling *C. odorata* to maintain the competitive stature essential to its survival.

ACKNOWLEDGMENTS

HLR would like to thank J. J. Ewel (Dept. of Botany, University of Florida) for the opportunity to participate in the Research for Undergraduates Program (funded by National Science Foundation, grant #BSR09000089). We thank J. Haggar and P. Zimba for comments on the manuscript and M. Colon and W. Hussein for guidance on starch extraction procedures.

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