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Using Plant Volume To Quantify Interference In Corn (*Zea mays*) Neighborhoods[1]

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Abstract. **Measurements of above-ground plant volume were used to quantify corn interference with common cocklebur and velvetleaf. Separate experiments were carried out for each weed species in which neighborhoods with a radius of 50 cm were established around target plants of both species, selected from a range of corn plus cocklebur or velvetleaf densities. Height and canopy area of target plants and neighbor corn and weed populations were measured periodically during the growing season. Target plant (corn, cocklebur, or velvetleaf) size as well as corn and weed population size within each neighborhood were quantified as cylindrical volumes. Regression analysis was used to quantify the relationship between target plant seed production and cylindrical volumes of the target and neighbor species. Both target and neighbor plant volumes were correlated with target plant seed production for all species. The ratio of target plant volume to total neighborhood plant volume (volume ratio) was the independent variable that accounted for the most variation in target plant seed production. These volume-based variables may be used to develop competitive indices in physico-empirical based interference models. Nomenclature: Common cocklebur, *Xanthium strumarium* L. #[3] XANST; velvetleaf, *Abutilon theophrasti* Medic, ABUTH; corn, *Zea mays* L. 'Pioneer 3787.'**

Additional index words: **Interference, target plant, neighborhood, *Abutilon theophrasti, Xanthium strumarium,* ABUTH, XANST.**

INTRODUCTION

The ability to make successful weed management decisions depends upon accurate prediction of the impact of weed populations on crop yields. Several methods have been used to establish predictive relationships between weed density and crop yield (3, 5, 6, 18). Most yield-density relationships have been based on the average performance of a group of plants. However, as plant populations often are composed of a hierarchy of individuals with a few large dominants and a greater number of small suppressed plants, average plant performance may not represent the most common plant in a population (6, 30). Averaging plant performance across all individuals in a plot may obscure the effects of spatially heterogeneous resource concentrations that can alter the outcome of competitive interactions (8, 23). These limitations may be overcome by using an individual-plant-centered neighborhood approach (25).

A neighborhood approach allows for individual plant measurements that effectively characterize the response of a target plant to interference from neighbor plants (6, 7, 25, 30). The mechanism whereby one plant inhibits another is generally resource reduction (24). Successful capture of resources by an individual plant depends on its size, emergence time relative to neighboring plants, distance from neighbor plants, morphology and physiology, and the morphology and physiology of its neighbors (6, 27). Models of weed and crop competition based on weed density (number of plants per unit area) alone do not adequately account for all of these factors (6, 13). More of the variation in plant performance may be accounted for if size characteristics of competing plants are incorporated in empirical relationships (25, 29), because size is a direct measure of morphology, reflecting relative emergence time, spatial arrangement, and plant physiology (3, 6).

Total plant dry weight is often used to measure plant size. Determining dry weight requires destructive sampling, which prevents season-long study of the same individuals. White and Harper (31) suggest that plant weight is a function of the volume of space it occupies. Therefore, a measure of plant volume should provide a non-destructive index of total plant weight as well as morphology and subsequent resource use. Plant volumes could assume any number of shapes. Cylindrical volumes are easily determined from height and canopy area measurements and may be sufficient for development of simple empirical models of plant interference.

This study was conducted to determine the potential for using cylindrical plant volume measurements as variables for assessing corn interactions with common cocklebur and velvetleaf in neighborhoods. The overall goal of this work was to establish the best empirical relationships that characterize interference between these species. Specific objectives were a) to determine how volume of an individual plant is related to its biomass and seed yield, b) to understand the relationship between individual plant seed production and neighbor plant density, canopy area, and volume, c) to determine a biologically realistic combination of target and neighbor plant cylindrical volume measurements for predicting target plant seed production, and d) to compare this combination variable to total neighborhood density as a predictor of target plant response. Common cocklebur and velvetleaf were chosen for study because these weeds have the potential to grow very large, they cause severe yield losses in corn (4, 32), and they are easy to measure.

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[3]Letters following this symbol are a WSSA approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

MATERIALS AND METHODS

Study site. Field experiments were carried out in 1991 and 1992 at Rosemount, Minnesota, on a Waukegan silt loam soil (fine-silty over sandy, mixed, mesic Typic Hapludoll) with approximately 3% organic matter. Previous crops were corn on the 1991 site and peas followed by alfalfa on the 1992 site. Sites were located adjacent to one another in the same field and were disked and fertilized with 116 kg ha^{-1} N in 1991 and 84 kg ha^{-1} N, 31 kg ha^{-1} P, and 94 kg ha^{-1} K in 1992, as recommended by the University of Minnesota Soil Testing Laboratory for corn production. Planting dates were May 14, 1991, and May 8, 1992. Soil moisture was presumed adequate throughout the growing season in 1991 with 11.51 cm of rain the first 5 wk after planting but dry in 1992 for the first 5 wk after planting, receiving only 3.45 cm of rain. Soil and air temperatures generally were cooler in 1992, with slight frost damage during the last week of May. Accumulated growing degree days were calculated with a minumum base of 10 C and a maximum of 30 C.

