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DISPLACEMENT OF ANDROPOGON SCOPARIUS ON THE NEW JERSEY PIEDMONT BY THE SUCCESSIONAL SHRUB MYRICA PENSYLVANICA[1]

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ABSTRACT

Andropogon scoparius, a perennial grass found in old fields on the New Jersey Piedmont, can be invaded and displaced by a nitrogen-fixing shrub, *Myrica pensylvanica*. The progression of *Andropogon* displacement was followed over a season, and possible contributing mechanisms (shading, allelopathy, physical effects of *Myrica* litter) were tested through field and greenhouse experiments. In the field, *Andropogon* seedling growth was inhibited beneath *Myrica* clumps, and mature plant living crown area was reduced. In the greenhouse, *Andropogon* seedling growth was reduced significantly in pots with mature *Myrica*. Both seedling and mature growth of *Andropogon* were reduced under shaded conditions. No inhibitory physical effects of *Myrica* litter on *Andropogon* seed germination or mature plant growth were found; however, there may ba allelopathic effects of *Myrica* litter leachate on *Andropogon* seedlings growing under shade or within grass litter, and on mature *Andropogon* in shaded conditions. *Andropogon* displacement appears to be the result of a complex interaction of *Myrica* shade, allelochemic, and competitive effects, rather than being attributable to any single mechanism.

ANDROPOGON SCOPARIUS MICHX.[2], little bluestem, is a successional member of old-field communities on the New Jersey Piedmont. The perennial, caespitose habit of this grass (Smith and Leinweber, 1971) and its extensive, fibrous root system (Clements and Weaver, 1924) permit it to rapidly attain dominance and persist in almost pure stands at many sites. Bard (1952) investigated a series of fields on the New Jersey Piedmont which varied in time since abandonment after farming. In 2-yr-old fields, she recorded *Andropogon* present. In those abandoned 5 yrs, she found it "appreciable," and it was represented in various amounts throughout the remaining age sequence of fields, including those which had been abandoned for 60 yrs. Blizzard (1931), who reported that a population of *Andropogon* on a Long Island terminal moraine had persisted for at least 150 yrs, suggested that the species, along with co-occurring mosses and lichens, formed an association which "served to retard vegetational change."

Stands of *Andropogon* may be invaded, and eventually displaced, by *Myrica pensylvanica* Loisel. (bayberry). This woody shrub reproduces both by seeds and by horizontal, primarily subterranean stems (Elias, 1971) which send up shoots around the parent plant (Blizzard, 1931; Thieret, 1966). Its fruits, which mature by early fall, appear to be dispersed mostly by birds such as tree swallows (Welty, 1962), chickadees, and especially myrtle warblers (Chrysler, 1930).

The vegetative reproduction of *Myrica* leads, over time, to almost pure patches, or clumps, within *Andropogon* stands. Bard (1952) recorded *Myrica* present in fields as young as 2 yrs in Somerset County, New Jersey. It occurred in varying amounts in all older fields of her study sequence, with its greatest representation in those abandoned 60 yrs. Blizzard (1931) suggested that *Myrica* actively invaded the long-persisting *Andropogon* association on Long Island through outward growth from the clumps; eventually, it displaced the grass and transformed the area into a shrub association.

Previous investigations have indicated that a variety of mechanisms, including competition (Keever, 1950), allelopathy (Rice, 1972; Jackson and Willemsen, 1976), and complex interactions with both the physical and biotic environment (Raynal and Bazzaz, 1975) may contribute to the decline of herbaceous plant populations in old-fields. Additionally, both the timing of, and species involved in, these processes may be influenced by plant life cycle lengths (Keever, 1950), life history strategies (Keever, 1950; Werner, 1976, 1977), the soil

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[2] Nomenclature from Gleason and Cronquist (1963).

seed bank (Oosting and Humphreys, 1940; Raynal and Bazzaz, 1973), and dispersal into the site (Bazzaz, 1968). The objectives of the present research were: 1) to examine *Andropogon-Myrica* interactions and the progression of grass displacement in the field, and 2) to experimentally investigate potential displacement mechanisms.

MATERIALS AND METHODS—*Study sites*—Two abandoned fields in Franklin Township, Somerset County, in central New Jersey, were chosen for the investigations of *Andropogon-Myrica* interactions. These areas are separated by 2.9 km. Both receive about 110 cm of precipitation annually (NOAA, 1978) and are located on loam soils underlain by Triassic red shale of the Brunswick formation (Kummel, 1940). In the forest site, a 17-yr-old field in the W. L. Hutcheson Memorial Forest, *Myrica* has not invaded; stands of *Andropogon* occur among a mosaic of woody and herbaceous vegetation. In the second site, however, a 37-yr-old field bordering Spooky Brook Golf course, the shrub is well established. *Myrica* and woody thickets composed mainly of *Juniperus virginiana* enclose "islands" of nearly pure *Andropogon*. The grass-shrub transition areas are quite sharp.

Andropogon-Myrica interactions—Myrica seedlings/established Andropogon: To investigate early *Myrica* establishment, its germination and seedling survival, twenty 25 × 25-cm^2 plots were established in December 1977, both within and outside *Andropogon* stands in the 17-yr-old field. Two hundred *Myrica* seeds were scattered on the soil surface in each of ten plots in each type of area. The remaining ten plots in each area received no seeds. Seedlings were counted weekly throughout the 1978 growing season. An additional count was made in June 1979.

