EFFECT OF THE INVASION OF DIPSACUS SYLVESTRIS ON PLANT COMMUNITIES IN EARLY OLD-FIELD SUCCESSION

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ABSTRACT

EFFECT OF THE INVASION OF DIPSACUS SYLVESTRIS ON PLANT COMMUNITIES IN EARLY OLD-FIELD SUCCESSION

By

Patricia Werner

The response of early old-field plant communities to colonization by an experimentally introduced biennial species, Dipsacus sylvestris Huds. (teasel) is studied over a three-year period (1969 to 1971) in eight fields in Kalamazoo County, Michigan. The dynamics of community change in natural and teasel-treated areas were measured in terms of changes in species composition, community diversity, net primary productivity of species, various reproductive strategies, and over-all community physical structure.

The study was designed to explore the response of a plant community and the changes in the partitioning of the site's resources when a new plant species successfully invades. The empirical evidence provided by this study should contribute to testing theoretical models of species colonization and species co-existence.

Results showed that teasel communities had significantly higher diversities (using the Shannon-Weaver function, H') and greater "evenness" values (J') than check communities from one to three years after teasel introduction. An over-all increase in number of species other than teasel was found in teasel communities.

Annual net primary productivity of the two communities was not significantly different when teasel was in its rosette form. When teasel produced flowering stalks, annual net primary productivity of the teasel community was significantly greater than in the check communities. The observed increase is attributed to teasel itself since the productivity of individual indigenous species was the same in both communities.

Qualities inherent in "biennialness" and in "tall diffuse" morphology are discussed in relation to the effects seen in this study. A conceptual model of terrestrial secondary succession in plant communities based on these data and current literature is proposed.

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By

Patricia Werner

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INTRODUCTION

An understanding of the processes underlying community organization is central to the science of ecology. In order to study such processes, one must be able to detect and examine changes occurring in communities. Accordingly then, succession, the developmental phase of a sere, is one of the most fruitful areas of study for ecologists interested in community dynamics.

Successional changes are directional (therefore predictable), self-regulating, and culminate in a stabilized community in which "maximum biomass and symbiotic functions between organisms are maintained per unit of available energy flow" (Odum, 1969). Once a steady-state is reached, further change presumably occurs through the longer-term process of evolution.

Most studies of succession have been descriptions of communities (or parts of whole communities, as plants, insects, phytoplankton, etc.) in various stages of development (Drew, 1942; Oosting, 1942; Keever, 1950; Bard, 1952; Quarterman, 1957; Olson, 1958; Odum, 1960; Golley, 1965; Margalef, 1965, 1967; Golley and Gentry, 1966; Witkamp, Frank, and Shoopman, 1966; Monk and McGinnis, 1966; Cooke, 1967; Bazzaz, 1968). This approach yields information about the structure of communities of various ages and often allows one to make inferences about possible mechanisms that account for the directional changes.

The time involved in community development generally necessitates that comparisons be made across space (sites) as well as across time (stages of development); hence it is difficult to separate effects due to the many variables on different sites and those effects due to time (development). The ideal approach is one where time is one variable and any others are quantitatively and qualitatively identified. In this way one is more confident in identifying processes responsible for given changes in community structure. The experimental approach can often be useful in this respect. Recent investigators have explicitly called for experimentation to help explain many-species interactions (Milthorpe, 1961; Pianka, 1966a; Miller, 1967, 1969; Cavers and Harper, 1967; Whittington and O'Brien, 1968; Harper, 1969; Price, 1971).

Processes thought to be operating in the community may also be isolated and experimentally tested in the laboratory. Indeed, laboratory experimentation is often necessary to understand phenomena observed in the field. However, the inferences from such experiments are often limited when one applies them to interpretations of the complexities found in the natural system (Harper, 1964; McIntosh, 1970).

Of course, the problems of obtaining experimental data on the community level are great. Obstacles include the difficulty in replication of experimental units, the length of time often required for changes to occur, the uncontrollability of many variables, and the still uncertainty as to which parameters are important which results in the current time-consuming practice of measuring "everything."

Experiments which have been performed on whole communities have contributed insight into processes that organize community structure (Likens, et al., 1967; Simberloff and Wilson, 1969; Hall, Cooper, and Werner, 1970; Hurd et al., 1971; Stephenson, 1972). Additional experimentation manipulating the biotic component against a natural physico-chemical background would be in order.

Since every species found in a community was at one time a successful colonizer on the site, the following questions appear crucial: what allows the species to become established at one time and not another? When a new species successfully invades the community, what is the response of the individual indigenous species? What changes in the partitioning of the site's resources are observed, if any?

Theoretical models of species colonization and species co-existence have been developed that may predict answers to these questions (Margalef, 1957, 1963;

MacArthur and Levins, 1964, 1967; Schoener, 1965; MacArthur and Wilson, 1967; MacArthur, 1967, 1969, 1970; Pielou and Pielou, 1967; Levins, 1968; Simberloff, 1969; McNaughton and Wolf, 1970; Horn, 1971; Price, 1971). Empirical evidence to test the theoretical models, however, has mainly been limited to studies of pest outbreaks, epidemic diseases, and post-disturbance changes in natural populations of plants and animals such as those discussed by Elton (1958). Studies of experimental additions of a species to a natural community have been concerned mainly with the population dynamics of the new species rather than with community response (Sagar and Harper, 1960, 1961; Cavers and Harper, 1967; Putwain and Harper, 1970). "It would be . . . convincing to be able to show with appropriate controls, that the experimental addition . . . of a species affects the realized niche distribution of another. This has seldom been attempted, in spite of the potential value of such experiments" (Miller, 1967).

The objective of my study is to gain experimental evidence on the response of early old-field plant communities to colonization by an introduced plant species, Dipsacus sylvestris Huds. The dynamics of community change over three years time in natural and treated areas were measured in terms of changes in species composition, community diversity, net primary productivity of species,

various reproductive strategies, and over-all community physical structure. Interpretation of the results provides insight into some of the processes that may be operating in the development of a plant community.
A generalized conceptual model of terrestrial succession of primary producers based on these data and current knowledge is proposed.

MATERIALS AND STUDY SITE

Two factors which are important in a study of the response of a plant community to an introduced alien species are (1) the selection of a plant species that is easy to census, and (2) the presence of study sites where the species is absent, even though it would not be unusual to find it growing there. The latter requirement allows the experimenter to control the level of input into the community and to compare treatment quadrats with natural community quadrats.

In this study, *Dipsacus sylvestris* Huds.,[1] commonly called teasel, was chosen to be introduced into early old-field communities in Southern Michigan. *Dipsacus* is usually found in openings undergoing later stages of succession, in meadows, and in ruderal communities where turnover periods are longer than one year (Ehrendorfer, 1965). In Michigan, as in Southern Ontario (Cavers *et al.*, unpubl.), *Dipsacus* seeds are normally dispersed in the autumn within a few meters of the parent plant (Tallon, unpubl.) and typically germinate the following spring,

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[1] Or *Dipsacus fullonum* L. See Ferguson and Brizicky, 1965, for a discussion of the taxonomic dispute on the binomial.

although a few seeds germinate throughout the summer months. No cold treatment is required for germination but perhaps an after-ripening period is necessary. Some delay in germination to the second or third spring after dispersal has been observed. Seedlings form rosettes which, as their horizontally oriented leaves enlarge, become physically oppressive to adjacent vegetation. The rosettes overwinter and those surviving may produce a flowering stalk 0.5 to 2.5 meters high in a subsequent summer and die after seeds are formed. Only occasionally will a rosette bolt and form a flowering stalk in the first growing season. As is common with most "biennials," the duration of the rosette phase is variable (Harper and Ogden, 1970).

A census of the species is relatively simple since individual plants are easily recognized in all stages of the life cycle and no vegetative reproduction occurs.

The study area was a 100 x 100 meter portion of a former corn field located on Michigan State University W. K. Kellogg Biological Station property at the intersection of Gull Lake Drive and B Avenue, Ross Township (T. 1 S, R. 9 W.), Kalamazoo County, Michigan. The soil is well-drained Fox Sandy Loam (Typic Hapludalf) on flat to gently rolling glacial drift of Cary Age. The site had been farmed since about 1850. Its more recent history includes a hybrid walnut tree crop planted in 1938 (Holt, 1969, USDA photo BDB-3-50). General farming was employed between 1950 and 1955 (USDA photos BDB-1G-95 and BDW-1P-47). Between 1960 and 1964 the site was planted with wheat, alfalfa, and corn. Fertilizer (250 pounds/acre 6-24-24 and 100 pounds actual nitrogen) was last applied in 1964 on a corn crop. Various herbicides were last applied in November 1962 and May 1963, for a demonstration of quack-grass (Agropyron repens (L.) Beauv.) control.

Studies of old-field succession were initiated on the site in the autumn of 1964 (Cantlon et al., unpubl.). The area was divided into twenty-five 16 x 16 meter plots separated by four-meter buffer strips, and grouped into five blocks. Blocks III, IV, and V were established with respect to topography; Blocks I and II, both on level ground, were partitioned to minimize effects due to two surviving black walnut (Juglans nigra L.) trees left in the field. Each year from 1964 to 1968 one plot from each block was selected at random, ploughed, and left fallow. In 1970, the former 1965 plots were again ploughed and left fallow. Davis (1968) and Cantlon et al. (unpublished data) have documented the plant community composition each year from 1964 to 1971 in the 100 x 100 meter study area. During this time Dipsacus was completely absent from the naturally-occurring plant communities.

Sites for the present study were available only on the east and west sides of each block in the large study area. These strips of ground were approximately 2.5 x 13 meters in size, and were parallel to the plow furrows. Eight of these sites were chosen in 1969, four in blocks left fallow since 1967 and four in blocks left fallow since 1968. Hence, the fields would be entering their third and second growing seasons after abandonment, respectively. For convenience, strips within the third year (1967) blocks are designated Fields A, B, C, and D; those within the second year (1968) blocks are designated Fields J, K, L, and M. (Figure 1)

Vascular plant nomenclature follows Gleason and Cronquist (1963). Voucher specimens, collected in cooperation with Darlene Valasek, have been deposited in the Beal-Darlington Herbarium, Michigan State University.

FIGURE 1

Distribution of Blocks and Teasel Introduction Fields. The numbered squares represent the portions of the study area under study by Cantlon *et al.* The Roman numerals indicate the block number, the arabic numerals indicate the year of fallowing, and the letters indicate fields used in the teasel introduction study.

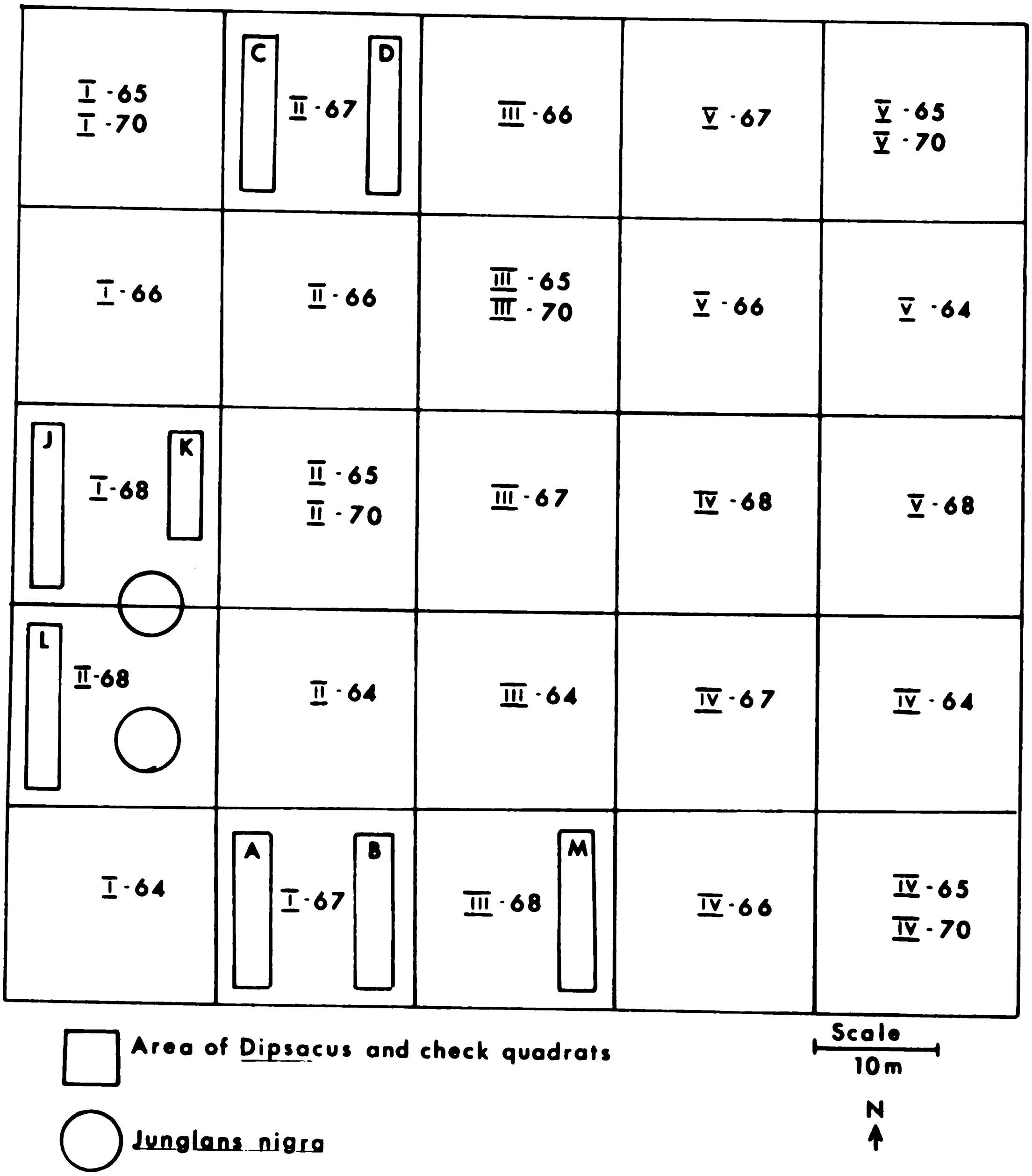
I-65
I-70
C
II-67
D
III-66
V-67
V-65
V-70
I-66
II-66
III-65
III-70
V-66
V-64
J
I-68
K
II-65
II-70
III-67
IV-68
V-68
L
II-68
II-64
III-64
IV-67
IV-64
I-64
A
I-67
B
III-68
M
IV-66
IV-65
IV-70
Area of Dipsacus and check quadrats
Junglans nigra
Scale
10m
N

FIGURE 1

METHODS

Treatment

Dipsacus seeds were collected October 15, 1968, from a naturally-occurring population in Lenawee County (Hudson Twp., Sec. 19), Michigan, and stored in ventilated glass containers in the dark at room temperature (23^{o}-28^{o} C).

Within each study field 52 randomly selected one-half by one-half meter quadrats[1] were measured out and permanently marked with wooden stakes. Half of these quadrats were randomly selected to receive teasel seeds, the other half were designated as "check" quadrats.

Seeds were sown at the rate of 150 seeds per treatment quadrat during March 15-17, 1969. The seeds had previously been divided into lots of 150 seeds in the laboratory, put into sealed envelopes, and then opened in the field and broadcast by hand to simulate the pattern of natural dispersal.

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[1] In Fields K and L, adjustments in number of quadrats had to be made for two black walnut trees. Forty-eight and eighty quadrats were selected, respectively.

Estimates of potential first-year field germination were assessed from laboratory germination tests. In February 1969, twelve lots of 50 seeds each were placed on moist blotters in petri dishes, then three replicates were left at room temperature (24°C) and the remainder were put in a 4°C cold room. The seeds left at room temperature showed 100% germination after 8 days. The cold treatment was terminated after the eighth day since it was no longer necessary to determine the length of time for any possible obligate cold period. Cold treatment was not applied to seeds used in the field.

Estimates of potential second-year field germination were assessed in similar laboratory tests conducted at room temperature. Results showed germinability had dropped to 63.3 ± 12.0%. A tetrazolium test showed the ungerminated seeds were dead.

Field Data Collection

In a subsample of 24 quadrats, teasel seed germination and seedling survival were assessed from April 1, 1969, until June 1, 1969, the end of the initial germination pulse, each week marking newly-germinated teasel seedlings with different-colored plastic toothpicks. Second-year seedling germination counts were conducted in the same way, only at 2-week intervals. Percent cover readings and census of teasel plants by seedling, rosette size, and flowering plant size were taken in each of the study's 220 treatment quadrats within three days before or after the following dates: September 1, 1969, June 1, 1970, September 1, 1970, June 1, 1971, and September 1, 1971.

Floristic composition was assessed in each treatment and check quadrat by visual estimation of the percent cover of each species as well as the recording of the life stage of each species (seedling, rosette, flowering) in August 1969 and August 1970. Floristic composition values for 1968 were obtained from my analysis of unpublished data collected by Cantlon *et al*., which was in the form of estimates of percent cover for the species.

Above-ground standing crop of individual species and their life stage was determined in August 1970 and August 1971. In each field a subsample of nine of the treatment quadrats and nine of the check quadrats were randomly selected for sampling. Vegetation within the vertical boundaries of each selected quadrat was clipped at ground level, placed in a plastic bag for transport to the laboratory, cooled to 4°C, separated by species and life stage, then dried for 24 hours at 100°C, and weighed. The litter (dead, horizontal plant material at ground level) was similarly removed from each sample quadrat, transported to the laboratory, separated into monocotyledonous or dicotyledonous litter, dried, and weighed.

Flowering heads of teasel plants were removed prior to seed dispersal in August 1970 with the exception of one quadrat in each of Fields L and M. Establishment success (ecesis) of the teasel population was determined in June 1971, by counting new germinated seedlings in natural vegetation near these untouched quadrats.
A three-year study of the population dynamics of Dipsacus will appear at a later date.

Any quadrat that was clipped for sampling or had flowering heads removed in 1970 was not chosen for clipping in 1971.

The term "teasel community" as used in this paper refers to the plant community within the boundaries of quadrats sown with teasel seed (teasel quadrats). The terms "indigenous community" or "natural community" refer to the plant community outside teasel quadrats, and usually within marked check quadrats not treated with teasel seeds.

Additional Determinations

In August 1970, a separate study was made to determine the relationship between the above-ground biomass and the diameter of a teasel rosette in order to be able to estimate dry weight without sacrificing the plant, i.e., by measuring its diameter. One hundred and thirty-two rosettes of various sizes were measured for diameter in the field and then removed to the laboratory, dried at 100°C for 24 hours, and weighed. The following weight-diameter relationship was determined by regression analysis using the method of least squares: $y = 0.0466 + 0.0011x^2$ $(r = 0.8561, n = 132)$, where x is the teasel rosette diameter (median in each of nine classes) in centimeters and y is the above-ground weight in grams (Table 1; Figure 2). This mathematical relationship is used to estimate above-ground dry weight of teasel rosettes for selected fields in 1969.

Estimates of teasel below-ground biomass were obtained by shoot/root ratio techniques (Bray, 1963; Monk, 1966a). Whole rosette plants from field collections in June and August, 1970, and from greenhouse plantings in March and April, 1970, were dried at 100°C for 24 hours, divided into shoot and root portions and weighed separately. A shoot/root ratio of 5.66 ± 0.92 $(n = 96)$ was calculated for teasel rosettes. Whole flowering plants were collected in August 1970, and prepared similarly. Results yielded a shoot/root ratio of 9.17 ± 0.87 $(n = 7)$ for the flowering plants.

TABLE 1

MEAN ABOVE-GROUND DRY WEIGHT OF TEASEL ROSETTES IN NINE DIAMETER CLASSES

Diameter class (cm)	Above-Ground Weight (gms)	
	Mean	Standard Error
<2.5	0.0028	0.00004
2.5 - 5.0	0.0249	0.0052
5.1 - 12.6	0.1857	0.0195
12.7 - 17.7	0.3435	0.0375
17.8 - 27.9	0.8135	0.1741
28.0 - 35.5	0.8600	0.0748
35.6 - 50.7	2.1800	0.2458
50.8 - 60.9	3.4567	1.2952
61.0 - 72.0	4.7333	2.3447

FIGURE 2

The Relationship Between Teasel Rosette Weight and Teasel Rosette Diameter. The dotted line is drawn through the mean weights of each of nine classes of diameters. The solid line shows the mathematical function $y = 0.0466 + 0.0011\, x^2$ which is obtained when the weights of 132 rosettes are regressed on diameter measurements. Weight values are expressed in grams; diameter values are expressed in centimeters.

