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An Ecological Study of Naturalized Hemp (Cannabis sativa L.) in East-Central Illinois

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ABSTRACT: Naturalized populations of hemp (*Cannabis sativa* L.) on a range of sites in E-central Illinois were intensively studied. Fifty-one independent (site) and 26 dependent (plant) parameters were quantified from 101 randomly selected stands. All site variables that could be quantified were examined statistically. These included soil physical and chemical properties, competition, physical site characteristics and stand histories. Correlations between dependent parameters and linear relationships between dependent and independent parameters were examined prior to multiple correlation analysis of each dependent variable. Extreme variation was found in most dependent variables. In only a few instances could a significant portion of the variance in a dependent variable be partitioned by multiple regression. Regression did permit an evaluation of the relative importance of each specific independent variable to any given dependent variable and to the overall ecology of hemp. Those parameters were particularly important that influenced seed production in this annual plant whose seeds do not long retain viability in the soil. Important parameters that influenced seed production were interspecific competition, especially from grasses, exposure to sunlight, soil disturbance the previous year, soil aeration and available phosphorus and potassium. Viable seed production ranged from 0 to 34,433 per sq m, with a mean of 4555. Two important agents effected some degree of biological control. *Alternaria alternata* (Fr.) Keissler, a common fungal pathogen of many plants, destroyed an average of 20.5% of developing seeds, while larvae of *Grapholitha tristrigana* Clements (Lepidoptera : Tortricidae) destroyed 7.1%. Although a few stands had no damage by the insect, every stand suffered attack from the fungus which destroyed up to 45.5% of seeds in extreme cases.

INTRODUCTION

Cannabis, generally considered a monotypic genus, is one of the most widely distributed plants. Probably originating in Asia, numerous ecotypes and cultivars now are found throughout most of the temperate and tropic regions of the world. Use of hemp for food, fiber and drug, which to a great extent led to its widespread distribution, is well documented with evidence suggesting that this is one of the oldest cultivated plants. Literature on origin, nomenclature and uses of *Cannabis* was summarized most recently by Schultes (1970).

Hemp may have been introduced into United States as early as 1629 (Boyce, 1900). In North America, the plant grows from Quebec to British Columbia in Canada and S throughout the United States and Mexico. Based on botanical collections, a study by Haney and Bazzaz (1970) found naturalized hemp to be rare in United States S of 37° N. latitude. Although widely cultivated, hemp apparently has not become naturalized in Mexico, an observatioa that seems to apply to most of the tropical and subtropical areas where it is grown, although Arnold (1968) reported that hemp is escaped in Hawaii.

Commercial fiber production from hemp was established in Virginia soon after the original introduction in New England, and in Kentucky by 1775. From Kentucky seed sources, hemp plantations were established in Missouri about 1835, in Illinois in 1875, in Nebraska in 1887 and in California by 1912 (Dewey, 1913). Doubtlesslv. settlers carried seeds with them prior to these dates. Crop improvement, through selection of superior plants, was conducted" over many decades to increase hemp fiber yield and quality. Eventually, introduction, both accidental and intentional, occurred in every state, especially during the early part of World War II. Although abuse of the plant for drugs, paucity of trained labor for fiber production, and development of competitive fibers led to the discontinuation of hemp cultivation in United States by 1955, hemp had escaped and become well established in waste areas, particularly in the Midwest. De Schweinitz (1836) noted that "naturalized *Cannabis sativa* is very common in eastern United States." Brendel (1887), in an account of the vegetation, of one area in N-central Illinois, wrote that *Cannabis sativa was* "perfectly naturalized and common around Peoria in the year 1852."

Haney and Bazzaz (1970) suggested that the naturalized populations of hemp in United States still were expanding. The study reported here was undertaken to learn more of the ecology of naturalized hemp such that a better prediction could be made of the rate of spread and *habitat preferences, of hemp in the Midwest.

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REVIEW OF PERTINENT LITERATURE

No attempt will be made here to summarize exhaustively the literature pertaining to the ecology of naturalized hemp. The interested reader is referred to Joyce and Curry (1970), Eddy (1965) and Waller and Denny (197 1) for more complete summaries.

Hemp is an annual, dioecious forb; hermaphroditic flowers and polygamomonoecious plants rarely were present in our populations. The ratio of male to female plants reportedly is decreased by ultraviolet light exposure of seeds (Montemartini, 1926), increased by shorter day-length during the growing period (Schaffner, 1923, 1931), decreased by lower air temperature (Cheuvart, 1954), decreased by higher carbon monoxide concentrations (Heslop-Harrison, 1957), and increased by higher nitrogen concentrations in the soil solution (Arnoux, 1966a, 1966b). Although the genetic, basis of sexuality in hemp is not fully understood, it is thought to be under an XX = ♀ and XY = ♂ system (Miller, 1970). Hemp is wind-pollinated (Robbins et al., 1941).

Optimum germination of hemp seeds occurred in the dark (Stephan, 1928) in the laboratory and when planted at a depth of 1-2 cm in the field (Dewey, 1913). Koehler (1946) reported that seeds with high moisture content deteriorated more rapidly than seeds with low moisture when stored at 21 C, but moisture content of seeds was less a factor when seeds were stored at 0 C; fungicide treatment of seeds significantly reduced loss of viability, particularly at higher storage temperatures.. Goss (1924) found no germination of hemp seeds after 1-24 years' storage in the soil; however, Kondo *et al.* (1950) reported germination of hemp seeds stored for 19 years in the laboratory under desiccated conditions. Tuma and Eaton (pers. comm., B. J. Eaton, Eli Lilly and Co., Greenfield, Ind.) found that hemp seeds from Kansas populations declined in viability from 70 to 4.4% in 15 months of soil burial.

Hemp seeds are important food for many birds and probably many small mammals. Doves feed extensively on hemp seeds (Hanson and Kossack, 1963; McClure, 1943), as do bobwhite quail (Robel, 1969).

Fiber production in hemp crops was greatest on well-drained, friable soils that were high in nitrogen and organic matter (Dewey, 1913). Apparently based on fiber yields, plants were reported to be susceptible to moisture stress (Hackleman and Domingo,, 1943). Royle (1855) suggested that young hemp plants were easily damaged by frost and that "*Cannabis* will smother all weeds." Hackleman and Domingo (1943) reported that hemp controlled competing weeds, especially annuals. Hemp has few insect pests or diseases, and plants are seldom bothered by fungus infection unless they are growing on unfavorable sites, are germinated exceptionally late, or are damaged (Dewey, 1913). Robinson (1943) also reported that seedlings are remarkably free of disease. Broom rape (***Orobanche ramosa*** L.) was reported by Dewey (1913) to occasionally attack hemp in United States. Smith and Haney (1973) discussed the relationship of *Grapholitha tristrigana* Clemens (Lepidoptera: Tortricidae) to hemp. The larvae of this insect feed in the pith and seed clusters of hemp, effecting small but significant biological control.

METHODS

Beginning in May 1969, an extensive survey for naturalized populations of hemp was made in Champaign Co. in E-central Illinois. The study area, approximately 2333 sq km (900 sq miles), is on gently rolling to level topography, 200-220 m above mean sea level. Approximately 25 ha of hemp was found in nearly 900 stands. A stand was defined as a relatively homogeneous population with a density not less than 20 plants per sq m. Habitats ranged from streamside to upland glacial moranes. Most stands occurred in waste areas such as fence rows, abandoned fields and banks along streams and ditches. Soils varied from coarse to heavy. One hundred fifty-three stands, representing a range of sites on which hemp was found, were selected for intensive study by a stratified random sample.