Possible interactions between *Myrica* seedlings and mature *Andropogon* were also tested in the greenhouse. Eight pre-germinated seedlings were spaced equally around the perimeter of a 15-cm pot which contained either a mature *Andropogon* in loam soil or soil alone. A third set of pots held only an *Andropogon* plant. Nine replicates of each were established, and pots were placed in the Nelson Biological Laboratories greenhouse for 266 days; this growth period was interrupted once, after 100 days, for a 2-wk cold treatment at 5 C. *Andropogon* plants were clipped at crown level and measured for height of tallest culm both before the cold period and also at the termination of the experiment. After the full growth period, *Myrica* plants were cut at the root-shoot junction and their heights determined. All clippings were air-dried and weighed. Greenhouse temperatures ranged from 10 to 32 C with the maximum during a 24-hr period exceeding the minimum by 2–17 degrees. Pot soil moisture was estimated by oven-drying samples collected from all pots during a watering cycle subsequent to the final plant harvest.

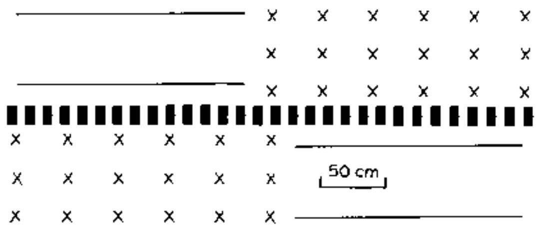

Fig. 1. *Andropogon-Myrica* transplant experiment in the 17-yr-old field. Rectangles = transplanted *Myrica* plants; X's = transplanted *Andropogon* ramets; lines = soil sample area.

Established Myrica/established Andropogon: Growth and survival of established populations of *Andropogon* and *Myrica* were investigated in the 37-yr-old field. Twelve 0.25 × 1.5-m quadrats, each divided into 24 6.25 × 6.25-cm blocks, were established at transition zones of the two species. One-half meter of each quadrat (eight blocks) extended into the *Myrica* litter area. The remaining meter was within the *Andropogon*. Seedlings of both species and *Myrica* sprouts were mapped weekly throughout the 1978 growing season. *Andropogon* vegetative growth was assessed by mapping living and dead crown area at the beginning and end of the observation period.

To determine if rapid chemical or biotic changes are brought about by shrub establishment within *Andropogon* stands, *Myrica* plants (many-stemmed and 25–65 cm in height) collected from the 37-yr-old field were transplanted in a 4-m long and 20-cm wide east-west row within an *Andropogon* area of the 17-yr-old field in October 1977 (Fig. 1). Twelve *Andropogon* plants, also taken from the 37-yr-old field, were each divided into three ramets and placed 10, 40, or 70 cm from the *Myrica* row (Fig. 1). Living and dead crown area of *Andropogon* and position of *Myrica* shoots relative to a midline established along the length of the transplanted *Myrica* were mapped in December 1977, in May and September 1978, and in June 1980. Pooled soil samples were taken from the upper 15 cm at 15 and 70 cm both north and south of the *Myrica* row (Fig. 1) and at both east and west ends of the row at 6-month intervals for textural and chemical analyses. The hydrometer method (Bouyoucos, 1953) was used for textural analysis, while soil pH was determined in a 1:1 soil-water suspension using a Fisher's Acumet model 230 pH meter. The methods of Flannery and Markus (1971) were used to determine concentrations of P, K, Mg, and Ca. Techniques for measuring NO_3-N concentrations were those of Kamphake, Hannah and Cohen (1967), while NH_4-N concentrations were determined by the methods of Mann (1963) and Bolleter, Bushman and Tidwell (1961).

Displacement mechanisms—Shading and soil enrichment in the field: To determine if *Andropogon* and *Myrica* areas of the 37-yr-old field have physical or chemical environmental differences which may affect grass displacement, pooled soil samples were taken from the upper 15 cm of the profile beneath each species in May 1979, and June 1980. These were analyzed for texture, pH, and ppm of Ca, Mg, P, K, NO_3-N, and NH_4-N using the methods outlined above. Light quantity at 0, 15, 30, and 60 cm above soil level within each species' litter area was measured with a Weston Illumination Meter (model 756) at 1:00 EDT on 12 cloudless days during spring 1979.

Greenhouse experiments on shading, allelopathy, and physical effects of litter: To test for possible effects of *Myrica* litter on *Andropogon* germination, seeds collected from the 37-yr-old field were divided into lots of 200. Each lot was secured inside a 1-mm mesh 10 × 10-cm nylon bag, and three bags were placed between layers of either "insulation grade" vermiculite, *Andropogon* litter, or *Myrica* litter in 25 × 25 × 6-cm plastic flats. Two replicate flats of each treatment were randomly placed in a block of "flat-size" depressions in the greenhouse courtyard and stratified for 150 days during the fall and winter of 1977–78. After this cold period, seeds of each lot were germinated at 30/20 C (15-h day, 9-h night) on water-saturated Rochester blue germination blotter paper in 11 × 11 × 3-cm closed plastic boxes placed in a model G-30 germinator (Controlled Environments, Inc.). The number of germinated seeds (1-mm coleoptile and radicle exposed) were counted each 2 days until no new seedlings were recorded for three consecutive counts.