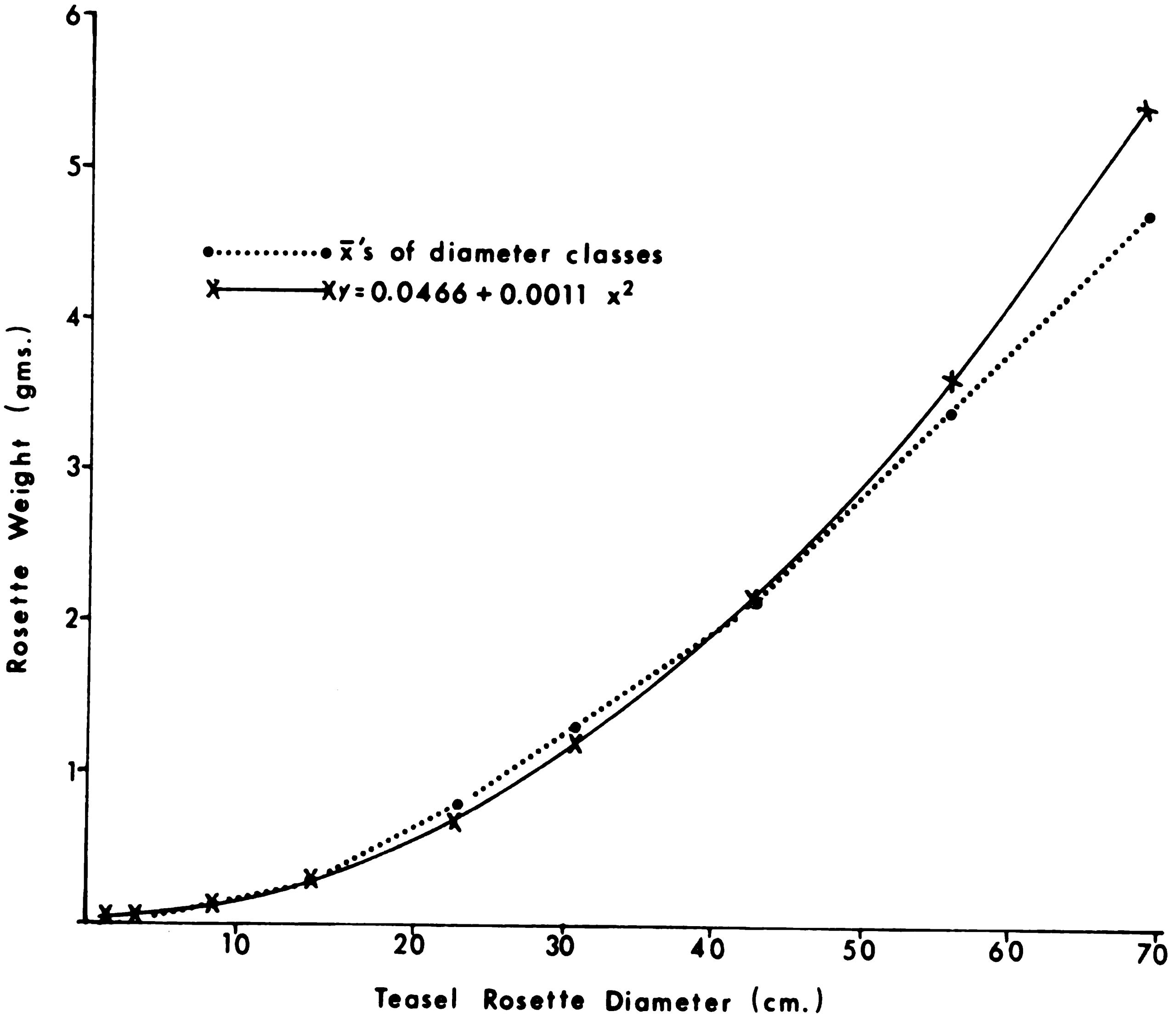
x̄'s of diameter classes
$y = 0.0466 + 0.0011\ x^2$
Rosette Weight (gms.)
Teasel Rosette Diameter (cm.)
0
1
2
3
4
5
6
10
20
30
40
50
60
70

FIGURE 2

ANALYSIS

Statistics

Tests of significance are based on standard procedures (t-test, Wilcoxon rank-sum), given by Steele and Torrie (1960) and Sokal and Rohlf (1969). Tests of significance between regression lines follow procedures presented by Ostle (1963). Means cited in the text and in tables are accompanied by their standard errors. Points on graphs representing means are shown with 95% confidence limits.

Diversity

Plant community diversity within each field was computed using the Shannon-Weaver (1963) formulation

$$H' = -\sum_{1}^{s} p_i \log_2 p_i$$

where s is the number of species in proportions p_1, p_2, ...p_s. Diversity is equated with the amount of uncertainty that exists regarding the species of an individual selected at random from a population. Ecologists are making increasing use of information content as a measure of diversity. (MacArthur, 1955, 1964; Margalef, 1957, 1958a;

Hairston, 1959; MacArthur and MacArthur, 1961; Crowell, 1961; Patten, 1962; Paine, 1963, 1966; Lloyd, 1964; Lloyd and Ghelardi, 1964; Pianka, 1966a; Pielou, 1966a, b, c).

The Shannon formulation assumes random selection and independent observations of units. Because of the patchiness of vegetation, that is, the tendency for species to occur in large single clumps, and the usual necessity of measuring plants by weight or percent cover rather than by discrete enumeration, it is impossible to obtain a random sample of independent observations of the species in a field. One quadrat will contain only a small portion of the vegetation pattern and only part of the species in the plant community. Therefore, any H' (the amount of uncertainty per individual unit) calculated on the species content within one quadrat will be smaller than the H' calculated on the entire community and will not be representative of the vegetation in the whole field (McIntosh, 1962, 1967; Lloyd and Ghelardi, 1964; Pielou, 1966a, b, d; Margalef, 1967; Hurlbert, 1971). Special care must be taken to ensure an accurate estimate of $H'_{\text{community}}$ (H'_{com}) whenever one is considering communities of plant species.

A good estimator of H'_{com} with corresponding variance term was calculated for each field and treatment by the method that follows (Good, 1953; Pielou, 1966a, b).

A total of z number of quadrats in each field were examined and chosen in random order for the mathematical operations. H'_1 is the calculated diversity of the first quadrat. Data from the second quadrat are added to those of the first and diversity is recalculated to obtain (the diversity of the pooled data). Continuing, a sequence of values H'_1, H'_2, $H'_3, \ldots H'_k, \ldots H'_z$ is obtained which are the diversities per individual unit of the pooled contents of the first k quadrats. A graph of the curve of H'_k against k shows H'_k increasing with sample area, then leveling off (Figure 3). A subjective decision is made as to where H'_k levels off; this k is labeled t. It is correct to assume that t or more random quadrats provide an adequate representation of the community.

The sequence $[H'_k]$ for $k \geqslant t$ are dependent estimates of H'_{com} and hence do not directly allow for a determination of standard error. However, a standard error can be estimated as follows:

For each $k > t$, calculate the increment in diversity per individual unit (h_k) that results from adding the kth quadrat to the first (k-1) combined quadrats:

$$h_k = \frac{M_k H'_k - M_{k-1} H'_{k-1}}{M_k - M_{k-1}}$$

where M_k = total units of all species in k-combined quadrats.

FIGURE 3

The Technique Used to Estimate H'_{com} with Corresponding Variance Term. A graphical representation of H'_k against k, where H'_k is the diversity of the pooled data in 1 through k quadrats. The kth quadrat where H'_k levels off is designated t. Data were collected from Field B, check community, in 1970.

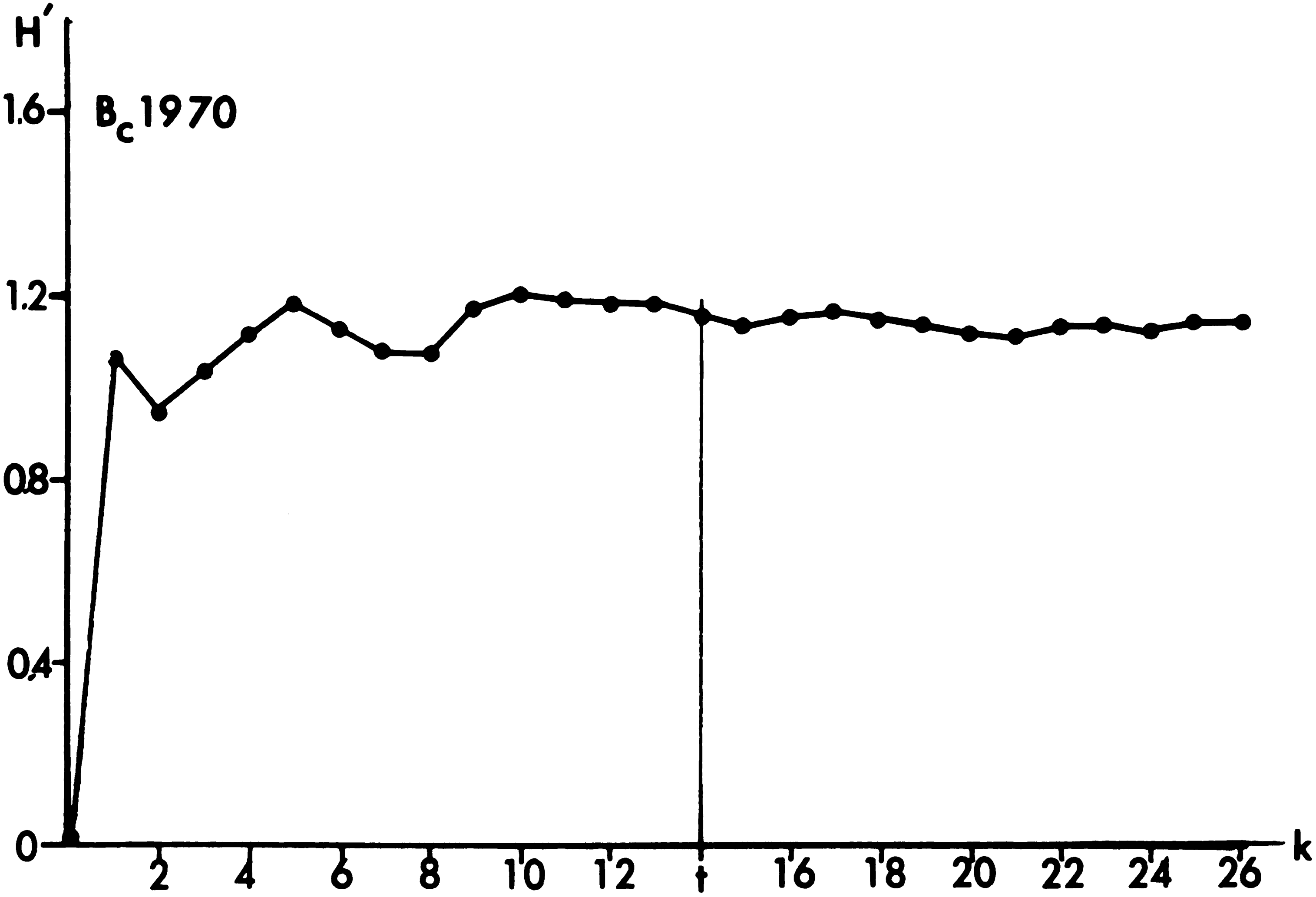

FIGURE 3

For all $k > t$, a sequence $h_{t+1}, h_{t+2}, \ldots$ of independent random variables is obtained such that $E(h_{t+r}) \simeq H'_{t+r}$ (where $r = z-t$).

Since when $k \geqslant t$, no change in diversity is expected as sample size is increased, it follows that $E(h_k) = \bar{h} = \tilde{H}'_{com}$ and also Var $(\bar{h}) = \widetilde{\text{Var}}\ (H'_{com})$ (Baer, 1953; Pielou, 1966a, b). All estimates of H'_{com} from 1969 to 1971 in this paper were derived by the method above, and will be designated H'_{com}.

The Evenness Component of Diversity

As a measure of evenness with which the total plant biomass is divided among species, it is common to calculate a ratio of the observed diversity to the maximum possible for the same number of species (Pielou, 1966a, b):

$$J'_{com} = \frac{H'_{com}}{H'_{max}} = \frac{H'_{com}}{\log s}$$

where s = number of species. This same value is sometimes calculated from the Shannon-Weaver equation directly, using log to the base s:

$$J'_{com} = -\sum_{1}^{s} p_i \log_s p_i$$

The evenness measure of diversity allows simple comparison among fields and treatments since the maximum value of J'_{com} is always 1. Again, valid comparisons of species evenness are possible for collections of equal size or if a variance is calculated (Hurlbert, 1971).

The Variety Component of Diversity

The measure of diversity that is very sensitive to the variety (number of species) component of diversity is the slope of the line resulting from the regression of individual species biomass ($\log_{10}$) determinations against their respective ranks (Motomura, 1932). Slope values are always negative, ranging from 0 to $-\infty$, or from maximum to minimum diversity; that is, as the slope approaches 0 diversity approaches maximum.

Slopes of the Motomura (1932) regression line, used as a measure of the variety component of diversity, indicated that teasel communities increased the number of species in a field or had no significant effect.

Productivity

The above ground standing crop in a field of herbaceous vegetation where all above ground parts die each winter is a reflection of the annual net primary productivity of the site (Wiegert and Evans, 1964; Golley, 1965). For any one growing season, the following should be considered. Annual plants and rosettes of biennials are produced during a given growing season. Net primary productivity contributed by biennials flowering during the same growing season can be compensated for by estimating and subtracting the previous year's stored underground reserves. Herbaceous perennials produce their above-ground portions during the current season from either stored or newly-made materials; if herbaceous perennials have maintained or increased above-ground biomass over the previous year, the increased yield most probably reflects net primary productivity of the current year.

Thus, in fields containing annuals, biennials, and herbaceous perennials (increasing or steady-state populations), it is valid to use standing crop biomass (dry weight yield) as an estimate of annual net primary productivity. This technique is especially useful in comparisons among various treatments within the same field where the standing crop is expected to be the same throughout.

Of course, a measure of the above-ground standing crop for a woody perennial does not give much information about the net primary productivity of that particular growing season, so other estimates must be employed (Ovington, 1957; Whittaker, 1961).

The fields chosen for teasel introduction are composed mainly of herbaceous plants as described earlier. A woody perennial, Rhus typhina (staghorn sumac), is gradually increasing in the larger 100 x 100 study area forming a shrub canopy over the older fields. In the fields used in this study Rhus is a recent invader and is patchy in distribution, usually being recorded as a zero in any sample quadrat. However, because of its relatively greater biomass, Rhus represents 75% of the standing crop in a few quadrats. Most of this weight is dense stem tissue produced in a previous year and never occupies more than two percent of the ground surface area of the quadrat. In quadrats where Rhus is recorded, the plant composition and total biomass of the remaining vegetation remain statistically unchanged from quadrats lacking Rhus (Table 12). Since this was true, I chose (1) to eliminate the problem associated with the inclusion of Rhus by subtracting woody perennial values to obtain corrected figures of total biomass, and (2) to make conclusions only about the annual net primary productivity of the herbaceous vegetation.

Herbaceous vegetation values were corrected further, where necessary, for "biennialness." This was found to be a minor correction in check communities since biennials made up less than five percent of the total biomass. However, in teasel communities, this became quite important. The correction methods applied to estimates of plant productivity for flowering teasels were designed so that, in any one season, the maximum possible biomass (both above and below ground weights) formed in rosettes the previous year was subtracted from the biomass measurement for the flowering plants formed in the current year. This technique assumes that all of the biomass in the previous year's rosette was stored in underground parts during the winter, and then emerged with the above ground parts the next spring into the new flowering stalk. Even though the estimate of annual net productivity is conservative, it will add to the validity of later conclusions. (Tables 2 and 3)

The study assumes equal within sample turnover, export, and herbivory in the two communities (teasel and check) in any one field. All standing crop (biomass) and annual primary productivity values are given on the basis of grams per square meter.

Functional Groups

Some ecologists have described vegetation on the basis of plant life forms (Raunkiaer, 1934; Dansereau, 1951) or horizontal layers (MacArthur and MacArthur, 1961; Golley, 1965). No causal factors were claimed in choice of categories, although in some studies these have become predictive tools. For example, MacArthur and MacArthur (1961) found that the number of bird species breeding in a small uniform area could be predicted in terms of the layers of vegetation and seemed independent of the number of plant species (MacArthur, 1967). Other investigators have recognized the possibility of taxocenoses (Margalef, 1967;

TABLE 2

ABOVE-GROUND TEASEL BIOMASS AND ESTIMATES OF BELOW-GROUND BIOMASS
($\bar{x}$ gms·m^{-2})

	$\bar{x}$ Rosettes			$\bar{x}$ Flowering Plants		
Year, Field	Above Ground	Below Ground	Total	Above Ground	Below Ground	Total
1969						
A	13.582	2.400	15.982	0		
B	5.772	1.020	6.792	0		
C	1.093	0.194	1.292	0		
D	2.292	0.405	2.694	0		
J	3.816	0.674	4.490	0		
K	0.349	0.062	0.410	0		
L	2.736	0.483	3.219	0		
M	10.177	1.798	11.975	0		
1970						
A	25.715	5.123	30.838	40.000	4.360	44.360
B	14.467	2.233	16.700	0		
C	1.257	0.251	1.508	0		
D	2.743	0.549	3.292	0		
J	2.350	0.470	2.820	3.900	0.425	4.325
K	1.600	0.320	1.920	0		
L	17.880	3.576	21.456	2.933	0.320	3.253
M	10.200	2.040	12.240	8.600	0.937	9.537
1971						
A	6.114	1.080	7.194	119.829	13.062	132.891
B	28.300	5.000	33.330	171.600	18.706	190.306
C	11.371	2.009	13.380	20.171	2.199	22.370
D	25.143	4.442	29.585	0		
J	1.920	0.339	2.259	0		
K	1.867	0.330	2.197	0		
L	10.200	1.802	12.002	105.000	11.446	116.446
M	18.465	3.262	21.727	204.600	22.303	226.903

Rosette S/R = 5.66 ± 0.92
Flowering Plant S/R = 9.17 ± 0.87

TABLE 3

CORRECTED VALUES FOR TEASEL ANNUAL NET PRIMARY PRODUCTIVITY ($\bar{x}$ gms$\cdot$m^{-2})

Field	Flowering: Above Ground Measurement	Previous Year's Rosette: Above and Below Ground (Table 2)	Flowering: Above Ground Corrected Value	Rosette: Above Ground	Teasel Total Above Ground Corrected Value
1969					
A	0			13.582	13.582
B	0			5.772	5.772
C	0			1.098	1.098
D	0			2.292	2.292
J	0			3.816	3.816
K	0			0.349	0.349
L	0			2.736	2.736
M	0			10.177	10.177
1970					
A	40.000	15.982	24.018	25.715	49.733
B	0			14.467	14.467
C	0			1.257	1.257
D	0			2.743	2.743
J	3.900	4.490	-0.590*	2.350	2.350
K	0			1.600	1.600
L	2.933	3.219	-0.286*	17.880	17.880
M	8.600	11.975	-3.375*	10.200	10.200
1971					
A	119.829	30.838	88.991	6.114	95.105
B	171.600	16.700	154.900	28.300	183.200
C	20.171	1.508	18.663	11.371	30.034
D	0			25.143	25.143
J	0			1.920	1.920
K	0			1.867	1.867
L	105.000	21.456	83.544	10.200	93.744
M	204.600	12.240	192.360	18.465	210.825

*Treated as 0 in total.

Hutchinson, 1967), or assemblages of species populations that are "likely to be of about the same size, to have similar life histories, and compete over both evolutionary and ecological time" (Deevey, 1969).