Neighborhood establishment. A range of weed and corn densities were established in 5 by 5 m plots in a randomized complete block design with three replications. Treatments included four weed seeding rates (0, 200,000; 400,000, and 800,000 seeds ha^{-1}), four corn planting rates (0; 32,000; 64,000, and 128,000 seeds ha^{-1}). Separate experiments were carried out for each weed species but treatments were randomized together so that comparisons could be made between common cocklebur and velvetleaf. Following seedbed preparation, a grid of 135 plots was laid out in three 45-plot blocks arranged along a slight change in soil type. Each block contained 18 corn + common cocklebur combinations, 18 corn + velvetleaf combinations, three corn monocultures, three common cocklebur monocultures, and three velvetleaf monocultures. Within each plot, a single target plant (weed or corn) was randomly chosen for study and a 50-cm radius neighborhood was established around it. Half of the 18 corn + weed combination plots were used for weed targets and the other half for corn targets.

Pre-measured quantities of deburred common cocklebur pods and acid scarified velvetleaf seed were hand scattered in the center 3.7 by 3.7 m of appropriate plots and incorporated with a disk. Pioneer 3787 hybrid seed corn was then uniformly sown at 5 cm depth in 76 cm wide rows at 64,000 seeds ha^{-1} in all plots, except those designated for weed monocultures. Additional corn rows were planted with a jab-type hand planter in 128,000 seed ha^{-1} corn plots. In 32,000 seed ha^{-1} corn plots, every other corn plant was removed with a hoe upon emergence.

Weed control. Propachlor [2-chloro-*N*-(1-methylethyl)-*N*-phenylacetamide] herbicide was applied PRE at a rate of 4.5 kg ha^{-1} to control annual grasses. Prior to common cocklebur emergence, bentazon [3-(1-methylethyl)-(1*H*)-2,1,3-benzothiadiazin-4(3*H*)-one 2,2-dioxide] was applied POST at 1.12 kg ha^{-1} to control indigenous velvetleaf seedlings in common cocklebur plots. Hand hoeing was required in 1992 to control woolly cupgrass (*Eriochloa villosa* Kunth.) and wild proso millet (*Panicum miliaceum* L.).

Measurements. Target and neighbor plants were measured approximately every 2 wk during the growing season in 1991 and weekly in 1992. Target plant measurements included height and canopy diameter. Height was measured from the soil surface to the highest point of living tissue in its natural state. Target plant canopy area was determined by measuring the width of the canopy at the widest point, then a second width perpendicular to the first. The mean of the two widths was used to calculate the canopy radius and circular canopy area. Neighborhood measurements included plant number, height of the tallest and average plant, and estimated canopy area for neighboring corn and weed plants. Neighbor plant canopy area was determined by visually estimating percent of total neighborhood area covered by each species (corn and weed). Height and canopy area measurements were used to compute the cylindrical volume of individual target plants and of each neighbor species. Relationships between individual plant volumes and above ground biomass were determined for all three species for a range of growth stages by measuring height and canopy area of randomly selected plants from areas adjacent to neighborhoods, harvesting them, and determining dry weights.

Harvest. Seeds of all target and neighbor plants were harvested by hand as they matured. Velvetleaf pods began to mature in late July and continued through September. To ensure that seed losses due to shattering were minimized, pods were collected approximately twice weekly as they matured prior to corn harvest. Seed was threshed from pods, dried at 60 C for 5 d, and weighed. Corn ears were harvested when grain moisture reached approximately 30% and was oven dried at 60 C for 5 d, and weighed. Whole common cocklebur plants were harvested with burs intact, dried at 60 C, and weighed. Burs were separated in the laboratory, counted, and then weighed. Seed production values are presented as bur counts rather than weight of seed produced, because bur morphology varied among target plants and could influence weights. Target corn and velvetleaf plants were harvested after all seed had been collected and dry weights were determined.

Statistical analysis. Correlations and regressions (linear and non-linear) were performed using SAS (20). Differences between regression lines were determined based on 95% confidence intervals for parameter estimates. Approximate R^2 values were computed for nonlinear regressions according to the following equation: Approximate $R^2 = 1 -$ (residual sum of squares/total corrected sum of squares).

RESULTS AND DISCUSSION

Predicting target plant biomass from cylindrical volume. Vegetative biomass of individual target plants was related to cylindrical volume for all species (Figure 1). Data from four sampling periods in 1991 and eight in 1992 were pooled and showed a consistent linear relationship ($R^2 \geq .76$) between biomass and volume. Close examination of corn and velvetleaf scattergrams (Figure 1) and some indication of systematic deviation in residual plots (data not shown) revealed slight curvature near the origin. This deviation from linearity may indicate that plant volume density is changing over time. When mutual as well

