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Biotic and abiotic control of the dynamics of gray dogwood (*Cornus racemosa* Lam.) shrub thickets

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Summary

1 Gray dogwood is the most abundant shrub in old-fields and utility rights-of-way in the Hudson Valley, New York, USA. It is present across an extremely broad range of environments, but most abundant on relatively wet sites. Once a site has been colonized, it spreads primarily through vegetative production of new shoots from extensive networks of horizontal roots (runners).

2 Remeasurement of permanent quadrats revealed that gray dogwood cover increased, on average, in all community types between 1987 and 1990, but most in communities on moist soils. The few quadrats with declining dogwood cover in this period were in communities on drier sites.

3 Analyses of stem densities, recruitment, growth, and mortality along transects through dogwood thickets showed that the thickets expand by gradual infiltration of a wide zone around the margin of the closed shrub canopy. The closed shrub margin expands through slow lateral development of the crowns of widely scattered stems outside the current margin.

4 Matrix projections of the transitions between understorey, subcanopy and canopy stems between 1989 and 1990 in three different positions within thickets showed that the observed stage distributions differed from expected stable distributions, except in the centres of thickets in dry sites. Stem population growth rates in wet and mesic sites declined with increasing thicket size as individual stem diameters and crown areas increased. Elasticity analysis showed that changes in stem density in all three positions and all three environments were most sensitive to canopy and subcanopy stem survivorship.

5 A field experiment demonstrated that surrounding grass and herb-dominated communities provided little inhibition of the rate of spread of dogwood thickets except on wet sites. In contrast, the experiment confirmed results from our field censuses that thicket expansion was very sensitive to soil moisture regimes. On dry sites, the rate of spread of dogwood was slow because of slow growth and high mortality of stems in the periphery of the thicket, regardless of the presence or absence of surrounding vegetation. Nonetheless, the presence of extensive dogwood thickets on even very dry sites indicates that gray dogwood is ultimately capable of dominating such sites under selective management regimes that protect it from major disturbance and prevent it from being overtopped by trees.

Keywords: competition, eigenvalue elasticity, old-field succession, rights-of-way, shrub thicket expansion, shrub stem demography, soil disturbance

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Introduction

Although shrubs are a common growth form over large regions of the earth, their dynamics have received much less attention than other plant growth forms (Harper 1977). In North America, most studies of the population dynamics of shrubs have been done in environments where they represent a dominant, stable growth form. These include deserts of the south-western USA (Vasek 1980), shrub/steppe communities of the Great Basin (West *et al.* 1979), chaparral communities of the California coast (Schlesinger

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et al. 1982), and Arctic tundra (Douglas 1989). In the north-eastern USA, shrubs are a persistent, dominant growth form only in some wetlands (Huenneke 1987) and marginal environments (primarily bogs and barrens). However, shrubs are also a major component of intermediate stages of secondary succession on abandoned agricultural land (Mellinger & McNaughton 1975) and on sites, such as utility rights-of-way, where succession is arrested (Niering & Goodwin 1974) through selective removal of trees. While old-fields and utility rights-of-way are currently extremely common within the landscape of the north-eastern USA, the old-field and right-of-way shrubs have received much less attention than the herbaceous species that precede them or the tree species that normally follow them in succession.

One reason for the lack of research on shrubs is that many of the most common species form extensive thickets through vegetative reproduction (e.g. Gilbert 1966; Abrahamson 1975; Taylor 1980; Huenneke 1987). Clonal plants, whether herbs, shrubs or trees, present unique challenges for studies of population dynamics (Barnes 1966; Sarukhán & Gadgil 1974; Harper 1977; Cook 1985; Pitelka & Ashmun 1985; Peterson & Squiers 1995). Most studies have adopted the approach championed by Harper (1977), and have focused on the linkages between the demography of above-ground shoots and the spread of the clone, with varying degrees of emphasis on the physiological integration of the thickets through interconnecting roots (Pitelka & Ashmun 1985; Huenneke 1987).

Gray dogwood (*Cornus racemosa* Lam.) occurs in open (high-light) environments throughout the eastern United States (Gleason & Cronquist 1963). Studies of vegetation in both old-fields and along rights-of-way in the Hudson Valley of New York (Canham & Kays 1993; Canham & Wood 1993; and unpublished data) have identified it as the single most common shrub within these sites. It reaches its greatest abundance on moist to wet soils, but is present on even very dry sites throughout New York State (Mellinger & McNaughton 1975; Johnston & Bramble 1981; Canham & Kays 1993). The species forms extensive thickets 1–2 m tall, whose canopy density is relatively uniform, although the thickets break up and ultimately disappear once a forest canopy develops (Glitzenstein *et al.* 1990). Gray dogwood produces copious numbers of fruits that are dispersed by birds, but once a site has been colonized, the shrub spreads primarily through vegetative production of new shoots from an extensive network of horizontal roots (runners), and true seedlings are then rare (personal observations). The thickets often have relatively distinct margins, although scattered gray dogwood stems with narrow crowns are quite common in a fairly broad zone surrounding the margin of a thicket (Fig. 1). Harrington *et al.* (1989a, 1989b) have compared the physiology and growth patterns of gray dogwood to several other native and exotic shrubs.

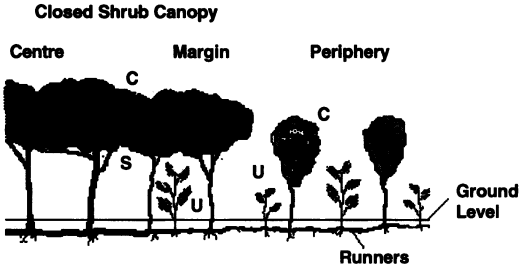

Fig. 1 Diagrammatic structure of a gray dogwood thicket. The closed shrub canopy is arbitrarily divided into centre and margin. The periphery is characterized by stems with narrower crowns that do not form a closed canopy. C, S, and U refer to canopy, subcanopy, and understorey stems, respectively.