The possibility of persistent compounds in *Myrica* soil that might be inhibitory to *Andropogon* seedling growth, as well as the overall effects of mature *Myrica* on *Andropogon* seedlings, were investigated by equally spacing 50 grass seeds around the perimeter of 30-cm clay pots which contained either a *Myrica* plant, "*Myrica* soil" which was obtained from within *Myrica* stands in the 37-yr-old field, or "non-*Myrica* soil" obtained from outside the *Myrica* areas. To compensate for the volume occupied by the shrub root system in pots not containing *Myrica*, 1.5-mm mesh plastic cylinders (25 cm diam × 15 cm ht) were filled with red shale fragments before the appropriate soil was added. Seedling numbers and heights were recorded weekly for 61 days; seedlings were then cut at soil surface level and their heights measured. During the experiment, pots were subirrigated with 300 ml water daily and misted at 3-day intervals. Soil moisture was determined after seedling removal; an 8-cm^3 soil plug was taken from each pot, placed in a soil tin, and weighed before and after a 24-hr drying period at 105 C. Greenhouse temperatures ranged from 16 to 34 C with the daily maximum exceeding the minimum by 2–14 degrees. Light (measured with a Weston Illumination Meter model 756) reaching seedling height in the "*Myrica* soil" and "non-*Myrica* soil" treatments at 9:00, 1:00, and 5:00 EDT on cloudless days was 462, 1,240 and 735 ft-c, respectively.

To determine specifically how *Myrica* might influence *Andropogon* seedling growth, plastic flats (25 × 25 × 6 cm), each containing 200 grass seeds distributed on a 1:1 (*Myrica* : non-*Myrica*) soil mixture, were set up in three ways. Potential chemical and physical effects of *Myrica* litter were investigated by incorporating seeds into 1 cm deep chopped dead leaf material which had been collected from the ground in the 37-yr-old field and air-dried. Chemical effects of litter were tested by spraying or pouring litter leachate over seeds covered by a 0.25-cm layer of soil. The leachate was collected from 25 × 25 × 6-cm plastic flats which had been covered with 1.5-mm plastic mesh and positioned in the ground beneath *Myrica* stands so that their surfaces were flush with the soil level. Dead *Myrica* leaves were spread over the mesh and the resulting leachate, washed into the flat by rainfall, was collected as soon after accumulation as possible and applied equally to flats of the "leachate" treatment at 3- to 5-day intervals. A third set of flats, again containing seeds on 4.25 cm of soil and covered by a 0.25-cm layer of soil, was established to monitor seedling growth in the absence of *Myrica* influences (control flats). Flats of all treatments were given an equivalent amount of water. Five replicates of each treatment and the control flats were placed inside a frame covered by green saran shading material (48.5% light reduction). An additional five replicates were left unshaded. These latter flats received about 39% of full sunlight. Those within the shading frame received about 20%. This experiment was begun on January 2, 1979, and greenhouse temperatures during its 58-day duration ranged from 12 to 31 C with the maximum exceeding the minimum by 2–10 degrees during a 24-hr period. To examine possible effects of summer drought in the field, a 2-wk drought was begun for all flats 25 days after initiation of the test. The dry period was followed by a week of watering; then a final drought was given until only a few seedlings survived. The living plants were then cut, measured, air-dried, and weighed.

The lack of litter in four of the six types of flats described above affected moisture levels and may have influenced seedling growth. Hence, the above experiment was repeated (beginning on April 27, 1979) with one modification. Seeds of flats not receiving *Myrica* litter were incorporated into 1 cm of *Andropogon* litter which had been collected from the 37-yr-old field, air-dried, and chopped.

To investigate potential effects of *Myrica* on mature *Andropogon* growth, 20 grass plants, collected from the 37-yr-old field, were each divided into six ramets and placed in 15-cm pots. After a recovery period, the ramets were clipped to crown level and subjected to the six regimes described above for the flats containing *Andropogon* seeds. Pots receiving *Myrica* litter had a 1.25-cm-deep layer of chopped material placed around the *Andropogon* plants. Pots were arranged on the greenhouse bench to form four blocks. Two blocks were unshaded (30% of full sunlight received at pot surface height), and two were shaded with green saran (53% light reduction). Pots were watered every 3 days. Additionally, 300 ml of water or litter leachate, the latter obtained by pouring 6,000 ml of water through an equivalent volume of *Myrica* leaf litter freshly collected from beneath shrubs in the 37-yr-old field, were applied at weekly intervals. Greenhouse temperatures ranged from 13 to 36 C with the maximum exceeding the minimum by 2–15 degrees in a 24-hr period. Plants were clipped following flowering and seed set (102 days after initiation of the experiment), and height of tallest culm was measured; clippings were air-dried and weighed. Soil moisture in the pots was assayed by removing an 8-cm^3 soil plug from a randomly chosen one-third of the pots of each treatment each day for 3 days. Each set of soil plugs was weighed before and after a 24-hr drying period at 105 C to obtain moisture levels comparable to those occurring during the watering cycle.

Statistical analyses—Field observational data were not analyzed statistically. Means of results from field and greenhouse experiments were compared by either *t*-tests or one-way Analyses of Variance (ANOVA) (Sokal and Rohlf, 1969). Groups with unequal variance, as determined by an *F*-max and Bartlett's Test for Homogeneity of Variance (Sokal and Rohlf, 1969), were transformed prior to analysis by either arc-sin or $\log_{10}$ transformation. Means found to vary significantly at the 0.05 level by an ANOVA were individually compared by the Duncan Multiple Range (DMR) procedure (Steel and Torrie, 1960).