In an attempt to look at the plant community in some way other than as a collection of interacting taxonomic species, I constructed two other sets of classifications which might have biological significance, one based on plant life forms and another based on reproductive strategies.

Physical Structure

The delineation of categories in this classification scheme was made prior to the collection of data in 1969. Plants were recorded by physical form throughout the study, in addition to species designations. The categories include (1) forms with long, linear, mainly vertical leaves, as grasses; (2) seedlings of herbaceous plants, usually less than 5 centimeters in height; (3) rosettes, usually over 5 centimeters in height and diameters greater than height measurements; (4) tree seedlings; (5) "diffuse" forms, 5 to 100 centimeters in height; (6) vines; (7) "diffuse" forms, greater than 100 centimeters in height; (8) shrub canopy; (9) appressed to the ground, living; (10) on the ground, dead. Any single species does not necessarily remain in the same category for its entire life span (Figure 4; Table 4).

FIGURE 4

Diagramatic Representation of Categories in the Physical Structure Classification.

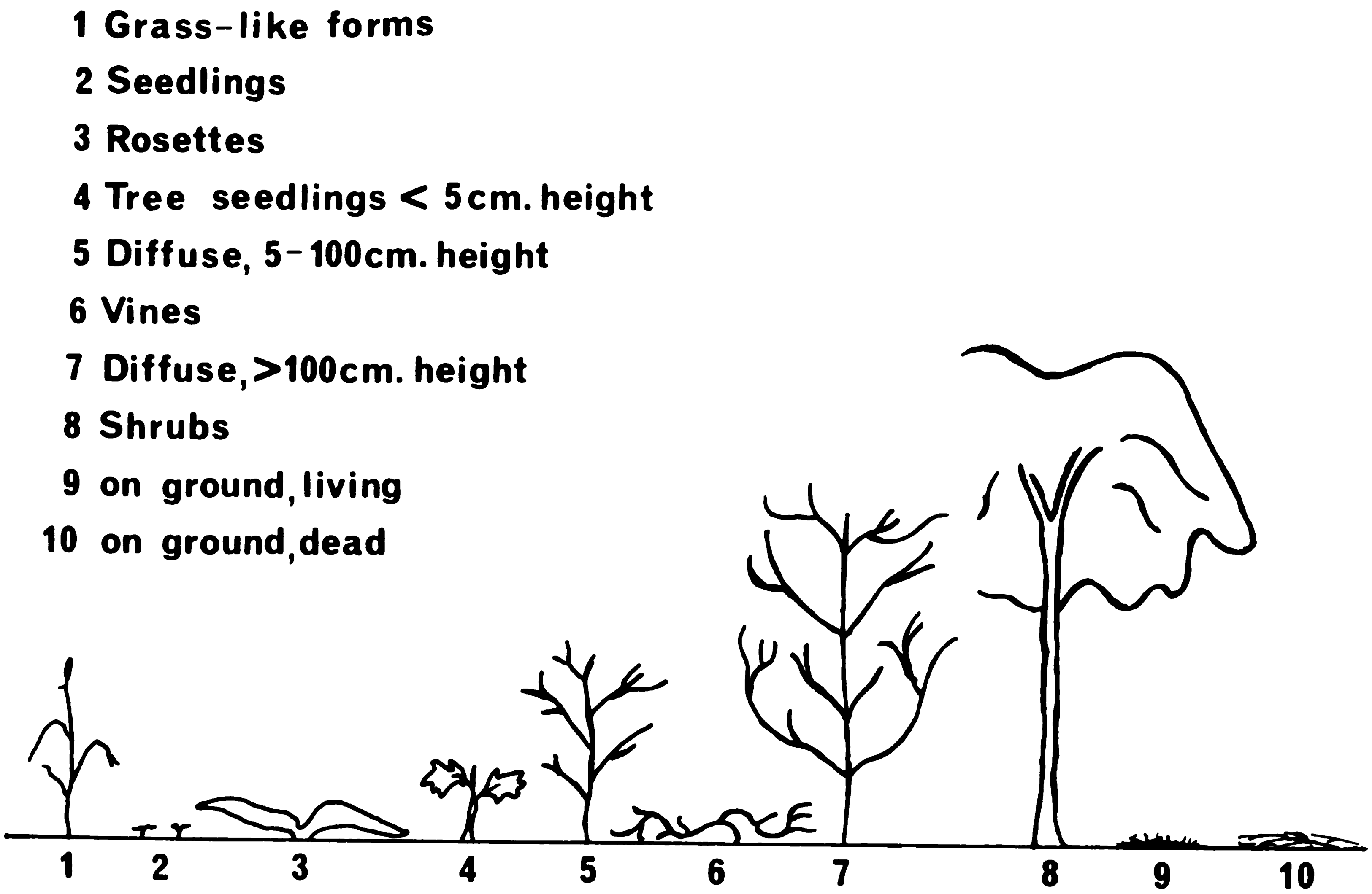
1 Grass-like forms
2 Seedlings
3 Rosettes
4 Tree seedlings < 5cm. height
5 Diffuse, 5–100cm. height
6 Vines
7 Diffuse, >100cm. height
8 Shrubs
9 on ground, living
10 on ground, dead
1
2
3
4
5
6
7
8
9
10

FIGURE 4

TABLE 4

THE PHYSICAL STRUCTURE CLASSIFICATION

1. Grass-like Forms

    Agropyron repens
    Agrostis stolonifera
    Bromus inermis
    Carex spp.
    Dactylis glomerata
    Digitaria sanguinalis
    Juncus spp.
    Muhlenbergia frondosa
    Panicum capillare
    Panicum spp.
    Phleum pratense
    Poa spp.
    Setaria glauca
    Setaria viridus

2. Seedlings of Herbaceous Plants

    Ambrosia spp. seedling
    Asclepias syriaca sdlg.
    Aster pilosus sdlg.
    Aster sagittifolius sdlg.
    Erigeron annuus sdlg.
    Erigeron canadensis sdlg.
    Erigeron strigosus sdlg.
    Lactuca spp. sdlg.
    Melilotus spp. sdlg.
    Potentilla norvegica sdlg.
    Potentilla recta sdlg.
    Rumex acetosella sdlg.
    Seedlings, unknown
    Solidago spp. sdlg.

3. Rosettes

    Achillea millefolium sdlg.
    Barbarea vulgaris sdlg.
    Circium spp. rosette
    Daucus carota sdlg.
    Dipsacus sylvestris rosette
    Oenothera biennis rosette
    Rumex crispus sdlg.
    Taraxacum officinale
    Verbascum thapsus rosette

4. Tree Seedlings

    Acer rubrum sdlgs.
    Acer saccharum sdlgs.
    Cornus racemosa sdlgs.
    Prunus virginiana sdlgs.
    Rhus typhina sdlgs.

5. Diffuse Forms, 5-100 cm. height

    Acalypha virginica
    Achilles millefolium adult
    Ambrosia spp. adult
    Arabis spp.
    Barbarea vulgaris adult
    Berteroa incana
    Capsella bursa-pastoris
    Cerastium vulgatum
    Chenopodium album
    Euphorbia spp.
    Galium spp.
    Geranium spp.
    Hieracium spp.
    Hypericum perforatum
    Lepidium spp.
    Lotus corniculata
    Lychnis alba
    Malva neglecta
    Medicago lupulina
    Nepeta cataria
    Oxalis stricta
    Plantago spp.
    Polygonum aviculare
    Polygonum pensylvanicum
    Polygonum persicaria
    Potentilla argentea
    Potentilla norvegica mature
    Potentilla recta mature
    Rumex acetosella
    Salvia spp.
    Sonchus oleraceus
    Stellaria media

continued

TABLE 4--Continued

Thlaspi arvense
Tragopogon pratensis
Trifolium pratense
Trifolium repens
Veronica arvense
Veronica peregrina

6. Vines

Lonicera spp.
Parthenocissus quinquefolia
Polygonum convolvulus
Ribes spp.
Rubus spp.
Vicia villosa
Vitis spp.

7. Diffuse Forms, > 100 cm. height

Asclepias syrica mature
Aster pilosus mature
Aster sagittifolius mature
Aster hybrid mature
Circium spp. mature
Daucus carota mature
Dipsacus sylvestris mature
Epilobium angustifolium
Erigeron annuus mature
Erigeron canadensis mature
Lactuca biennis mature
Lactuca canadensis mature
Melilotus spp. mature
Rumex crispus mature
Solidago canadensis mature
Solidago graminifolia mature
Verbascum blattaria mature
Verbascum thapsus mature

8. Shrub (canopy)

Rhus typhina

9. Appressed to Ground, Living

Mosses
Tree trunk

10. On Ground, Dead

Bare ground, Rocks
Corn litter
Dicot litter (excludes wood)
Monocot litter (excludes corn)
Wood litter

Species names with author citation may be found in Table 5.

Biological Structure

In this classification, categories include (1) annual grasses; (2) perennial grasses; (3) perennial monocots, exclusive of grasses; (4) summer annual dicots; (5) winter and spring annual dicots; (6) biennials; (7) woody perennials; (8) herbaceous perennial dicots; (9) mosses; (10) miscellaneous (Table 5).

TABLE 5

BIOLOGICAL STRUCTURE

1. Annual Grasses

    Digitaria sanguinalis (L.) Scop.
    Panicum capillare L.
    Panicum spp.
    Setaria glauca (L.) Beauv.
    Setaria viridus (L.) Beauv.

2. Perennial Grasses

    Agropyron repens (L.) Beauv.
    Agrostis stolonifera L.
    Bromus inermis Leyss.
    Dactylis glomerata L.
    Muhlenbergia frondosa (Poir.) Fern.
    Phleum pratense L.
    Poa spp.

3. Other Perennial Monocots

    Carex spp.
    Juncus spp.

4. Summer Annuals (Dicots)

    Acalypha virginica L.
    Ambrosia spp.
    Cerastium vulgatum L.
    Chenopodium album L.
    Galium spp.
    Lychnis alba Mill.
    Malva neglecta Wallr.
    Oxalis stricta L.
    Stellaria media (L.) Cyrill.

5. Winter, Spring Annuals (Dicots)

    Arabis spp.
    Barbarea vulgaris R.Br.
    Berteroa incana (L.) DC.
    Capsella bursa-pastoris L.
    Erigeron annuus (L.) Pers.
    Erigeron canadensis L.
    Erigeron strigosus Muhl.
    Euphorbia spp.
    Geranium spp.
    Lepidium spp.
    Medicago lupulina L.
    Polygonum aviculare L.
    Polygonum convolvulus L.
    Polygonum pensylvanicum L.
    Polygonum persicaria L.
    Thlaspi arvense L.
    Veronica arvense L.
    Veronica peregrina L.

6. Biennials (Dicots)

    Daucus carota L.
    Dipsacus sylvestris Huds.
    Lactuca biennis (Moench.) Fern.
    Lactuca canadensis L.
    Melilotus spp.
    Oenothera biennis L.
    Sonchus oleraceus L.
    Tragopogon pratensis L.
    Verbascum blattaria L.
    Verbascum thapsus L.

7. Woody Perennials

    Acer rubrum L.
    Acer saccharum Marsh.
    Cornus racemosa Lam.
    Lonicera spp.
    Parthenocissus quinquefolia (L.) Planch
    Prunus virginiana L.
    Rhus typhina
    Ribes spp.
    Rubus spp.
    Vitis spp.

continued

TABLE 5--Continued

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8. Herbaceous Perennials (Dicots)

   Achillea millefolium L.
   Asclepias syriaca L.
   Aster pilosus Willd.
   Aster sagittifolius Willd.
   Aster hybrid
   Cirsium spp.
   Epilobium angustifolium L.
   Hieracium spp.
   Hypericum perforatum L.
   Lotus corniculata L.
   Nepeta cataria L.
   Potentilla argentea L.
   Potentilla norvegica L.
   Potentilla recta L.
   Rumex acetosella L.
   Rumex crispus L.
   Salvia spp.
   Solidago canadensis L.
   Solidago graminifolia (L.) Salisb.
   Taraxacum officinale Weber.
   Trifolium pratense L.
   Trifolium repens L.
   Vicia villosa Roth.

9. Mosses

10. Miscellaneous

   Bare ground, Rocks
   Corn litter
   Dicot litter (excludes wood)
   Monocot litter (excludes corn)
   Seedlings, unknown
   Tree trunk (ground level only)
   Wood litter

RESULTS

Teasel Introduction

Although teasel seeds were introduced at the same rate and time in the eight fields, the success of teasel germination and growth varied among fields due to the interaction between the introduced teasel plants and the natural vegetation. Success of teasel introduction was examined in the light of the various ages of fields, previous herbicide treatments, litter cover, amount of bare ground, initial amounts of *Agropyron repens*, *Rhus typhina*, and biennials, and the dominance and diversity of the natural plant communities. A detailed accounting and systems analysis of these and other factors as variables affecting teasel population dynamics in old fields is in preparation (Werner and Caswell, unpubl.). Data from a separate two-year field study on the effects of litter on teasel invasion are also undergoing analysis (Werner, unpubl.).

Since the current analysis deals with the effects of teasel on the community enumeration data is not reported here, but rather, measurements of teasel that relate it to the other plant species, i.e., percent cover, standing crop biomass, etc. To serve as background information, percent cover values of teasel in each field from August 1969 to August 1971 are presented in Table 6 and Figure 5. The total percent cover of teasel was estimated independently from separate readings for rosettes and flowering plants.

Teasel Effect on Diversity

Number of Species

A simple comparison of the number of plant species found in teasel communities vs. check communities was made in each field and at each sample time (August 1969, 1970, and 1971). Results of a Wilcoxon rank-sum test showed that over all fields and times the number of species in teasel communities significantly exceeded that in check communities ($P < 0.005$, $T=40$, $N=24$). This held true even when a correction was made excluding Dipsacus in the species count (Table 7; Figure 6).

Also, the difference between the number of species in teasel communities and check communities, averaged over all fields, increased each year after treatment (Table 8).

Later in this paper, Fields B and M are singled out for further analyses; comparisons of slopes as a measure of diversity are presented in Table 9 for these two fields. For any one year and field, the t-value tests the hypothesis that the slope values for the teasel and check communities are the same. Results show that slopes of regression lines

TABLE 6

PERCENT COVER OF DIPSACUS

Field	Date	Rosettes Alone $\bar{x}$ ± s.e.		Flowering Plants Alone $\bar{x}$ ± s.e.		Total Cover $\bar{x}$ ± s.e.	
A	8/69	10.06	2.46	0		10.06	2.46
	5/70	17.06	4.29	3.46	3.09	20.52	5.09
	8/70	19.84	4.83	1.65	0.96	21.50	5.28
	5/71	19.22	5.87	2.78	2.26	22.83	6.39
	8/71	16.64	4.40	14.72	5.56	29.52	7.36
B	8/69	7.01	1.42	0		7.01	1.42
	5/70	22.13	3.34	0.87	0.87	23.00	3.86
	8/70	24.54	3.73	1.15	1.15	25.69	4.02
	5/71	28.73	3.83	10.48	4.02	41.29	7.74
	8/71	40.10	4.77	11.14	4.16	53.50	7.86
C	8/69	1.16	0.35	0		1.16	0.35
	5/70	5.39	1.13	0		5.39	1.13
	8/70	6.87	1.63	0.69	0.69	7.56	1.97
	5/71	15.32	2.97	2.63	2.63	16.37	3.37
	8/71	19.21	3.76	3.00	3.00	22.21	4.09
D	8/69	1.40	0.35	0		1.40	0.35
	5/70	5.07	0.91	0		5.07	0.91
	8/70	6.65	1.27	0		6.65	1.27
	5/71	20.42	3.61	0		20.42	3.61
	8/71	28.37	4.91	0		28.37	4.91
J	8/69	4.80	1.37	0		4.80	1.37
	5/70	6.58	1.99	0		6.58	1.99
	8/70	5.49	1.74	0		5.49	1.74
	5/71	4.31	1.93	0		4.31	1.93
	8/71	5.06	2.36	0		5.06	2.36
K	8/69	0.59	0.18	0		0.59	0.18
	5/70	2.09	1.09	0		2.09	1.09
	8/70	2.55	1.20	0		2.55	1.20
	5/71	3.00	1.38	0		3.00	1.38
	8/71	2.25	1.43	0		2.25	1.43

continued

TABLE 6--Continued

Field	Date	Rosettes Alone $\bar{x}$ ± s.e.		Flowering Plants Alone $\bar{x}$ ± s.e.		Total Cover $\bar{x}$ ± s.e.	
L	8/69	3.86	1.48	0		3.86	1.48
	5/70	8.04	2.68	0.50	0.35	7.99	2.95
	8/70	9.57	3.56	0.55	0.39	10.12	3.84
	5/71	8.74	3.62	4.19	2.88	12.94	6.37
	8/71	6.07	2.54	5.00	3.42	11.06	5.83
M	8/69	13.00	2.80	0		13.00	2.80
	5/70	15.75	3.19	1.92	1.15	18.16	4.25
	8/70	24.46	4.62	1.35	0.76	25.80	5.13
	5/71	23.83	5.79	8.44	2.78	32.28	7.51
	8/71	21.28	4.92	17.78	6.37	39.05	8.55

FIGURE 5

Percent Cover Values of Teasel in Each of Eight Fields from August 1968 to August 1971.

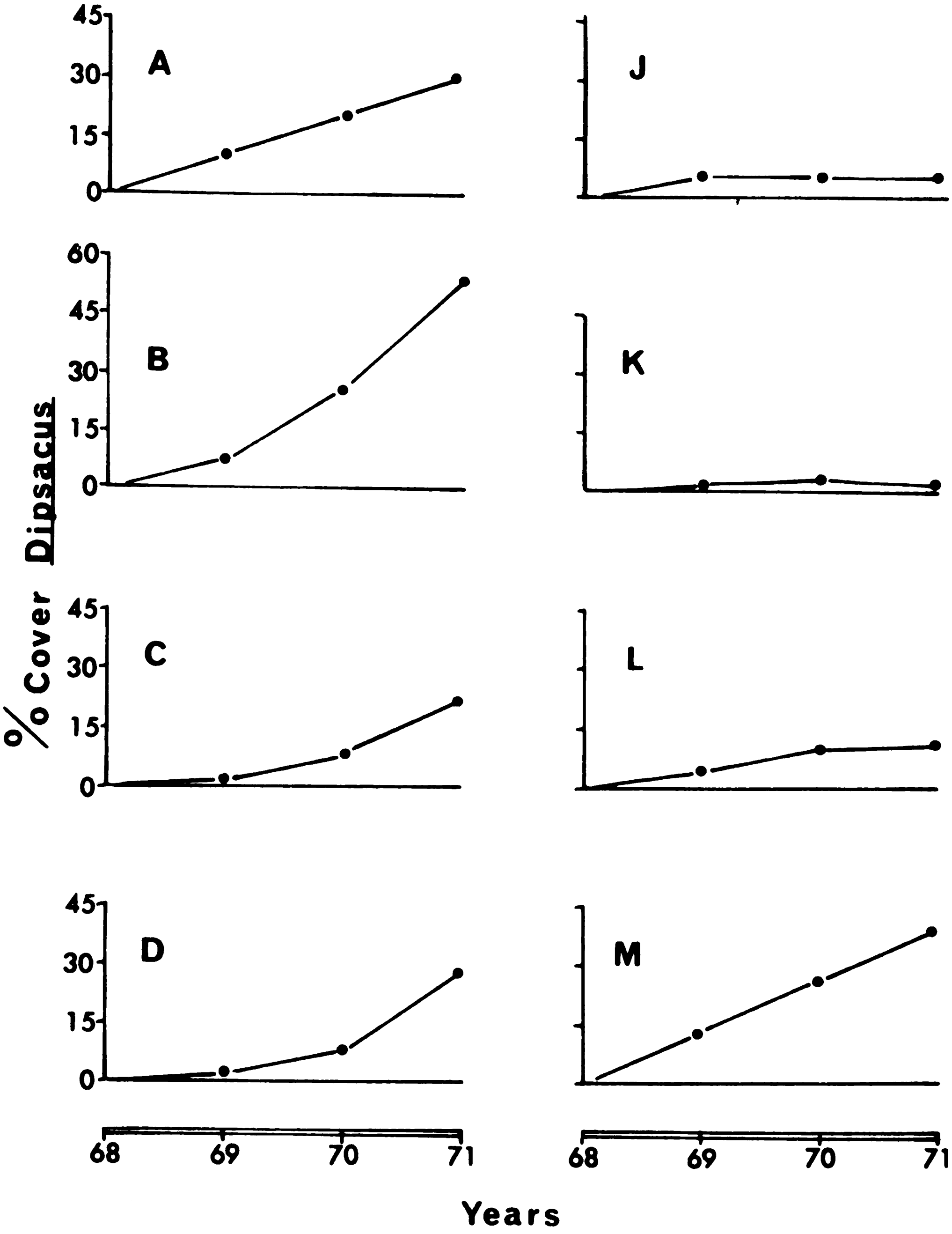

% Cover Dipsacus
A
45
30
15
0
B
60
45
30
15
0
C
45
30
15
0
D
45
30
15
0
J
K
L
M
68
69
70
71
68
69
70
71
Years

FIGURE 5

TABLE 7

NUMBER OF PLANT SPECIES IN TEASEL AND CHECK COMMUNITIES

Field	Date	Teasel Comm. No. species	Check Comm. No. species	Difference ($N_t - N_c$)
A	8/68		34	
	8/69	17	12	5
	8/70	21	18	3
	8/71	17	11	6
B	8/68		36	
	8/69	13	14	-1
	8/70	25	25	0
	8/71	18	14	4
C	8/68		34	
	8/69	9	9	0
	8/70	19	17	2
	8/71	17	17	0
D	8/68		43	
	8/69	15	17	-2
	8/70	37	31	6
	8/71	24	16	8
J	8/68		41	
	8/69	24	19	5
	8/70	26	21	5
	8/71	16	11	5
K	8/68		32	
	8/69	4	3	1
	8/70	9	11	-2
	8/71	5	3	2
L	8/68		41	
	8/69	23	21	2
	8/70	32	31	1
	8/71	14	10	4
M	8/68		38	
	8/69	13	14	-1
	8/70	26	18	8
	8/71	14	15	-1

FIGURE 6

Graphical Representation of the Difference Between the Number of Species in Teasel Communities and the Number of Species in Check Communities ($N_t - N_c$) for Each of Eight Fields from August 1968 to August 1971. The solid line indicates a base line where there is no difference in number of species.