There has been a great deal of public interest in the use of native communities of shrubs and herbaceous species to inhibit tree invasion and arrest succession along utility rights-of-way in the north-eastern USA, thereby reducing both the costs and the environmental consequences of more intensive management using mowing or nonselective herbicide application (Niering & Egler 1955; Niering & Goodwin 1974; Bramble & Byrnes 1976). Gray dogwood thickets have a relatively high resistance to invasion by tree seedlings, due to the effects of both competition between the shrubs and tree seedlings (Putz & Canham 1992) and herbivory by vertebrates foraging within the thickets (Hill *et al.* 1994). Selective removal of the relatively low numbers of tree saplings that emerge above the shrub stems is clearly necessary to maintain an intact thicket (personal observations). The ultimate role of gray dogwood in ecologically based management regimes, however, will depend on the natural dynamics of the establishment, maintenance and spread of thickets within the matrix of other old-field shrubs and herbaceous species.

The general objectives of this study were to (1) document the rate of spread of gray dogwood across a range of environments and community types, and (2) to test the importance of competition, soil disturbance, and environment in regulating the dynamics of dogwood thickets. We have used three different techniques – remeasurement of shrub cover in permanent quadrats, a comparative study of rates of stem recruitment, growth and mortality in different environments, and a field experiment – to examine these questions. In a related study, Dickinson *et al.* (1993) have examined the responses of dogwood thickets to disturbance and the processes that maintain closed dogwood canopies.

Methods

VARIATION IN RATE OF SHRUB EXPANSION AMONG COMMUNITIES AND ENVIRONMENTS

Sixteen sites were chosen in 1987 for a study of vegetation mosaics (Canham & Wood 1993) and the demography of tree seedling invasion (Hill *et al.* 1994) in old-field communities found along utility rights-of-way. The sites encompass the regional variation in physical environments present within the Hudson Valley. At each site, we had established 30 2-m^2 quadrats at random locations within a 60 m long plot that spanned the width of the right-of-way. For this study, a set of these quadrats was recensused in summer 1990. Seven of the original 16 sites were excluded because they were either outside of the range of environments in which gray dogwood occurs (five sites in the Catskill and Shawangunk Mountains) or were already heavily dominated by other species of shrubs (two sites). For the remaining nine sites, 262 of the 270 original quadrats were relocated and shrub cover was estimated visually. In both 1987 and 1990, nine cover classes were identified: absent; < 1%; 1–5%; 5–10%; 10–20%; 20–40%; 40–60%; 60–80%; and > 80% cover. Thus, the cover scale provides the greatest resolution for changes in shrub cover at the lowest levels of absolute shrub cover. In 1990 we also counted the number of dogwood stems per plot, differentiating between understorey stems (defined as stems with their crowns overtopped by adjacent plants) and canopy stems.

In 1987 the low-growing vegetation in each quadrat was classified into one of 12 different component community types (Canham & Wood 1993). Seven of these community types occurred in our sample of recensused quadrats: little bluestem (*Schizachyrium scoparium*) meadows (SCSC); little bluestem meadows with a moss understorey (SCMO); a mixed grass/creeping shrub community dominated by little bluestem and northern dewberry (*Rubus flagellaris*) (RUSC); a mixed herb/creeping shrub community dominated by goldenrods (primarily *Solidago rugosa*) and northern dewberry (SORU); a perennial herb community dominated by purple loosestrife (*Lythrum salicaria*) (LYSA); a grass/erect shrub community dominated by a diverse mixture of grasses (primarily *Agrostis* spp. and *Anthoxanthum odoratum*) and scattered gray dogwoods (GRCO); and shrub thickets dominated by gray dogwood (CORA). More complete descriptions of the community types and the environments in which they are most common are provided in Canham & Wood (1993) and Canham & Kays (1993).

SHRUB STEM DYNAMICS WITHIN GRAY DOGWOOD THICKETS

We selected nine gray dogwood thickets in three different environments in old-fields at the Institute of Ecosystem Studies in Millbrook, New York, for detailed study of the dynamics of shrub stem density, recruitment, mortality and growth. Three thickets were in dry sites (primarily hilltops and slopes) surrounded by a matrix of little bluestem communities (SCSC, SCMO, and RUSC community types). Three thickets were chosen in mesic environments located in lower-slope positions. These thickets were surrounded primarily by the goldenrod/creeping raspberry (SORU) community type. The remaining three thickets were located in wet sites (primarily along drainage channels and in local depressions), where gray dogwood was very abundant, and where individual thickets were surrounded primarily by communities of mixed grasses and goldenrods with scattered gray dogwood stems (the GRCO community type). The wet sites were all seasonally flooded in the spring, although standing water disappeared early in the growing season.

A single 50-cm-wide transect was laid out through the centre of each thicket. The transect was orientated in a randomly chosen compass direction, and extended out from the centre in both directions as far as necessary until there were no gray dogwood stems for at least 1 m in either direction along the transect. The transects were divided into three sections (Fig. 1). The two ends of the transect from the endpoints to the beginning of the closed shrub canopy were pooled to form the 'periphery'. The segment of the transect within the closed shrub canopy was divided into four equal parts, the two outer ones were the 'margin' and the inner ones the 'centre'. For all gray dogwood stems within the transects, we recorded their location, diameter at 10 cm height, total height, reproductive status (seed bearing or not), and whether they were in the canopy or understorey. Understorey stems were defined as stems with > 50% of their crown overtopped by other plants (both shrubs and herbaceous species). Initial measurements were done in July 1989, and then repeated in July 1990.

Demographic data were analysed as a split-plot analysis of variance (SAS 1988) with the nine thickets as main plots (i.e. three environment types (dry, mesic and wet) replicated by three thickets), and place within thickets (periphery, margin and centre) as the subplot factor. The dependent variables were (1) stem density (number of live stems per m^2) (2) mortality (proportion of stems that died during the study period, after angular transformation) (3) recruitment (number of new stems per m^2) (4) mean stem height, and (5) change in stem height (growth, 1989–90). Understorey and canopy stems were analysed separately. Differences among environments were tested with the environment by thicket interaction as the error term. The residual mean square was used to test the effect of place within thicket.

We also reconstructed profiles of shrub stem age along each of the transects, using age-diameter relationships from samples taken in other thickets along rights-of-way. The age diameter relationships were estimated using stems collected from three thickets located in each of the environment types (wet, mesic and dry). In each thicket, two 0.25-m × 0.75-m quadrats, one in the closed canopy and one in the periphery, were chosen. All stems (total = 190) were collected (cut at the base), and their age was determined in the laboratory by counting annual rings with a microscope. For each environment type, the relationship between age, stem diameter at 10 cm above ground level, place within thicket (closed canopy or periphery) and vertical position (canopy or understorey) was established using multiple linear regression ($P \leqslant 0.0001$, $R^2 \geqslant 0.719$ for the three environments).