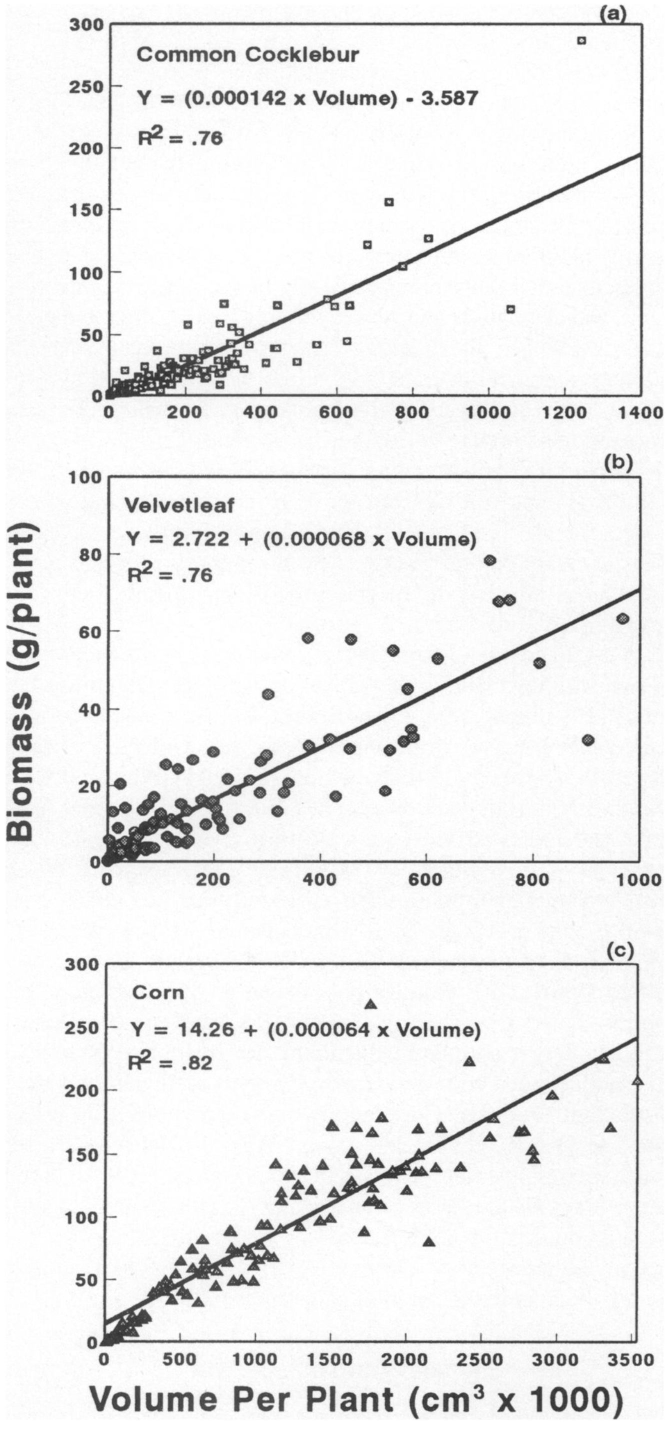


Figure 1. Relationship between individual plant biomass (Y) and cylindrical volume for common cocklebur (a), velvetleaf (b), and corn (c). Data were pooled from several measurement periods in 1991 and 1992. All regressions were significant ($p < 0.001$).

as neighbor shading intensifies following canopy closure, synthesis of carbohydrate may drop sufficiently to reduce the rate of storage, resulting in lower tissue densities or longer internodes, which would result in reduced leaf area per total canopy volume. Changes in stem density resulting from removal of competing vegetation are well documented in woody species (33). This deviation was minor and did not justify a nonlinear model. Regardless of the specific form of the relationship, these results indicate that plant volume is an appropriate surrogate variable for vegetative biomass production.

Predicting target plant seed production from cylindrical volume. Correlations between target plant cylindrical volume and

Table 1. Correlation between seed production and volume for target common cocklebur and corn plants in the common cocklebur experiment.[a]

Date	DAP[b]	GDD[c]	Correlation coefficient	
			Corn	Common cocklebur
			r	
1991				
5/29	15	255	.14	–0.04
6/11	28	524	.15	–0.13
6/26	43	858	.62*	0.00
7/08	55	1156	.78*	.53*
7/17	64	1363	.84*	.66*
1992				
6/01	23	323	.39*	–0.05
6/17	39	619	.20	–0.08
6/30	52	792	.48*	–0.08
7/14	66	1029	.65*	.58*
7/28	80	1232	.62*	.57*

[a] All correlations marked with an asterisks were significant ($p \geq 0.05$).

[b] Days after planting.

[c] Accumulated growing degree days (GDD) based on a minimum of 10 and a maximum of 30 C.

Table 2. Correlation between seed production and volume for target velvetleaf and corn plants in the velvetleaf experiment.[a]

Date	DAP[b]	GDD[c]	Correlation coefficient	
			Corn	Velvetleaf
			r	
1991				
5/29	15	255	.38*	.25
6/11	28	524	.16	.40*
6/26	43	858	.42*	.55*
7/08	55	1156	.60*	.83*
7/17	64	1363	.50*	.76*
1992				
6/01	23	323	.04	.08
6/17	39	619	.10	.05
6/30	52	792	.32*	.07
7/14	66	1029	.61*	.48*
7/28	80	1232	.70*	.78*

[a] All correlations marked with an asterisk were significant ($p \geq 0.05$).

