COPPICE SPROUTS IN *CORDIA ALLIODORA*

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HUMMEL, S. 2000. Coppice sprouts in *Cordia alliodora*. Coppice treatments were applied in 5-y-old experimental plots of *Cordia alliodora* to investigate whether 1) sprouts are produced more often by retaining a stump (consistence), 2) more sprouts are produced on a stump (profusion), and 3) sprout production is related to the diameter of the "parent" tree. In each of 3 replicated plots, 8 trees were cut with a 0.5-m stump retained and 8 trees were cut flush to the ground. The 48 treatment trees were inspected for sprouts after 136 days. All 24 of the trees with 0.5-m stumps sprouted, but only 8 of the 24 flush-cut stumps sprouted. The 0.5-m stumps averaged 16.33 sprouts, while the flush-cut sites averaged only 0.71 sprouts per tree. Statistical analyses confirmed that the 0.5-m stumps sprouted both more consistently ($p > 0.02$) and more profusely ($p > 0.0001$) than did the flush-cut sites. The diameter of the "parent" tree was not strongly associated with sprout production or with the mean number of sprouts. Results of this study confirm that *C. alliodora* is a facultative sprouter and suggest that silvicultural treatments to coppice *C. alliodora* should retain a stump rather than cutting trees flush to the ground. Trees such as *C. alliodora* that sprout facultatively can be useful for reforestation of severely disturbed sites.

Key words: Vegetative reproduction - La Selva - silviculture - Costa Rica - laurel

HUMMEL, S. 2000. Tunas kopis dalam *Cordia alliodora*. Rawatan kopis dijalankan di petak kajian *Cordia alliodora* berusia 5 tahun untuk menyiasat sama ada 1) tunas lebih kerap dihasilkan dengan mengekalkan tunggul (konsisten), 2) tunas lebih banyak dihasilkan pada tunggul (banyak), dan 3) penghasilan tunas berkaitan dengan garis pusat pokok "induk". Lapan batang pokok di setiap tiga petak yang seiras ditebang dengan meninggalkan tunggul setinggi 0.5 m, sementara lapan batang lagi ditebang separas dengan tanah. Penghasilan tunas diperhatikan pada 48 batang pokok yang dikaji ini selepas 136 hari. Kesemua 24 batang pokok yang bertunggul 0.5 m bertunas, tetapi hanya 8 daripada 24 tunggul yang separas dengan tanah bertunas. Tunggul 0.5 m menghasilkan purata 16.33 tunas sementara tunggul separas dengan tanah menghasilkan cuma 0.71 tunas. Analisis statistik mengesahkan bahawa tunggul 0.5 m bertunas secara lebih konsisten ($p > 0.02$) dan lebih banyak ($p > 0.0001$) berbanding tunggul yang separas dengan tanah. Garis pusat pokok "induk" tidak begitu berkait rapat dengan penghasilan tunas atau dengan min bilangan tunas. Keputusan kajian ini mengesahkan bahawa *C. alliodora* merupakan penunas fakultatif selain mencadangkan bahawa rawatan silvikultur terhadap kopis *C. alliodora* sepatutnya meninggalkan tunggul dan tidak menebangkan pokok sampai ke tanah. Pokok seperti *C. alliodora* yang bertunas secara fakultatif berguna untuk penghutanan semula tapak yang terganggu teruk.

Introduction

Successional dynamics in forests are influenced by disturbance patterns (e.g. Reiners & Lang 1979) and by plant reproductive strategies (e.g. Grime 1979). Disturbed forests regenerate via germination of seeds, growth of surviving trees or seedlings and vegetative sprouts. The intensity and type of disturbance, as well as the stage of stand development at the time of disturbance, affect which regeneration strategy is most successful (Oliver & Larson 1996). Severely disturbed sites regenerate predominantly via germination of the soil seed bank (e.g. Marks 1975) or via sprouts (e.g. Kauffman 1991), while mild disturbances favour the growth of pre-existing seedlings. On severely disturbed sites, trees that reproduce both vegetatively and from seed (facultative sprouters) can have a competitive advantage over trees that reproduce only from seed (obligate non-sprouters) because sprouts grow faster than seedlings (Kozlowski *et al.* 1991).