In June and July each stand selected for intensive study was visited. Based on the site and plant variation, the hemp population at each site was delimited and soil samples were taken at O-10, 10-20, 25-40 and 46-61 cm depths within the defined area. Slope steepness and aspect were determined and site history obtained from landowners. Visual classification of site disturbance during the previous year was made: sites were scaled from l-5 with increasing degree of soil disturbance. Rating 1 was set for sites with no disturbance of any kind; 2 represented minor disturbance such as from an early summer mowing; 3 designated moderate disturbance such as burning; 4 involved some soil disruption as from erosion or light disking; and 5 indicated major disturbance such as plowing. Populations that were disturbed during the 1969 growing season, such as'by mowing, spraying or illicit collection for marihuana, were excluded from subsequent study. Fifty-two of the 153 stands selected were eliminated because of -disturbance, most due to apparent illicit collecting.

In late August and early September, at the time of maximum seed maturity, each hemp population was sampled by use of randomly placed, (0.25 sq m) circular frames. Alien species in each plot were clipped at the soil surface; grasses and forbs were bagged separately. Hemp plants within quadrats were carefully dug to obtain as much of the root systems as possible, separated by sex, and measured for total height from root collar to terminal leaves (without extending branches). Diameter of the stem at 5 cm above the root collar was measured. Plants were placed in labeled paper bags with care taken to avoid shattering of leaves and seeds. Dead hemp plants were dug and bagged separately. Exposure of the population to direct light was estimated by measuring the degrees from the eastern horizon to the western horizon from the average height of taller hemp plants, correcting for overhanging structures.

Bagged plants were placed in a forced-air drying room at 30 C (86 F) from l-3 months while processing continued. Leaves and flowers (when present) were removed from plants within each sample and roots were severed from stems. Roots were washed and redried to constant weight. Foliage, stem and roots of each sample were weighed. Female hemp plants were processed in the same manner as males except all seeds were separated from the foliage. Samples of female foliage were analyzed for drug; constituents. The drug analyses are reported elsewhere (Haney and Kutscheid, 1973). Total seed weight was recorded and seeds were preserved for further examination. Grasses and forbs collected with each sample were weighed and discarded.

By using 5 g subsamples, hemp seeds from the samples were visually separated into chaff, mature, green (immature), necrotic and insect-destroyed categories. Separation of green from mature seeds was based on germination experiments that showed the development of a mottled seed coat corresponded closely to development of a viable embryo. Each subsample of seeds was counted and weighed, and data were proportionately expanded to represent the total sample. Chaff weight was added to the sample foliage weight. Germination experiments were run on seeds collected outside sample quadrats in each stand. Seeds were divided into two lots, one of which was stored at room temperature and the other at 3 C. Five sets of 20 seeds were removed from each lot at regular intervals over a 32-week period and germinated in the dark on moist filter paper in covered petri dishes.

Soil samples were dried at 49 C (120 F) to constant weight, weighed, ground with a mortar and pestle, and sieved through a '2 mm mesh. Material remaining on the sieve was weighed and discarded; soil passing the mesh was used for all analyses. Textural analyses were made by the Bouyoucos (1951) method. Exchangeable bases and hydrogen were determined for each sample by the method developed by Brown (1943). Organic matter was estimated by the Walkley-Black wet-oxidation method as modified by Richards (1954). Sod reaction was measured by slowly wetting 20-30 g samples with distilled water until a visible film appeared on the stirred mixture, letting samples set for 1 hr, then measuring *p*H directly with a glass electrode *p*H meter. Total soil nitrogen was determined by a modified Kjeldahl method. Phosphorus was estimated as molybdovando-phosphoric acid using the procedure outlined by Greweling and Peech (1965). Calcium was measured by atomic absorption spectroscopy of solutions prepared by leaching 10 g of soil with 230 ml neutral normal ammonium acetate over an 8-hr period and adjusting the volume to '250 ml. All other cations were determined by atomic absorption spectroscopy of solutions prepared by the quick shake method (Greweling and Peech, 1965).

Data were examined statistically and graphically. All data were transformed to approximate standard normal distributions. The "z" transformation was used (Steel and Torrie, 1960; see p. 188-190) . The resulting distribution for most variables was intermediate between normal and platykurtic. All data were tested after transformation. A correlation matrix was developed to establish the linear relationship between every combination of variables, including the correlations within the set of independent (site) variables and within the set of dependent (plant) variables. Selected independent variables were plotted against each dependent variable, using raw data, to determine the linearity of the correlation. Graphs were plotted of both highly and lowly correlated variables, but especially, variables that we intuitively believed should be related. From this we determined that few variables appeared to be linearly correlated, but the variance in all cases was so great that further transformation did not improve correlations.

To reduce the probability of erroneous conclusions in multiple regression analyses stemming from substantial overlap of independent variables, data first were analyzed by principal-axis factor analysis (Harmon, 1960). Eigenvectors were computed and scaled to generate the principal-axis factors which were examined for closely interrelated sets of independent variables. For example, we were reasonably certain beforehand that soil nitrogen would be related closely to soil organic matter and that nitrogen in the 0-10 cm depth Gould be related to nitrogen at the 10-20 cm depth. This statistical procedure established not only these obvious relationships, but others that were more subtle. Table 1 shows the functional grouping of 36 independent variables. In each of the functional groups, the variables were considered carefully and one to three were selected to represent the group for further analyses. Selection of specific variables from related groups was based on the extent and reliability of data, the correlation between variables. as well as the ease of observing the variable and evidence of overlap between parameters. In all, 18 variables, including those indicated in Table 1, were selected to represent the 51 independent variables for which we had obtained data. Using only these 18 variables and selected interactions between them (Table 2), a stepwise multiple regression was run for each dependent. variable and a multiple correlation determined. The rationale for the statistical methods used is presented in the Discussion.

TABLE 1. Relationships between independent variables as shown by a principal-axis factor analysis. Consistently related factors in each group are identified by common superscripts. Variables chosen to represent each group are italicized

Vector 1	Vector 2
% sand 0-10 cm[1]	***%** organic matter 0-10 cm*[1]
% silt 0-10 cm[1]	***% nitrogen 0-10 cm***[1]
% fine gravel 0-10 cm	***pH 10-20 cm***
% sand 10-20 cm	% organic matter 10-20 cm
% silt 10-20 cm	% nitrogen 10-20 cm
% fine gravel 10-20 cm	pH 25-35 cm
% sand 25-35 cm	% organic matter 25-35 cm
% sand 46-61 cm	% nitrogen 25-35 cm
% silt 46-61 cm	pH 46-61 cm
% fine gravel 46-61 cm	% organic matter 46-61 cm
	% nitrogen 46-61 cm
Vector 3	Vector 4
Calcium 0-10 cm	Phosphorus 0-10 cm[1]
***Phosphorus** 10-20 cm*[1]	***Potassium 0-10 cm***
Potassium 10-20 cm	***Magnesium 0-10 cm***
Phosphorus 25-35 cm[1,2]	Potassium 10-20 cm[1]
Potassium 25-35 cm[2]	Magnesium 10-20 cm
Calcium 25-35 cm	
Phosphorus 46-61 cm[2]	
Calcium 46-61 cm	Vector 5
	Cation exchange capacity 0-10 cm[1]
	Phosphorus 0-10 cm[1,2]
	Calcium 0-10 cm
	Magnesium 0-10 cm[2]
	Calcium 10-20 cm

RESULTS

The mean, standard error and range of values for the dependent variables examined in this study are listed in Table 3.