[b] Days after planting.

[c] Accumulated growing degree days (GDD) based on a minimum of 10 and a maximum of 30 C.

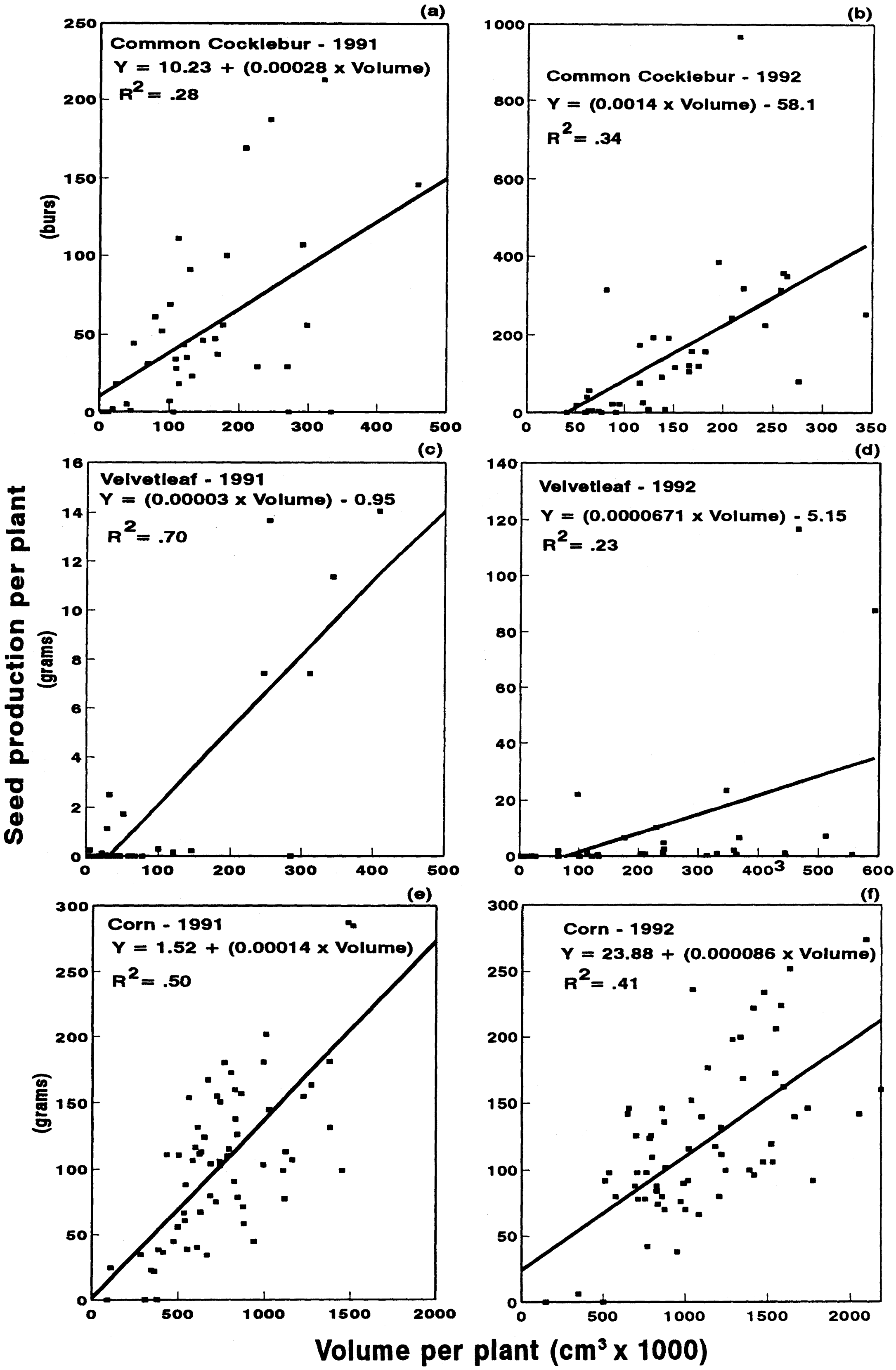


Figure 2. Relationship between target plant seed production (Y) and cylindrical volume measured July 8, 1991, and July 14, 1992, on common cocklebur (a and b), velvetleaf (c and d), and corn (e and f) target plants. All regressions were significant ($p < 0.005$).