Vegetative reproduction in trees is described according to origin. Thus, a root sucker originates from the roots, a sprout originates from a dormant bud on the lower stem and epicormic branches originate from the main stem (Ford-Robertson 1983). The silvicultural term 'coppice' is used when forest regeneration is secured via vegetative means, or to describe the ability of a tree to reproduce vegetatively. Knowledge of tree reproductive strategies is a basic requirement for understanding stand dynamics, as well as for silviculture.

This study investigated sprouting in the neotropical tree *Cordia alliodora* (Ruiz & Pav.) Oken. *Cordia alliodora* has a native range from Mexico to Argentina, or 25° N to 25° S latitudes in the American tropics (Liegel & Stead 1990). In Costa Rica, as elsewhere in its range, the tree is often grown together with crops of cacao and coffee (e.g. McCaffrey 1969, Schlonvoigt 1993). In such agroforestry systems, *C. alliodora* trees offer several benefits. They shade the growing crop (Somarriba & Beer 1987), provide seasonal inputs of nutrient-rich litterfall (Glover & Beer 1984), and can be harvested for timber after twenty years or more (CATIE 1994). The wood of *C. alliodora* is known locally as "laurel" and is prized for structural and decorative uses (Cordoba *et al.* 1990). Costa Rican farmers can receive a premium for laurel; between 1988 and 1993, the stumpage price increased 60.9% (Howard 1995). For this reason, *C. alliodora* was a popular species for plantations and reforestation projects in the 1980s (Butterfield 1994).

Cordia alliodora grows over a range of site conditions and elevations. These include flat coastal lowlands with infertile soils and low organic matter such as in Surinam, mountainous uplands with volcanic soils high in organic matter found in Columbia (Johnson & Morales 1972), and riparian areas and forest edges (Opler *et al.* 1975). The seeds of *C. alliodora* are wind dispersed (Liegel & Stead 1990) and retain viability for a year when properly stored (Stead 1979). Previous observations of vegetative growth in *C. alliodora* suggest it is probably a facultative sprouter. For example, Marshall (1939) commented that "young and medium-sized trees" of *C. alliodora* were observed sprouting in Trinidad and Tobago. Other observations of sprouting in *C. alliodora* were made in Vanuatu (Neil 1984), in Costa Rica (Beer 1979), and in Mexico (Miller 1999). Johnson and Morales (1972) recorded the presence of root suckers, while epicormic branching was noted by Barrance (1985). Vegetative growth in stems and branches was observed during tree improvement work in Columbia (Koenig & Melchior 1978). To date, however, there are no published results from an experiment on the sprouting response of *C. alliodora.* This study was therefore designed to investigate whether 1) sprouts are produced more often by retaining a stump (consistence), 2) more sprouts are produced on a stump (profusion), and 3) sprout production is related to the diameter of the "parent" tree.

Methods

Site description and experimental design

This study made use of experimental plots of *C. alliodora* planted at La Selva Biological Station (La Selva) in 1991. La Selva (10°26'N, 84°00'W) lies within the tropical moist forest life zone (Holdridge *et al.* 1971), and has an annual mean temperature of 24 °C and annual average precipitation of 4000 mm. The history, setting and physical and biotic characteristics of La Selva are described in McDade and Hartshorn (1994).

The experimental plots are on an alluvial floodplain where the soils are classified as mixed Isohypothermic, possibly Andic, Fluventic Dystropepts (Haggar & Ewel 1994). Each plot of *C. alliodora* (50 m × 40 m) was replicated three times. Each tree in the experimental plots was assigned a unique, 4-digit identification number when planted. A complete description of the site, design and initial hypotheses of the original experiment is explained in Haggar and Ewel (1994). The trees were growing in monocultural plots and were all 5 y old when sampled. The population from which the sample was drawn were those trees previously marked for thinning. Although thinning operations often target trees of inferior vigour or size, this thinning was done to regulate spacing. The sample trees were, therefore, representative of the variation in the plantation.