FIELD EXPERIMENT ON THE LATERAL SPREAD OF GRAY DOGWOOD THICKETS

The effects of environment vs. competition from surrounding vegetation on the dynamics of the lateral spread of gray dogwood thickets were tested with a field experiment. Along the outer perimeter of each of the three replicate thickets in each of the three environment types (dry, mesic, wet), we measured the recruitment, mortality and growth of dogwood stems in response to three experimental treatments: (1) killing all plants other than gray dogwood through highly selective application of an herbicide (glyphosate), but without disturbing the ground (2) the herbicide treatment described above, but with the removal of the root systems of the grasses and herbaceous species, and (3) a control. The two different manipulations were designed to allow us to test for physical effects of the presence of the often dense root mats of little bluestem and the rhizome mats of goldenrods on dogwood stem emergence. We took great care to minimize damage to dogwood roots during the removal of the root systems of other species.

The experimental manipulations of surrounding vegetation were applied to nine quadrats per thicket: three replicates for each of the three treatments. The 0.5-m^2 quadrats (70 cm × 70 cm) were located $\approx$ 1–2 m outside the current margin of the closed shrub canopy (Fig. 1). All of the quadrats had at least three existing dogwood stems to ensure the presence of dogwood roots within the quadrat. All existing gray dogwood stems were tagged, and their height and diameter at 10 cm above the ground were measured when the treatments were initiated in late June – early July of 1989. The effects of the treatments (recruitment of new stems, growth, and mortality) were measured in September, 1989, and again in late July, 1990.

The experiment was analysed with a split-plot analysis of variance (for height growth and mortality) or covariance (for density and recruitment), with initial stem density as the covariate (SAS 1988). Environment type (main plot) was replicated by three thickets each, and manipulations of vegetation surrounding the thickets (the subplot factor) were replicated by three quadrats per treatment. Mortality rates were transformed using an angular transformation prior to analysis (SAS 1988). Effects of environment on stem recruitment, growth and mortality were tested using the environment by thicket interaction term as the error term. The effect of vegetation treatment and its two- and three-way interactions with environment type and thicket differences were tested using the residual mean square as the error term.

TRANSITION MATRIX MODELS OF DOGWOOD DYNAMICS

We used transition matrix models to test the stability of the observed structure of the different sections (centre, margin, periphery) of thickets in the three environments (dry, mesic and wet) (Werner & Caswell 1977; Bierzychudek 1982; Huenneke & Marks 1987; Crouse *et al.* 1987; Caswell 1989). Transition probabilities were calculated using 1989 and 1990 censuses of stems assigned to three functional height classes: understorey stems (U) were below the foliage of canopy stems; subcanopy stems (S) were within the canopy, but not exposed to direct sunlight; and canopy stems (C) reached to the top of the canopy. In the periphery (i.e. outside the closed shrub canopy), understorey and subcanopy height classes were defined relative to the scattered canopy shrub stems. Transition a_{ij} denotes the probability that an individual stem will change to stage i (U, S, or C) in the July 1990 census from stage j in July 1989. Vegetative recruitment of new understorey stems (U), relative to the number of canopy stems, was used as the 'fecundity' term a_{UC} in the 3 × three transition matrix. This was done because canopy stem density was the only factor with a significant effect on the recruitment of new understorey stems [$P = 0.0005$ in an ANCOVA with environment type, thickets (with their interaction as error term), location within thickets and its interaction with environment (vs. residual mean square), and canopy stem density as covariate]. However, because there were also canopy stems that reverted to the smallest category due to severe browse or dieback, this probability was added to the recruitment rate to obtain the canopy-to-understorey transition a_{UC}.

There were no structural zeros (i.e. denoting biologically impossible transitions) in the transition matrices. However, zeros caused by very low probabilities as a consequence of small sample sizes and the integer nature of individuals would distort the results of the projections. Therefore we set all zero transitions to a value near zero (0.001).

Population growth rates λ (the dominant right eigenvalues), stable stage distributions (the right eigenvectors) and reproductive values (left eigenvectors) were determined for all 27 datasets [i.e. the three sections (periphery, margin and centre) of three replicate thickets in each of three environments (wet, mesic and dry)]. Stability of the observed stage distributions was tested by comparing the observed initial frequencies with those expected assuming a stable distribution based on the projections. We used maximum likelihood tests (G-tests) for extrinsic expected frequencies (Sokal & Rohlf 1981). Effects of environment and position within thicket on projected population growth rates (λ) were tested using ANOVA. The additional effect of thicket size was tested in an ANCOVA.

Under the assumptions of the matrix model, the effect of a change in transition a_{ij} on λ depends on the reproductive value of stage i (v_i), and the proportion of individuals in stage j in the stable stage distribution (w_j) (Crouse *et al.* 1987). Thus, the proportional sensitivity of l to changes in transition rates can be examined using elasticity values (Crouse *et al.* 1987; Caswell 1989)

$$e_{ij} = (a_{ij}/\lambda) \times [(v_i w_j)/\langle \mathbf{v}, \mathbf{w} \rangle].$$

Elasticities are standardized for the value of a_{ij}, which is usually larger for probabilities involving the production of new individuals than for other transitions (Crouse *et al.* 1987; Caswell 1989). Elasticity analysis also facilitates qualitative evaluation of differences in demography between environments and positions within thickets.

Results

VARIATION IN RATE OF SHRUB EXPANSION AMONG COMMUNITIES AND ENVIRONMENTS

Gray dogwood increased in cover in 76% of the 262 quadrats between 1987 and 1990. Gray dogwood was absent from 45% of the quadrats in 1987, but was present with at least 5% cover in all of those quadrats by the time of the 1990 census. Dogwood stem densities, however, were still quite low in those recently colonized quadrats (averaging < one stem m^{-2} for both canopy and understorey stems combined) (Fig. 2). Dogwood cover had not changed in 17% of the quadrats, and declined in only 7% of the quadrats. Most of the 64 quadrats with either no change or a decline in shrub cover were in quadrats already dominated by gray dogwood (CORA) (40 of 64 quadrats) or by the mixed grass/dogwood community (GRCO) (13 of 64 quadrats) (Table 1). The quadrats with no change in shrub cover also had the highest densities of canopy dogwoods in 1990 (Fig. 2).