Table 3. Correlations between target plant seed production and neighbor variables for each species in the common cocklebur experiment.[a]

	Correlation coefficient					
	Corn vs. neighbor			Common cocklebur vs. neighbor		
Date	Total density	Canopy area	Volume	Total density	Canopy area	Volume
	r					
1991						
5/29	–.73*	–.67*	–.49*	–.39*	–.39*	–.36*
6/11	–.73*	–.76*	–.64*	–.39*	–.42*	–.34*
6/26	–.73*	–.79*	–.69*	–.43*	–.38*	–.44*
7/08	–.71*	–.73*	–.57*	–.41*	–.33*	–0.26
7/17	–.73*	–.56*	–0.24	–.39*	–.34*	–0.28
1992						
6/01	–.42*	–.48*	–.48*	–.58*	–.62*	–.54*
6/17	–.39*	–.43*	–.44*	–.51*	–.61*	–.61*
6/30	–.38*	–.48*	–.54*	–.49*	–.69*	–.65*
7/14	–.43*	–0.30	–.47*	–.54*	–.54*	–.71*
7/28	–.42*	–0.19	–.39*	–.56*	–.68*	–.71*

[a]All correlations marked with an asterisk were significant ($p \geq 0.05$).

seed yield for corn, common cocklebur, and velvetleaf revealed an increasingly positive relationship over time and growing degree day accumulation (Tables 1 and 2). By early to mid July, a strong positive correlation was observed for each species, indicating that accumulated height and canopy area development in the first 8 wk after planting was important to seed production. These results are consistent with findings from several studies in which seed yield was positively related to plant size across and within genotypes of numerous species (1, 2, 9, 14, 19). Several researchers have suggested that relationships between plant biomass and seed production are most often linear (16, 19, 22). Regressions of target plant seed yield on early July target plant volume indicated no clear departure from linearity (Figure 2), although residual plots for velvetleaf and common cocklebur showed non-constant variance as yield increased. Increases in corn and common cocklebur volumes appeared to have similar effects on seed yield in 1991 and 1992, but increasing velvetleaf volume did not have a consistent impact between years (Figure 2). It is apparent from the point scatters and R^2 values for all three species that early size development does not account for all of the variability in seed production, particularly velvetleaf. Aarssen and Clauss (2) suggested that competition may have a direct impact on reproductive resource allocation and number of seeds produced per plant, independent of size.

Table 4. Correlations between target plant seed production and neighbor variables for each species in the velvetleaf experiment.[a]

	Correlation coefficient					
	Corn vs. neighbor			Velvetleaf vs. neighbor		
Date	Total density	Canopy area	Volume	Total density	Canopy area	Volume
	r					
1991						
5/29	–0.03	–.36*	–.31*	–.37*	–.44*	–.37*
6/11	–0.03	–.43*	–.58*	–.37*	–.37*	–.35*
6/26	–0.12	–.48*	–.52*	–.41*	–.27*	–.41*
7/08	–0.13	–.56*	–.58*	–.43*	–0.27	–0.32
7/17	–0.22	–.44*	–.44*	–.41*	–.35*	–.38
1992						
6/01	–0.01	–.53*	–.52*	–.48*	–.38*	–.31*
6/17	–0.05	–.31*	–.42*	–.49*	–.47*	–.38*
6/30	–0.07	–.36*	–.48*	–.47*	–.56*	–.47*
7/14	–0.11	–0.28	–.47*	–.49*	–.53*	–.46*
7/28	–0.14	–0.30	–.51*	–.47*	–.52*	–.51*

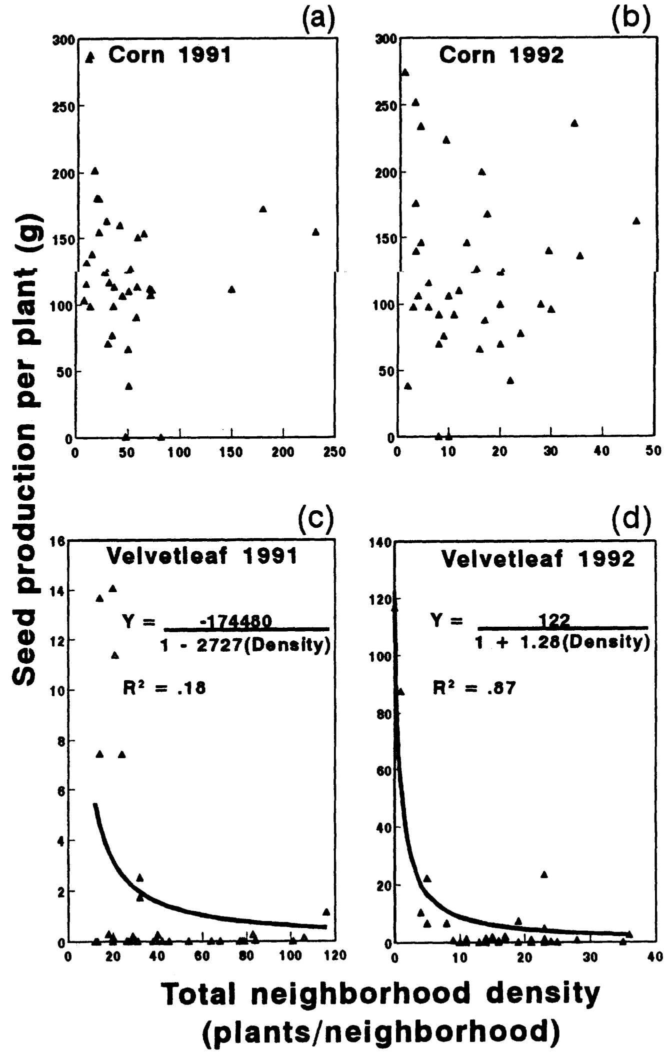
[a]All correlations marked with an asterisk were significant ($p \geq 0.05$).