TABLE 2.-List of the 18 independent variables and interactions used in the stepwise multiple correlation analysis

Independent factors tested	Interactions tested
1. % sand 0-10 cm depth	
2. Cation exchange capacity of 0-10 cm soil (C.E.C.)	2 x 3
3. % base saturation of 0-10 cm soil (B.S.)	1 x 4
4. % total nitrogen in 0-10 cm soil (N)	5 x 9
5. Potassium (ppm) in 0-10 cm soil (K)	5 x 6
6. Calcium (ppm) in 0-10 cm soil (Ca)	6 x 9
7. Magnesium (ppm) in 0-10 cm soil (Mg)	7 x 9
8. *p*H of 10-20 cm soil	11 x 12
9. Phosphorus (ppm) in 10-20 cm soil (P)	11 x 13
10. % clay in 46-61 cm soil	1 x 2
11. Potassium (ppm) in 46-61 cm soil	14 x 14
12. Calcium (ppm) in 46-61 cm soil	15 x 15
13. Magnesium (ppm) in 46-61 cm soil	17 x 18
14. % slope on which stand was growing	1 x 3
15. Exposure of plants to direct solar radiation	1 x 5
16. Soil disturbance	3 x 5
17. Biomass of Graminaceous plants in stand	3 x 6
18. Biomass of forbs (other than *Cannabis*) in stand	3 x 8

TABLE 3.-Mean, standard deviation and range of observations of dependent variables in 101 stands of naturalized hemp

Parameter	Mean	Standard deviation	Range
Density of male plants (No./m²)	36.6	32.5	0 - 184
Density of female plants (No./m²)	76.4	62.9	4 - 376
% male plants	32.6	16.7	0 - 83.3
% dead plants/total live plants	31.0	22.0	0 - 87.5
Average height of male plants (cm)	99.6	38.1	16.3 - 236.2
Average diameter of male stems (cm)	1.07	0.56	0.28 - 4.09
Male foliage biomass (g/m²)	39.66	62.08	0.02 - 456.92
Male stem biomass (g/m²)	166.88	217.84	0.08 - 1092.52
Male shoot biomass (g/m²)	206.61	266.12	1.72 - 1293.48
Male root biomass (g/m²)	31.11	43.72	0.12 - 226.84
Male root/shoot ratio	.150	0.079	0.003 - 0.507
Average height of female plants (cm)	83.3	33.1	16.5 - 165.6
Average diameter of female stems (cm)	1.10	0.68	0.28 - 5.41
Female foliage biomass (g/m²)	211.76	280.49	5.12 - 1721.92
Female stem biomass (g/m²)	379.64	545.70	4.08 - 3558.00
Female shoot biomass (g/m²)	588.92	818.46	10.80 - 5279.92
Female root biomass (g/m²)	72.30	107.52	0.92 - 724.40
Female root/shoot ratio	0.128	0.099	0.063 - 1.039
Total seed production (No./m²)	9351.2	13862.0	44 - 71664
Good seed produced (No./m²)	4554.9	73 18.5	0 - 34433
Good seed weight (g/1000 seeds)	7.302	1.644	4.041 - 12.598
% good seeds (of total)	37.1	22.1	92.7
% of seeds destroyed by borer	7.1	5.2	0 - 25.2
% of seeds destroyed by fungus	20.5	11.8	2.8 - 45.5
% of seeds immature at harvest	25.1	12.8	2.7 - 59.9
Good seeds per female plant	94.8	257.4	0 - 2474.2

Male plants began flowering about 2 weeks before females in most stands; a few males reached anthesis by the 1st week in July, whereas female plants seldom began flowering before the middle of July. Most males became senescent before the middle of September, as indicated by lack of continued growth and flowering, yellowing and abscising of leaves, and drying of stems; females rarely were senescent before frost. Both sexes shed lower, shaded leaves as plants grew, but this tendency was much more pronounced in male plants. The first viable seeds were present in most stands by the 2nd week in August; in all cases, females continued to set seeds until frost.

Some seeds were capable of germination within 3 weeks after full maturity in the field. Full maturity is defined here as the development of a mottled seed coat. Seeds stored at room temperature reached maximum germinability in 3 months, whereas seeds stored at 3 C reached maximum germinability only after 5 months (Fig. 1). Seeds nearing maturity in the field were capable of germination only after much longer storage time.

Hemp plants were occasionally blighted but rarely killed by a fungus identified as *Alternaria tenuis*. This fungus, however, attacked developing seeds (discussed below) and was present in every stand. Hartowicz et *al.* (unpubl. abstract) reported that *Alternaria tenuis* was also a common disease on hemp in Kansas. Larvae of *Grapholitha tristrigana* Clemens (Lepidoptera : Torticidae) also were important in seed destruction. Observations on this insect are reported elsewhere (Smith and Haney, 1973).

Density of male plants averaged 37 per sq m with a range from 0 to 184. Male density was significantly correlated with female density but was negatively related to height and stem diameter of male plants (Table 4) . The higher the density, the smaller the plants,

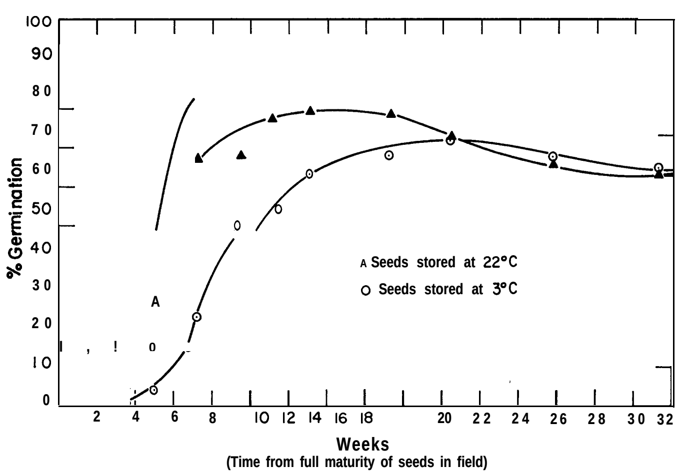

Fig. 1.—Germination percentages for mature hemp seed stored at 3 C and 22 C over a 32-week period. Seeds were stored dry in sealed cartons

although population biomass tended to peak at intermediate densities. Therefore, conditions leading to large plants tended to be negatively correlated with density.