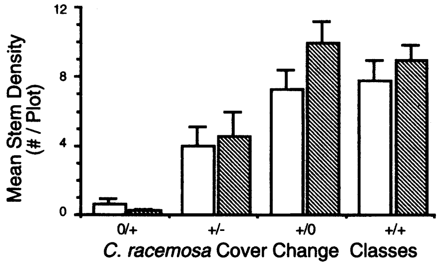

Fig. 2 Means and standard errors of density of canopy stems and understorey stems in four categories of change in gray dogwood cover from 1987 to 1990. Cover change classes: 0/+, quadrats in which dogwood was absent in 1987 but present in 1990; +/–, dogwood present in 1987 but declined in cover by 1990; +/0, present in 1987, but no change in cover by 1990; +/+, present in 1987, and increased in cover by 1990.

Table 1 Change in gray dogwood cover from 1987 to 1990. The classes indicate changes in cover from 1987 to 1990: 0/+, absent during the 1987 census but present in 1990; +/–, present in 1987, but declined in cover by 1990; +/0, present in 1987, but no change from 1987 to 1990; +/+, present in 1987, and increased in cover by 1990. The last two columns give the mean and standard error of relative change in percent cover, by community type, for the 145 plots where gray dogwood was present during 1987. See text for a description of the community type abbreviations

Community type	Cover change class				Relative change in % cover
	0/+	+/–	+/0	+/+	(mean ± SE)
SORU	42	1	2	8	1.955 ± 0.832
GRCO	9	5	8	19	1.234 ± 0.516
CORA	3	11	29	31	0.466 ± 0.143
LYSA	29	0	0	4	2.750 ± 1.548
SCSC	21	0	2	3	1.000 ± 0.548
SCMO	8	2	3	9	0.643 ± 0.243
RUAN	5	0	1	7	2.250 ± 0.818
Total	117	19	45	81	

In the 145 quadrats in which gray dogwood was present in 1987, shrub cover increased, on average, for all seven of the community types (Table 1), although the magnitude of the increase in dogwood cover varied significantly among the seven communities (one-way ANOVA, $F_{6,138} = 2.54$, $P = 0.0229$). The dogwood thickets, as expected, showed only a minor increase, and most of that increase was attributable to quadrats that were on the edges of thickets in 1987 and had been engulfed by the thicket in the intervening three years. The low relative change in shrub cover in the existing dogwood thickets also reflects the fact that most of those quadrats were already in the 60–80% cover class in 1987, and where shrub cover was at the low end of the range there would have to be a substantial increase (i.e. to > 80% cover) to register as a change during the three year period. Among the remaining six community types, the greatest increases came in the two types dominated by perennial herbs (LYSA and SORU) on moist sites and the creeping raspberry/little bluestem (RUSC) communities on intermediate to dry sites. (Table 1). The communities dominated by little bluestem (SCSC and SCMO) that are characteristic of drier sites, had the smallest increases in dogwood cover.

THICKET STRUCTURE AND DEVELOPMENT

Canopy stem dynamics

Split-plot analysis of variance revealed no significant variation in the density of canopy-sized stems among either the three environments (wet, mesic, and dry) or among the three positions (periphery, margin, or centre of the thicket) (Table 2). Stem densities in the centres of thickets were approximately 8–10 stems m^{-2} in all three environments (Table 2). There was greater variation among the environments in stem densities in both the margins and the peripheries of thickets; however, the large variance among thickets weakened the patterns. If the thickets from the mesic environments are analysed separately with a simple anova, stem density does vary significantly among the three positions ($F_{2,4}$ = 10.95, $P = 0.0238$). However, our results indicate that the boundary between the closed shrub canopy and the surrounding periphery is not necessarily marked by a pronounced decline in dogwood stem density.

Canopy stem height growth rates varied marginally among the three environments ($F_{2,11} = 6.08$, $P = 0.061$), but not among the three positions within thickets ($P > 0.5$). Height growth was lowest in the dry sites. While the densities, growth rates, and mortality rates of stems in the periphery were not significantly different from mortality rates for canopy stems located within the closed margin of the thicket, canopy stems in the periphery were characterized by much smaller crowns in all three environments (Fig. 3) (effect of position: $F_{1,55} = 11.445$, $P = 0.0013$; effect of environment: $F_{2,4} = 0.581$, $P = 0.601$).

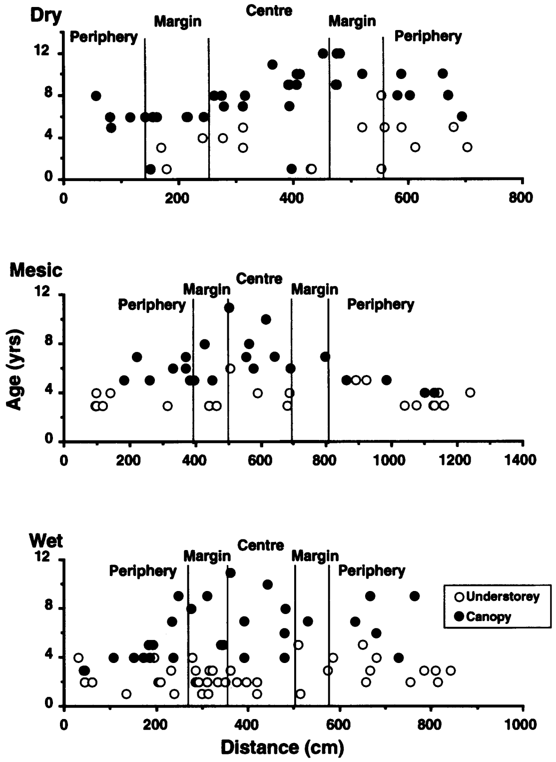

Fig. 3 Distributions of canopy and understorey stem ages along representative transects through dogwood thickets in each of the three environments.