Predicting target seed yield from neighborhood parameters. Total neighborhood density, canopy area, and cylindrical volume were negatively correlated with target plant seed production for all species (Tables 3 and 4). The strength of these linear correlations changed across variables and species. Overall, neighbor volume exhibited the most consistent linear correlation to target plant seed production for all species across years in both experiments. Correlations were weakest for corn targets in mixture with velvetleaf, where no clear relationship appeared to exist between seed yield and total neighbor density. This indicates that number of velvetleaf plants had little impact on corn target plant yield. Further analysis based on nonlinear regression of individual corn plant yield on neighbor velvetleaf density verified that no clear relationship existed (Figure 3).

Several studies have shown that individual plant seed production is reduced as neighbor plant density, canopy area, or biomass increased (11, 28). These relationships were best described by a negative hyperbolic curve (6, 7, 17, 21, 26, 28, 32). Regression analysis confirmed that yield density curves were best described by the negative hyperbolic curve developed by Weiner (28) based on the inverse yield law (10) (Figures 3 and 4). Regression analyses also revealed that neighbor canopy area and volume were related to target plant seed production in a negative hyperbolic form (results not shown).

Predicting target plant seed production from volume ratio. Because both target plant volume and total neighbor volume were related to target plant yield, biologically tenable combinations of these variables were investigated for improving prediction of target plant seed yield. Multiple linear regressions of target plant yield on target and neighbor volume resulted in higher adjusted R^2 values than simple linear regressions with either dependent variable above (results not shown), but these multiple linear models did little for elucidating the mechanisms driving interference between target and neighbor plants.

A more biologically plausible composite of the independent variables with good predictive power was the ratio of target cylindrical volume to total neighborhood cylindrical volume (including the target plant). This fraction, which was designated "volume ratio," describes the volume of space occupied by the target plants relative to the volume occupied by all plants in the neighborhood including the target. A target plant growing alone has a volume ratio of 1, while a stunted target plant with many neighbors approaches a volume ratio of 0. It is a measure of the prominence of the target plant which to some degree reflects the share of total resources received. It also may reflect differences in relative size based on different emergence times. This approach is similar to the relative leaf area relationships developed by Kropff and Spitters (12) who suggested that competitive strength of a species is determined by its share of leaf area at the moment when canopy closure occurs (11). Kropff and Spitters (12) did not specifically consider the dimension of height, whereas volume ratio assumes that competitive strength of individuals is determined by their relative share of 3-dimensional space.



As volume ratio increased, seed yield increased for all target plant species (Figures 5 and 6). This is expected since plants of a given species that are larger relative to neighbors should have greater potential for seed production. Linear functions consistently provided the best fit for relating volume ratio to target plant seed yield and represent reasonable predictions because crop plants in production fields will most often exhibit volume ratios over the middle to upper portions of the graphs, where the relationship is most linear. However, further testing of the predictive functions over more years and sites are required to verify their utility.

The relationship between target plant seed yield and volume ratio tended to be weaker at early measurement dates than later dates based on the percentage of variation explained (Table 5).

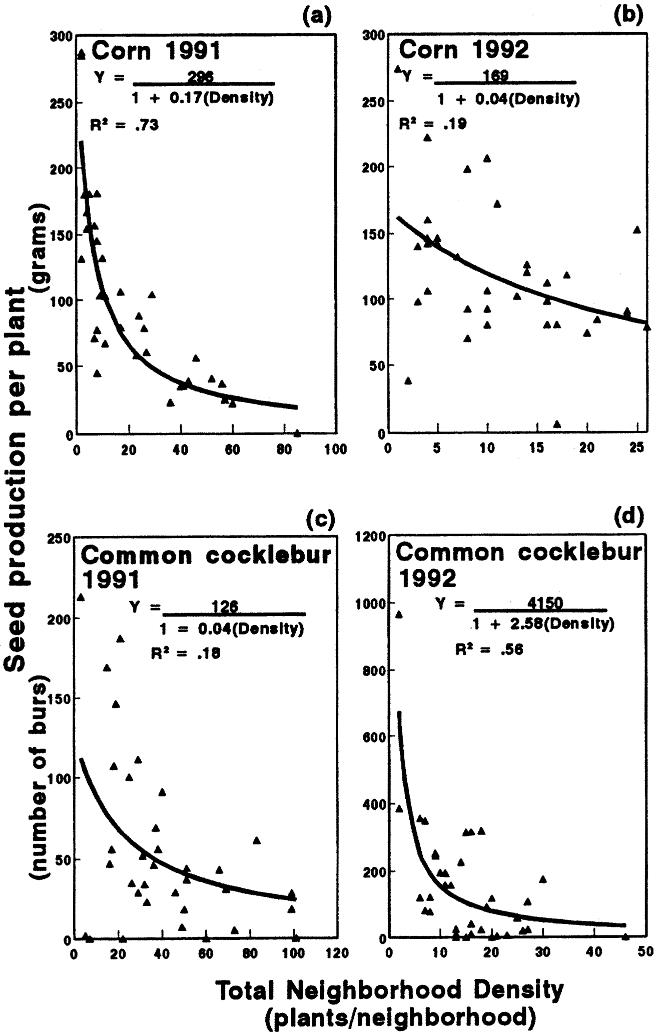


Figure 4. Hyperbolic relationships between target plant seed production (Y) and total neighbor number (Density) for corn in 1991 (a) and 1992 (b), and common cocklebur in 1991 (c) and 1992 (d) when the two species were grown in mixture. Values for R^2 are approximate.