Female plants averaged 76 per sq m and ranged from four to 376. Density of male plants exceeded density of female plants in only eight of the 101 stands examined. Percent of plants, that were male averaged 32.6, with a range of 0 to 83%. Stands with larger male plants tended to have a higher percentage of males (Table 4). Multiple correlations for male and female densities are given in Table 5. Over

	Male density	Female density	Percent male	Mortality	Male height	Male diameter	Male foliage biomass	Male stem biomass	Male shoot biomass	Male root biomass	Male root/shoot ratio	Female height	Female diameter	Female foliage biomass	Female stem biomass	Female shoot biomass	Female root biomass	Female root/shoot ratio	Total seed production	Good seed production	Good seed weight	Percent good seeds	Percent wormy seeds	Percent necrotic seeds	Percent green seeds
Female density	*.654*																								
Percent male	*.408*	*-.236*																							
Mortality	-.164	.165	*-.445*																						
Male height	*-.228*	*-.332*	.178	-.108																					
Male diameter	*-.275*	*-.342*	.184	-.135	*.880*																				
Male foliage biomass	.191	-.060	*.334*	-.166	*.483*	*.490*																			
Male stem biomass	.212	.029	*.246*	-.077	*.653*	*.665*	*.722*																		
Male shoot biomass	.218	.010	*.274*	-.102	*.647*	*.659*	*.825*	*.987*																	
Male root biomass	.125	-.019	*.289*	-.083	*.610*	*.686*	*.593*	*.872*	*.852*																
Male root/shoot ratio	-.142	-.061	.001	-.068	.114	.178	-.081	-.003	-.020	*.311*															
Female height	*-.288*	*-.448*	.142	-.158	*.773*	*.725*	*.447*	*.459*	*.480*	*.382*	.018														
Female diameter	*-.293*	*-.420*	.123	*-.240*	*.664*	*.793*	*.375*	*.416*	*.428*	*.402*	.060	*.885*													
Female foliage biomass	.099	.021	.061	-.147	*.531*	*.634*	*.534*	*.700*	*.697*	*.594*	-.030	*.608*	*.717*												
Female stem biomass	.043	.014	-.002	-.088	*.542*	*.647*	*.486*	*.702*	*.688*	*.614*	.008	*.599*	*.701*	*.966*											
Female shoot biomass	.065	.017	.022	-.106	*.539*	*.646*	*.508*	*.709*	*.699*	*.614*	-.006	*.605*	*.711*	*.985*	*.996*										
Female root biomass	-.030	-.013	-.065	-.106	*.530*	*.646*	*.393*	*.610*	*.591*	*.551*	.116	*.599*	*.730*	*.922*	*.945*	*.945*									
Female root/shoot ratio	-.218	-.099	-.158	-.116	.038	.050	-.105	-.090	-.098	-.029	*.458*	.075	.089	-.032	-.028	-.029	*.229*								
Total seed production	.133	.107	-.022	-.048	*.326*	*.332*	*.252*	*.563*	*.520*	*.504*	.082	*.332*	*.331*	*.729*	*.694*	*.709*	*.675*	.051							
Good seed production	.018	.012	-.098	.023	*.363*	*.377*	.186	*.529*	*.476*	*.483*	.102	*.316*	*.317*	*.648*	*.637*	*.641*	*.627*	.060	*.931*						
Good seed weight	-.079	-.021	-.067	.143	.192	.124	.007	.059	.050	.128	.064	.137	.049	.046	.046	.046	.018	-.156	.077	.061					
Percent good seeds	*-.250*	-.095	*-.191*	-.015	*.286*	*.320*	.001	*.261*	.214	*.280*	.176	.197	.192	.203	.215	.209	*.227*	.152	*.356*	*.540*	-.072				
Percent wormy seeds	.163	-.097	*.274*	-.157	.070	-.019	.145	-.094	-.043	-.070	.052	.065	.004	-.022	-.112	-.079	-.028	.194	-.040	-.134	.085	*-.420*			
Percent necrotic seeds	.043	-.180	*.231*	.007	*-.262*	*-.292*	.160	-.162	-.094	*-.222*	*-.322*	-.030	-.056	-.096	-.135	-.118	*-.221*	*-.250*	*-.288*	*-.448*	.072	*-.738*	.099		
Percent green seeds	.165	-.050	.167	-.074	.089	.100	.138	.037	.064	.043	-.051	.175	.207	*.248*	*.241*	*.247*	*.260*	.026	.023	-.217	.204	*-.796*	.192	*.253*	
No. good seeds/female	-.142	-.166	.059	.041	*.275*	*.810*	.015	.124	.105	.124	.066	*.404*	*.470*	*.415*	*.333*	*.361*	*.381*	.060	*.503*	*.611*	.093	*.327*	.045	*-.268*	-.181

TABLE 4.-Linear correlation between dependent parameters from 10 1 stands of naturalized hemp in E-central Illinois. Significant correlations ($p \leqslant 0.05$) are suggested by darkened, italicized coefficients

TABLE 5.-Results of stepwise multiple regression of factors relating to density and mortality of hemp. Independent variables are listed in order of importance to each multiple correlation as determined ***by*** the contributor of the variable to the multiple correlation. Cutoff for entry was determined by F level '($P \leqslant 0.05$)

A. Number of male plants per sq m
Multiple correlation = 0.9542
Dependent variable intercept = 20.94
Standard error of estimate = 9.88

Independent variables

Per cent slope
K (O-10 cm) x P (10-20 cm)
IS (46-61 cm) x Mg (46-61 cm)

B. Number of female plants per sq m
Multiple correlation = 0.4286
Dependent variable intercept = 75.39
Standard error of estimate = 57.37

Independent variables

K ***(46-61*** cm) x Mg (46-61 cm)
Grass biomass x forb biomass

C. Males as percent of live plants
Multiple correlation = 0.4341
Dependent variable intercept = ***23.30***
Standard error of estimate = 15.23

Independent variables

K (0-10 cm) x Ca (O-10 cm)
Grass biomass x forb biomass

D. Ratio of dead to live plants at harvest '(expressed as a percentage)
Multiple correlation = 0.5956
Dependent variable intercept = 25.83
Standard error of estimate = ***17.74***

Independent variables

K (O-10 cm) x P (10-20 cm)

90% of the variance in male density was accounted for by three independent variables. In contrast, less than 20% of variance in female density could be statistically absolved.

Mortality was greatest in June and early July. Over 90% of dead hemp plants examined were sexually immature. Mortality was negatively correlated ($P \leqslant 0.05$) to percent of living plants that were males, suggesting that females tended to survive better than males. This observation is supported by the prevalence of females in most stands. Also, after flower initiation, when plants could be sexed, we observed that males tended to wilt sooner and generally showed signs of stress before females. in the same population. Furthermore, dead male plants were common but only rarely were dead female 'plants observed. Analysis of multiple correlations between independent variables and mortality data are presented in Table 5.

Tables 6 and 7 present the results of multiple correlation analyses between significant independent variables and dependent growth variables for male and female plants, respectively. It was apparent from the field as well as from statistical analyses that soil disturbance the previous year aided growth of hemp. Plant size was extremely variable between stands but quite homogeneous within stands. Largest plants consistently grew on fertile, well-drained sites with ample moisture. Smallest plants were found in dense shade or on infertile, poorly drained sites, such as eroded stream banks or spoil from gravel quarries. Plants from stands growing in close competition with grasses also were stunted.