There were no significant differences in rates of canopy stem mortality among the three environments or the three positions within thickets ($P > 0.10$ for all main effects and interaction terms in the split-plot ANOVA) (Table 2). Mortality rates were relatively high overall, and exceeded 10% of stems per year in most of the nine environment by position categories (Table 2). The average age of canopy stems varied significantly among the three positions within the thicket ($F_{2,12} = 12.62$, $P = 0.001$), but not among the three environments ($F_{2,12} = 2.92$, $P = 0.165$). While stems in the periphery of the thickets were generally younger than stems in the centres of the thickets, the differences were not very large (2–3 years on average) (Table 2). The relatively young average age of canopy stems in the centres of the thickets is a reflection of

Table 2 Means and standard errors of canopy stem density (No. of stems m^{-2}), mortality (proportion of stems), stem age (years) and height growth (cm) in three environment types (with n = three thickets each), and results of split-plot ANOVAS with environment type (d.f. = 2) and thicket differences (d.f. = 2) tested against the environment by thicket interaction (d.f. = 4), and place within thickets (d.f. = 2) tested against residuals (d.f. = 12)

Response	Position	Dry	Mesic	Wet	ANOVA results	
Density	Centre	10.59 ± 1.98	8.08 ± 1.311	7.92 ± 0.96	Environment	$F = 1.490$, $P = 0.3285$
	Margin	7.64 ± 1.32	4.79 ± 1.29	10.49 ± 3.70	Thickets	$F = 0.444$, $P = 0.6699$
	Periphery	8.33 ± 1.69	3.00 ± 1.27	10.98 ± 5.59	Place w/in Thicket	$F = 0.336$, $P = 0.7211$
Mortality*	Centre	0.000 ± 0.000	0.102 ± 0.054	0.119 ± 0.067	Environment	$F = 0.758$, $P = 0.5260$
	Margin	0.098 ± 0.069	0.241 ± 0.145	0.092 ± 0.092	Thickets	$F = 1.431$, $P = 0.3398$
	Periphery	0.092 ± 0.056	0.024 ± 0.024	0.244 ± 0.046	Place w/in Thicket	$F = 0.691$, $P = 0.5199$
Stem age	Centre	7.723 ± 0.859	6.88 ± 0.433	5.947 ± 0.638	Environment	$F = 2.920$, $P = 0.1652$
	Margin	8.667 ± 0.959	7.263 ± 0.385	5.610 ± 0.899	Thickets	$F = 2.571$, $P = 0.1915$
	Periphery	6.579 ± 0.519	6.158 ± 0.803	5.668 ± 0.373	Place w/in Thicket	$F = 12.620$, $P = 0.0011$
Height growth	Centre	–0.688 ± 11.077	4.35 ± 2.451	7.919 ± 1.058	Environment	$F = 6.076$, $P = 0.0613$
	Margin	15.905 ± 6.112	16.083 ± 2.917	20.100 ± 3.676	Thickets	$F = 9.566$, $P = 0.0299$
	Periphery	7.074 ± 9.715	11.109 ± 10.129	16.359 ± 4.278	Place w/in Thicket	$F = 1.513$, $P = 0.2627$

*Tested after angular transformation

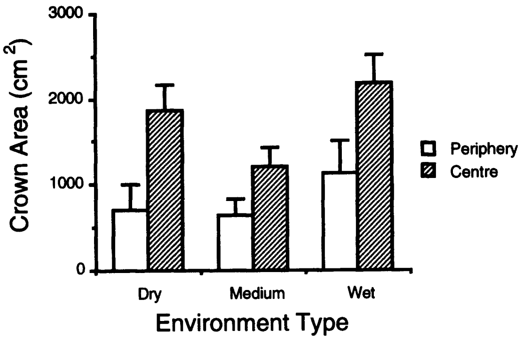

Fig. 4 Means and standard errors of projected crown areas of canopy dogwood stems in the periphery vs. the centres of thickets for the three environments.

the high mortality rates and the correspondingly high turnover of stems within intact thickets. As expected, maximum canopy stem ages decreased along the transects from the centre of the thickets to the periphery (Fig. 3).

While the densities, growth rates, and mortality rates of stems in the periphery were not significantly different from rates for canopy stems located within the closed margin of the thicket, canopy stems in the periphery were characterized by much smaller crowns in all three environments (Fig. 4) (effect of position: $F_{1,55} = 11.445$, $P = 0.0013$; effect of environment: $F_{2,4} = 0.581$, $P = 0.601$).

Understorey stem dynamics

In contrast to the canopy layer, both the total density of understorey dogwood stems and the number of new understorey stems produced annually varied significantly with thicket position (density: $F_{2,12} = 4.30$, $P = 0.039$; recruitment: $F_{2,12} = 4.59$, $P = 0.033$). In all three environments, understorey stem density was lowest in the peripheries of the thickets (5–10 stems m^{-2}) (Table 3). Variation in the number of new stems produced annually ('recruitment') was greatest in the dry sites, where > 9 stems m^{-2} emerged in the centres of the thicket during the year between censuses (Table 3). Stem recruitment rates were much lower (< 4 stems m^{-2}) and fairly uniform across all of the other eight combinations of environment and thicket position (Table 3).

While recruitment and density varied along the transects, mortality rates of understorey stems did not vary significantly among either the environments or positions within thickets ($P > 0.2$ for all main effects and interaction terms in the split-plot ANOVA). Mortality rates of understorey stems were extremely high ($\sim$ 20–40% year^{-1}) regardless of environment or position (Table 3). As a result of these high rates of mortality, the average ages of understorey stems were uniformly low ($\approx$ 2 years) ($P > 0.10$ for all main effects in the split-plot ANOVA). Mean understorey stem height growth was more variable (Table 3), but there was no statistically significant variation in growth because of large variation among thickets ($P > 0.25$ for all main effects in the split-plot ANOVA). Understorey height growth rates tended to mirror growth rates of canopy stems: growth rates were lowest in the dry sites, and stems in the periphery or on the margin of the thicket tended to have higher growth rates than stems in the centre of the thicket (Table 3).