The 4-digit tree identification numbers and a random number table were used to select *C. alliodora* trees to receive one of two coppice treatments. Eight trees were randomly assigned a stump treatment and eight trees were randomly assigned a flush-cut treatment in each of the three replicated plots. The diameter (at 1.3 m) of each tree before applying the coppice treatments was recorded in June 1996 (Table 1). All 48 trees were cut with a chain-saw: half were cut at an approximate 45° angle, at a height of 0.5 m, while the remainder were cut flush with the ground. After 136 days, the 48 treatment trees were inspected and recorded as to whether any sprouts were present, and, if so, the total number of sprouts per tree.

Data analyses

The first analysis was a test of proportion using normal theory. A Z-test was used to evaluate the null hypothesis that no significant difference in the production of sprouts existed between treatments. The second analysis used analysis of covariance (ANCOVA) techniques in SAS® to test whether the profusion of sprouts was

Table 1. Range of tree diameter (dbh) (cm) prior to coppice treatment (S=0.5-m stump, F=flush-cut)

Replicate	Treatment	n	Mean dbh	Max.	Min.	SD
1	S	8	6.2	8.8	4.4	1.61
	F	8	10.4	13.5	7.5	2.07
2	S	8	8.4	11.2	6.3	1.59
	F	8	10.4	13.0	8.1	1.66
3	S	8	8.8	12.4	7.0	1.91
	F	8	11.9	20.2	8.1	3.66

significantly different between treatments after accounting for variation in "parent" tree diameter. Prior to the analyses diagnostics such as residual plots were prepared and, subsequently, a square root transformation of the data was done. The power of the Z-test and the ANCOVA were calculated for all replicates.

Results

Cordia alliodora produced sprouts in both the 0.5-m stump and the flush-cut treatments, which confirms that the tree is a facultative sprouter. However, both the production of sprouts (consistence) and the mean number of sprouts per stump (profusion) were strongly related to the coppice treatment method and therefore the null hypothesis of no treatment difference is rejected. Trees cut with a 0.5-m stump retained sprouted both more consistently (replicate one: $p > 0.001$, replicate two: $p > 0.0209$ and replicate 3: $p > 0.0019$) and more profusely than did the flush-cut trees ($p > 0.0001$ for all replicates respectively). Overall, one hundred percent of the 0.5-m stumps produced sprouts, while only one-third of the flush-cut stumps produced sprouts (Table 2). The power ($\alpha = 0.01$) of test for all replicates was at least 0.93.

There was no significant relationship between the diameter of the parent tree and sprout profusion in the 0.5-m stump treatment ($p > 0.0001$ for all replicates) (Figures 1, 2 and 3). For the flush-cut sites, no significant relationship between diameter and profusion existed in either replicate one ($p > 0.5570$; Figure 1) or replicate two ($p > 0.1155$; Figure 2). In replicate three, however, sprout profusion in the flush-cut sites was associated with diameter ($p > 0.0018$).

Discussion

Results of this study provide strong evidence that *C. alliodora* is a facultative sprouter. This conclusion is supported by previous observations of vegetative growth in *C. alliodora.*

The range of conditions in which *C. alliodora* produces sprouts is still unknown, however. I did not, for example, investigate the relationship between tree age, disturbance type or season of coppice and sprout production. Nor did I investigate survival and mortality of the sprouts produced. Any or all of these factors may also influence the production, profusion and long-term viability of sprouts.

Coppice sprouting in *C. alliodora* probably varies with tree age. Young trees that do not yet produce viable seed may rely on sprouting for regeneration. Older trees

Table 2. Total number of *Cordia alliodora* trees with sprouts and mean number of sprouts per tree 136 days after coppice treatment (S= 0.5 m stump, F= flush-cut)

Replicate	Treatment	n	With sprouts	Without sprouts	Mean #sprouts per tree	SE	Max # sprouts	Min # sprouts
1	F	8	2	6	0.375	0.26	2	0
	S	8	8	0	21.5	2.96	34	9
2	F	8	4	4	1.375	0.73	6	0
	S	8	8	0	13.875	1.81	22	4
3	F	8	2	6	0.375	0.26	7	0
	S	8	8	0	13.625	1.7	20	6