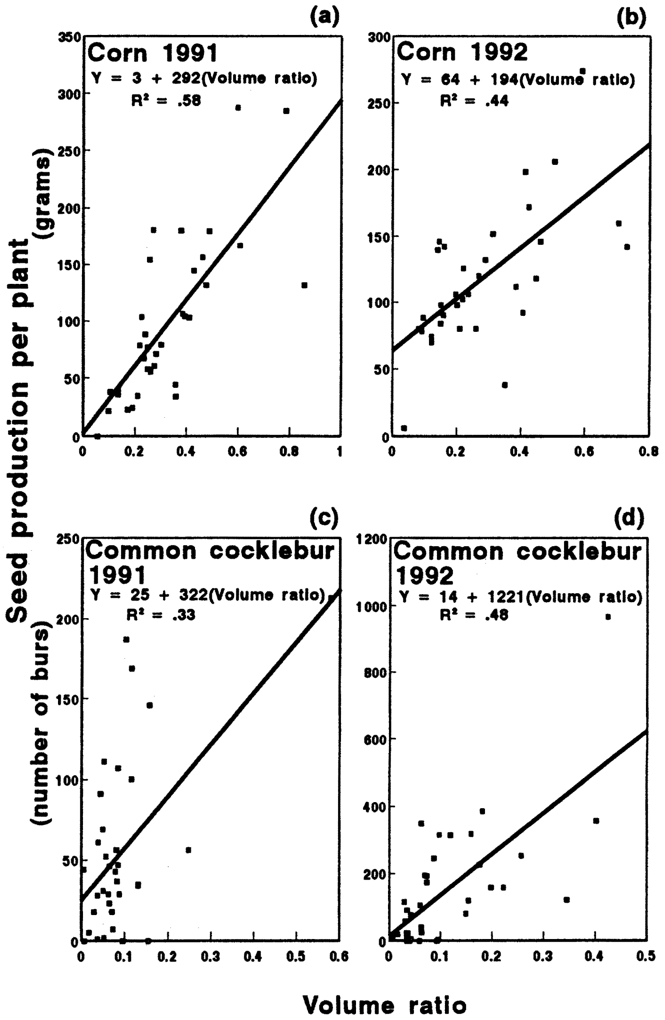


Figure 5. Relationships between target plant seed production (Y) and volume ratio for corn in 1991 (a) and 1992 (b), and common cocklebur in 1991 (c) and 1992 (b) when the two species were grown in mixture. Volume ratios were determined between June 9 and June 18 in both years. All regressions were significant ($p < 0.0003$).

This may be a result of the difficulty in making accurate measurements when plants were small. This also may be due to delay in time before plants exhibited morphological changes due to competition. These points may be particularly important for velvetleaf and common cocklebur, which in general did not exhibit clear relationships between seed production and volume ratio as early as corn plants.

Volume ratio was a better predictor of target plant seed production than total density, consistently accounting for more variation across species (Figures 3, 4, 5, and 6). In the velvetleaf experiment, no clear relationship existed between target corn plant seed yield and total neighborhood (corn + velvetleaf) density (Figure 3), but more than 45% of the variation in yield was accounted for with volume ratio. Density has proven to be unreliable as a predictor of individual plant performance in other studies (6, 29). Substantial improvements in functional relationships has been achieved by adding distance and various measures of neighbor size to models relating yield to neighbor density (7, 17). Wagner and Radosevich (25) found that neighbor canopy area, which simultaneously accounts for size and density, was the best predictor of individual plant growth. Our findings suggest that volume-based variables, especially volume ratio, may provide superior empirical relationships upon which to base weed threshold levels.