Table 3 Means and standard errors of understorey stem density (no. of stems m^{-2}), recruitment (no. of new stems m^{-2}), mortality (proportion of stems), stem age (years) and height growth (cm) (means and standard errors) in three environment types (with three thickets each), and results of split-plot ANOVAs with environment type (d.f. = 2) and thicket differences (d.f. = 2) tested against the environment by thicket interaction (d.f. = 4), and place within thickets (d.f. = 2) tested against residuals (d.f. = 12)

Response	Position	Dry	Mesic	Wet	ANOVA results	
Density	Centre	12.96 ± 4.14	9.32 ± 6.13	16.12 ± 6.75	Environment	$F = 0.829$, $P = 0.5000$
	Margin	7.37 ± 1.61	10.22 ± 7.26	19.66 ± 3.93	Thickets	$F = 0.855$, $P = 0.4906$
	Periphery	5.82 ± 2.64	5.51 ± 2.18	10.49 ± 4.60	Place w/in Thicket	$F = 4.301$, $P = 0.0390$
Mortality[a]	Centre	0.217 ± 0.084	0.308 ± 0.108	0.234 ± 0.046	Environment	$F = 0.048$, $P = 0.9535$
	Margin	0.347 ± 0.120	0.351 ± 0.218	0.335 ± 0.068	Thickets	$F = 2.515$, $P = 0.1962$
	Periphery	0.412 ± 0.048	0.294 ± 0.047	0.342 ± 0.048	Place w/in Thicket	$F = 0.634$, $P = 0.5475$
Recruitment	Centre	9.035 ± 3.620	2.253 ± 1.958	3.165 ± 1.473	Environment	$F = 1.974$, $P = 0.2532$
	Margin	2.683 ± 1.199	1.176 ± 0.669	2.654 ± 0.691	Thickets	$F = 1.665$, $P = 0.2977$
	Periphery	1.874 ± 1.529	0.607 ± 0.496	2.216 ± 1.389	Place w/in Thicket	$F = 4.588$, $P = 0.0331$
Stem age	Centre	1.996 ± 0.628	3.037 ± 0.262	2.691 ± 0.276	Environment	$F = 2.156$, $P = 0.2316$
	Margin	2.527 ± 0.704	2.612 ± 0.307	2.751 ± 0.143	Thickets	$F = 0.002$, $P = 0.9984$
	Periphery	1.431 ± 0.219	1.737 ± 0.057	2.154 ± 0.092	Place w/in Thicket	$F = 2.793$, $P = 0.1010$
Height growth	Centre	9.000 ± 12.166	5.972 ± 1.100	6.369 ± 2.177	Environment	$F = 1.815$, $P = 0.0613$
	Margin	5.687 ± 2.410	17.817 ± 10.973	20.382 ± 2.059	Thickets	$F = 1.710$, $P = 0.0299$
	Periphery	8.080 ± 3.307	17.410 ± 6.498	20.501 ± 3.291	Place w/in Thicket	$F = 1.471$, $P = 0.2627$

[a] Tested after angular transformation

Stability of structure and density in gray dogwood thickets

All but three of the 27 stage distributions observed in the 1989 censuses differed significantly from the stable distributions derived from the 1989–90 transition probabilities (Table 4). Only the central parts of two of the thickets in dry sites, and one in a wet site did not deviate significantly from stability. The discrepancies were to a large extent caused by the proportions of subcanopy stems, which were either much lower or much higher than expected based on matrix projection.

Population growth rates λ (Table 4) varied between thickets and between locations within thickets. Values ranged from 0.50 (rather rapid decline in the margin of one of the thickets of mesic sites) to 1.128 (relatively rapid increase in the margin of one of the wet thickets). The other λ's were equal or close to unity, indicating very slow decrease (in 13 cases) or increase (six cases), or no change (eight cases). Using a split-plot ANOVA as described above, λ was not significantly affected by either environment type or location within thicket, or by their interaction. However, substituting thicket identity by thicket size, which differed between 'replicate' thickets per environment, we found a significant negative correlation between λ and thicket size ($R^2 = 0.195$, $P = 0.0214$). This was mainly the result of the inverse relation between stem population growth rates in the centre and margin of the wet and mesic thickets with thicket size ($R^2 = 0.725$, $P = 0.0014$). Neither the projected changes in stem densities in the periphery of the thickets of wet and mesic sites, nor those in all locations in the thickets of dry sites varied with thicket size.

Elasticity analysis (Table 4) showed remarkable consistency in the sensitivity of λ to proportional changes in demographic rates. Stem recruitment (a_{UC}) contributed not more than 11% to the sensitivity of λ, usually much less. In the majority of the samples, λ was most affected by changes in canopy stem survivorship (a_{CC}), i.e. the probability of remaining in the canopy stem stage as opposed to dying or reverting to the subcanopy (e_{CC} from 35 to 99%). In the six remaining cases, the most important transition was the probability of remaining in the subcanopy layer (a_{SS}). Demographically, these results are caused by the high reproductive values of the canopy (or subcanopy) stems, coupled with high proportions of those stems in the stable stage distributions.

EFFECTS OF ENVIRONMENT, COMPETITION AND SOIL DISTURBANCE ON THICKET EXPANSION

In our experimental quadrats outside the margins of the thickets, dogwood mortality varied significantly across the three environments ($F_{2,54} = 8.84$, $P = 0.034$), but did not vary in response to the experimental manipulation of adjacent vegetation (Table 5). In contrast, initiation of new stems ('recruitment') did vary significantly in response to the manipulations ($F_{2,53} = 11.64$, $P = 0.0001$), but did not vary across environment types (Table 5). Removing surrounding vegetation increased the recruitment of new dogwood stems, and our data suggest that the competitive inhibition of dogwood recruitment was greatest on the wet sites (Table 5). Stem recruitment showed the greatest response to the combined treatment of herbicide and removal of the root systems of species other than gray dogwood. As a result, it is possible that the response of dogwood to the manipulations (particularly in the dry and mesic sites) was primarily due to direct effects of soil disturbance on the initiation of new dogwood root sprouts, rather than a response to a change in competition from surrounding herbaceous vegetation. However, the increase in recruitment on wet sites in response to the removal of only above-ground living biomass suggests that soil disturbance and removal of roots cannot account for all of the response documented in Table 5.