The average height, average diameter, foliage, stem and root biomasses of hemp from the stands were significantly correlated both within and between sexes (Table 4). Height of male plants averaged 99.6 cm (39.2 inches), whereas. female plants averaged 83.3 cm (32.8 inches) (Table 3). Height of male plants was extremely variable between stands, much more so than for females. Much of the difference in height between sexes arises during flowering. At sexual maturity, a terminal raceme rapidly elongates on male plants. Female flowers, on the other hand, develop in the axils of leaves, and rate of growth in height decreases at onset of sexual maturity. Females tend to develop more lateral branches, leading to greater foliage and stem biomass '(Table 3).

Root development of hemp plants varied greatly with soil texture. In coarse-textured soils lateral root development is minimal. and the greatly elongated primarv root may extend to over 2 m depth. In heavv or fine-textured soils roots are verv shallow. often within 10-20 cm of the surface. The primary root may be scarcely discernible. In heavy soils of low fertility, plants usually are quite small, and roots are very poorly developed with neither vertical nor lateral development. In medium-textured soils both vertical and lateral development of roots occur. Under these conditions lateral roots tend to occur near the surface and at a depth of about 1 m with few lateral roots between. Both the shallow and deep laterals may extend several meters from a vigorous plant. Lateral roots from plants near cultivated fields often extended into the field near the surface of the soil and, in corn or soybeans, concentrated along rows. Under these conditions roots were poorly developed into the fence row or uncultivated edge, except at the deeper levels. Roots of male plants generally were developed more poorly than female roots but followed the patterns de-

TABLE 6.-Results of stepwise multiple regression of factors relating to growth of male plants. Independent variables are listed in order of importance to multiple correlation as determined by the contribution of the variable to the multiple correlation. Cutoff for entry was determined by F level ($P \leqslant 0.05$)

A. Mean height of plants in stand
Multiple correlation = 0.6 102
Dependent variable intercept = 42.85
Standard error of estimate = 11.96

Independent variables

K (O-10 cm) x P (10-20 cm)

B. Mean diameter of plants in stand
Multiple correlation = 0.5 705
Dependent variable intercept = 0.471
Standard error of estimate = 0.182

Independent variables

K (O-10 cm) x P (10-20 cm)

C. Biomass of foliage (leaves and flowers) of plants/m^2
Multiple correlation = 0.7292
Dependent variable intercept = -57.60
Standard error of estimate = 43.13

Independent variables

Sand (O-10 cm) x % N (O-10 cm)
Soil disturbance class
K (O-10 cm) x P (10-20 cm)

D. Biomass of stems of plants/m^2
Multiple correlation = 0.6758
Dependent variable intercept = -95.73
Standard error of estimate = 162.20

Independent variables

Soil disturbance class
K (O-10 cm) x P (10-20 cm)

E. Biomass of shoot (stems plus foliage) of plants/m^2
Multiple correlation = 0.6986
Dependent variable intercept = -130.05
Standard error of estimate = 192.36

Independent variables

Soil disturbance class
K (O-10 cm) x P (10-20 cm)

F. Biomass of roots of plants/m^2
Multiple correlation = 0.6227
Dependent variable intercept = -20.62
Standard error of estimate = 34.56

Independent variables

Soil disturbance class
K (O-10 cm) x P (10-20 cm)

G Root/shoot ratio of plants
Multiple correlation = 0.79 17
Dependent variable intercept = 0.0589
Standard error of estimate = 0.04908

Independent variables

Biomass of competing forbs
K (46-61 cm) x Ca (46-61 cm)
Biomass of forbs x biomass of grass
Soil disturbance class

scribed above. Root/shoot ratios tended to be less for female plants, primarily because of disproportionately greater foliage.

Seed production averaged 9351 seeds per sq m but ranged from 44 to 71,664 per sq m. The number of viable seeds produced per square meter, however, was substantially less, averaging 4555 and ranging from 0 to 34,433. The weight of viable seeds ranged from 4.041 to 12.598 g per 1000 seeds with a mean of 7.302. Multiple correlations of independent variables to seed data are given in Table 8.

TABLE 7.—Results of stepwise multiple regression of factors relating to growth of female plants. Independent variables are listed in order of importance to multiple correlation as determined by the contribution of the variable to the multiple correlation. Cutoff for entry was determined by F level ($P \leqslant 0.05$)

A. Mean height of plants in stand
Multiple correlation = 0.5333
Dependent variable intercept = 35.72
Standard error of estimate = 11.42

Independent variables

K (0-10 cm) x P (10-20 cm)

B. Mean diameter of plants in stand
Multiple correlation = 0.4144
Dependent variable intercept = 0.479
Standard error of estimate = 0.245

Independent variables

K (0-10 cm) x P (10-20 cm)

C. Biomass of foliage (leaves and flowers) of plants/m^2
Multiple correlation = 0.7164
Dependent variable intercept = -166.61
Standard error of estimate = 197.69

Independent variables

Soil disturbance class
K (0-10 cm) x P (10-20 cm)

D. Biomass of stems of plants/m^2
Multiple correlation = 0.4423
Dependent variable intercept = 475.75
Standard error of estimate = 491.89

Independent variables

K (0-10 cm) x P (10-20 cm)

E. Biomass of shoot (stems plus foliage) of plants/m^2
Multiple correlation = 0.7874
Dependent variable intercept = -556.89
Standard error of estimate = 509.61

Independent variables

Soil disturbance class
K (0-10 cm) x P (10-20 cm)

F. Biomass of roots of plants/m^2
Multiple correlation = 0.4147
Dependent variable intercept = 90.05
Standard error of estimate = 98.33

Independent variables

K (0-10 cm) x P (10-20 cm)

G. Root/shoot ratio of plants
Multiple correlation = 0.6294
Dependent variable intercept = 0.218
Standard error of estimate = 0.078

Independent variables

K (0-10 cm) x Ca (0-10 cm)
% base saturation (0-10 cm) x K (0-10 cm)

TABLE 8.-Results of stepwise multiple regression of factors relating to seed production of hemp. Independent variables are listed in order of importance to multiple correlation as determined by the contribution of the variable to the multiple correlation. Cutoff for entry was determined by F level ($P \leqslant 0.05$)

A. Total number of seeds produced per ¼ m^2
Multiple correlation = 0.5939
Dependent variable intercept = -3365.36
Standard error of estimate = 2830.98

Independent variables

Exposure x exposure
Soil disturbance class
K (O-10 cm) x P (10-20 cm)

B. Total number of good seeds produced per sq m
Multiple correlation = 0.866 1
Dependent variable intercept = -64936.7
Standard error of estimate = 3753.48

Independent variables

Exposure x exposure
% slope x % slope
Soil disturbance class
K (O-10 cm) x P (10-20 cm)
% sand '(O-10 cm) x K (O-10 cm)

c. Weight in g per 1000 good seeds
Multiple correlation = 0.4166
Dependent variable intercept = 7.574
Standard error of estimate = 1.502

Independent variables

K (0-10 cm) x P (10-20 cm)

D. Percent of total that were good seeds
Multiple correlation = 0.6827
Dependent variable intercept = 38.45
Standard error of estimate = 16.30

Independent variables

K (O-10 cm) x P (10-20 cm)
Biomass of competing grass

E. Percent of total seeds destroyed by borers
Multiple correlation = 0.3792
Dependent variable intercept = 7.93
Standard error of estimate = 4.87

Independent variables

K (O-10 cm) x P (10-20 cm)