TABLE 1. *Stem numbers, height, and weight of mature* Andropogon *plants and* Myrica *seedlings grown alone or together in 15-cm pots in the greenhouse*[a]

Treatment	Mean stem no.	Mean maximum ht (cm)	Mean wt (g)	Soil moisture (%)
GROWN ALONE				
Andropogon	4.2	50.0	5.33	11.59
Myrica	6.8*	13.3*	6.70*	13.09
GROWN TOGETHER				
Andropogon	11.3	45.2	9.42	—
Myrica	4.2*	7.2*	1.17*	11.30

[a] Means for the same species within a column which differ significantly at the 0.05 level are followed by an asterisk.

RESULTS AND DISCUSSION—*Andropogon-Myrica interactions—Myrica seedlings/established Andropogon:* The mean numbers of new *Myrica* seedlings recorded in spring 1978 and 1979, in seed plots within *Andropogon* stands of the 17-yr-old field were 4.4 and 1.8, respectively. In plots outside grass areas, fewer seedlings were recorded in both years (1.8 in 1978 and 0.5 in 1979), although in the second season the difference was not statistically significant. The percent survival of seedlings over the first growing season was also greater within *Andropogon* (56.8%) than in plots outside (24.9%); this resulted in a significantly higher mean number of surviving plants within *Andropogon* plots. In fall 1978, 2.5 *Myrica* seedlings per plot were found within *Andropogon* areas; only 0.4 seedlings per plot were recorded in non-grass sites. Pre-germinated *Myrica* also grew in the greenhouse with mature *Andropogon*, although their mean number, height, and weight were significantly lower than those of seedlings grown alone (Table 1). In the 17-yr-old field, however, seedling survival ultimately was more affected by the overall physical environment than by biotic interactions; all first-year plants in plots both within and outside *Andropogon* died over the 1978–79 winter. Such seasonal mortality may be partially offset by germination occurring

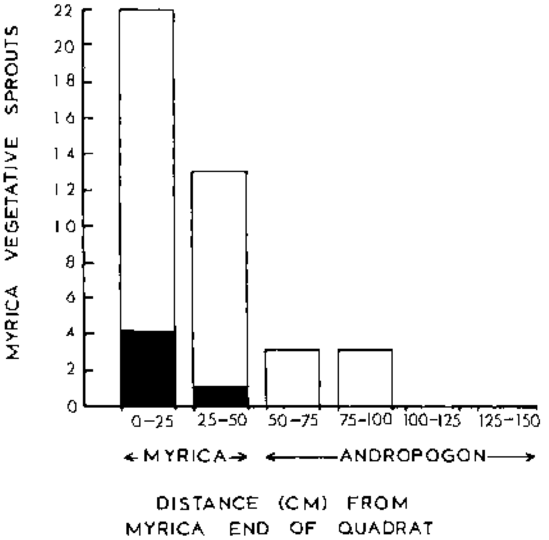

Fig. 2. *Myrica* sprout occurrence with distance from stand edges in the 37-yr-old field. Numbers are totals for 12 quadrats. Shaded area = number dying between May and November 1978.

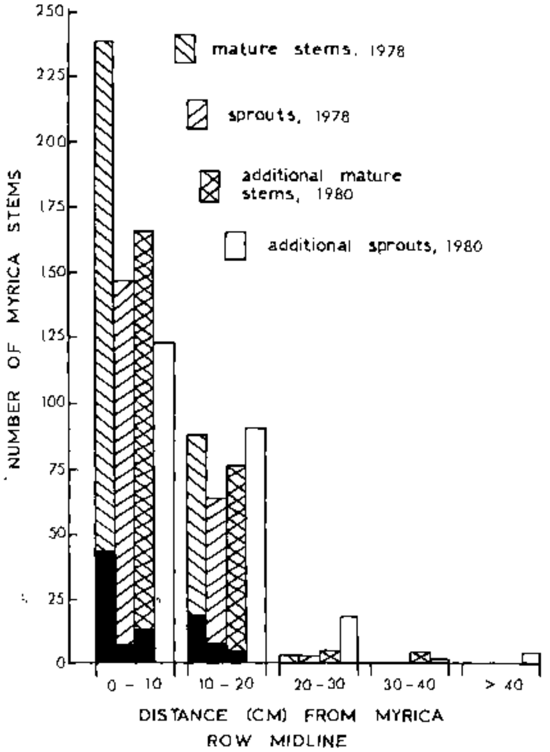

Fig. 3. Transplanted-*Myrica* stem distribution in 1978 and 1980. Shaded area = dead stems or sprouts.

over several years. Some plants from a seed population might thus be placed under more favorable yearly conditions, especially within *Andropogon* stands, which seemed more amenable for *Myrica* germination and early seedling growth.