Table 4 Projected stem population growth rates (λ) and transitions with the highest elasticity (Max e_{ij}) and G statistics for tests of the stability of the stage distribution for each of the 27 combinations of environment, thicket, and position within thicket

		Periphery			Margin			Centre		
Env.	Thicket	λ	Max e_{ij}	G	λ	Max e_{ij}	G	λ	Max e_{ij}	G
Dry	1	1.009	CC	32.8**	0.747	CC	9.5*	0.857	CC	26.7**
	2	0.999	SS	243.7**	0.893	CC	40.1*	1.042	CC	3.4
	3	0.997	SS	1106.6**	1.008	CC	44.8*	1.209	CC	4.9
Mesic	1	1.000	CC	14.4**	0.818	CC	9.5*	0.692	CC	29.7**
	2	1.000	CC	116.9**	1.009	CC	68.2**	1.000	CC	46.4**
	3	1.000	SS	319.9**	0.997	SS	139.2**	0.999	CC	101.9**
Wet	1	0.777	CC	48.2**	1.037	SS	10.4**	1.000	CC	61.6**
	2	0.999	SS	246.7**	1.128	CC	6.5*	1.000	CC	28.0**
	3	0.945	CC	13.7**	0.890	CC	39.1**	0.878	CC	1.3**

* $P < 0.05$, ** $P < 0.01$.

Table 5 Means and standard errors of recruitment (no. of new stems/quadrat), mortality (proportion of stems dying during the experiment), stem turnover (net change in no. of stems/quadrat) and change in stem height (cm) in 0.7-m × 0.7-m experimental quadrats immediately outside the closed shrub canopy, and results of split-plot ANOVAs with environment type (d.f. = 2) and thicket differences (d.f. = 2) tested against the environment by thicket interaction (d.f. = 4), and treatments (d.f. = 2) and their interactions tested against residuals (d.f. = 54)

		Treatment				
Response	Environment	Control	Removal	Removal + Disturbance	ANOVA results	
Recruitment	Dry	1.889 ± 0.735	1.667 ± 0.764	5.778 ± 1.460	Environment	$F = 0.013$, $P = 0.9874$
	Mesic	1.778 ± 0.683	2.444 ± 0.835	4.556 ± 1.168	Thickets	$F = 0.670$, $P = 0.5609$
	Wet	1.889 ± 0.807	3.111 ± 1.230	3.778 ± 1.038	Treatments	$F = 9.056$, $P = 0.0004$
Mortality*	Dry	0.365 ± 0.075	0.458 ± 0.117	0.499 ± 0.085	Environment	$F = 8.627$, $P = 0.0354$
	Mesic	0.224 ± 0.083	0.071 ± 0.038	0.155 ± 0.069	Thickets	$F = 0.632$, $P = 0.5776$
	Wet	0.205 ± 0.060	0.191 ± 0.069	0.283 ± 0.039	Treatments	$F = 1.177$, $P = 0.3161$
Stem Turnover	Dry	−0.778 ± 0.572	−1.333 ± 0.624	−1.222 ± 1.839	Environment	$F = 3.202$, $P = 0.1478$
	Mesic	0.111 ± 0.655	1.444 ± 0.444	3.333 ± 1.155	Thickets	$F = 0.133$, $P = 0.8792$
	Wet	0.667 ± 1.041	0.778 ± 1.152	−0.333 ± 1.691	Treatments	$F = 0.263$, $P = 0.7694$
Height growth	Dry	−0.267 ± 1.636	−7.667 ± 2.857	−4.700 ± 1.767	Environment	$F = 4.451$, $P = 0.0961$
	Mesic	−1.933 ± 2.489	−0.756 ± 2.963	−9.911 ± 2.374	Thickets	$F = 0.692$, $P = 0.5520$
	Wet	6.333 ± 2.532	5.500 ± 2.748	4.200 ± 3.031	Treatments	$F = 3.106$, $P = 0.0528$

*Tested after angular transformation

Given the relatively high mortality rates, there was little net change in dogwood stem density at the end of the year following the treatments (Table 5). Stem density actually declined, on average, for all three of the treatments in the dry sites. Dogwood height growth showed marginally significant responses to both environment and vegetation manipulation (environment: $F_{2,4} = 4.45$, $P = 0.096$; manipulation: $F_{2,54} = 3.11$, $P = 0.0528$). In both the dry and mesic environments, there was no net growth during the year in the control plots because of dieback on many stems (mean heights actually declined slightly, Table 5). In both of those environments, either just killing surrounding vegetation or killing it and removing the roots actually reduced the average height of the dogwood stems during the year following the manipulations (Table 5). In the wet environment, dogwood stems had positive net growth in all three treatments, and there was no significant effect of vegetation manipulation on stem growth ($P = 0.78$ using a separate ANOVA to test for effects of the treatments on change in height in the wet sites only).

Thus, we found no strong evidence that the presence of the intact communities of grasses and herbaceous species inhibited the growth of gray dogwood stems. If anything, our experiment suggests that the surrounding vegetation facilitates growth of dogwood stems in dry and mesic sites. We cannot absolutely rule out the possibility that the vegetation manipulation treatments (either careful, selective herbicide application to grasses and herbaceous species, or soil disturbance associated with weeding out roots of the grasses and herbs) reduced dogwood growth through injury or herbicide drift. However, the lack of treatment effects in the wet site (where herbaceous biomass was greatest, and the associated herbicide use and soil disturbance required to remove the vegetation was also the greatest) suggests that the effects observed in the dry and mesic environments (Table 5) were not artefacts of the treatments.

While we have evidence of modest competitive inhibition of dogwood recruitment (but not growth), there is clear evidence in the experiment of the effects of environment on the dynamics of lateral spread in dogwood thickets (Table 5). Both stem mortality and growth in the periphery surrounding the thickets varied significantly in response to environment, and the patterns are in agreement with our results from both the censuses of change in dogwood cover in permanent quadrats, and our detailed study of the demography of dogwood stems along transects through thickets. Dry sites are characterized by high mortality and low growth of dogwood stems, particularly on the periphery of thickets, while wet sites have lower mortality and higher growth rates.

Discussion

Our results indicate that gray dogwood is actively increasing in abundance in a wide range of environments and successional communities within old-fields and rights-of-way in the Hudson Valley. The current pattern of greatest dogwood abundance on wet to mesic sites is a reflection of the more rapid spread of dogwood on those sites. While rates of increase in dogwood cover were relatively low on drier sites, our observations of well-developed thickets even on very dry sites within the region suggest that gray dogwood is ultimately capable of dominating such sites under selective management regimes that protect it from major disturbance and prevent it from being overtopped by trees.