F. Percent of total seeds destroyed by fungus
Multiple correlation = 0.6930
Dependent variable intercept = 19.48
Standard error of estimate = 8.61

Independent variables

K (O-10 cm) x P (10-20 cm)
Biomass of competing grass

G. Percent of seeds immature at harvest
Multiple correlation = 0.6 123
Dependent variable intercept = 21.44
Standard error of estimate = 10.24

Independent variables

K '(O-10 cm) x P (10-20 cm)
Mg (O-10 cm) x P (10-20 cm)

H. Number of good seeds produced per female plant
Multiple correlation = 0.7 18 1
Dependent variable intercept = -217.56
Standard error of estimate = 181.87

Independent variables

% sand (O-10 cm) x % base saturation (O-1 0 cm)
K (0-10 cm) x P (10-20 cm)
Biomass of competing grass

Along with the phosphorus-potassium interaction, which was significantly correlated with every seed parameter examined, exposure greatly influenced the number of seeds produced. Exposure was not significantly correlated to other dependent variables examined. Hemp growing in the field under full or partial shade often was as large as adjacent plants in full sunlight, but shaded plants produced fewer seeds. Competition was a consistent factor in seed production as well as growth of hemp. Grasses, in general, reduced plant size and seed production more than comparable amounts of forbs. The importance of competition was manifested through correlations with soil disturbance as well as with the biomass of competing grasses and forbs. More recently disturbed areas tended to have more forbs and less grass. Figure 2 presents a dichotomization of viable seed production data as influenced by exposure, slope and soil disturbance. Lack of adequate sample numbers prevented further extension of those data which are based on the multiple correlation analyses

Germination experiments indicated no differences between the largest and smallest seeds in either germinability or vigor of resulting seedlings as measured by the rate of radical extension. Viable seed production per female plant averaged 95 and ranged from 0 to 2474 seeds in exceptional stands (Table 3) . Larger females, in general, produced more seeds than small females, but production per unit area tended to be highest in stands with higher densities of intermediate-size plants.

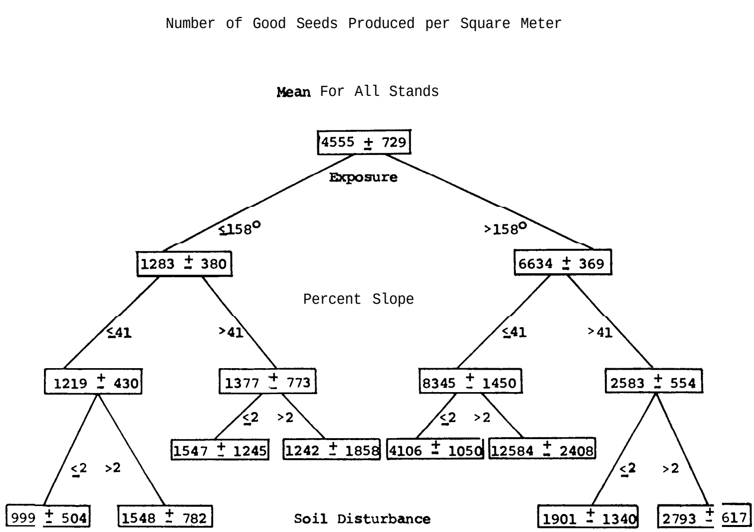

Fig. 2.—Influence of three environmental parameters on viable seed production in naturalized hemp stands. Data are mean and standard deviation of seeds per square meter from 101 randomly sampled stands. Equal numbers of stands were compared for each extreme of the factor examined. Factors were Jdentified by significant multiple correlations

The number of viable seeds produced was influenced not only by environmental factors but also by insect predation and fungus blight (Table 8). Viable seeds averaged slightly more than 37% and ranged from 1 to 93 %. An average of 7'. 1% of seeds were destroyed by insect larvae (range: 0 to 16.7%) and 20.5% were destroyed by fungus (range: 2.8 to 45.5%). Rate of seed maturity was a factor in the viable seed production estimates because onlv single collections were made at peak maturity in stands. An average of 25.1% of seeds were immature at collection with a range from 2.7 to 59.9%. There is no evidence to suggest that inadequate pollination was a factor in seed production. For example, male density and size of male plants were not significantly correlated with total seed production. Even in stands with no living males, seed set was clearly within the range of variation for stands with high'male populations.

DISCUSSION

At the outset of this study, we wished to make as few assumptions as possible concerning which factors. might be most important in the biology of naturalized hemp. Therefore, we collected data on all factors that we could justify ecologically within the limits of our time and resources. Limitations of the statistical procedures available to deal with this type of biological question necessitated our making later assumptions about factors. In many cases these assumptions are ecologically sound; in others they were simply necessary to validate the statistical procedures.

A transformation was used to normalize the platvkurtic distribution of the data. Because we hoped to order the 'most important factors that affected the dependent variables) we observed, it was necessary to set some kind of confidence limits in our multivariate analyses. These analyses depend upon reasonable proximities to normal distributions. Because we were sampling discontinuous populations as opposed to one large population, we assumed our data would not be normally distributed unless a very large number of samples were taken. With 101 samples, we still found the need to transform data.

The most obvious way of identifying the important ecological factors is to run first-order correlations between each of the independent and dependent variables. We did this, recognizing, however, that a plant does not respond to isolated factors but to a system of factors. The actual response to any single factor may be greatly modified by levels of other factors present. Thus, conclusions from first-order correlations may be very misleading. Analysis of variance provides a statistical wav of examining up to four or five factors together. but becomes totallv impractical for large numbers of factors. We, therefore, choose 'multiple regression "analysis as the only reasonable alternative.

Multiple regression ideally requires that only uncorrelated factors be entered. The analysis is not invalidated by the use of closely related factors, but interpretation becomes difficult. We chose to do a preliminary analysis to determine how our 51 independent variables were related. Five distinct groupings of factors were found (Table 1). Although it was recognized that the factors in each group were-closely correlated, this did not mean that they were physically or biologically related in their effects on hemp. Consequently, we elected to select one to several factors from each group, justifying each selection on the following criteria. If there was an obvious physical or chemical relationship between the factors in a group, only one was selected according to criteria outlined in Methods. In Vector 1 (Table 1), for example, there was a clear physical relationship of the soil textural components, and only one factor was selected. If factors in a vector were not obviously related in a close way, based on linear correlations between the factors or on the suspected effects of the factors on hemps, two or more were chosen by same selection criteria suggested above. In Vector 2, for example, subsoil *p*H was considered sufficiently isolated from surface soil nitrogen, in terms of effects, so that both were used. Likewise, subsoil calcium in Vector 3 could vary substantially from a close relationship to surface calcium and both could be relatively unrelated to subsoil phosphorus; yet all three could account for part of the behavior of hemp.

Use of unequal numbers of factors to represent vectors precluded our drawing conclusions on the ecological importance of vectors. The more factors entered from a vector, the more likely the vector will be represented in the final multiple regression, especially if the factors had different effects or were those least highly correlated. Because we were more interested in the factors than the vectors, this did not present a problem. Use of two or more related factors, whether the relationship is spurious or not, may jeopardize identification of important factors. If two related factors are offered, selection of one greatly reduces the chance that the second will be identified. Consequently, one must use extreme caution and a great deal of judgment in drawing conclusions from multiple regression analyses involving related factors.