Established Myrica/established Andropogon: Only two *Myrica* seedlings were found in spring 1978, beneath established shrub clumps in the 37-yr-old field; both of these died while still in the cotyledon stage. Recruitment to the *Myrica* areas was exclusively by vegetative sprouts. These were distributed primarily within the shrub litter area (Fig. 2), but were infrequently found as far as 0.5 m into the adjacent *Andropogon.* A similar distribution of older living *Myrica* stems suggests both a past shrub "invasion" and a future spread into the surrounding grass. Transplanted *Myrica* in the 17-yr-old field also showed this pattern of vegetative growth (Fig. 3). After one season (1978), both mature stems and vegetative sprouts were distributed primarily within 0–10 cm of the *Myrica* row midline and found no further from the line than 30 cm. After three growing seasons (1980), both stems and sprouts were found further than 30 cm; the number of sprouts within 10–20 and 20–30 cm from the midline (Fig. 3, unshaded bars) exceeded both the number of sprouts recorded in these areas in 1978 and the number of mature stems found there in both years.

Recruitment of *Andropogon* within grass areas of the 37-yr-old field was both by seedlings (Fig. 4) and vegetative growth (Fig. 5). However, rather than expanding its borders, *Andropogon* appears to be growing only within its own litter area. None of the 36 seedlings recorded within the *Myrica* regions of the 12 quadrats survived for the entire growing season, while within the grass 42 of 63 seedlings remained alive until fall (Fig. 4). *Andropogon* vegetative growth, as measured by living crown area (Fig. 5), also differed across the transition area, increasing from only 74 cm^2 (31%) in the shrub litter area to 343 cm^2 (52%) within the adjacent grass.

The greater percentage of dead *Andropogon* crown area beneath *Myrica* (Fig. 5) suggests that vegetative as well as seedling growth may be inhibited within shrub clumps. Results from the transplant experiment in the 17-yr-old field indicate that this, if it occurs, might be a gradual process. Vegetative growth of *Andropogon* was not significantly affected by proximity to *Myrica* after one season; mean living crown area increased only slightly from 36.2 cm^2 at 10 cm to 39.3 cm^2 at 40 cm, and 42.9 cm^2 at 70 cm from the *Myrica* row. Nor were significant effects of *Myrica* seen by the third season. Mean living crown area at 10 cm (34.4 cm^2) was slightly lower, and at 40 and 70 cm

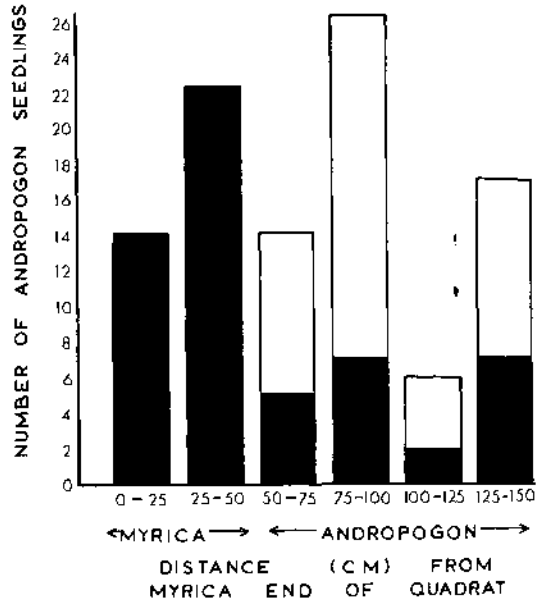

Fig. 4. *Andropogon* seedling distribution with distance from the *Myrica* end of the 12 quadrats in the 37-yr-old field. Shaded area = seedlings dying between May and November 1978. Numbers are totals for all quadrats.

(41.4 cm^2 at both distances) similar to that at the end of the first season. Although the mean area of dead *Andropogon* was greater in the third season (25.8 cm^2 at 10 cm, 33.8 cm^2 at 40 cm, and 32.3 cm^2 at 70 cm) than the first (16.7 cm^2, 11.8 cm^2, and 15.8 cm^2 at 10, 40, and 70 cm, respectively), there was no significant relation of shoot mortality to distance from *Myrica* in either year.

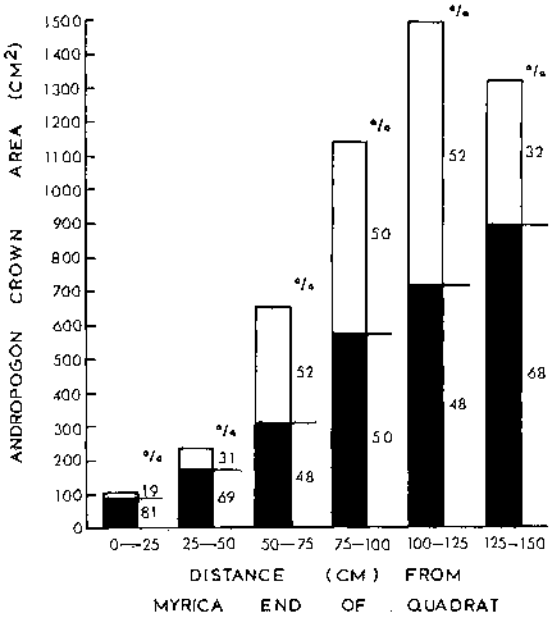

Fig. 5. Mature *Andropogon* occurrence with distance from the *Myrica* end of the quadrats in the 37-yr-old field. Shaded area = crown area dead in 1978. Areas are totals for 12 quadrats.

Displacement mechanisms—Shading: The importance of competition for light in successional dynamics and the tendency for less shade tolerant plants to be replaced by taller or more tolerant species have been noted in several studies (e.g., Oosting, 1942; Bormann, 1953). Blizzard (1931) suggested that *Myrica* shade is the primary mechanism of *Andropogon* displacement.