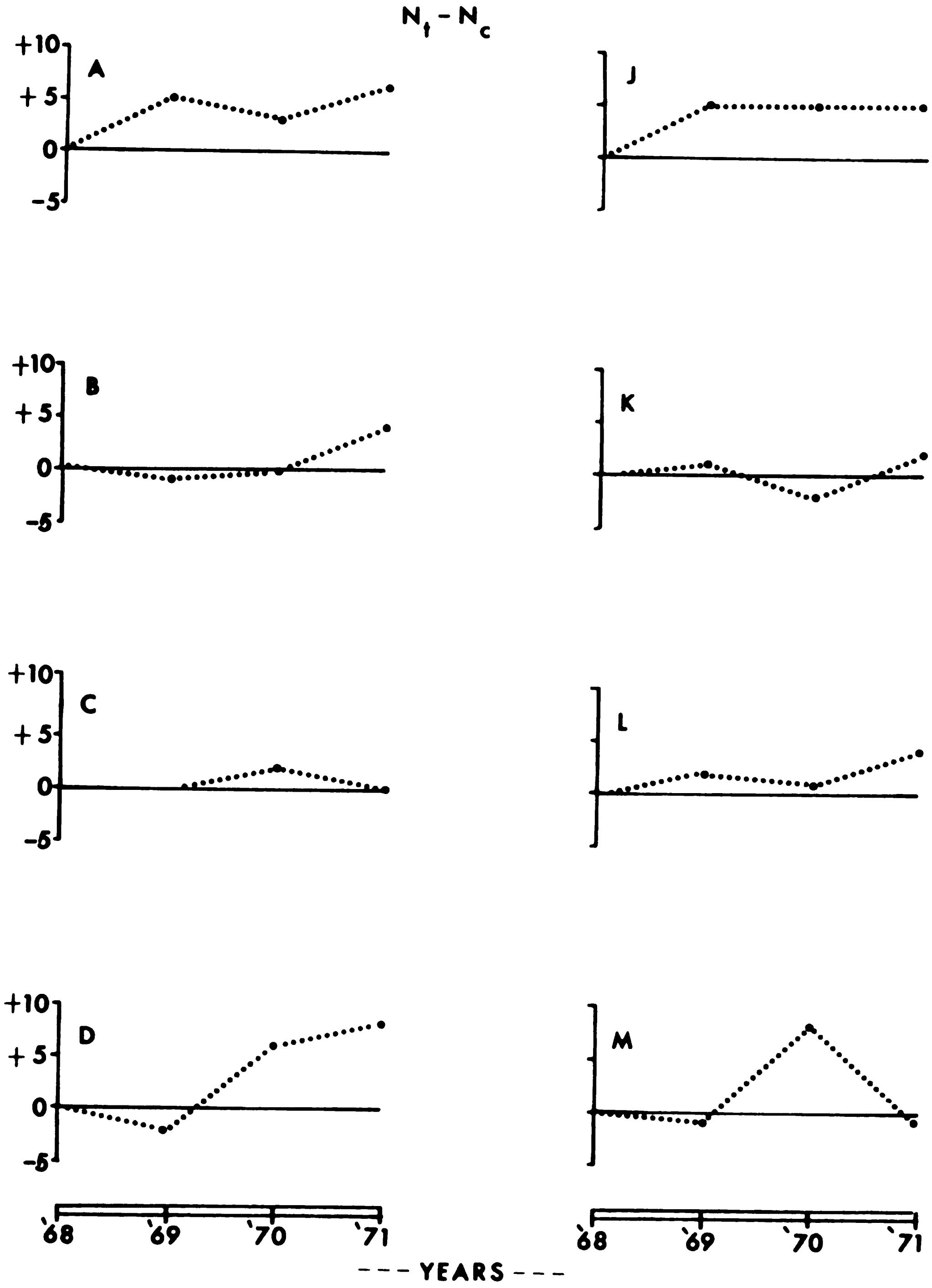


FIGURE 6

TABLE 8

THE MEAN DIFFERENCE, OVER ALL FIELDS, BETWEEN THE NUMBER OF SPECIES IN TEASEL COMMUNITIES AND CHECK COMMUNITIES

Year	$\bar{d}$ $(N_t - N_c)$	s.e.
1969	1.1250	0.9531
1970	2.8750	1.1716
1971	3.5000	1.0690

TABLE 9

SLOPES OF THE MOTOMURA REGRESSIONS AS MEASURES OF THE VARIETY COMPONENT OF DIVERSITY

		Teasel community		Check community		t		
Field	Year	Slope	s.e.	Slope	s.e.	value	df	P
B	1970	-0.3469	0.0543	-0.6690	0.1334	2.4461	14	*
	1971	-0.2369	0.0200	-0.3074	0.0374	1.7625	28	n.s.
M	1970	-0.2316	0.0210	-0.5280	0.0744	4.3144	20	**
	1971	-0.2922	0.0205	-0.2458	0.0226	-1.4900	25	n.s.

n.s. = $P > 0.05$, not significantly different

* = $0.01 < P < 0.05$

** = $P < 0.01$

in teasel communities are significantly greater than those for check communities in both fields in 1970; hence, there were a greater number of species.

Information Measure of Diversity

Estimates of community diversity with accompanying standard errors were calculated in each community at each sample point in time (Figures 7, 8, 9, and 10).

Differences in diversities (H'_{com} values) between teasel communities and check communities in each of the eight fields and for each time, were used in a Wilcoxon rank-sum test to determine, on an overall basis, the effect of teasel treatment on the indigenous plant communities. Results show that teasel communities had a significantly higher H'_{com} ($P < 0.005$, $T=29$, $N=24$).

Within each field, a non-pooled t-test was used to compare the two communities at each time (Table 10). In three of the eight fields (A, B, and M) teasel communities had significantly higher diversities than their corresponding check communities for three summers (1969, 1970, 1971) after teasel was introduced. In three fields (C, J, and K) the diversity of the teasel community was significantly higher than the check communities for two years after teasel introduction. In one field (L) diversity was higher in the teasel community for the first year only; in Field D, no significant difference in diversity is demonstrated for any year.

FIGURE 7

Diversity Measures for Teasel Communities and Check Communities in Fields A and B from 1968 to 1971. Each H' is accompanied by a bracketed line showing 2 standard errors above and 2 standard errors below. The dotted line represents measurements for teasel communities and the solid line represents measurements for check communities.

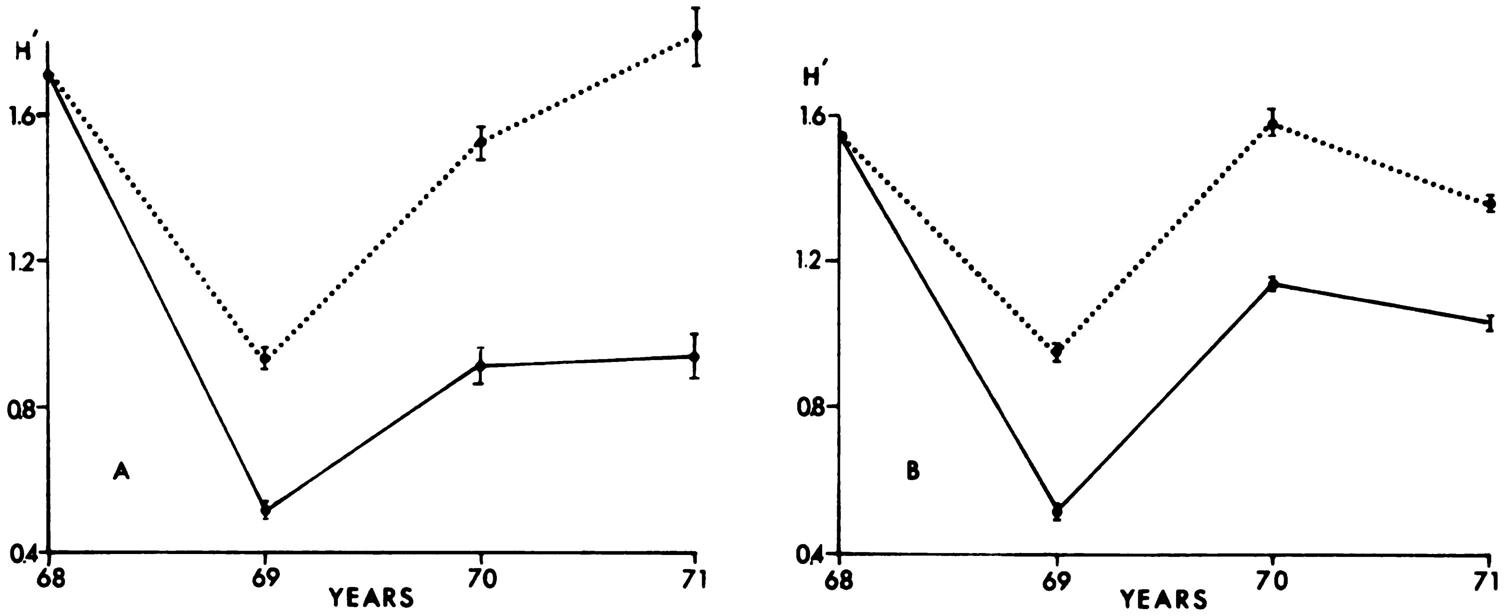


FIGURE 7

FIGURE 8

Diversity Measures for Teasel Communities and Check Communities in Fields D and C from 1968 to 1971. Each H' is accompanied by a bracketed line showing 2 standard errors above and 2 standard errors below. The dotted line represents measurements for teasel communities and the solid line represents measurements for check communities.

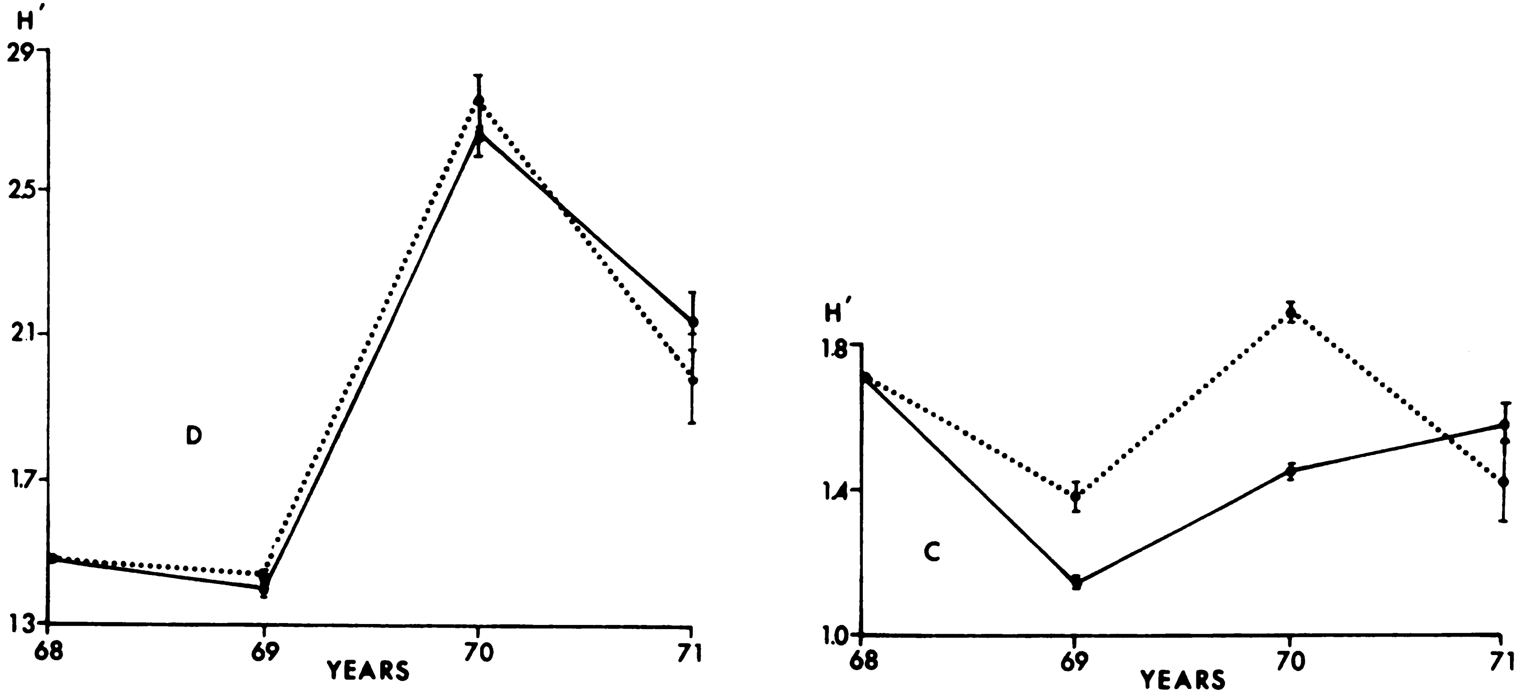


FIGURE 8

FIGURE 9

Diversity Measures for Teasel Communities and Check Communities in Fields J and K from 1968 to 1971. Each H' is accompanied by a bracketed line indicating 2 standard errors above and 2 standard errors below. The dotted line represents measurements for teasel communities and the solid line represents measurements for check communities.

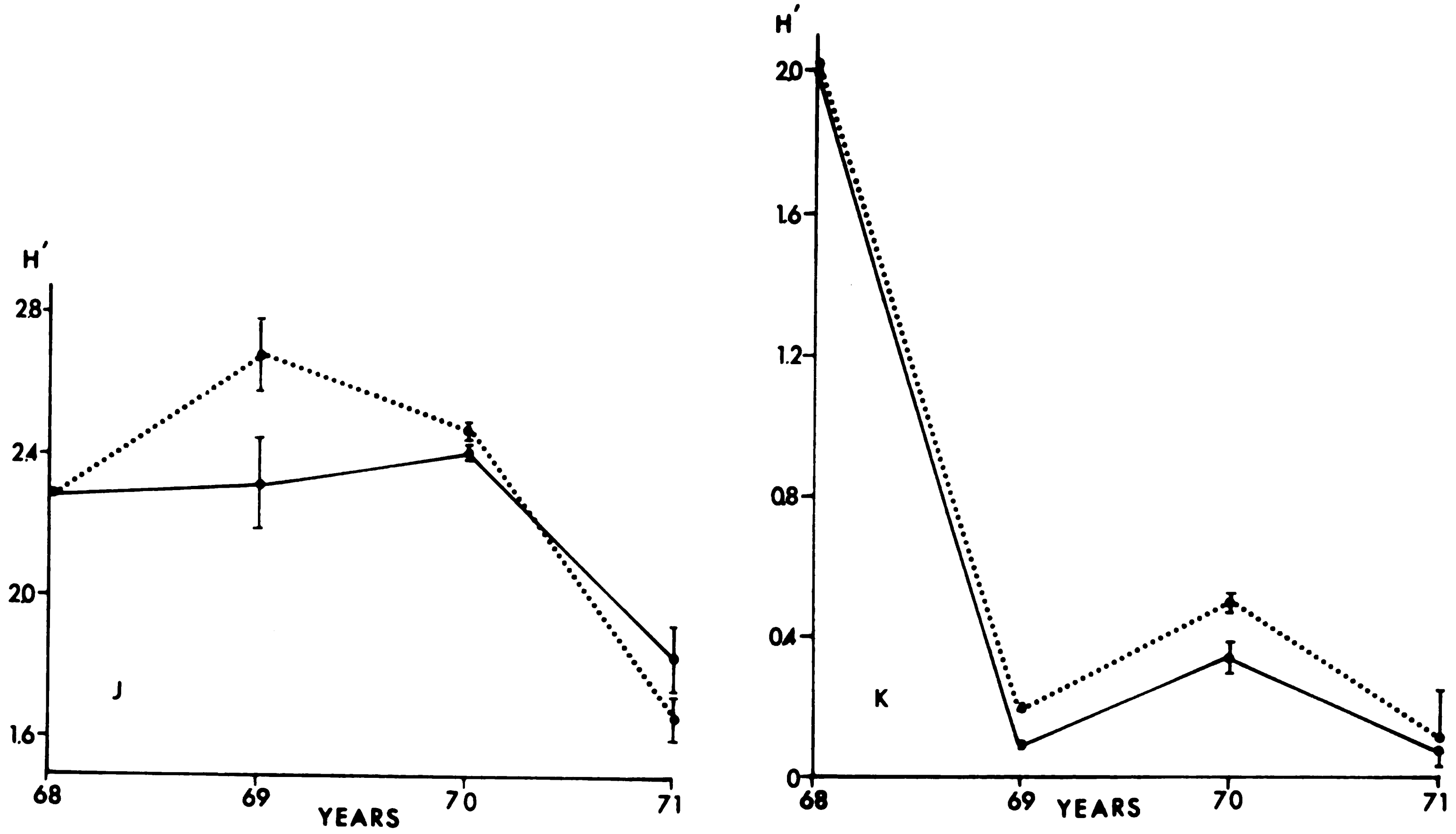


FIGURE 9

FIGURE 10

Diversity Measures for Teasel Communities and Check Communities in Fields L and M from 1968 to 1971. Each H' is accompanied by a bracketed line indicating 2 standard errors above and 2 standard errors below. The dotted line represents measurements for teasel communities and the solid line represents measurements for check communities.

