Canopy gap closure in thickets of the clonal shrub, *Cornus racemosa*[1]

Matthew B. Dickinson
Department of Biological Science, Florida State University, Tallahassee, FL 32306

Francis E. Putz
Department of Botany, University of Florida, Gainesville, FL 32611-2009

Charles D. Canham
Institute of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545

ABSTRACT

DICKINSON, M. B. (Department of Biological Science, Florida State University, Tallahassee, FL 32306), F. E. PUTZ (Department of Botany, University of Florida, Gainesville, FL 32611-2009), AND C. D. CANHAM (Institute of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545). Canopy gap closure in thickets of the clonal shrub, *Cornus racemosa*. Bull. Torrey Bot. Club 120: 439–444. 1993.—We investigated the rates and mechanisms of canopy gap closure and changes in thicket age, stem density, crown size, and canopy closure with height in thickets of the clonal shrub, *Cornus racemosa* Linnaeus. We conducted the study in a well drained upland old field with nutrient-poor soil and a poorly drained lowland old field with more nutrient-rich soil in New York's Hudson Valley. As thickets grow taller, canopy closure tends to decrease because lateral growth of canopy stem crowns does not completely offset decreases in canopy stem density. When stems die, they generally die standing and singly, forming gaps in the canopy. Single stem gaps formed by standing-dead stems were closed predominantly by lateral growth of the branches in the crowns of stems surrounding the gaps. Mean closure rates of experimentally created gaps were greater on average in the wetter and more nutrient-rich lowland site (15.0 cm/yr) than in the upland site (5.0 cm/yr). Gaps closed by 85%/yr at the lowland site and 21%/yr at the upland site. The fates of understory stems differed between sites, more understory stems reached the canopy in upland thickets. Stem lean contributed to both the opening and closing of individual gaps at both sites. On average, lean opened gaps in upland thickets and had no effect on lowland gap closure rates. Stem lean after gap creation increased with canopy stem density. Larger gaps should take longer to close, allowing more opportunity for understory stems to contribute to gap closure.

Key words: *Cornus racemosa*, clonal shrubs, canopy gaps, canopy dynamics, succession, invasion resistance.

Rates of tree seedling invasion within intact *Cornus racemosa* Linnaeus (gray dogwood) thickets are quite low (Egler and Anderson 1982). Within shrub thickets, root and shoot competition reduces tree seedling growth rates (Putz and Canham 1992) and tree seeds and seedlings are subjected to heavy herbivore pressure (Niering et al. 1986). Understanding the maintenance of gray dogwood thickets will facilitate their management as a means of suppressing tree regeneration in areas, such as powerline right-of-ways, where trees are not desired. Other means of controlling tree regeneration in powerline right-of-ways are problematic; mechanical control is expensive and blanket herbiciding controversial (Egler and Anderson 1982). Our main objective in this study was to derive a mechanistic understanding of canopy gap formation and closure in gray dogwood thickets as the basis for a better understanding of shrub thicket persistence.

Canopy gap dynamics has been little studied in shrubs, but forest canopy gaps are closed by lateral branch growth of gap margin individuals (Runkle and Yetter 1987), by growth of understory plants (e.g., Brokaw 1985), by vegetative recovery of damaged trees (Putz and Brokaw 1989), and potentially by bending of branches and boles of gap-margin trees towards the gap center. In shrub thickets, the continual produc-

tion of new stems has been emphasized in the maintenance of canopy cover (Balogh and Grigal 1987; Kurmis and Sucoff 1989; Luken 1990; Tappeiner et al. 1991).

This study was designed to address the following questions relative to canopy gap closure in gray dogwood thickets. Are natural gaps generally formed by the death of single or multiple stems? How quickly do gaps close? What is the relative contribution of understory stem growth, lateral growth of the branches of gap edge stems, and lean of gap edge stems to the closure of experimentally created gaps in gray dogwood thickets? How does the mode of gap formation influence the contribution of stem lean to gap closure? Do stem densities decrease and canopies become more open as thickets age or does crown expansion tend to maintain canopy closure with decreases in stem density? We addressed these questions at two sites at either end of a continuum from low to high water and nutrient availability in order to estimate the range we could expect in the rate and process of gap closure where gray dogwood occurs in New York's Hudson Valley.