Observations at the 37-yr-old field revealed differences in light intensity between grass and shrub areas. Light quantity (percent of full sunlight) was 26.4% at 0 cm (soil surface), 28.6% at 15 cm, 40.6% at 30 cm, and 44.6% at 60 cm in height under *Myrica* canopy, while within *Andropogon*, light penetration was much greater (74.6% at 0 cm, 79.2% at 15 cm, 80.5% at 30 cm, and 81.9% at 60 cm). Transition areas received intermediate amounts.

In flats of *Andropogon* seeds exposed to potential *Myrica* displacement mechanisms (shade, and physical and chemical effects of litter; Table 2), seedlings of each shaded treatment (light reduced to 20% of full sunlight) tended to have lower percent survival than plants in the corresponding unshaded test. However, these differences were not statistically significant, nor was the growth (mean height and weight) of shaded seedlings lower than that of their unshaded counterparts (Table 2). In a second, similar experiment with *An-*

TABLE 2. *Effects of* Myrica *litter,* Myrica *leachate, and shade on* Andropogon *seedling growth in flats in the greenhouse (January 2–March 1)*[a]

	Initial seedling no.	Percent seedlings surviving after 2 drought periods	Mean ht (cm) surviving seedlings	Mean wt (g) surviving seedlings
UNSHADED				
Control (no litter) or leachate)	107.6a	1.76b	8.36a	0.67a
Myrica litter	106.0a	94.32a	8.69a	0.73a
Myrica leachate	107.2a	1.82b	9.80a	0.88a
SHADED				
No litter or leachate	104.8a	0.62b	9.95a	0.83a
Myrica litter	93.0a	89.10a	10.14a	0.70a
Myrica leachate	105.8a	0.52b	7.13a	0.53a

[a] Means in a column followed by the same letter are not significantly different at the 0.05 level.

TABLE 3. *Effects of* Myrica *litter,* Myrica *leachate, and shade upon growth of* Andropogon *seedlings in flats in the greenhouse (April 27–June 24).*[a] *In this experiment, seeds of flats not receiving* Myrica *litter were incorporated into 1 cm of* Andropogon *litter*

	Initial seedling no.	Percent surviving seedlings drought I[b]
UNSHADED		
Control (*Andropogon* litter)	142.6a	17.04d
Myrica litter	160.0a	24.52cd
Myrica leachate with *Andropogon* litter	151.4a	6.40e
SHADED		
Andropogon litter	183.8a	71.90b
Myrica litter	178.0a	99.70a
Myrica leachate with *Andropogon* litter	149.8a	39.12c

[a] Means in a column followed by the same letter are not significantly different at the 0.05 level.

[b] Angular transformation was done before statistical analysis.

TABLE 4. *Effects of* Myrica *plants,* Myrica *soil, and non-*Myrica *soil on* Andropogon *seedling growth in 30-cm pots in the greenhouse*[a]

	Mean no. surviving	Mean ht (cm)	Mean wt (mg)	Soil moisture (%)
Myrica soil	13.33a	21.86a	18.7a	11.53a
Non-*Myrica* soil	18.25b	19.22a	18.6a	12.02a
Myrica plants	5.78c	10.09b	8.3b	7.26b

[a] Means in a column followed by the same letter are not significantly different at the 0.05 level.

dropogon litter added to all flats without *Myrica* litter (Table 3), an insufficient number of seedlings survived drought II for analysis. After the first 2-wk drought, seedlings in each shaded treatment had a significantly greater percent survival than those in the corresponding unshaded tests. This experiment, however, was run under higher temperatures, which would have magnified the effects of drought through a higher rate of moisture loss, especially from the unshaded flats.

During dry periods, low soil moisture may occur within *Myrica* clumps in the field. If so, interactive effects of shade and moisture stress may affect *Andropogon* seedling growth and survival. In the greenhouse, seedlings in pots with *Myrica* (where light reaching seedling height was reduced by ca 61% beneath the shrub canopy, and mean soil moisture was lower than that of pots without the shrub) had significantly reduced mean survival, height, and weight (Table 4). In these pots, soil moisture and *Andropogon* weight had a correlation coefficient of 0.699, while for moisture and height, $r = 0.273$. The shading of the *Myrica* canopy apparently produced etiolation and thus affected seedling growth.

Roos and Quinn (1977) reported that *Andropogon* can grow and reproduce successfully in only 16% of full sunlight, although these plants were significantly shorter and flowered later than those under 25% of full sunlight. In the present research, greenhouse results reveal that shoot weight of mature *Andropogon* in all shaded treatments (light reduced to 14% of full sunlight) was significantly lower than that of unshaded plants, which received 30% of full light (Table 5). However, no unshaded greenhouse plants received light quantity comparable to that within *Andropogon* in the field (74.6% of full sunlight), and light reduction within the shaded treatments was much greater than found beneath the *Myrica* canopy at the 37-yr-old field. Although the greenhouse results may thus not be directly applicable to field conditions, *Myrica* shade effects do appear to contribute to the decline of the grass area.