Volume ratio may explain more of the variation in individual plant seed production than neighbor density because, in part, it accounts for genetic and microsite differences between individuals. It also accounts for neighbor size, spatial distribution, relative emergence time, and number. Volume ratio may therefore be a much more stable predictor across sites and years than neighbor density. Relationships between target corn plant seed yield and

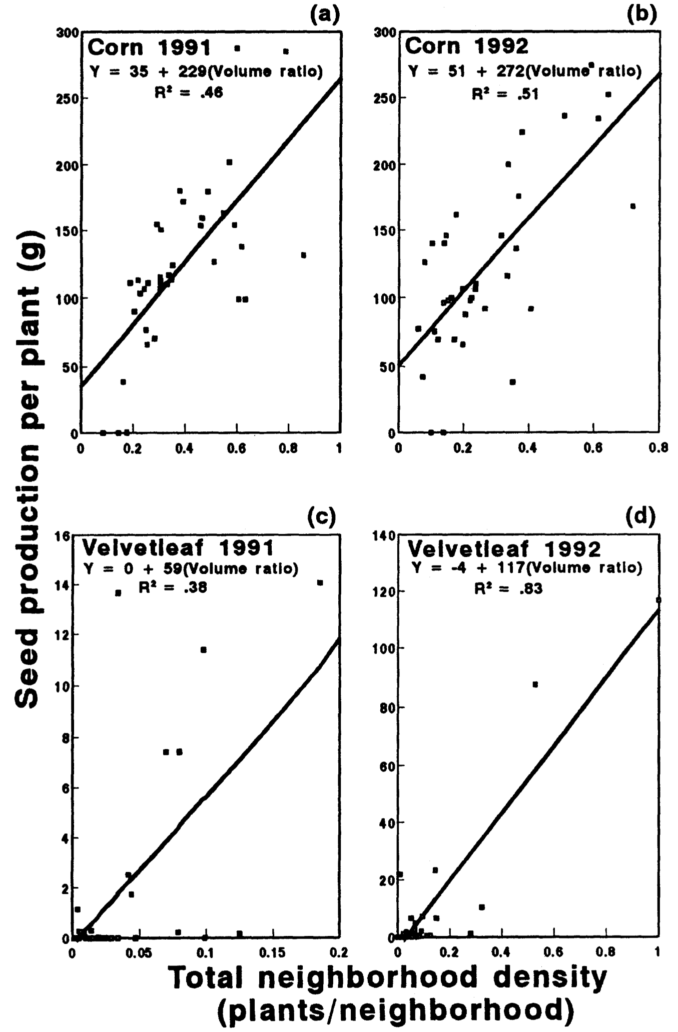


Figure 6. Relationships between target plant seed production (Y) and volume ratio for corn in 1991 (a) and 1992 (b), and velvetleaf in 1991 (c) and 1992 (d) when the two species were grown in mixture. Volume ratios were determined between June 9 and June 18 in both years. All regressions were significant (p 0.0002).

total neighbor density, on the other hand, were different from year to year in both the common cocklebur and velvetleaf experiments.

Parameter values for corn target plant yield in the velvetleaf experiment were not different from year to year for volume ratios determined between June 9 and June 23. Parameter values were stable across years when volume ratios were determined between June 18 and July 7 for corn target plant yield with common cocklebur neighbors. These findings suggest that relationships between corn plant yield and volume ratio may be consistent over time and perhaps space. The stability of volume ratio relationships, however, may depend upon crop and weed maturity, which can influence measurement accuracy.

Volume ratio and total density were inconsistent from year to year for predicting seed production of common cocklebur and

Table 5. R^2 values for linear regressions of target plant seed production on volume ratio for each target species.

	Cofficient of determination			
Date	Common cocklebur in corn	Corn in common cocklebur	Velvetleaf in corn	Corn in velvetleaf
	R^2			
1991				
5/29	0.00	.26	.21	.21
6/11	0.00	.58	.16	.47
6/26	.15	.71	.47	.41
7/08	.36	.71	.63	.49
1992				
6/01	.10	.54	.78	.30
6/17	.48	.41	.83	.44
6/30	.41	.65	.77	.48
7/14	.49	.51	.72	.54

velvetleaf. This may be due to wide genetic diversity within each weed species allowing for a broad range of responses to factors such as pathogens, predators, and physical gradients as well as interference from other plant species.

Volume ratio may be an improvement over density as an independent variable to quantify intra- and inter-specific interference on corn yield. Volume ratio captures the result of different emergence times and variation in growth rates as well as the number of neighbors. Bioeconomic models and weed management decision aids have been plagued with the common problem of a requirement to reparameterize the interference component of the models for different regions and over time. This study has provided evidence that volume ratio captures enough of the mechanism driving interference between corn and arboreous growth form weeds to be accurate as well as consistent over time and space. The predictive power and utility for use of volume ratio to quantify intra- and inter-specific impacts on weed seed production may be less useful because of inconsistency over time. The utility of these interference models in weed management decision aids may be better judged based on the economic impact of their predictions. Volume ratio might be used most effectively in the development of physio-empirical-based weed control decision models as the foundation for more accurate competitive indices for modifying growth of individual plants and competing species over time and predicting yield as a result of season-long interference. A model of this type is currently under development (15).

This research has shown that plant volume measurements can be used to predict individual plant seed production in two separate two-species mixtures. These results suggest that volume ratio can predict individual plant performance for other two-species mixtures and for multispecies mixtures, but this must be verified. Because soil fertility and moisture were high in these experiments, competition was assumed to be primarily for light. We predict, however, that volume measurements would in fact reflect the share of all resources that plants are receiving, as above-ground morphology is a function not only of available light but also available soil resources (24). The volume-based relationships in this study must be tested in situations where competition is mainly for soil resources.

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