Materials and Methods. SPECIES STUDIED. Gray dogwood is a common shrub in abandoned agricultural fields in the Hudson Valley of New York. It reaches its greatest cover on mesic sites, but sometimes dominates even dry, rocky sites. It forms dense thickets ranging from 3–20 m in diameter and up to 5 m tall with most thickets 2–3 m tall. The thickets generally have well defined canopies. The shrub spreads vigorously by runners and produces copious seed crops. Gray dogwood seedlings are present within thickets, but their importance to thicket dynamics relative to vegetatively produced stems is unknown.

STUDY SITES. We conducted the study on two abandoned agricultural fields on the grounds of the Mary Flagler Cary Arboretum near Millbrook, New York (41°50′N, 73°45′W). Mean annual precipitation is 1020 mm, mean annual temperature is 9.4°C, January temperatures average −4.2°C, and July temperatures average 22.4°C (Glitzenstein et al. 1990). The upland field has well drained gravelly loam soil derived from glacial outwash (Secor et al. 1955) and, until about 20–30 years ago, was used primarily for pasture. The lowland field was cut for hay until about 25 years ago and prior to that supported row crop agriculture. The soil at the lowland site is silty clay loam derived from alluvial material (Secor et al. 1955).

The two sites are dominated by gray dogwood thickets, forbs, and grasses. Occasional *Lonicera* spp. and *Rubus* spp. thickets are also present. Forbs and grasses reach their highest cover in the spaces between thickets.

STEM AND THICKET CHARACTERISTICS. We measured canopy stem density, thicket height, stem age, canopy cover, and horizontal crown diameter per stem on a random selection of almost all the thickets > 1 m in height and the two old fields. From this sample, we excluded thickets in which more than ¼ of their canopy stems had died and the few thickets with overtopping trees. To estimate stem density, we counted canopy stems within two adjacent or (in small thickets) a single 2 m² quadrat. Stems fused near the base were counted as separate stems and stems branching > 30 cm above the base were counted as a single stem. We measured the height of the three tallest stems within each quadrat and averaged the values. To estimate thicket age, we cut the tallest stem within each quadrat and counted the number of rings 5 cm from the base. We estimated canopy cover with a spherical densiometer 1 m below the canopy (Lemon 1956). None of the canopy cover measurements included visible single or multiple stem gaps. To estimate horizontal crown diameter, we measured crown diameter at the widest point and its perpendicular on five or six canopy stems in the center of each thicket and averaged the values. Spearman Rank correlation was used to test the significance of relationships between thicket characteristics.

We also tested for differences in stem growth rates between sites. This was done by testing whether or not the slope of the regression of stem age on stem height for the lowland site was equal to that of the upland site. If there is a significant interaction between site and stem age in a two-way analysis of variance (stem height is the dependent variable), then the null hypothesis of equality of slopes is rejected.

To find out how many stems died to form canopy gaps, we randomly selected thickets > 1.5 m in height from all the thickets in both the upland (N = 12) and lowland (N = 18) sites. For all the gaps in each thicket we recorded how many stems had died to form each gap. We made no attempt to distinguish between recent and older gaps.

GAP CLOSURE. In nine randomly selected thickets > 1.5 m tall, we created one gap by defoliating and stripping the basal 10 cm of bark

from a randomly selected stem. In the lowland site, one to three adjacent stems were defoliated if the single stem gap was small (<28 cm average gap diameter). These gaps were created in August 1989, and all defoliated stems were dead in July 1990. In order to create an unambiguous gap, we removed any stems with foliage in the canopy, but over-topped by the gap-forming stem. Thicket canopies were generally distinct and were defined as the volume between the lowest and highest leaf forming an edge of the vertically projected two dimensional gap.

To facilitate measurement and remeasurement of gap dimensions we drove a permanent stake into the center of each gap and suspended a plumb line over the stake from a temporary scaffolding placed above the canopy. At 45 degree intervals starting at 0 degrees, we measured from the plumb line to the nearest canopy leaf and to a tag placed on the branch to which that leaf was attached.

We remeasured gaps in early July 1990 and estimated total radial closure by subtracting the 1990 measurement of distance from the plumb line to the nearest leaf from its corresponding 1989 measurement. We estimated radial closure by canopy branch and stem lean from the net movement of tags towards or away from the plumb line. To estimate growth of canopy branches, we subtracted the measurement of lean from the measurement of total radial closure at each of the sampling points around the gap. We excluded from the analysis one lowland canopy gap in a thicket in which many stems, including gap edge stems, had died between sampling dates. We noted whether or not a tagged branch was dead or alive in 1990 (all tagged branches were alive when tagged in 1989). Spearman Rank correlations were used to test the significance of the relationships between closure and thicket characteristics.