Soil enrichment and subsequent succession: Rice (1964) found *Andropogon scoparius* to be capable of inhibiting nitrifying bacteria, while Bold (1949) demonstrated that it could inhibit nitrogen-fixing algae. The NO_3-N content of soil taken from the upper 15 cm beneath grass areas of the 37-yr-old field in April 1977, was only 4–5 ppm (Galuten, 1977). These levels were less than $^1/_{10}$ those in soil taken concurrently from beneath *Myrica* clumps, although the NH_4-N levels beneath both species were

TABLE 5. *Effects of* Myrica *litter,* Myrica *leachate, and shade on mature* Andropogon *in 15-cm pots in the greenhouse*[a]

	Mean ht (cm)	Mean shoot wt (g)	Mean wt per 10 tillers (g)	Soil moisture (%)
UNSHADED				
Control (no litter) or leachate)	69.3a	6.49a	5.77a	8.51a
Myrica litter	78.5a	8.56a	6.13a	10.36a
Myrica leachate	69.5a	6.91a	3.78ab	7.90a
SHADED				
No litter or leachate	59.9a	4.15b	2.26c	8.20a
Myrica litter	58.4a	3.50b	2.71bc	10.22a
Myrica leachate	55.0a	3.37b	2.24bc	9.02a

[a] Means in a column followed by the same letter are not significantly different at the 0.05 level.

similar, ranging from 6.5 to 9 ppm (Galuten, 1977). *Myrica* litter may contain nitrogen concentrations representing 16–32 g/m^2/yr under pure shrub clumps (Benson, 1978). This addition of nitrogen to litter and soil beneath *Myrica* results partially from fixation by the shrub, since the species has been shown to be capable of nitrogen-fixation (Morris et al., 1974), and plants are nodulated in the field.

In the greenhouse, mature *Andropogon* plants in pots with nodulated *Myrica* seedlings, where accumulation of nitrogen could occur relatively rapidly, had greater mean weight and number of stems than plants grown alone (Table 1). In the field, soil enrichment in shrub areas may be favorable to growth of not only *Andropogon*, but also of later successional species which may eventually interfere with the grass and contribute to its displacement. Galuten (1977) observed that *Acer rubrum* seedlings in the 37-yr-old field tended to be associated with *Myrica* areas but not with *Andropogon*. On Long Island, Blizzard (1931) recorded the presence of "secondary invaders" such as *Acer rubrum* and *Sassafras albidum* within larger (i.e., older) *Myrica* clumps and described the subsequent development of a young forest.

Results from the present research indicate that accumulation of nitrogen and other minerals does not occur immediately upon *Myrica* establishment. Concentrations of minerals in soil samples taken over a 30-month period from both 15 and 70 cm from the narrow row of transplanted *Myrica* in the 17-yr-old field (Table 6) showed no tendency to be greater in the closer (15 cm) samples, nor were they higher in later samples than in those taken shortly after shrub transplanting. Additionally, nitrogen concentrations within established shrub clumps may not always be greater than those in surrounding areas. Analyses of soil taken in May 1979, and June 1980, from both *Andropogon* and *Myrica* regions of the 37-yr-old field (Table 7) revealed that concentrations of NH_4-N within shrub clumps were slightly lower than those in the surrounding grass areas, while NO_3-N levels were similar beneath both species. It appears, therefore, that soil enrichment beneath *Myrica* may not explain the *Andropogon* displacement beneath young shrub clumps observed by Blizzard (1931). Nor may nitrogen levels be consistently higher within larger clumps, although these clumps often do contain later successional species which may eventually contribute to grass displacement through competitive or allelopathic effects.

TABLE 6. *Minimum and maximum values of soil chemical composition from five samples over a 30-month period at either end of, and at 15 and 70 cm from, the transplanted* Myrica *row*

		pH 1:1	Mg	P	K	Ca	NO_3-N	NH_4-N
			ppm					
Ends	East	4.9	56	7	93	238	4	4
		5.2	104	12	124	573	11	11
	West	4.9	56	8	75	150	3	4
		5.1	99	13	140	629	11	22
15 cm	North	5.0	63	7	80	250	3	4
		5.2	107	18	106	646	12	9
	South	4.9	63	8	80	225	4	4
		5.2	101	16	117	517	10	11
70 cm	North	4.9	67	9	88	238	3	3
		5.0	97	19	160	629	25	17
	South	5.0	77	7	85	263	3	4
		5.2	97	11	144	629	12	11

TABLE 7. *Soil chemical composition of the upper 15 cm of substrate beneath* Andropogon *and* Myrica *stands in the 37-yr-old field*

Sample	pH 1:1	Mg	P	K	Ca	NO_3-N	NH_4-N
		ppm					
Andropogon							
1979	4.5	20	11	78	100	10	28
1980	4.3	18	13	55	197	6	15
Myrica							
1979	4.2	33	8	45	185	10	12
1980	4.1	24	9	47	225	9	12

Allelopathy: The high mortality of *Andropogon* seedlings (Fig. 4) and the low occurrence of living mature grass (Fig. 5) or other species beneath established shrub clumps suggest possible allelopathic effects of *Myrica* litter, litter leachate, and/or materials exuded into the surrounding soil by shrub roots. However, the presence of a few grass seedlings within *Myrica* clumps in the spring (Fig. 4) indicates that *Andropogon* germination is not totally inhibited by compounds released from *Myrica* litter over winter. Experimental results reinforced this observation: the percent germination of *Andropogon* seeds stratified outdoors in *Myrica* litter (25.2%) did not differ significantly from that of seeds in either *Andropogon* litter (25.8%) or "insulation grade" vermiculite (22.5%).