Except on the sandy, acidic soils at higher elevations in the Catskill Mountains, where a diverse community of ericaceous shrubs dominates nonforested sites, no other shrub species in the region appears to be capable of dominating open sites through clonal spread (Canham & Kays 1993; Canham & Wood 1993). In the Hudson Valley, the rate of old-field succession from early stages dominated by grasses and perennial herbs to dominance by gray dogwood appears to be under stronger control by abiotic conditions, particular soil moisture, than by competitive inhibition from earlier successional stages (i. e. the tolerance model of Connell & Slatyer 1977). The extent and duration of gray dogwood dominance in late stages of old-field succession appears ultimately limited by the rate of invasion by trees and concomitant reduction in light levels.

Our study of stem dynamics reveals that gray dogwood thickets have a remarkably consistent structure, regardless of environment. The patterns of stem density were particularly striking. Our results indicate that the distinction between a closed shrub canopy and the surrounding periphery is not due to variation in stem density, but rather due to differences in height and crown dimensions of canopy stems. The margin of the closed shrub canopy is frequently surrounded by a wide zone in which total stem density is as high as it is in the centre of the thicket. However, those peripheral stems are smaller (in diameter, height, and crown area), have slow growth rates, and individual stems frequently die back in a given year. Moreover, mortality rates, particularly of new (understorey) stems are quite high (20–40%). As a result, expansion of the thicket is a gradual process of vertical height growth and crown expansion of many stems in a relatively wide zone (1–5 m) surrounding the margin of the thicket. In effect, our results suggest that thickets expand as individual stems in these broad zones coalesce around the existing margin. Thus the dynamics of gray dogwood thickets combine elements of both the 'guerrilla' mode of clonal spread through the advance of widely scattered, individual shoots (Lovett-Doust 1981), and 'phalanx' models of clonal expansion through a discrete, advancing wave front (Barclay-Estrup & Gimingham 1969; Keatinge 1975; Wallen 1980; Lovett-Doust 1981).

The strong effects of variation in canopy and subcanopy stem survivorship on stem population growth rates suggests that factors affecting stem dieback and mortality, such as drought stress and browsing by white-tailed deer (*Odocoileus virginianus*), are critical factors in the maintenance of stem density. The sensitivity of gray dogwood stem dynamics to variations in canopy stem survivorship contrast sharply with both *Alnus incana*, a shrub with basal shoot production studied by Heunneke & Marks (1987) using similar matrix projection methods, and with the clonal *Ranunculus* species studied by Sarukhán & Gadgil (1974), where λ was most strongly affected by changes in ramet (new stem) production. The dynamics of stem density in gray dogwood thickets more closely resemble tropical tree population dynamics, where population growth rates are highly sensitive to changes in survivorship of large individuals (Hartshorn 1975; Caswell 1978; Enright & Ogden 1979), and to a lesser extent, species such as *Dipsacus sylvestris* (Caswell 1978; Werner & Caswell 1977) and *Dryas octopetala* (McGraw & Antonovics 1983), where growth of young shoots to larger size classes was most important.

All of our results confirm that soil moisture regimes exert an important control on the rate of spread of dogwood in a site. While the patterns of stem density were relatively uniform across the environments, dogwood stems generally had higher growth rates and lower mortality rates in wet sites than in dry sites. However, our field experiment provided relatively little evidence of inhibition of dogwood by grass and herb-dominated communities that surrounded the thickets. The combination of killing the surrounding vegetation and removing the root mat stimulated dogwood shoot production in all three environments, but simply killing the surrounding vegetation (without disturbing the soil) produced a response only in the wet sites. Thus, the strongest evidence of competitive inhibition of the spread of gray dogwood came from the environment that most favoured the performance of the shrub. Although the evidence for competitive inhibition of clonal spread by the surrounding herbaceous vegetation is scant, we found even less evidence of facilitation. In fact, the additional effect of root removal on thicket spread in the mesic and wet sites suggests that herbaceous species may physically inhibit the spread of the thicket. It also illustrates the potential importance of soil disturbance for vegetation dynamics (Platt 1975; Loucks *et al.* 1985; Gutterman 1988; Gutterman *et al.* 1990; Shachak *et al.* 1991; Boeken & Shachak 1994). There is little evidence of significant amounts of soil disturbance by animals along rights-of-way in the Hudson Valley (Canham *et al.* 1993). Vehicle traffic associated with vegetation management may be a significant cause of mortality to shrub stems, but it may also accelerate the rate of spread of the thicket through soil disturbance in zones surrounding the closed canopy.

The distribution of stems in understorey, subcanopy and canopy size classes differed in nearly all cases from the stable distribution expected if the transition rates observed in 1989–90 were constant over time. This was not unexpected, and there seems to be little reason to expect constancy over time in either the size class distribution or density of stems in a species where stem establishment, growth and mortality is highly sensitive to an abiotic factor such as soil moisture that varies significantly over time. Although stem size structure and density are obviously important aspects of thicket dynamics, expansion of the closed-canopy portion of the thicket appears to depend more on the rate at which peripheral canopy stems expand their crowns, and coalesce to form a wider closed canopy. We do not have any direct data on the rates of lateral growth of crowns of peripheral stems, but suspect that they are equally sensitive to variation in abiotic conditions. Thus we expect that rates of expansion of the closed portion of the thicket vary significantly over time in response to variation in soil moisture availability.

The maximum stem ages estimated for the thickets (10–20 years) are fairly similar to results from other studies of north-eastern USA shrubs (Gilbert 1966; Tappeiner 1971; Huenneke 1987). Our results suggest that even closed thickets are characterized by a relatively high rate of turnover of canopy stems. However, canopy gaps formed by the death of individual dogwood stems are closed very rapidly (within 1–2 years) through a combination of lateral growth of adjacent stems and recruitment of new stems (Dickinson *et al.* 1993). While the research described here has focused on the rate of spread of the species, the ultimate effectiveness of the species at resisting invasion by tree species will depend on the degree to which the species maintains a relatively uniform, closed canopy following the death of the first and subsequent generations of canopy stems (Niering & Egler 1955).

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