For the reasons outlined above, we have avoided extensive interpretation of many of the relationships suggested by the multiple regression analyses. These analyses were helpful, however, in identifying factors of lesser importance. Relatively few independent parameters were significantly related to the dependent parameters we examined. This does not mean that unrelated factors are ecologically unimportant to hemp but does suggest that they have a minor role in the ecology of hemp relative to other factors, at least in our populations and area of study.

Male plants tended to react to environmental stimuli in strikingly different ways than females. Although differential response between sexes is well known in animals, it has not been widely observed in plants. Some of the observed differences between sexes were clearly results of selective pressure; for example, differential survival under stressed conditions. Because hemp is wind-pollinated, and because each male plant produces such a prodigious quantity of pollen, a few males can adequately fertilize a great many female plants. Genetic control of sex in hemp apparently is determined in the zygote by the XX-XY chromosome system whereby each sex has an equal chance of occurring in each fertilized egg (Miller, 1970). Two mechanisms can give rise to unequal representation of the sexes at maturity, sex reversal and differential survival. Sex reversal in hemp has been extensively investigated. In all known instances, the degree of sex reversal in hemp is relatively small or is not likely to act in a field situation. Thus, our data, supported by field observations, led us to conclude that differential survival is far more important than sex reversal in naturalized populations of hemp. As resources became limiting to a population, male plants died much sooner than females. In most instances. this 'natural thinning process appeared to be accomplished with the sacrifice of little- seed production. Poor root development in male plants relative to female plants was the only discernible difference between sexes that might account for differential mortality.

We can see no evolutionary strategy for earlier flowering of males. Conceivably, in other areas, environmental conditions might be such that flowering of the two sexes would fall more in line. Both sexes are clearly short-day plants, but flower initiation varies up to 2 weeks for plants of the same sex in the same stand. Frequently, individuals will initiate flowering 2 or 3 weeks in advance of the rest of a population. Precocious individuals. however, are invariablv males.

Seed germination studies indicate that no stratification is required but an after-ripening period is needed. Storage near freezing resulted in a longer ripening 'period. Occasional seeds should germinate in autumn in the field. but we have never observed this. Low temperatures apparently prevent most germination until spring. Hemp seeds, in general, began germination in early April at lower temperatures than most other weedy annuals of our area. Contrary to the observation by Royle (1855), we never observed frost damage to hemp seedlings although the average date of the last killing frost in the studv area is 21 April.

Hemp seedlings are well established when most other species begin germination. Early germination and rapid growth provide an advantage to hemp in colonizing disturbed sites. Only rarely are young hemp plants overtopped by competing annuals. Usually, other annuals disappear from the rapidly growing hemp stands. One notable exception is giant ragweed (***Ambrosia trifida*** L.), the most common associate of hemp on recently disturbed sites of high fertility. Giant ragweed also germinates early and grows rapidly, often exceeding hemp in rate of height growth. Giant ragweed stands, however, are rarely so dense that significant hemp mortality results within a single year, although continued cohabitation would appear to lead to decline in hemp.

Root development in hemp demonstrated an important adaptation to a range of site conditions. 'Except in tight soils, where development was greatly inhibited, apparently by inadequate oxygen, root systems developed to maximize effectiveness. In coarse soils, where very low water potentials were frequent, plants were deep-rooted. Laterals were developed in medium-textured soils at the expense of deeper root systems. These observations confirm those of Boyce (1900). On edges of disturbed sites, such as cultivated fields, laterals extended into the cleared soil but not into the less disturbed soil supporting dense vegetation. These responses can be explained in terms of available moisture. nutrients and oxygen.

Seed'production data probably provide the greatest insight to the ecology of hemp. Total seed production per unit area was extremely variable, but production of viable seed is-more important. Assuming all viable seeds survive over winter, it takes an average of four viable seeds per female plant to reproduce a stand. Two plants from these four seeds will die before reaching sexual maturity, one plant will be female, and one will be a male at maturity. Slightly over 20% of the 1969 stands produced fewer than four good seeds per female. Only one of these stands, by our definition of 20 plants per m^2, was present in 1970. Four of these stands. otherwise undisturbed. produced no hemp plants in 1970. Other stands were disturbed or 'had only scattered hemp plants among other vegetation. Because of overwinter mortality in seeds and mortality during germination and early establishment of seedlings, considerably more than four seeds per female are needed for stand reproduction. There was a threshold of about 10 good seeds per female plant in 1969 below which stands did not reproduce. Thirty-five percent of the 1969 stands yielded fewer than 10 good seeds per female. Of these, only three had regenerated at least '2'0 plants per m^2 by June 1970. In many cases, however, nearby disturbances led to new stands not present in 1969. Of stands producing more than 10 seeds per female in 1969, and not disturbed, nearly 70% were present in 1970. Not considered here are the normal successional processes that occur in absence of continual disturbances. The establishment of perennial vegetation tends to reduce the probability that hemp stands will reproduce. Although conclusions from the above observations are tenuous, they do reinforce the observation that hemp is strictly a disturbed-site species. Given ample soil disturbance, stands very successfully reproduce, even on poor sites, for growth and seed production. The poorer the site, the more hemp is dependent upon soil disturbance.. This also suggests that hemp is more and more restricted to optimum and disturbed sites toward the limits of its potential range.

One is led to believe from the literature that hemp responds readily to nitrogen (Royle, 1855; Dewey, 1913; Miller, 1970). Our data tend to refute this. Both potassium and phosphorus were much more important than nitrogen in affecting a broad range of growth and seed parameters. As indicated in Tables 5, 6, 7 and 8, few other factors were so consistently important to hemp growth and seed production. Nitrogen, on the other hand, had little effect when potassium and phosphorus levels were held constant. Usually the effects of potassium and phosphorus were interacted and the interactions were much more important than first-order effects.

Based on information from the multiple regression analyses and field observations, Figure 3 was prepared to suggest the general trends of biomass, seed production, density and mortality as functions of the most important site variables. Biomass was the dependent variable used to establish the basic model, and the other dependent variables are examined along the same independent axis. Data are so variable as to preclude use of mathematical models for these relationships.

Mortality was consistently less on poor sites and tended to vary as a function of biomass. The larger the hemp plants, the fewer there were. On very poor sites, plants were stunted but usually very dense. This suggests either that gerrnination or survival was much better on poor sites assuming comparable seeds were available. Our data suggest that seeds were probably more available on the better sites where production was much higher. We could discern no reason why germination should be less on good sites, but we did observe greater mortality in stands of larger hemp plants. Judging from the size of the dead plants, we found that mortality tended to occur early in the growing season when moisture stress is less severe. Cause of death seldom was apparent. 'These data do suggest that hemp plants on poor sites grow so slowly that dominance is seldom expressed. On good sites, a few plants achieve early dominance and suppress the rest of the population, often to the point of heavy mortality.