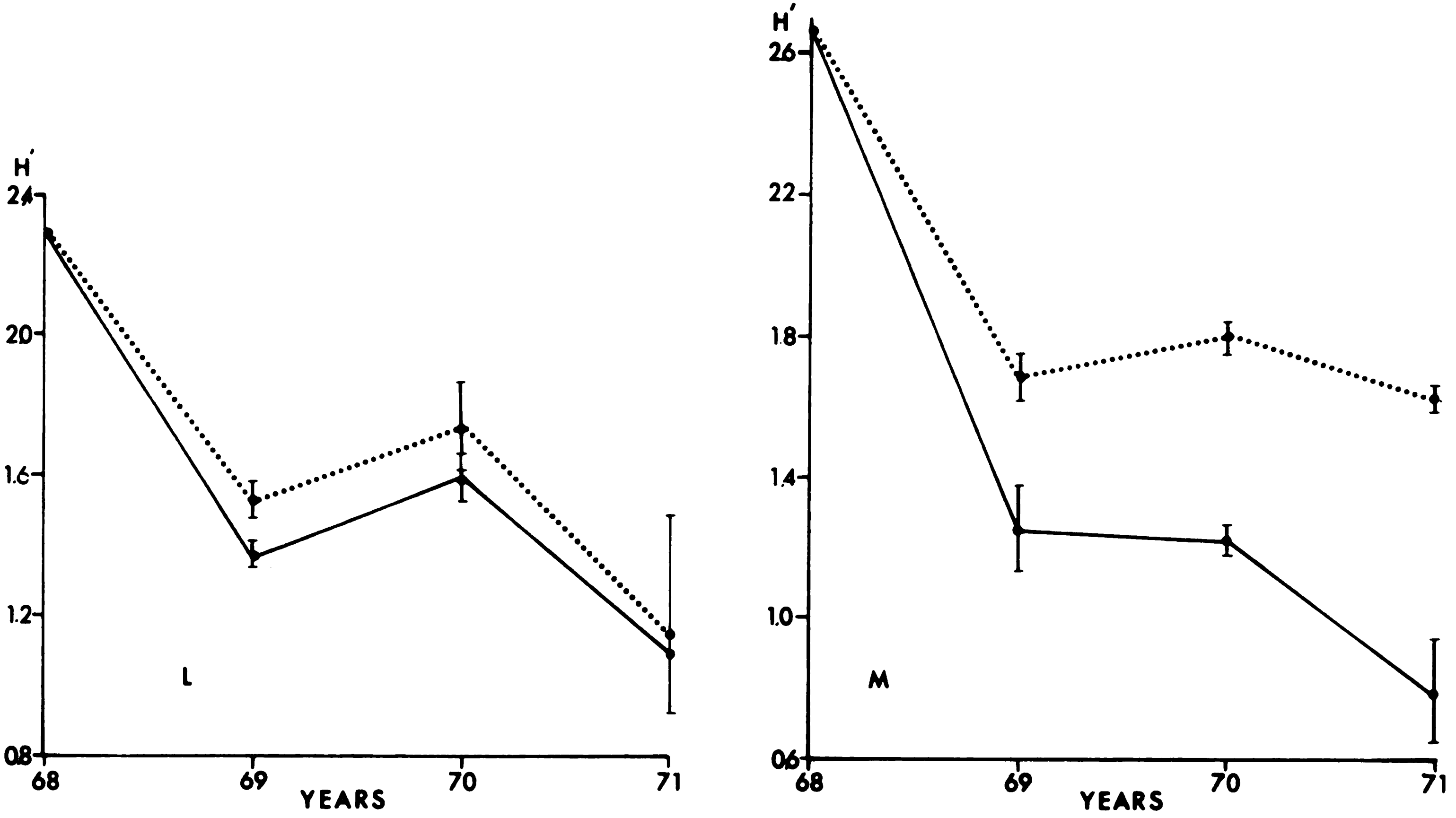

H'
2.4
2.0
1.6
1.2
0.8
68
69
70
71
YEARS
L
H'
2.6
2.2
1.8
1.4
1.0
0.6
68
69
70
71
YEARS
M

FIGURE 10

TABLE 10

DIFFERENCES IN DIVERSITY (H') IN TEASEL AND CHECK COMMUNITIES IN EIGHT FIELDS FROM 1968 TO 1971

Field	Date	Treatment		Check		t-Value	Degrees freedom	Probability
		H'_{com}	s.e.	H'_{com}	s.e.			
A	8/68			1.71				
	8/69	0.92909	0.01549	0.51133	0.01140	21.72438	12	<<0.01 **
	8/70	1.52350	0.01949	0.90937	0.02449	19.62076	17	<<0.01 **
	8/71	1.80750	0.03987	0.94333	0.03178	16.94783	3	<<0.01 **
B	8/68			1.55				
	8/69	0.94947	0.01048	0.50900	0.00707	34.84731	14	<<0.01 **
	8/70	1.58142	0.01303	1.13769	0.00447	32.20101	9	<<0.01 **
	8/71	1.36000	0.00836	1.02500	0.00948	26.50316	4	<<0.01 **
C	8/68			1.71				
	8/69	1.37833	0.01843	1.14578	0.00632	11.93175	14	<<0.01 **
	8/70	1.88769	0.01140	1.45200	0.01095	27.55787	13	<<0.01 **
	8/71	1.42333	0.05357	1.58500	0.02863	- 2.66167	4	0.05<P<0.10 ns
D	8/68			1.48				
	8/69	1.39714	0.01048	1.43000	0.01140	- 2.12136	15	0.05<P<0.10 ns
	8/70	2.66944	0.04159	2.74545	0.03714	- 1.36316	19	0.10<P<0.20 ns
	8/71	2.1400	00.03754	1.98000	0.06090	2.23619	3	0.10<P<0.20 ns

J	8/68			2.28					
	8/69	2.68692	0.05167	2.31714	0.06565	4.42638	13	<0.01	**
	8/70	2.47571	0.01341	2.41857	0.01140	3.24659	6	0.01<P<0.02	*
	8/71	1.66500	0.03492	1.84000	0.04582	- 3.03766	2	0.05<P<0.10	ns
K	8/68			2.02					
	8/69	0.19750	0.00000	0.08666	0.00316	35.07594	4	<<0.01	**
	8/70	0.49500	0.01341	0.34500	0.02213	5.79598	6	<0.01	**
	8/71	0.12500	0.06496	0.07500	0.02489	0.71870	2	--	ns
L	8/68			2.28					
	8/69	1.52363	0.02701	1.37333	0.01760	4.66191	9	<0.01	**
	8/70	1.74200	0.06625	1.59555	0.03316	1.97665	9	0.05<P<0.10	ns
	8/71	1.14600	0.17291	1.10166	0.08899	0.22800	5	--	ns
M	8/68			2.66					
	8/69	1.68421	0.03224	1.25265	0.06212	6.16514	15	<0.01	**
	8/70	1.79714	0.02302	1.21642	0.01974	19.14671	13	<<0.01	**
	8/71	1.62250	0.01870	0.78666	0.07791	10.43235	3	<0.01	**

** Very significantly different (99% confidence)

 * Significantly different (95% confidence)

ns Not significantly different

It appears that the introduction of teasel tends to increase diversity in almost all fields (87.5%) during the first year after treatment, even when the percent cover of teasel rosettes is as low as 1% (as in Fields C and K). This influence of teasel introduction on diversity may continue for the following two growing seasons, either leveling off, or continuing to increase. There was no correlation between percent cover of teasel and the change in diversity (H'_{com}) ($r = 0.5212$, $n = 24$).

The Evenness Component of Diversity

In an attempt to determine if the higher diversity in teasel communities was due mainly to a difference in "evenness", H'_{com} and standard error values were converted to an H' and s.e. in base s (s = number of species), designated J'_{com}. The results of a Wilcoxon rank-sum test, using values over all fields and points in time, show that teasel communities have a significantly higher J'_{com} than check communities ($P < 0.005$, $T=53$, $N=24$); that is, the plant species are more evenly distributed in relative amounts within the teasel communities than within the check communities.

Examination of J'_{com} values in individual fields (Table 11) show that in five of the eight fields, teasel communities had a more even distribution of species than did the check communities. Three of these (A, B, and M)

TABLE 11

DIFFERENCES IN EVENNESS (J') IN TEASEL AND CHECK COMMUNITIES IN EIGHT FIELDS FROM 1968 TO 1971

Field	Date	Treatment			Check				Confidence Limit Overlap
		J'_{com}	s.e.	n	J'_{com}	s.e.	n	$J'_{Tcom}-J'_{Ccom}$	
A	8/68				0.34		34		
	8/69	0.22730	0.00378	17	0.14263	0.00318	12	0.09	**
	8/70	0.34686	0.00443	21	0.21809	0.00587	18	0.13	**
	8/71	0.44222	0.00975	17	0.27269	0.00918	11	0.17	**
B	8/68				0.30		36		
	8/69	0.25659	0.00283	13	0.13369	0.00185	14	0.12	**
	8/70	0.34054	0.00280	25	0.24499	0.00096	25	0.10	**
	8/71	0.32617	0.00200	18	0.26922	0.00248	14	0.06	**
C	8/68				0.34		34		
	8/69	0.43482	0.00581	9	0.36146	0.00199	9	0.07	**
	8/70	0.44438	0.00268	19	0.35524	0.00267	17	0.08	**
	8/71	0.34822	0.01310	17	0.38778	0.00700	17	-0.04	*
D	8/68				0.27		43		
	8/69	0.35762	0.00268	15	0.34986	0.00278	17	0.01	--
	8/70	0.51245	0.00798	37	0.55417	0.00749	31	-0.04	*
	8/71	0.46677	0.00818	24	0.49501	0.01522	16	-0.03	--

J	8/68				0.42		41		
	8/69	0.58606	0.01127	24	0.54548	0.01545	19	0.05	*
	8/70	0.52671	0.00285	26	0.55064	0.00259	21	-0.02	**
	8/71	0.41626	0.00873	16	0.53190	0.01324	11	-0.11	**
K	8/68				0.40		32		
	8/69	0.09875	0.0000005	4	0.05467	0.00199	3	0.05	**
	8/70	0.15615	0.00423	9	0.09973	0.00639	11	0.06	**
	8/71	0.05383	0.02797	5	0.04732	0.01570	3	0.00	--
L	8/68				0.42		41		
	8/69	0.33683	0.00597	23	0.31267	0.00400	21	0.03	*
	8/70	0.34840	0.01325	32	0.32206	0.00669	31	0.03	*
	8/71	0.30100	0.04541	14	0.33164	0.02678	10	-0.03	--
M	8/68				0.51		38		
	8/69	0.45515	0.00871	13	0.32901	0.01631	14	0.13	**
	8/70	0.38235	0.00489	26	0.29173	0.00473	18	0.09	**
	8/71	0.42616	0.00491	14	0.20135	0.01994	15	0.23	**

** 99% confidence limits do not overlap the means being compared

* 95% confidence limits do not overlap the means being compared

-- 95% confidence limits overlap the means being compared

n Number of species

show significant differences for three summers (1969, 1970, 1971) after teasel-introduction and two (K and L) show significant differences for the first two years.

Productivity

Mean values of above-ground standing crop (grams dry weight per square meter) and accompanying standard errors, corrected for woody perennials and biennials, are given in Table 12 for 1970 and 1971. These values estimate the herbaceous plant above-ground annual net production (henceforth called "productivity").

Differences in productivity between teasel and check communities in each of the eight fields and for the two sampling times were used in a Wilcoxon rank-sum test to determine, on an over-all basis, the effect of teasel introduction on the productivity of the indigenous plant communities. Results failed to show any over-all effect ($P > 0.05$, $T=44$, $N=16$).

When the fields with flowering plants of teasel (A, 1970, 1971; B, 1971; C, 1971; J, 1970; L, 1970, 1971; M, 1970, 1971) are considered separately from those containing only teasel rosettes (B, 1970; C, 1970; D, 1970, 1971; J, 1971; K, 1970, 1971) and Wilcoxon rank-sum tests are applied to each of the groups, the results are different. In fields where some teasel plants have reached flowering stage, productivity is significantly greater in

TABLE 12

ABOVE-GROUND PRODUCTIVITY: TEASEL AND CHECK COMMUNITIES ($\overline{x}$ gms$\cdot$m^{-2})

Field	Year		Field Sample		Corrected for Woody Perenniels		Corrected for Teasel "Biennielness"	Difference Between Teasel and Check Communities	Confidence Intervals Overlap
			$\overline{x}$	s.e.	$\overline{x}$	s.e.			
A	1970	T	430.89	31.72	429.74	32.20	413.76		
		C	343.12	42.77	343.04	42.82		70.72	n.s.
	1971	T	610.99	68.75	504.02	35.30	473.18		
		C	529.41	64.29	422.01	38.99		51.17	n.s.
B	1970	T	248.69	24.55	239.55	27.23	239.55		
		C	278.82	9.16	249.72	26.72		-10.17	n.s.
	1971	T	626.95	66.31	594.65	56.357	577.95		
		C	627.73	164.69	422.60	30.75		155.35	**
C	1970	T	523.19	76.05	313.37	42.12	313.37		
		C	422.96	66.19	278.56	23.83		34.81	n.s.
	1971	T	684.36	114.09	298.59	31.48	297.08		
		C	419.74	63.14	308.38	53.99		-11.30	n.s.
D	1970	T	238.37	23.99	186.25	10.94	186.25		
		C	234.26	19.85	233.30	20.15		-47.05	*
	1971	T	425.95	89.11	246.46	17.44	246.46		
		C	521.15	132.39	273.31	33.27		-26.85	n.s.

	1971	T	425.95	89.11	246.46	17.44	246.46		
		C	521.15	132.39	273.31	33.27		-26.85	n.s.
J	1970	T	441.72	136.25	208.28	20.72	208.28		
		C	663.05	22.75	209.55	22.29		- 5.17	n.s.
	1971	T	805.56	114.76	226.93	22.07	204.38		
		C	878.53	282.61	219.73	56.75		7.20	n.s.
K	1970	T	333.64	15.66	324.17	20.33	324.17		
		C	332.88	32.75	312.48	13.29		11.69	n.s.
	1971	T	315.91	65.98	311.51	65.33	311.51		
		C	367.64	68.83	362.97	68.51		-51.46	n.s.
L	1970	T	352.86	46.71	343.40	49.88	340.47		
		C	381.09	29.52	377.67	30.82		-37.20	n.s.
	1971	T	450.66	83.39	423.11	90.09	401.65		
		C	526.49	130.92	361.69	43.22		39.96	n.s.
M	1970	T	338.08	23.75	333.77	24.73	315.01		
		C	283.00	37.26	245.47	17.52		69.54	**
	1971	T	604.39	81.29	563.67	67.37	551.43		
		C	390.84	11.77	368.68	20.55		182.75	**

T = teasel community
C = check community
* = 95% confidence interval does not overlap mean being compared
** = 99% confidence interval does not overlap mean being compared
ns = no significant difference

teasel communities than in check communities ($P=0.027$, $T=6$, $n=9$). In fields where all teasel plants are in the rosette stage, no significant differences in productivity occur ($P > 0.05$, $T=9$, $n=7$). That is, in fields where the introduced teasel has developed to the point of producing flowering stalks, there is a significant increase in community primary productivity over that of the indigenous non-teasel plant community.

A more detailed look at differences between teasel community productivity and check community productivity by individual field and date (Table 12) show significantly higher productivities in teasel communities in Fields B (1971) and M (1970 and 1971). These two fields promised to be the most interesting to analyze further.

Graphic representation of 1970 and 1971 productivity in Fields B and M are found in Figures 11 and 12. Here it is more readily evident that (1) total community productivity increased from 1970 to 1971, and that (2) teasel communities had a greater productivity than check communities, the differences being accounted for by productivity of the flowering plants of teasel.

Field B and Field M productivity totals are broken down into species values in Tables 13 and 14. Where comparison of means and standard errors are possible, there is no significant difference in the productivity of any species (other than Dipsacus) between the teasel community and check community for either 1970 and 1971.

FIGURE 11

Net Primary Productivity in Teasel Communities and Check Communities in Field B in 1970 and 1971. In each case productivity measures for teasel flowering plants, teasel rosettes, and other vegetation are represented. The horizontal dotted line through the teasel flowering plant category shows the corrected total productivity when the community productivity is corrected for "biennialness." Total productivity values are accompanied by line segments representing a 95% confidence limit.

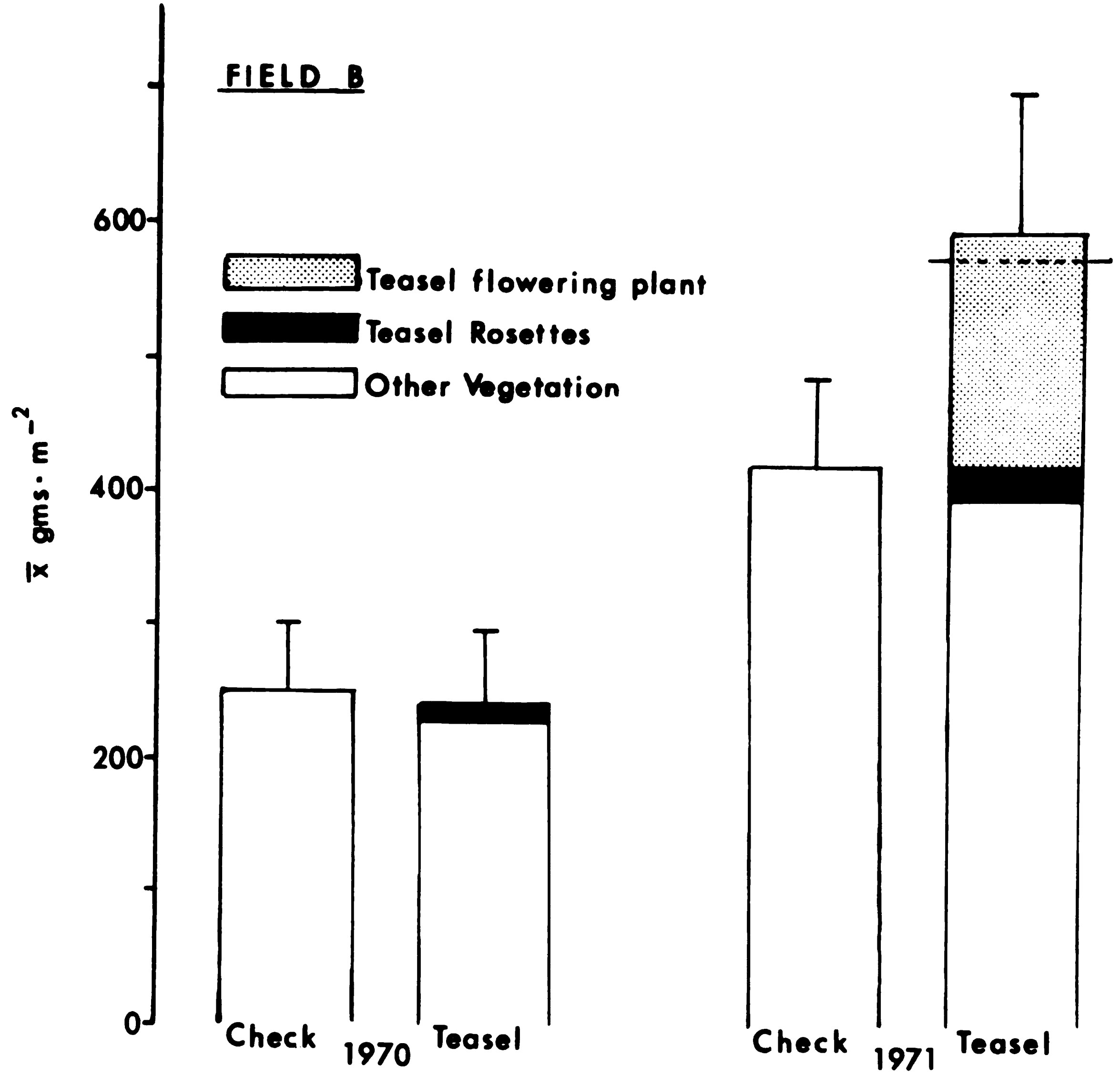

FIELD B
Teasel flowering plant
Teasel Rosettes
Other Vegetation
$\bar{x}$ gms · m^{-2}
600
400
200
0
Check
1970
Teasel
Check
1971
Teasel

FIGURE 11

FIGURE 12

Net Primary Productivity in Teasel Communities and Check Communities in Field M in 1970 and 1971. In each case productivity measures for teasel flowering plants, teasel rosettes, and other vegetation are represented. The horizontal dotted line through the teasel flowering plant category shows the corrected total productivity when the community productivity is corrected for "biennialness." Total productivity values are accompanied by line segments representing a 95% confidence limit.