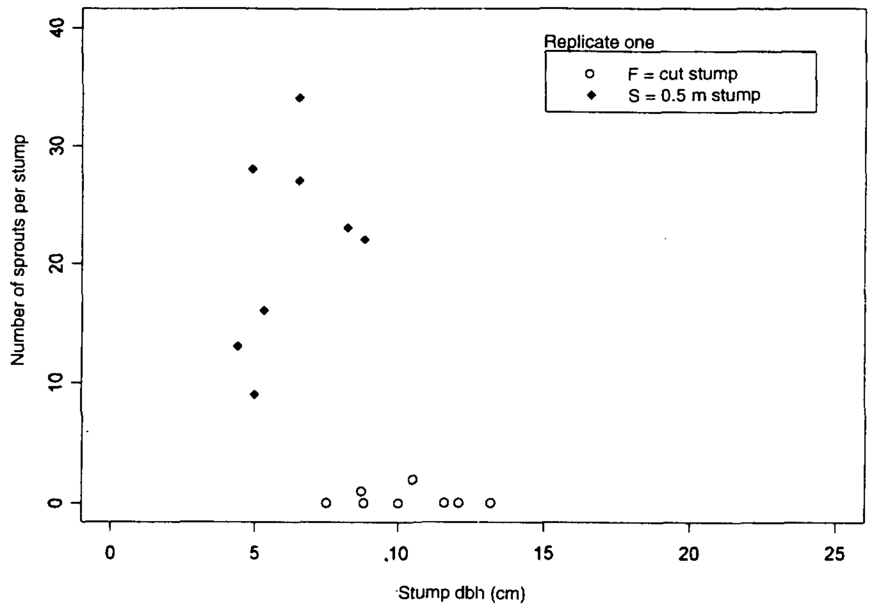

Figure 1. Relationship between tree diameter (dbh at 1.3 m) and number of sprouts 136 days after coppice treatment in *Cordia alliodora*

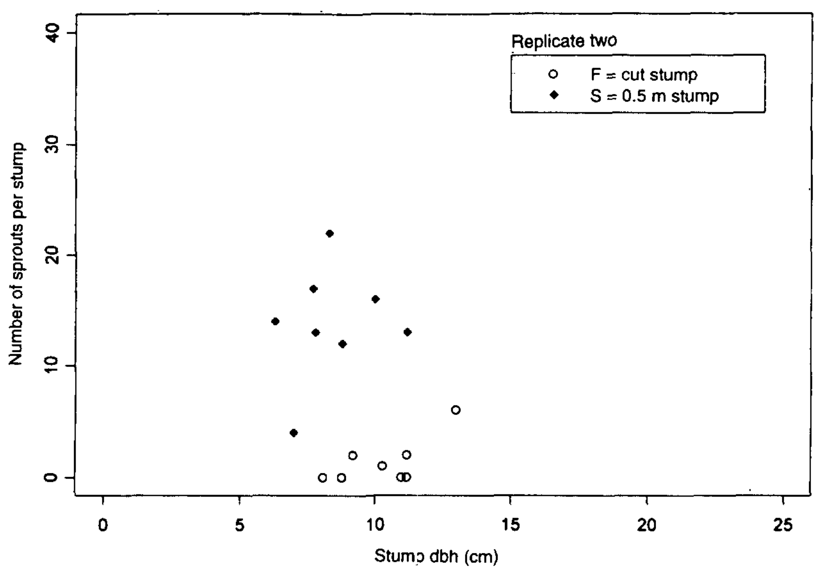

Figure 2. Relationship between tree diameter (dbh at 1.3 m) and number ot sprouts 136 days after coppice treatment in *C. alliodora*