We report gap closure rates and rates of entrance of understory stems into the canopy as yearly rates. This was done by dividing the observed values by 11. This procedure slightly underestimates the actual rates because the missing month occurred during the summer when the plants were still growing.

To determine the fates of understory stems, we tagged and measured the height growth of all understory stems within 0.75 m of the center of each experimental gap. Also, stems were categorized based on whether or not they increased in size, died, were browsed, or were otherwise damaged during the year of the study. Percentages of stems in each category were calculated

for each gap and the data were log transformed. The damaged category was dropped in the analysis so that percentages were not constrained to sum to 100%. Also, data from one gap in the upland site that had only one stem were dropped from the analysis. Hotelling's T^2, a multivariate statistic, was calculated to test for differences between site means. One-way analyses of variance also were done to test for differences between means of individual variables. A probability value of $P = 0.02$ was used to judge significance of tests (adjusted downward from $P = 0.05$) in an attempt to avoid spurious conclusions.

We created five additional gaps in order to determine the extent to which gaps formed by stem removal (as opposed to gaps formed by stems that died in place) were closed or further opened by leaning of stems adjacent to the gaps. These gaps, created in thickets near the upland site in July 1989, ranged from 9 to 20 cm diameter. Gaps were remeasured 5 weeks later. In order to estimate height : diameter ratios, we also measured the height and diameter of five stems surrounding each artificial gap.

Results. STEM AND THICKET CHARACTERISTICS. Upland and lowland thickets differed only in canopy closure (Table 1). Thicket age, height, stem density, and crown radius did not differ between sites. However, as thickets grow taller, canopy stem density decreases, while crown diameter increases in both upland and lowland thickets (Table 2). Also, older thickets were taller. The relationship between percent canopy closure and thicket height was weak in upland thickets and not significant in lowland thickets. Heavy stem mortality (mortality of >¼ canopy stems) had occurred in 16% of upland thickets and 6% of lowland thickets.

GAPS. Upland and lowland gray dogwood thickets had an average of 8 and 2 canopy gaps in their canopies of which 72 and 75%, respectively, were formed by mortality of standing, single stems (Fig. 1). A total of 93 gaps from 12 thickets were recorded at the upland site and 36 gaps from 18 thickets were recorded at the lowland site. There was no relationship between number of dead stems in thickets and thicket age at either the upland ($r = -0.289$, N = 12, $P > 0.05$) or lowland site ($r = -0.261$, N = 18, $P > 0.05$).

Total radial closure, growth, and lean varied between the upland and lowland sites (Tables 3 and 4). Total radial closure, lean, and growth varied among upland gaps, while only lean var-

Table 1. Means (sample size, range) of thicket characteristics of the rhizomatous shrub *C. racemosa* from an upland and a lowland site and results of Mann-Whitney *U*-tests for differences between sites (NS $P > 0.05$, * $P < 0.05$).

	Uplands (N = 33)	Lowlands (N = 28)	U
Age (yr)	10 (28, 5–21)	8 (23, 5–15)	279.5 NS
Height (cm)	185 (33, 113–265)	191 (23, 143–280)	287.5 NS
Canopy stems/m²	15 (33, 5–26)	17 (23, 10–26)	362.5 NS
Canopy closure (%)	91 (28, 86–96)	93 (22, 85–97)	209.5*
Crown diameter (cm)	51 (33, 30–85)	42 (21, 22–68)	263.0 NS

ied among lowland gaps (Table 4). Within the lowland site, the process of closure was less variable. Experimental gap radius at the time of creation (in thickets >1.5 m tall) averaged 23 cm (14 to 29 cm) and 17 cm (14 to 19 cm) in upland and lowland thickets, respectively. Gaps decreased in radius by an average of 85% in lowland and 21% in upland thickets over one year.

Total radial closure and radial closure by lean and growth were sometimes negative (Table 3). Negative values of radial closure by growth occurred when branches died during the study period. The proportion of gaps in which more tagged branches died than lived was much less in the lowlands (15%) than in the uplands (85%, the probability that these proportions are the same is $P = 0.0001$). There was no evidence of browsing on canopy branches.