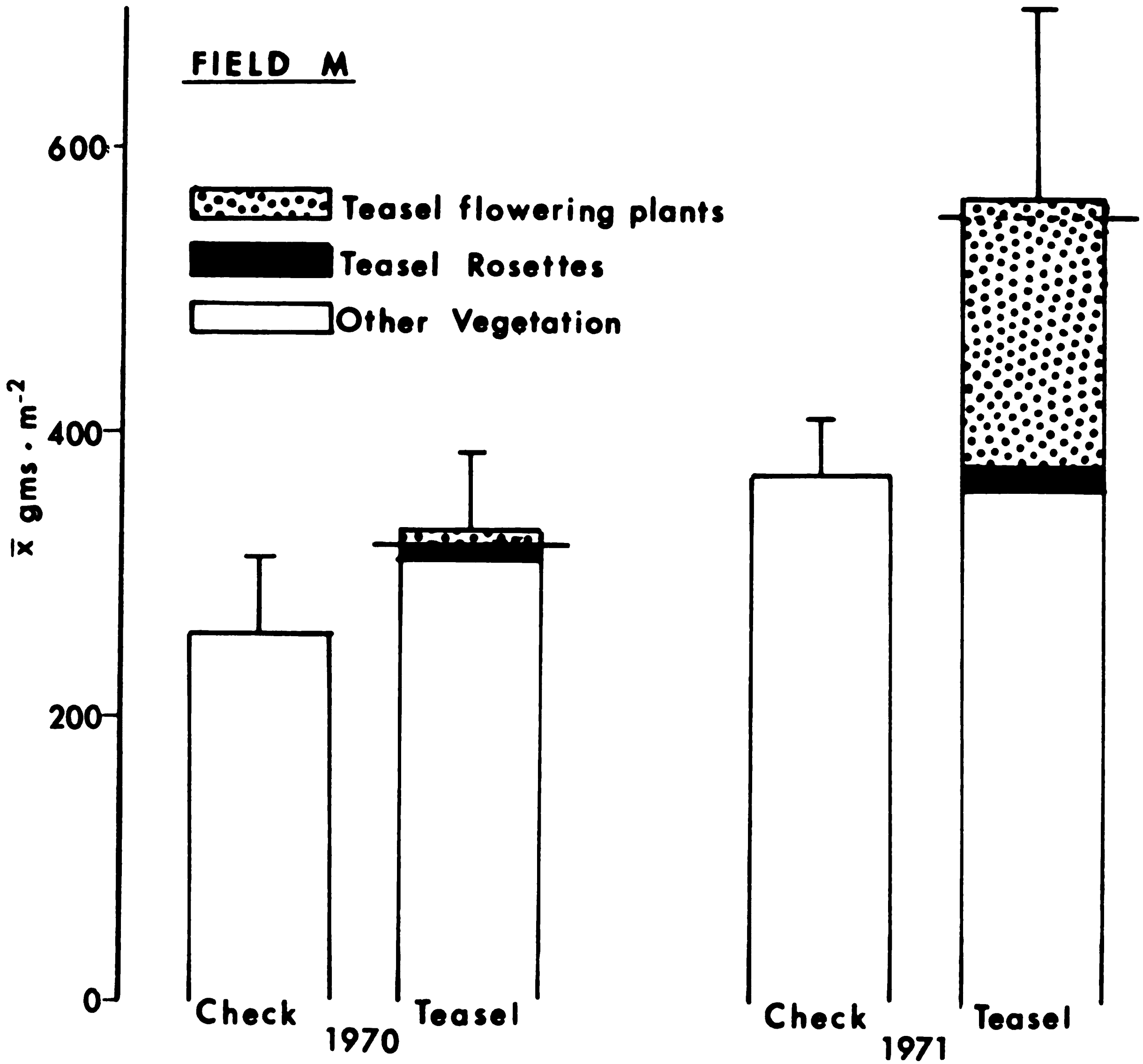

FIELD M
Teasel flowering plants
Teasel Rosettes
Other Vegetation
$\bar{x}$ gms · m^{-2}
600
400
200
0
Check
Teasel
1970
Check
Teasel
1971

FIGURE 12

TABLE 13

PRIMARY PRODUCTIVITY OF SPECIES IN FIELD B IN 1970 AND 1971

Above-ground Productivity (gms·m^{-2})	1970				1971			
	Teasel Comm.		Check Comm.		Teasel Comm.		Check Comm.	
Field B	$\overline{x}$	s.e.	$\overline{x}$	s.e.	$\overline{x}$	s.e.	$\overline{x}$	s.e.
Achillea millifolium	0		0		0		0.667	0.667
Agropyron repens	223.933	28.119	249.100	26.670	377.150	48.379	414.600	33.092
Ambrosia spp.	0.067	0.067	0.030	0.030	0		0	
Aster pilosus	0		0		1.030	0.996	0.107	0.085
Barbarea vulgaris	0		0		0.015	0.015	0.020	0.020
Chenopodium album	0		0		0.015	0.015	0	
Circium arvense	0.400	0.327	0		0.200	0.107	0.267	0.267
Dipsacus sylvestris	14.467	3.214	0		199.900	49.897	0	
Erigeron annuus	0.067	0.067	0.080	0.080	0.180	0.147	0.040	0.025
Erigeron canadensis	0		0		0.050	0.050	0.020	0.020
Erigeron strigosus	0.267	0.198	0.230	0.192	0		0	
Lactuca biennis	0.067	0.067	0		0		0	
Lychnis alba	0		0		0.300	0.300	1.467	1.176
Medicago lupulina	0.067	0.067	0.300	0.300	0		0	
Melilotus spp.	0		0.030	0.030	0.200	0.200	0	
Oxalis stricta	0		0		0		0.040	0.025
Poa spp.	0		0		1.450	1.339	4.200	4.200
Potentilla recta	0		0		0.650	0.650	0.067	0.067
Rumex crispis	0		0		12.700	12.700	0	
Salvia spp.	0.133	0.133	0		0		0	
Solidago canadensis	0		0		0.580	0.546	0	
Taraxacum officinale	0		0		0.015	0.015	0.040	0.025
Trifolium repens	0.020	0.020	0		0		1.067	1.067
Verbascum thapsus	0		0		0.050	0.050	0	
Unknown mint seedling	0		0		0.165	0.103	0	
Total excluding Rhus**	239.55	27.23	249.72	26.72	594.65	56.36	422.60	30.75
Rhus typhina	9.133	8.065	29.100	22.528	32.300	14.767	205.133	168.228
Total including Rhus	248.69	24.55	278.82	9.16	626.95	66.31	627.73	164.69

TABLE 14

PRIMARY PRODUCTIVITY OF SPECIES IN FIELD M IN 1970 AND 1971

Above-ground Productivity (gms·m^{-2})	1970				1971			
	Teasel Comm.		Check Comm.		Teasel Comm.		Check Comm.	
Field M	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.
Achilles millifolium	0		0		0.015	0.015	0	
Agropyron repens	298.000	20.341	233.067	20.713	315.500	27.529	334.800	14.979
Aster pilosus	0.815	0.578	0.333	0.262	0.865	0.809	3.440	1.925
Aster sagittifolius	0.065	0.050	0		0		0	
Daucus carota	0.015	0.015	0		0		0.080	0.080
Dipsacus sylvestris	28.965	14.929	0		223.065	64.305	0	
Erigeron annuua	0.050	0.050	0.133	0.133	0.600	0.490	6.024	3.447
Erigeron canadensis	0		0		0.800	0.800	0	
Lactuca biennis	0.110	0.046	0		0		0	
Lychnis alba	0.230	0.197	0		1.150	0.776	0.320	0.320
Medicago lupulina	0.145	0.059	0.067	0.067	0		0	
Melilotus spp.	0		0		1.365	1.348	9.360	8.965
Oxalis stricta	0.015	0.015	0		0		0.024	0.024
Phleum pratense	1.550	1.550	0		0		0	
Plantago spp.	0		0		0		0.080	0.080
Poa spp.	3.050	2.775	0.333	0.333	9.115	3.807	13.440	8.844
Potentilla recta	0.100	0.100	0.067	0.067	0		0.160	0.098
Rumex crispis	0		0		2.050	2.050	0	
Solidago canadensis	0		11.467	10.387	8.950	8.950	0.240	0.240
Taraxacum officinale	0.315	0.298	0		0.150	0.105	0.288	0.069
Verbascum thapsus	0.350	0.232	0		0		0	
Unknown mint seedling	0		0		0.050	0.050	0	
Total excluding Rhus **	333.77	24.73	245.47	17.52	563.67	67.37	368.68	20.55
Rhus typhina	4.300	3.761	37.533	36.035	40.715	37.598	22.160	20.771
Total including Rhus	338.08	23.75	283.00	37.26	604.39	81.29	390.84	11.77

Thus, it would seem that not only does the total community productivity increase when teasel is successfully introduced, but that the indigenous plant species are relatively unaffected in their respective annual accumulations of dry weight biomass.

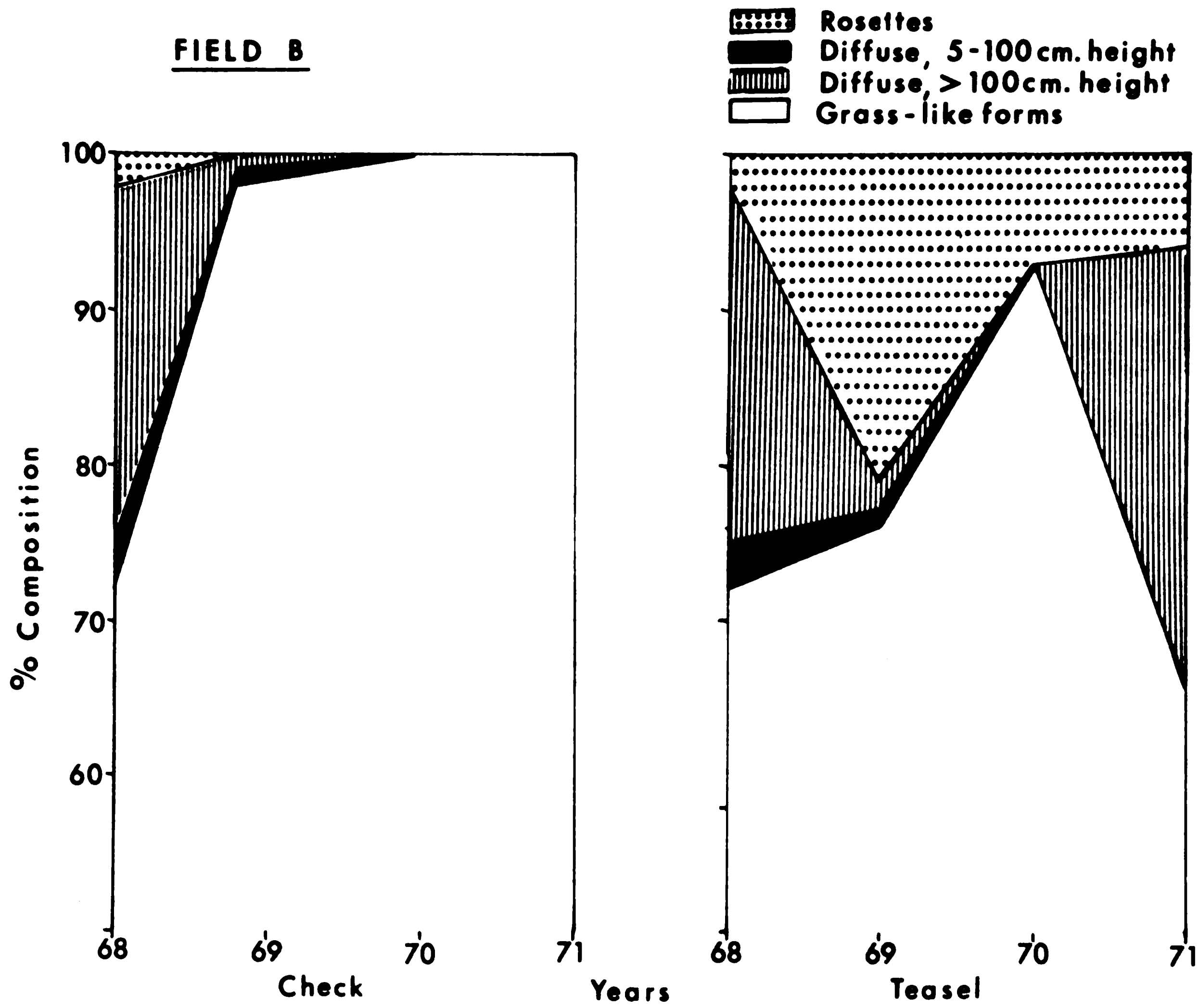
Physical Structure

In each field, the teasel and check communities were analyzed on the basis of the ten categories in the Physical Structure classification (Figure 4 and Table 4), and the results expressed as percent portions of the total plant community for each year from I968-1971. Fields B and M are used as examples. (Figures 13 and 14; categories less than one percent are excluded.) In the check communities of both fields, the general tendency is for the grass-like forms to increase in relative amounts (from 72 and 71% to 100 and 96%, respectively), with decreasing values for rosettes, 5-100 cm. diffuse forms, and >100 cm. diffuse forms.

However, in the teasel communities of both fields, the grass-like forms do not achieve such relative dominance. Instead, the rosette forms increase greatly the first year after teasel introduction (1969) (from 2 and 2% to 21 and 20%, respectively), then level off to between 3 to 7% for the next two years. The 5-100 cm. diffuse forms achieve the same relative percentages as those in the check communities, and are not found after 1969; the >100 cm. diffuse

FIGURE 13

The Physical Structure of Field B Expressed as Percent Portions of Each Category for the Check Community and for the Teasel Community from 1968 to 1971.



FIELD B

FIGURE 13

FIGURE 14

The Physical Structure of Field M Expressed as Percent Portions of Each Category for the Check Community and for the Teasel Community from 1968 to 1971.

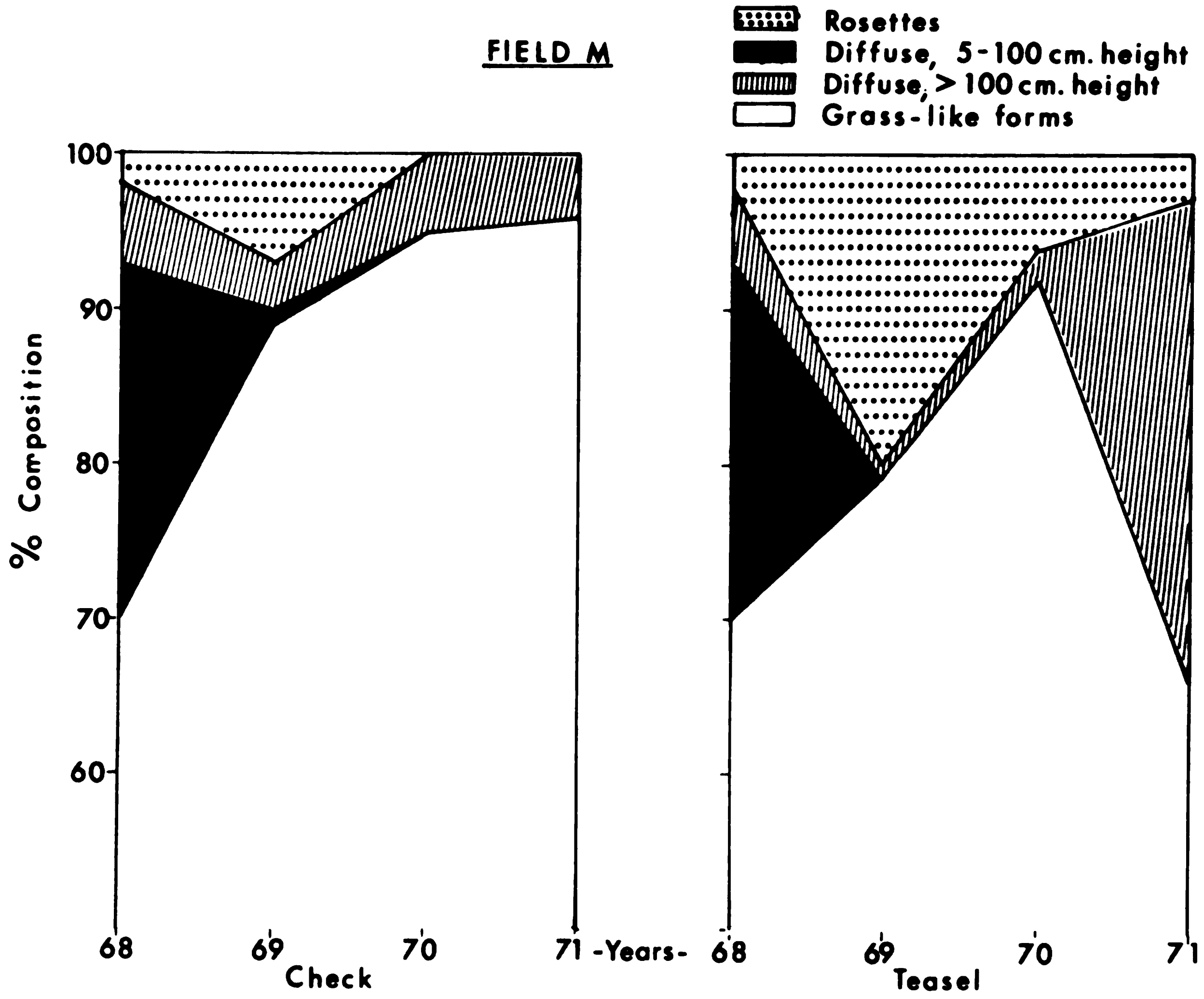

FIELD M
Rosettes
Diffuse, 5-100 cm. height
Diffuse, > 100 cm. height
Grass-like forms
% Composition
100
90
80
70
60
68
69
70
71
-Years-
68
69
70
71
Check
Teasel

FIGURE 14

forms also mimic those in the check communities until the third year after teasel introduction, when relative amounts go from near 0 and 2% in 1970 to 28 and 31%, in Fields B and M, respectively.

Absolute values of above-ground standing crop expressed as mean grams dry weight in Fields B and M in 1971 are presented in Figure 15. These data support the idea that (a) new physical form(s) (rosettes and >100 diffuse forms) had been added to the indigenous plant community, without decreasing the dominant grass-like forms in net productivity.

Biological Structure

In each field, the teasel and check communities were analyzed on the basis of the ten categories in the Biological Structure classification (Table 5), and the results expressed as percent portions of the total plant community for each year from 1968 to 1971. Fields B and M serve as examples (Figures 16 and 17; categories less than one percent excluded). In the check communities of both fields (in 1968, respectively entering the second and first growing season after abandonment), the general tendency is one found in much of the literature on early succession (Oosting, 1942; Odum, 1960; Bazzaz, 1968). There was an increase in relative amount of perennial grasses (from 71 and 67% to 99 and 96%, respectively) from 1968 to 1971, and a decrease in annual grasses and annual dicotyledonous plants (from a

FIGURE 15

The Physical Structure of Fields B and M Expressed as Productivity Values in Each Category for the Check Communities and for the Teasel Communities in 1971.