As indicated above, density of plants tended to be less on the best sites and highest on marginal sites. In the very poorest sites, where plants usually were extremely stunted and often did not flower, density was somewhat less. Our mortality data do not totally account for this

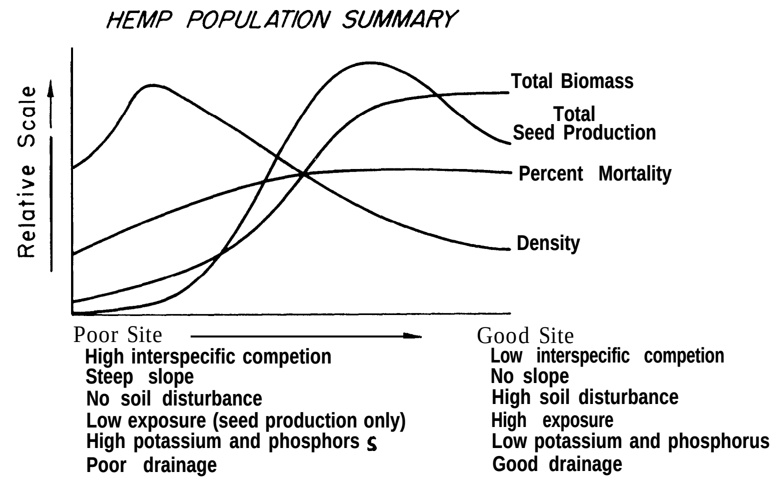

Fig. 3.-Generalized summary for relationship between four dependent parameters of naturalized hemp and the most important independent (site) parameters identified in this study. Total biomass was used as the basis for establishing the independent axis

variatioa in density. The reason, most likely, is that much mortality occurs during seed germination and the 1st few weeks of establishment. With few exceptions, those plants that died early in the growing season disintegrated before our collections and never appear in our data. Observations on individually marked seedlings in 10 stands during the 1st month of growth indicate that early mortality often exceeds 50%.

Seed production, expressed on an area basis, 'reached a peak in suboptimum stands. On the poorest sites, plants frequently were sterile. Seed production per female plant tended to increase from the worst to the best sites, but apparently the decreasing density, together with more foliage of plants on the best sites, resulted in an overall drop in seed production per unit area.

Total biomass was highly correlated to average plant height and stem diameter, but tended to be less variable within a set of comparable sites. Soil disturbance and fertilitv were the most important site factors correlated to biomass. Our data suggested a high degree- of interaction between phosphorus and potassium. More surprisingly, the data suggested a negative correlation to the level of these nutrients in the soil and most growth and seed production parameters. Because this was so contrary to our expectations. an experiment was run in the greenhouse to test 'the relationship of hemp growth to phosphorus and potassium. Results indicated a significant positive interaction which suggests that the effects of potassium-aphosphorus were suppressed in our analvsis by one or more other related factors. In our analyses, the computer simply calculated best fit of the data. The best fit utilized the most important and significant independent parameters, assigning either a positive or negative sign to arrive at the highest possible correlation. This, together with the great variation observed in the data, may have led to a negative multiple correlation when the simple linear correlation was positive. This points up the hazards of interpretation of multiple regression analyses.

In retrospect, much of our research effort was spent collecting data that could not be fully utilized because of statistical limitations. Yet without these efforts one runs the risk of being misled in his study by wrong conclusions of previous workers, as, for example, in the effects of nitrogen vs. potassium and phosphorus. Even with ample data, there is a great risk of faulty conclusions stemming from spurious relationships between factors. Thus, we see this study as a beginning, a beginning that should be followed by carefully controlled studies to further elucidate the probable relationships our results suggest.

CONCLUSIONS

This study suggests that hemp is adapted to essentially any soil where roots receive adequate aeration. The threshold of adequate aeration might be defined as those soils containing not more than 40% clay or 60% silt, nor less than 35% sand (Fig. 4). Optimum growth occurs on recently disturbed, sandy-loam soils with low competition and ample moisture. Moisture and fertility are limiting to the growth but not to the persistence of hemp on a site; the species will successfully reproduce on very infertile sites that are subject to extreme drought.

Apparently, in the upper Midwest hemp rapidly becomes established when seeds are introduced to a recently disturbed area. Seed dissemination, except by man, is low. The species will not long persist on sites in the absence of continued disturbance. Viable seeds persist in the soil for not more than 2 or 3 years. For these reasons, hemp is not expected to realize the full potential of its range; that is, suitable sites within the range will be sporadically occupied by the species. Following eradication or removal of the species through successional processes, hemp must be reintroduced to the sites when the habitat becomes suitable again in subsequent years. This is in sharp contrast to most other weedy annuals whose seeds are long persistent in soil or readily disseminated by birds or wind.

It is apparent from the literature that hemp has been established in the Midwest for over a century. At least in Peoria Co., Illinois, hemp was established before the now common *Stellaria media, Verbascum blattaria, Melilotus officinalis* and many others (Brendel, 1887). We have seen no evidence to suggest that *Cannabis sativa* is any less persistent in the region than these plants.

This suggests the close dependence of hemp upon man, not only for dissemination but especially for maintenance of suitable habitats.

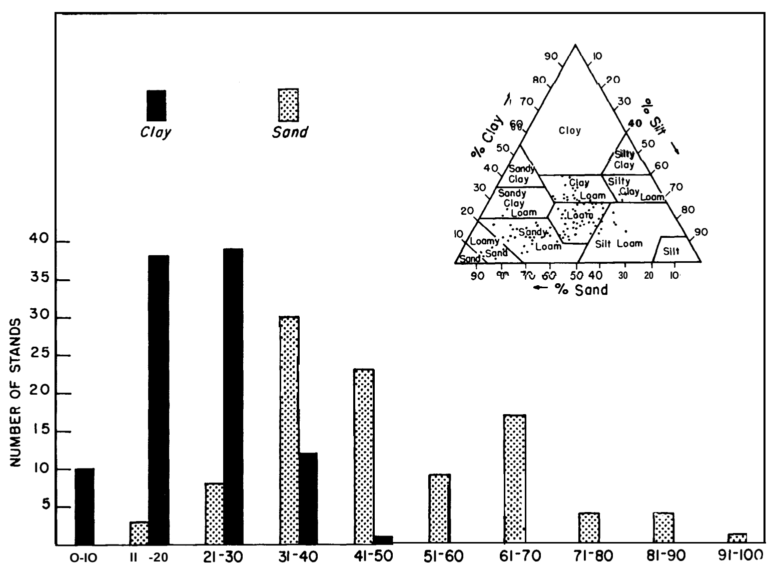

Fig. 4.-Relationship between soil texture and naturalized hemp stands. Dots on the inset graph denote natural percentages of sand, silt and clay for soils of the stands studied

Nearly all the populations we have observed were on sites repeatedly disturbed by cultural activities such as mowing, cultivation- of soil, stream channel improvements and refuse disposal. Side effects from these activities, such as flooding and erosion, maintain other habitats for hemp. Rarely does hemp occupy sites disturbed by animals such as the woodchuck. In these very local situations, it is doubtful that hemp could successfully maintain populations unless adequate seed pools were available from other nearby sites that were maintained by cultural activitv.

What has appeared to be continual spread of hemp over the past several decades (Haney and Bazzaz, 1970) is more likely a shifting of populations within the range alreadv established. Invasion of new sites does not result in permanent establishment unless the site is disturbed at least every 4 or 5 years. Because cultural patterns are stabilized in the upper Midwest, it is unlikely that hemp abundance is increasing significantly. The only exceptions that we have observed are found in the way of invasion along recently completed highways or improved roads and drainage channels where mowing or spraying may help maintain persistent stands.

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