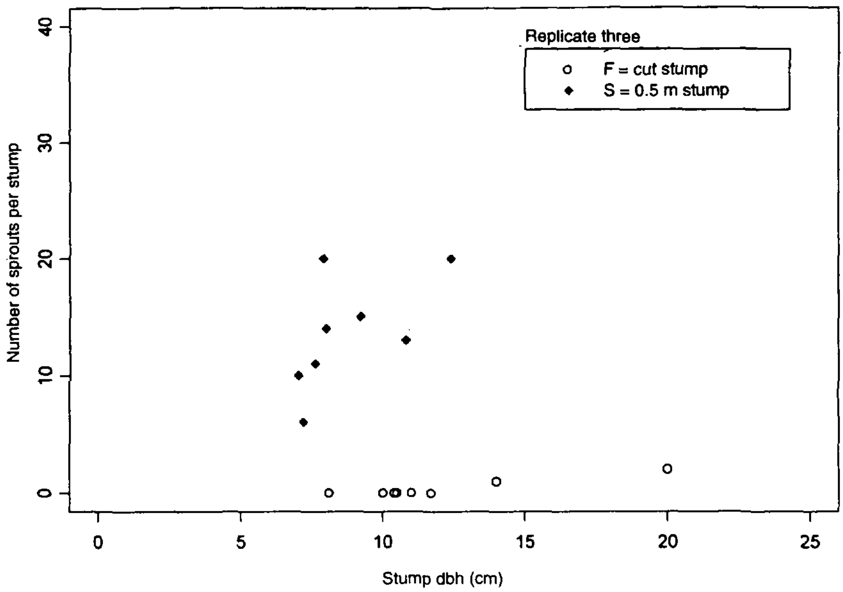

Figure 3. Relationship between tree diameter (dbh at 1.3 m) and number of sprouts 136 days after coppice treatment in *C. alliodora*

might reproduce via seed or sprout, depending on disturbance patterns and site conditions.

The type of disturbance will likely affect both sprouting and survival. This study only investigated sprouting response after cutting, and the response may well vary with, for example, fire. Miller and Kauffman (1998) observed in slash-and-burn plots in Mexico that it was disadvantageous for individuals to sprout before burning. Similarly, Sampaio *et al.* (1993) reported that 94% of individuals sprouted after slashing but only 10–43% sprouted after fire. In a comparative study in Paraguay and Venezuela, Kammesheidt (1999) found that the percentage of trees of sprout origin declined with stand age following fire, while this percentage slightly increased following logging.

These coppice treatments were installed in early summer, when the trees had just leafed out. Maximum seedfall for *C. alliodora* is typically in April and May (Liegel & Stead 1990). Kozlowski *et al.* (1991) observed that, in general, sprouting was least abundant at this time, as trees had low carbohydrate reserves. Instead, trees responded more vigorously to coppice treatments made in the dormant season, when there was a reserve of food material stored in roots. From observations made in India, Parkash and Khanna (1979) concluded that coppice treatments made after the dormant period resulted in a poorer and weaker sprout response. The coppice response observed in this study may change seasonally, or in relation to seed production.

The stability and survival of stems originating from sprouts were not addressed, but could influence management decisions about the choice of silvicultural systems.

Lamprecht (1993), for example, recommended coppice cuts "close to the ground" due to concerns about stability. Thus, although results from this study indicate that more sprouts are obtained by leaving a stump than not, the quality of the resulting stems still requires evaluation.

Oliver and Larson (1996) stated that the size of the "parent" stump influenced the early height growth of sprouts, and I expected stump diameter to be directly related to sprout production in *C. alliodora*. In this study, however, the diameter of the parent tree did not have a significant relationship with either the consistency or profusion of sprouts produced in the 0.5-m stump treatment. Similar results were obtained for the flush-cut treatments in all but replicate three, where the two largest trees in the experiment were located. Sprouts on these two trees, although few, were enough to suggest a weak relationship (Figure 3). If stump size is indeed a factor in sprout production, then measurements in addition to diameter may be needed to evaluate the relationship.

Recommendations

The reproductive strategy of a tree provides clues about the disturbance regimes to which it is adapted. Facultative sprouters such as *C. alliodora* can be strong competitors on severely disturbed sites. Such conditions might be found, for example, following intensive logging, flooding or fire. Results from this study indicate that the production and the profusion of stump sprouts in *C. alliodora* are related to the method of coppice. These results provide silvicultural information on an economically important tree species and may be used to manage *C. alliodora* in areas with similar rainfall, temperature and soil conditions.

Future experiments should include a wider range of stump height, tree age and tree diameter. Results from such experiments will improve our understanding of the range of conditions in which coppicing occurs in *C. alliodora*, as well as the optimal timing and height of coppice treatments.

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