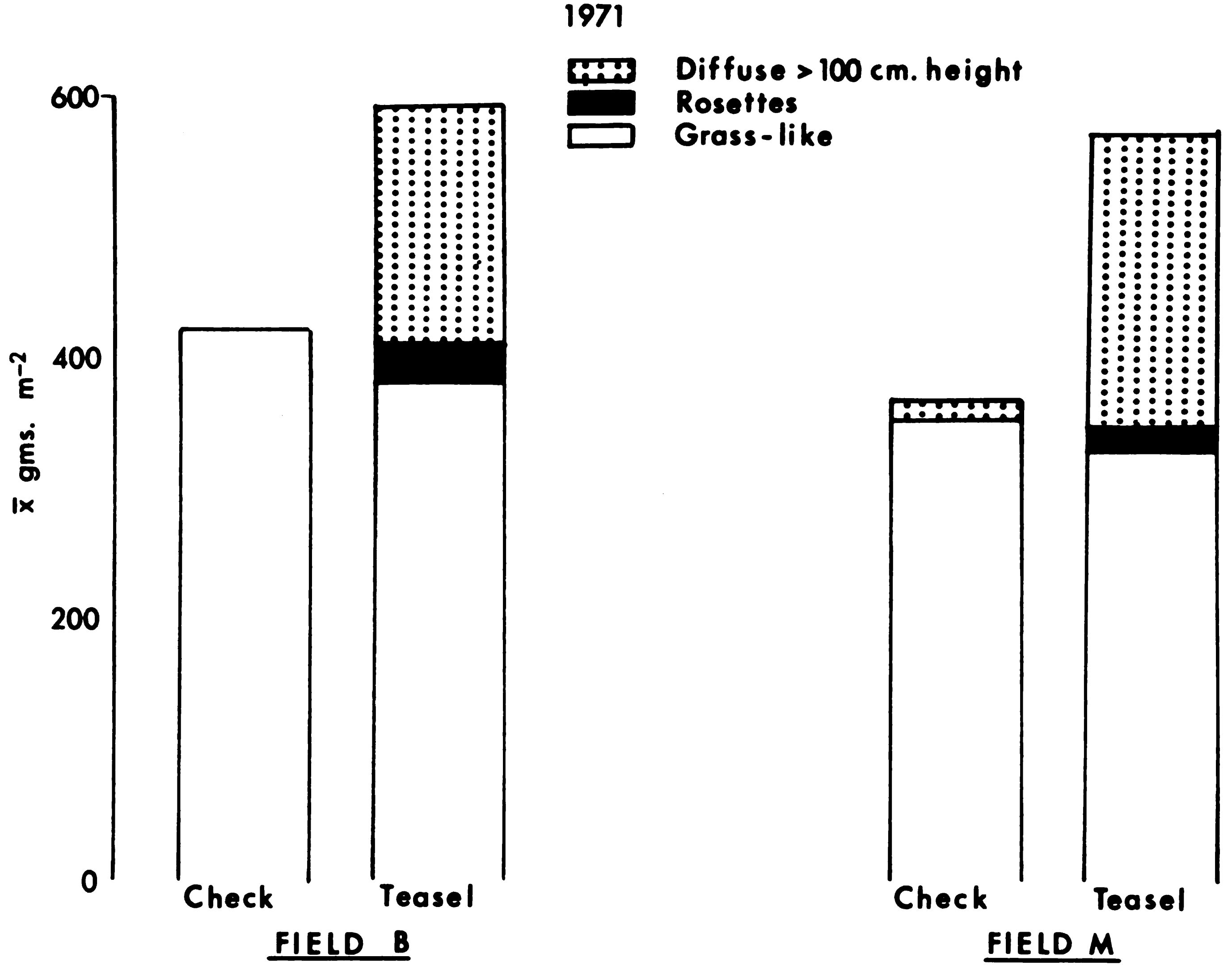

1971
▨ Diffuse > 100 cm. height
■ Rosettes
□ Grass-like
600
400
200
0
$\bar{x}$ gms. m^{-2}
Check
Teasel
FIELD B
Check
Teasel
FIELD M

FIGURE 15

FIGURE 16

The Biological Structure of Field B Expressed as Percent Portions of Each Category for the Check Community and for the Teasel Community from 1968 to 1971.

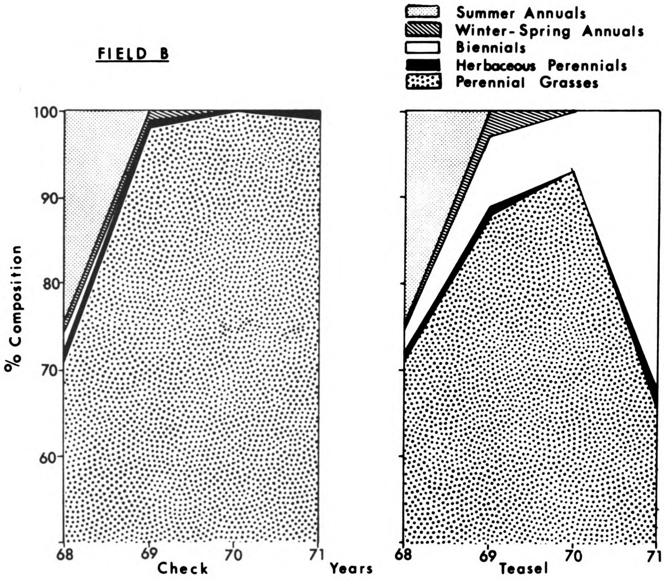

FIELD B
Summer Annuals
Winter-Spring Annuals
Biennials
Herbaceous Perennials
Perennial Grasses
% Composition
100
90
80
70
60
68
69
70
71
Check
Years
68
69
70
71
Teasel

FIGURE 16

FIGURE 17

The Biological Structure of Field M Expressed as Percent Portions of Each Category for the Check Community and for the Teasel Community from 1968 to 1971.

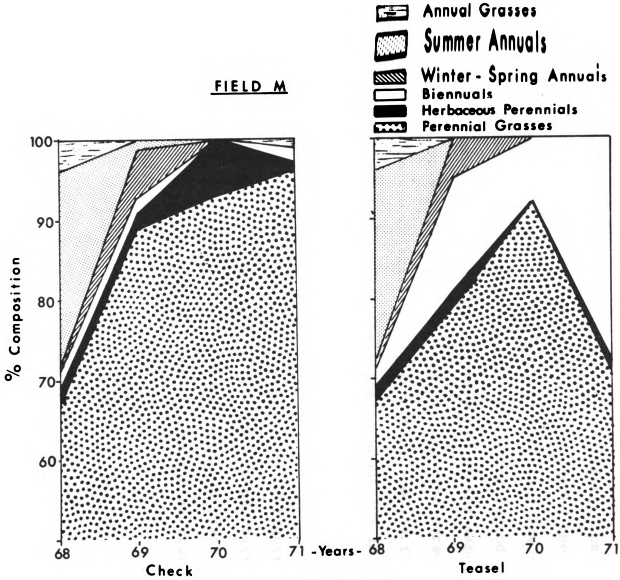

FIELD M
Annual Grasses
Summer Annuals
Winter - Spring Annuals
Biennuals
Herbaceous Perennials
Perennial Grasses
% Composition
100
90
80
70
60
68
69
70
71
-Years-
68
69
70
71
Check
Teasel

FIGURE 17

total of 26 and 29% to a total of 0 and 1%, respectively). In these fields, neither biennials nor herbaceous dicotyledonous perennials achieved more than a 7% portion of the total check communities for the years 1968-1971.

However, in the teasel communities, a different pattern emerged. Biennial reproductive forms expanded their relative portions from 8 and 14% in 1969 to 32 and 29% in 1971, in Fields B and M respectively. All other reproductive forms except perennial grasses remained at the same relative percentages as in check communities. The perennial grasses became relatively less important, moving from about 70% in 1968, up to 92%, then back to about 70% in 1971, when the biennials greatly increased.

Absolute values of standing crop in mean grams dry weight in Fields B and M in 1971 are presented in Figure 18. These data support the idea that a new reproductive form (biennials) had been added to the indigenous plant community without decreasing the dominant perennial grasses in net productivity.

FIGURE 18

The Biological Structure of Fields B and M Expressed as Productivity Values in Each Category for the Check Communities and for the Teasel Communities in 1971.

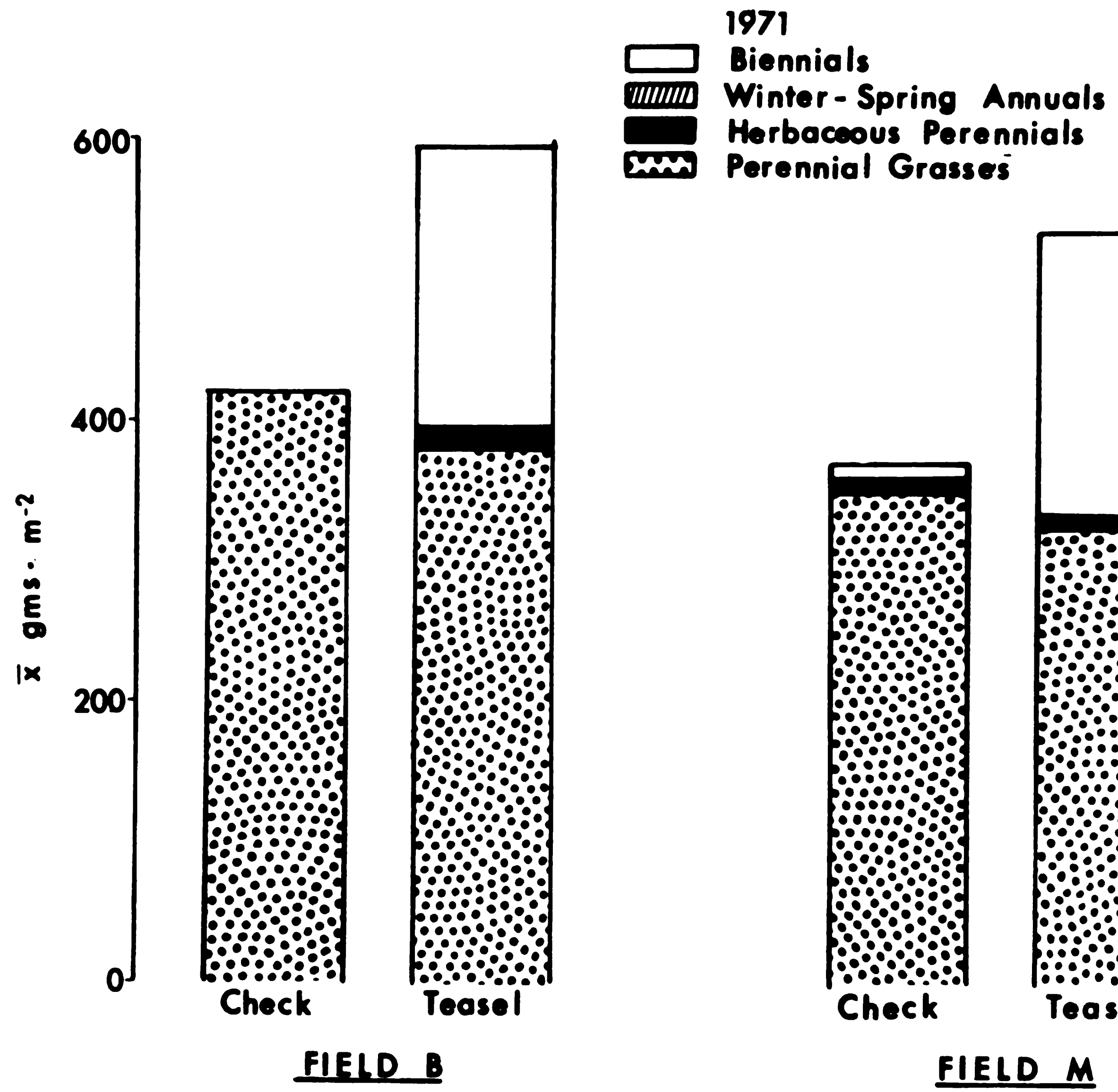

1971
Biennials
Winter-Spring Annuals
Herbaceous Perennials
Perennial Grasses
$\bar{x}$ gms · m^{-2}
600
400
200
0
Check
Teasel
FIELD B
Check
Teasel
FIELD M

FIGURE 18

DISCUSSION

I. The Effect of the Invasion of Teasel on Plant Communities

Summary of Results

Teasel communities had significantly higher diversities (H') and greater "evenness" values (J') than check communities from one to three years after teasel introduction. An over-all increase in number of species other than teasel was found in teasel communities. Annual net primary productivity of the two communities was not significantly different when teasel was in rosette form. When teasel produced flowering stalks, annual net primary productivity of the teasel community was significantly higher than in the check communities. The observed increase is attributed to teasel itself since the productivity of individual indigenous species was the same in both communities.

When one looks at the fields as collections of certain physical forms of plants, the increased productivity in the teasel communities may be attributed to an increase in diffuse forms over 100 centimeters in height. If the fields are analyzed on the basis of differences in reproductive strategies of plants, the increased productivity may be attr

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attributed to an increase in biennials in the teasel communities.

Diversity

The diversity index, H', is a function of both the number of species and the "evenness" with which these species are represented in relative numbers or biomass within the community. Increases in species other than teasel in the teasel communities had only a small effect on increasing H' because the individual biomass values were low. The successful addition of teasel itself was the main contribution to a higher H' in the teasel communities.

Number of Species: An examination of "extra" species in teasel communities shows that they were mainly dicotyledonous annual species, usually good colonizers (sensu Baker, 1965) taking advantage of any openings in vegetation. Such species are usually found in fields of an earlier successional status than the fields used in this study.

When a young teasel rosette died, an opening was left in the vegetation which was quickly colonized by the "extra" species. A second- or third-year rosette that is greater than 20 centimeters in diameter may form a flowering stalk; when this happened in the study fields the leaves of the old rosette died back, thus forming litter and subsequent openings in the ground layer vegetation. Such openings are not found in natural vegetation where a perennial grass (e.g. Agropyron) predominates. In such cases, there are few rosettes (Figures 13 and 14). In effect, the teasel rosettes acted as a perturbation at the ground level and opened up space in which seedlings became established. Where before the plant community structure was one of a relatively homogeneous cover of perennial grass, it became more heterogeneous, interrupted by patches of rosettes, dead rosette leaves, and ultimately exogenous annual species.

These rosette openings help explain the frequent presence of the annual species found in the teasel communities, even when teasel rosettes occupied 1% cover in a field. Each added species was represented mainly by seedlings and had a mean biomass measurement of 0.1 to 1.0 grams/m^2; in contrast, the very infrequent species found in both teasel communities and check communities had mean biomass measurements of less than 0.1 grams/m^2. The added seedlings were not observed to mature or to make up more than 1% of the biomass of the teasel community. They were always dependent on the rosettes for their presence, and did not reestablish themselves through reproduction on the site. Evidence of a more slowly-growing perennial species being established in these openings has not been detected to date.

It has been pointed out that the openings in vegetation around a dying teasel rosette or flowering stalk might be considered "islands" to be colonized. However, patches of open habitat are different from the oceanic islands described by MacArthur and Wilson (1967) in that the space surrounding the former is full of the colonizers, not barren as an ocean. A constant overflow from adjacent competing vegetation might not allow colonization by species that immigrated some greater distance. Thus, some species might find it harder to colonize a habitat island than a true island.

Present competition theory cannot directly handle second-order interactions such as occur when added species enter a community with teasel. It is known that certain species can provide spatial structure for the community and may create another level of diversity which then results in a potential increase in number of species (Margalef, 1958b; Whittaker, 1969). A somewhat analogous situation to this teasel introduction study was found in field experiments by Harper (1960) where the presence of wheat increased the frequency of microsites suitable for poppy (Papaver sp.) establishment.

Evenness: Evenness, measured by J', increased when one species (teasel) showed an increase in net production relatively greater than other species. In the few cases where check communities were more "even" than the teasel community (Fields C, 1971; D, 1970; J, 1970, 1971), the total productivity of the teasel community had dropped from the previous year due to a decrease in teasel, while the total productivity of the check community increased as it did in all fields.

Productivity and Niches

An expression of community evenness (especially when measured in terms of productivity) is an expression of total niche differentiation condensed into one term, J'. Possible insight into the relationships of various individual parts may be lost in the condensed term.

By niche differentiation I mean the manner in which the site's resources are partitioned among the biota, creating certain sized realized niches for each population. It is assumed here that a species population fills a realized niche, smaller than its potential or absolute niche, and regulated mainly by competitive interaction with others on the same trophic level which partially overlap, i.e., require parts of the same niche or common resource pool.

Numbers of and sizes of niches are hard to measure since the investigator observes only realized niches, the result of competition. As Connell and Orias (1964) have pointed out, it is also impossible to define a priori how many potential niches there are in an area since the "number of niches is partially a function of the number and type of species present." An estimate of relative niche size of species within a community may be obtained from production measurements if the realized productivity of a species is assumed to have some correspondence to the amount of resources it utilizes (Whittaker, 1969). Changes in realized niche sizes is most easily observed experimentally (Connell, 1961) or when a species invades an area (Price, 1971). Data from well-designed and well-executed experiments will be useful in testing theoretical models of species packing, i.e., the number of species that can coexist in an area (MacArthur and Levins, 1964, 1967; Schoener, 1965; Levins, 1968; MacArthur, 1969, 1970).

Changes in Niche Size During Invasion

What happens to the realized niche sizes of indigenous species when a new one on the same trophic level successfully invades? Conceptually, we may envision three categories of possible outcomes (Figure I9).

Case I: Total productivity of the site is increased by some amount. The added amount may be equal to the productivity of the new species, in which case a new niche effectively has been added. Or, the added productivity may be more than that of the new species and some one or more indigenous species enlarges its previous realized niche (positive feedback). In MacArthur's (1970) model of species packing, a new species can enter the system where resource utilization is not at its maximum if the addition of one reproductive unit will produce a total utilization even closer to the potential production of the community.

Case II: Total productivity is not changed. The new species must appropriate resources (niche space) from one

FIGURE 19

Diagramatic Representation of Three Cases Possible When a New Species Successfully Invades a Community. The area of each enclosure represents relative amounts of annual production for the species. Case I: Total productivity increases. Case II: Total productivity remains the same. Case III: Total productivity decreases. * is the invading species.

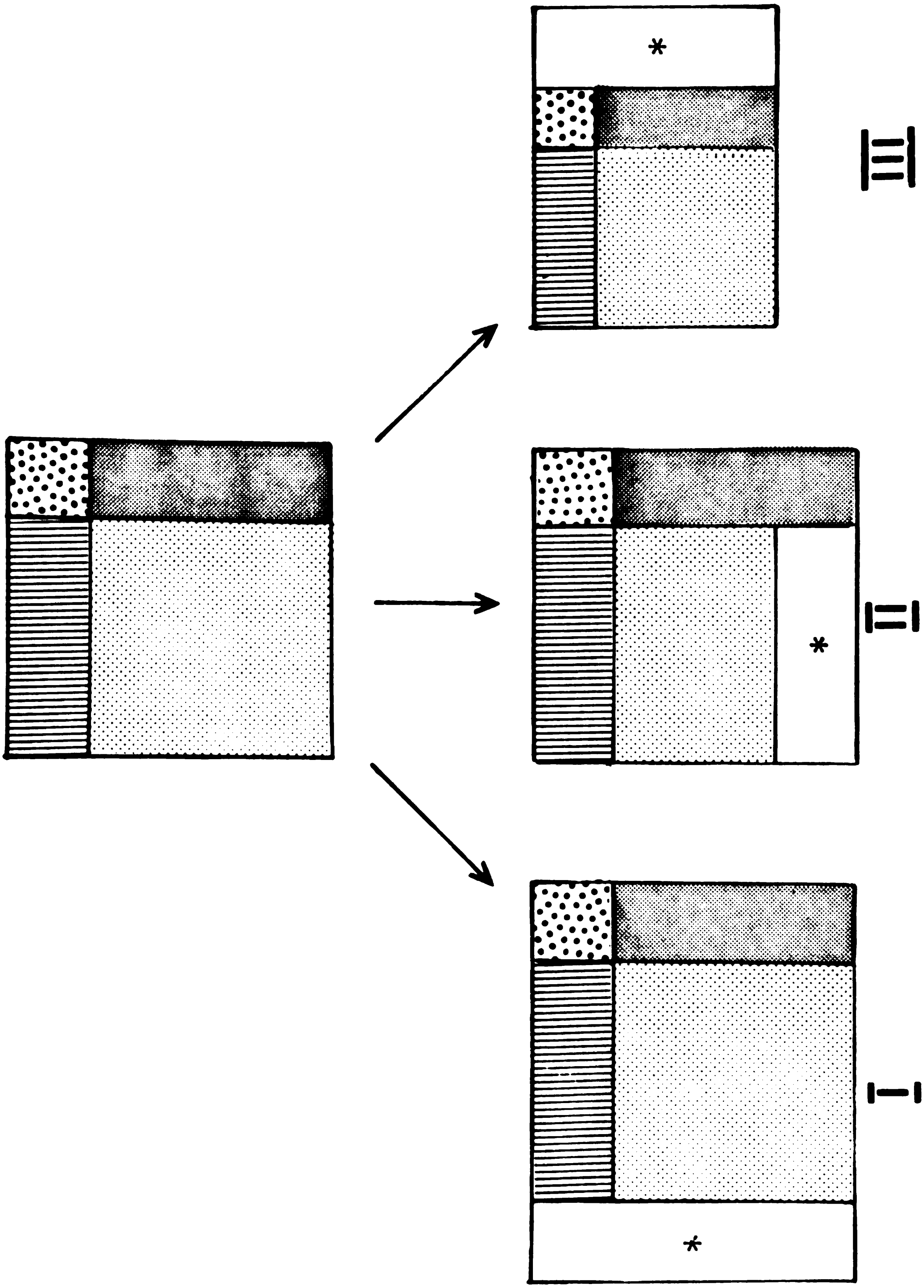

FIGURE 19

or more of the indigenous species. That is, the new species must help complete the total community utilization of the site's resources (MacArthur, 1969, 1970). In this case, the invading species must have competitive superiority to survive (Price, 1971). A problem of interpretation of results arises from the fact that it is impossible to distinguish between smaller niches and increased niche overlap (Pianka, 1966b).