Negative values of lean occurred when stems leaned away from the center of the gap. Lean was extremely variable and stems as often leaned away from as towards the center of gaps (Tables 3 and 4). The absolute value of stem lean increased with stem density at the lowland site ($r = 0.78$, N = 8, $P < 0.05$), but there was no significant relationship at the upland site ($r = 0.50$, N = 9, $P > 0.05$).

Gap closure rates were related to thicket characteristics in an effort to explain some of the variability between thickets. Total radial closure was not correlated ($P > 0.05$) with thicket age ($r = 0.62$, N = 8; $r = -0.45$, N = 7), thicket height

($r = 0.40$, N = 9; $r = 0.034$, N = 8), or crown area ($r = 0.47$, N = 9; $r = -0.35$, N = 8) at either the upland or lowland site, respectively.

Lean and growth added together do not exactly equal total radial closure (Table 3). This is because growth was estimated as the remainder in the subtraction of lean from total radial closure and some of the tags to which lean measurements were made were lost. Means in Table 3 are averaged over all measurements for each site and lower sample sizes for lean and growth resulted in less accurate estimates.

Only one understory stem contributed to the partial closure of an experimental gap. However, around the experimental gaps, 0.1 stems·m⁻²·yr⁻¹ in lowland and 0.8 stems·m⁻²·yr⁻¹ in upland thickets entered the canopy.

The fates of understory stems differed between sites (Hotelling's $T^2 = 14.02$; df = 3, 12; $P < 0.001$, Table 3). More stems were browsed in lowland than in upland thickets (F = 45.39, df = 1, $P < 0.001$) and marginally more stems in-

Table 2. Spearman rank correlation coefficients (sample size) of thicket height in cm with thicket age, canopy stem density, canopy closure, and crown diameter in upland and lowland thickets (NS $P > 0.05$, * $P < 0.05$, ** $P < 0.01$).

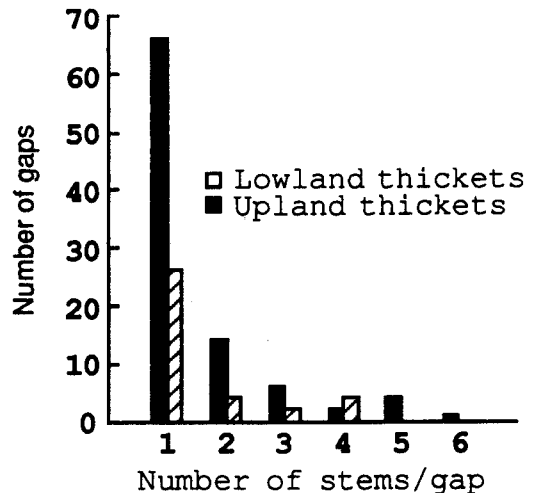|	Uplands	Lowlands
Thicket age (yr)	0.69 (23)**	0.54 (28)**
Stem density/m²	−0.64 (22)**	−0.39 (32)*
Canopy closure (%)	−0.44 (22)*	−0.05 (26) NS
Crown diameter (cm)	0.43 (22)*	0.50 (33)**

Fig. 1. Frequency distribution of canopy gaps in gray dogwood thickets formed by the death of different numbers of adjacent stems. Data are from 93 gaps in 12 upland thickets and 36 gaps in 18 lowland thickets.

Table 3.   A. Mean rates (cm/yr) of gray dogwood canopy gap closure by stem lean and canopy branch growth. Negative values indicate that gaps increased in area due to either lean of canopy stems away from the gap center, branch mortality, or both. The ranges are given in parentheses. B. Fates of understory stems in upland and lowland thickets over the study period. The stems that reached the canopy are included among the stems that increased in size.

	Uplands (N = 9)	Lowlands (N = 8)
A.		
Total	5.0 (−4.4 to 11.8)	15.0 (8.7 to 19.8)
Lean	−3.7 (−6.2 to 3.4)	−0.2 (6.8 to 7.6)
Growth	7.9 (−2.9 to 21.8)	14.6 (8.4 to 23.6)
B.		
Stems that reached the canopy	17 (20%)	2 (4%)
Stems that increased in size	51 (59%)	11 (20%)
Browsed stems	0 (0%)	17 (30%)
Stems that died	20 (23%)	21 (38%)
Total number of stems	88	51

creased in size in the upland thickets (F = 6.70, df = 1, P = 0.02). There was no difference between sites in the number of stems that died over the sample period (F = 0.12, df = 1, P = 0.738).