On the other hand, the percent survival of grass seedlings in "*Myrica* soil" was significantly lower than in "non-*Myrica* soil," possibly indicating the persistence of toxic compounds in shrub soil (Table 4). Also, in two subsequent experiments utilizing a 1:1 (*Myrica* : non-*Myrica*) soil mixture in flats of *Andropogon* seeds exposed to potential *Myrica* displacement mechanisms, some interactive effects of *Myrica* litter leachate were demonstrated. In the first experiment where no litter cover was provided those flats not receiving *Myrica* litter (Table 2), the initial seedling number, percent seedling survival, mean height, and mean weight of plants in both shaded and unshaded treatments given *Myrica* litter leachate did not differ significantly from values for the respective control plants which received only water. Nevertheless, slight interactive effects of leachate and shade were suggested by the unshaded leachate flats having a slightly greater mean height and weight than other unshaded flats as opposed to the shaded leachate flats having a somewhat lower percent survival and mean height and weight than other shaded flats. In the second experiment in which *Andropogon* litter was added to those flats not receiving *Myrica* litter (Table 3), seedling survival, after one 2-wk drought, in both shaded and unshaded trials with *Myrica* litter was higher than that of the control treatments (i.e., Shade-*Andropogon* Litter and *Andropogon* Litter). On the other hand, application of *Myrica* leachate to seeds in *Andropogon* litter significantly decreased survival under both shaded and unshaded conditions. There may thus be some interactive effects of *Myrica* litter leachate on *Andropogon* seedlings growing within grass litter—a situation which could occur in the field within the transition areas of the species.

Mature *Andropogon* vegetative growth (mean height of tallest culm and mean weight; Table 5) in unshaded treatments receiving *Myrica* litter leachate was similar to that of control plants given only water, but the mean weight per ten tillers of plants receiving *Myrica* leachate was 35% lower (Table 5). Also growth of shaded plants subjected to *Myrica* leachate tended to be lower than that of plants in shade only. These growth differences, although not statistically significant, may also indicate some interactive inhibition of vegetative growth by shade and *Myrica* litter leachate. In a study to evaluate possible volatile effects of *Myrica* on mature *Andropogon* growth, Galuten (1977) found that the growth (dry shoot weight) of *Andropogon* in pots surrounded by *Myrica* was 24% less (but not significant at the 0.05 level) than that of grass in pots removed from the *Myrica*, and that the mean weight per ten tillers of plants surrounded by the shrub was significantly lower. However, neither these inhibitory effects of *Myrica* litter leachate and volatile *Myrica* compounds on mature *Andropogon*, nor those of *Myrica* leachate on grass seedling growth, appear to be the sole causes of *Andropogon* displacement.

Physical effects of litter: Galuten (1977) suggested that young *Andropogon* seedlings within *Myrica* litter might be prevented by physical effects of the litter from producing a root and/or shoot adequate to obtain necessary light and/or water and thus have reduced growth and survival, especially during dry periods. In two greenhouse experiments, *Andropogon* seeds incorporated into 1 cm deep *Myrica* litter (Tables 2, 3) had initial germination similar to that of seeds in control treatments. After two droughts, seedlings of the first experiment in both shaded and unshaded flats with *Myrica* litter had a significantly higher percent survival than those in the control treatments without litter cover (Table 2). Survival in the second experiment, after one drought, was affected more by shade than by type of litter cover (Table 3). However, values for treatments with *Myrica* litter tended to be higher than those of the control treatments with *Andropogon* litter.

These results do not indicate direct inhibitory physical effects of *Myrica* litter in the field, providing it does not exceed 1 cm in depth. A deeper litter was used in the experiments of Galuten (1977), who measured a recognizable shrub litter of approximately 0.6–1.3 cm with an additional 0.6–1.3 cm unrecognizable decomposing material beneath. This additional litter may have had physical effects on *Andropogon* seedlings not accounted for by our greenhouse experiments which employed a litter depth equivalent to the average field depth measured in spring 1978.

CONCLUSIONS—*Andropogon* displacement does not appear to be the result of a single mechanism, but may be brought about by several properties of *Myrica*. The vigorous sprouts of mature shrub plants permit increasing penetration of the surrounding grass, which results in an enlarging *Myrica* area. Within shrub clumps, *Andropogon* seed germination is apparently not inhibited by chemical or physical effects of *Myrica* litter; however, first-year seedling mortality is high. Greenhouse results indicate that reduced growth of seedlings may be attributable to lower light beneath *Myrica* canopy, or to the interaction of shading and allelopathic effects of shrub litter. Etiolated seedlings with a lesser allocation to root development may also be more affected by dry periods in the field.

The amount of living mature *Andropogon* is lower within shrub clumps than in adjacent grass areas, while, on a percentage basis, the area of dead *Andropogon* is greater within *Myrica* litter regions. Greenhouse results suggest that mature *Andropogon* vegetative growth may be limited by the reduced light beneath *Myrica* canopy. Shrub litter leachate was also found to inhibit grass growth slightly in shaded conditions.

The reduced vegetative growth of mature *Andropogon* and the mortality of seedlings within enlarging *Myrica* clumps result in an increasingly smaller grass area. Additionally, soil enrichment beneath *Myrica*, partially due to the shrub's ability to fix nitrogen, may facilitate establishment of later successional species which may then also contribute to *Andropogon* displacement through competitive or allelopathic effects.

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