Five weeks after single-stem canopy gaps were made by removing stems from the canopy (as contrasted with gaps created by stems that die and remain in place), stem lean partially closed four gaps by 39, 38, 32, and 29%. During the same period, one gap opened by 17%. Stem height : diameter ratios averaged 140:1.

Discussion.   Gray dogwood thickets maintain intact canopies through branch growth of canopy stems and, to a lesser extent, growth of understory individuals into small natural gaps characteristically formed by the death of single stems. The rate of radial closure of small experimental gaps at both sites was 5–15 cm/yr. This rate of radial closure is remarkably similar to the 6–14 cm/yr reported by Hibbs (1982) for hemlock-hardwood forest gaps and the 18 cm/yr reported by Runkle and Yetter (1987) for mixed forests in the southern Appalachians. Thus, gaps in gray dogwood thickets are similar to forest gaps in that they are closed by branch and understory stem growth (Runkle and Yetter 1987; Brokaw 1985). They obviously differ from forest gaps in

that, given roughly equal rates of gap closure, small, single-stem gaps in gray dogwood thickets should close more quickly than small, single-tree forest gaps. Also, stem lean was an important mechanism of gap closure in shrub thickets at both sites, while lean has not been documented as a mechanism of forest gap closure.

The mechanism by which a gap is formed is likely to influence how it is closed. Stems in these gray dogwood thickets generally died singly, forming small gaps. The relative importance of understory stems would likely be greater in gaps formed by the death of many adjacent stems or in thickets in which large numbers of stems die throughout the thicket (e.g., Luken 1990).

In addition, the majority of natural gaps in thickets at the two sites were formed by stems that died standing. These standing stems appear to inhibit the lean of stems into the gap; lean opened upland gaps and had no effect on lowland gaps. In contrast, four out of five gaps formed by removing stems from the canopy (as might happen during an ice storm) were partially closed by lean of gap-margin individuals.

Gray dogwood stems have much higher height : diameter ratios (140:1) than are generally observed in trees (100:1, Halle et al. 1978) and consequently may be more flexible. In addition,

Table 4.   Nested analysis of variance of total radial closure and closure by lean and growth in canopy gaps in gray dogwood thickets in a lowland and an upland site.

Source of variation	df	F	P	df	F	P	df	F	P
Site	1	30.1	0.000	1	7.4	0.008	1	15.5	0.000
Lowland gaps	7	1.1	0.346	7	1.6	0.160	7	2.1	0.053
Upland gaps	8	2.3	0.023	8	3.9	0.001	8	9.2	0.000
Error	119			62			62		

in lowland thickets, stem lean was positively related to the stem density. These lines of evidence suggest that stems within dogwood thickets provide mechanical support to one another.

Rates of gap closure were slower on the dryer and more nutrient-poor upland site (Table 3). This may in part be related to the higher rates of mortality of individual branches in the drier site. Given that gaps are roughly circular and assuming no understory stems grew into gaps, we projected how long it should take gaps to close at the two sites. Gaps from 14 to 29 cm radius (the range in experimental gap size at the two sites) should close in 0.9 to 1.9 years at the lowland site and in 2.8 to 5.8 years at the upland site.

Understory processes potentially important to gap closure also differed between sites. The rates of entrance of understory stems into the canopy and the proportion of stems that increased in height were greater in upland than lowland thickets. This was due in part to heavy browsing by herbivores in lowland thickets and low levels of browsing in upland thickets. Higher rates of entrance of understory stems into the canopy coupled with slower rates of gap closure suggest that there would be opportunity for understory stems to contribute more to the closure of gaps in upland thickets than was observed in the first year.

Recent experiments (Boeken and Canham, unpubl. data) indicate that site conditions have an extremely strong effect on the dynamics of colonization and spread of gray dogwood thickets within old fields. Lateral spread of existing thickets is much faster on mesic than dry sites, and is largely unaffected by competition with surrounding herbaceous species (Boeken and Canham, unpubl. data). Our results indicate that, in addition to spreading more slowly, gray dogwood thickets on dry sites have a more open canopy, with higher rates of gap formation and canopy stem turnover, and slower rates of gap closure. These results suggest that site conditions will have a significant effect on the resistance of this dominant old field shrub to invasion by trees.

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