Case III: To maintain a consistent argument, the case is included where total productivity is decreased as the new species is added. Such a situation might occur if there were a large negative feedback to the other species, such as might result from invasion by a fast-growing, shading liana. It is thought that Case III is unlikely to occur in the early stages of natural successional communities since the group of species that have been evolutionarily selected to take part in the development of a plant community probably do so with an ever greater utilization of site resources (Harper, 1967a).

In all three cases above, second-order interactions may occur among the indigenous species. That is, even though as few as one indigenous species is directly in competition with the new species, any changes in that one interacting species will result in changes in other indigenous species. Thus, internal community adjustments in individual species productivity may occur secondarily to the direct effect of the teasel introduction. (One example is the added species in teasel communities discussed earlier.)

In the present study, teasel communities containing only teasel rosettes did not significantly increase or decrease total productivity over check communities (Case II). A slight, but not statistically significant, decrease in Agropyron was noted. Teasel communities containing teasel flowering stalks increased the total productivity in an amount equal to the productivity of the flowering stalk (Case I), thus, in effect, exploiting new resources or occupying a previously unexploited niche.

Figures 20 and 21 show the relative productivity of various species in Fields B and M for 1970 and 1971. Here, each enclosed area represents a species; the size of an area represents the amount of production of that particular species relative to the others.

Since teasel communities with only rosettes fit Case II and teasel communities with flowering plants fit Case I, it can be concluded that the rosettes compete for resources but flowering stalks have effectively escaped competition with the indigenous vegetation.

Explanation: Life Forms

How can these results be explained? Answers to this question might be found in data showing differences in reproductive and morphological groups between teasel communities and check communities. Recall that the increased

FIGURE 20

Diagramatic Representation of Relative Productivities of Plant Species in Field B, Teasel and Check Communities, 1970 and 1971. The area of each enclosure represents relative amounts of annual production for each species. Agro = *Agropyron repens*; Poa = *Poa* spp.; Dip = *Dipsacus sylvestris*.

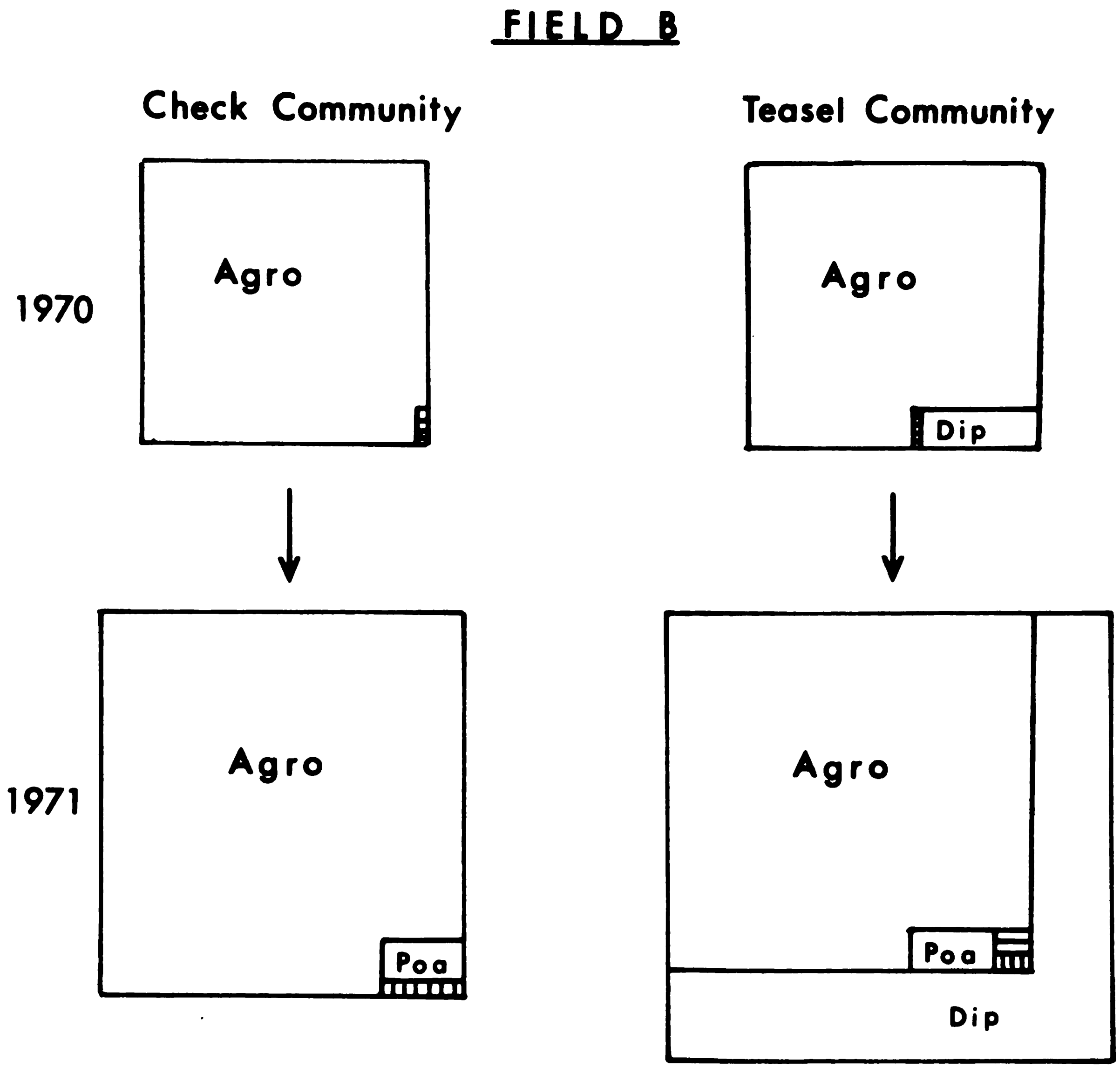
FIELD B
Check Community
Teasel Community
1970
1971
Agro
Agro
Dip
Agro
Poa
Agro
Poa
Dip

FIGURE 20

FIGURE 21

Diagramatic Representation of Relative Productivities of Plant Species in Field M, Teasel and Check Communities, 1970 and 1971. The area of each enclosure represents relative amounts of annual production for each species. Agro = *Agropyron repens*; Poa = *Poa* spp.; Sol cn = *Solidago canadensis*; Mel = *Melilotus* spp.; E an = *Erigeron annuus*; A p = *Aster pilosus*; R c = *Rumex crispus*; Dip = *Dipsacus sylvestris*.

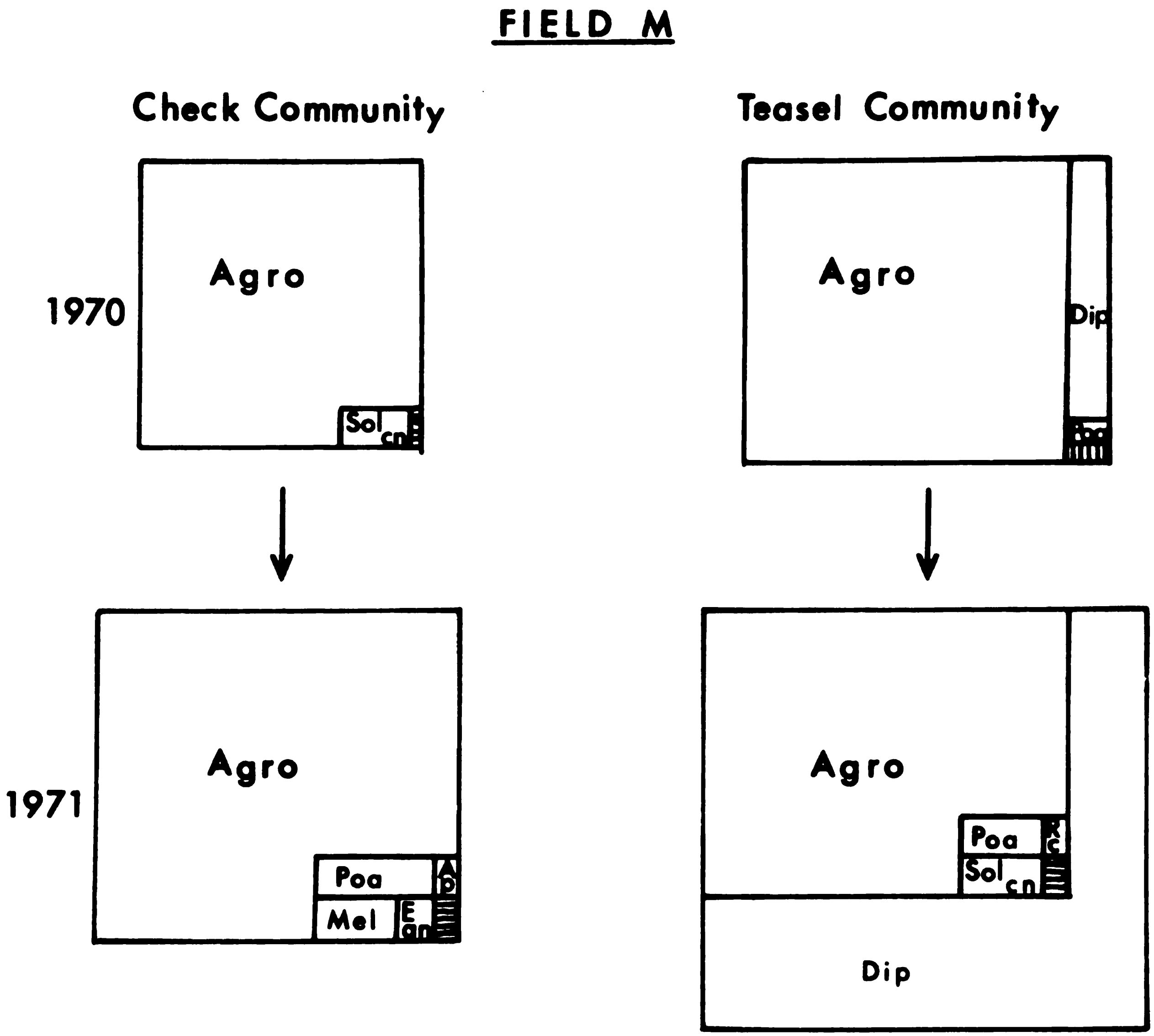
FIELD M
Check Community
Teasel Community
1970
1971
Agro
Sol
cn
Agro
Dip
Poa
Agro
Poa
Mel
E
an
Agro
Poa
Sol
cn
R
c
Dip

FIGURE 21

production of teasel communities could be accounted for by an addition of biennials or by an addition of diffuse forms over 100 centimeters in height. Teasel made up the majority of the community biomass found in each of these two categories. Qualities inherent in "biennialness" and in "tall diffuse" morphology are most likely related to the effects seen in this study.

Relationship to Nutrients: Many biennials, teasel included, produce a long thick tap root which is thought to serve as a storage organ during non-reproductive years. In contrast, annuals generally have shallow diffuse or relatively shallow tap roots and perennial grasses usually have diffuse or rhizomatous underground parts. The effects of plants with long tap roots "upon grasses is usually not marked except where they occur in unusually dense stands . . . (they) may have resulted from long adjustment to competition with the roots of grasses" (Weaver, 1958). Any competition that does occur between roots begins long before shoots are sufficiently developed to cause serious mutual shading (Donald, 1958, 1961; Aspinall, 1960; Milthorpe, 1961).

Results of the present study indicate that some competition occurs between teasel rosettes and indigenous species since total productivity in the teasel community does not increase above that of the check community and resources are divided among the new species (teasel) and

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the indigenous species (Case II). More time than this study allowed would be necessary to determine the final outcome of the competition between populations.

The changing pattern of nutrient supply with time to various plant species is unknown (Milthorpe, 1961). However, it is speculated in this study that at some point in development the teasel tap root reaches soil not yet reached by the indigenous plants and is able to exploit a new resource or a supply of common resources effectively unavailable to the other vegetation at that time. Thus, by the time the rosette produces a flowering stalk, the plant has been released from much of its interspecific root competition. It becomes greatly productive, effectively not infringing on soil resources of other species (Case I).

Relationship to Light: The teasel flowering stalk, a diffuse form greater than 100 centimeters in height, is taller than the indigenous vegetation. This large new physical form may have a mean percent cover value of up to 54% in a field and shades the indigenous species somewhat; yet the productivities of the various indigenous species are not significantly decreased. Apparently light is not limiting in the community at that point in time.

The actual area of leaves per unit area of ground (called the Leaf Area Index or LAI) is a relatively good indicator of primary production (Whittaker, 1963, Harper, 1967b). In a community dominated by one species, the LAI is not high enough to take maximum advantage of incoming light, due to a self-shading effect. Golley (1965) used figures of broomsedge production to estimate a reduction of 70% in community production due to leaf attitude and litter shading. An increase in the number of strata of photosynthetic tissue could compensate for this loss by more efficient use of the light (Odum, 1960). In fact, the development of vegetational strata in communities by the addition of species of varying heights and growth forms is observed in plant communities. Horn (1971) has produced a theoretical model of the development of plant communities on the basis of light interception and selective advantages of different morphologies at various points in time. Leaf Area Indices of 5.0 (Brougham, 1958), 2.0 to 3.0 (Blackman and Black, 1959), and 3.0 to 5.4 (Donald, 1963) have been calculated as being optimum to trap 95% of the sunlight in various plant mixtures. Apparently if there was any increase in LAI in teasel communities over check communities, it was not great enough to cause a reduction in effective sunlight utilization by the indigenous species.

In summary, annual net primary productivity of the community was not influenced by teasel rosettes but was significantly increased by teasel flowering stalks. The reproductive strategy and physical form of teasel appear to explain these results.

General Considerations of Life Forms: If teasel had not been a biennial or a tall diffuse form, different results might have been expected, depending on how much teasel differed from indigenous forms. Also, if one of these biological or physical forms had been in the natural community as a dominant, teasel might not have been able to compete with it successfully. The biology of each of the organisms is important to the outcome, including combinations of reproductive strategies, growth forms, physiological requirements, etc. These qualities cut across taxonomic lines that are themselves important in reproduction and natural selection.

Functional groups of organisms may be the ecological units of communities, not taxonomic species. Recognition of a taxonomic species implies a recognition that there once was some isolation that allowed divergence of characters, usually floral, but this does not necessarily recognize similarities in major functions of one species relative to another such as productivity, mineral cycling, shading, etc. Looking at each taxonomic species for answers to some types of questions on the community level may be confusing to the picture of the whole. In this study, reports of changes in diversity and productivity of plant groups, based on reproductive strategies and physiognomy, and ignoring individual species, yielded information on possible mechanisms responsible for observed differences; at the same time this approach can save a vast amount of time in sorting field samples.

Other Considerations of Results

Some consideration is given here to a discussion of ground-level space in the communities. In the teasel communities, rosettes of teasel often covered up to 50 to 80% of the ground. Agropyron percent cover readings were 80 to 90% in check communities and only 30 to 50% in teasel communities. Even so, there was no significant difference in production of Agropyron in teasel and check communities. This lack of difference may have been due to some decrease in competition in Agropyron in teasel communities which allowed increased densities in isolated microsites; or the effect may have been due to an artifact of the technique of reading percent cover estimates where density is hard to account for. I tend to support the latter explanation as the former one does not help account for the increase in productivity of Agropyron in both communities between 1970 and 1971.

Within both teasel and check communities, it can be said that resources were not fully utilized in 1970 because total production increased in 1971. Perhaps the reason that the 1970 total community primary production is lower than in 1971 is due in part to the allelopahthic qualities of decomposing plant tissue of Agropyron (Welbank, 1960, 1963; Grümmer, 1961; Winter, 1961; Ohman and Kommendahl, 1964;

Carley and Watson, 1968). These parts might have inhibited germination and growth of potential competitors while the more slowly-growing Agropyron gradually increased in the communities. The question remains in successional studies as to the extent that specific toxic substances may be responsible for the composition of plant communities (Bonner, 1950; Rice, Penfound, and Rohrbaugh, 1960; Rice, 1964; Muller, 1966; Tukey, 1970).

Herbivory is also important in determining plant community structure (Odum, Connell, and Davenport, 1962, Harper, 1969); however, few community studies have shown the proportion of annual net primary production that is eaten by herbivores. It is estimated from studies (Golley, 1960; Odum, et al., 1962; Teal, 1962; Bray, 1964; Wiegert and Evans, 1964) that 88 to 99% of the annual net primary production is uneaten and subsequently enters the litter-soil component (Weigert, Coleman, and Odum, 1969). In this study, the amount of predation on the natural vegetation is not known but is assumed to be equal in both teasel and check communities. No evidence of mammal herbivory on teasel plants was found, though results of minor insect herbivory were occasionally observed.

II. Secondary Terrestrial Succession of Plant Communities in Temperate Forest Areas

From the results of this study and current literature, I will construct a generalized conceptual model of secondary terrestrial succession of plant communities in terms of primary productivity, diversity, and the series of vegetational dominant forms.

Current Knowledge

Primary Productivity and Succession: By itself, a measurement of net primary productivity is important in a study of community ecology because it is a measure of energy fixed by plants that potentially supports all life in the community (Woodwell and Whittaker, 1968). Productivity, amounts of standing crop biomass, and diversity of communities are thought to be related in some way to the stability of communities (see Brookhaven Symposium, 1969).

It is assumed that both gross and net primary productivity on a particular site increase and level off at climax (Whittaker, 1953, 1963, 1966; Monsi and Oshima, 1955; Olson, 1963; Takeda, 1961; Odum, 1969), perhaps declining slowly after a maximum is reached (Loucks, 1970). Some studies on the early stages of succession in laboratory aquatic microcosms (Beyers, 1962; Cooke, 1967; Margalef, 1968) and fields (Odum, 1960) show relatively higher primary productivity initially, then a lowering to some relatively steady-state level. The microcosms in the laboratory are closed systems; in these systems more complex life forms do not migrate in and become established as does happen in later stages of natural terrestrial succession. It may be that open systems do not always experience an initial decline in net or gross productivity as do the closed (Odum, 1969), but in general, the pattern remains the same.

The high levels of productivity at initiation of the secondary successional sere can be attributed to "loose" nutrients (Odum, 1960; Ovington, Heitkamp, and Lawrence, 1963; Golley, 1965; Cooke, 1967). The decline comes as the available nutrient supply is depleted. A plateau (Ryther, _et al._, 1958, McAllister, _et al._, 1961) occurs at some level determined by the decomposition rate of the dead organisms, i.e., the rate of supply of "new," available nutrients. It has been demonstrated that phytoplankton productivity largely depends on nutrient availability (regeneration), not standing crop of nutrients (Ketchum, 1961; Pomeroy, 1960, 1970). Laboratory microcosms maintain productivity at this first plateau; field terrestrial productivity moves upward in a series of discontinuous steps (Margalef, 1968) or relays (Dansereau, 1951) or periods of adjustment toward specific levels (Odum, 1960; Olson, 1963) for the particular community.

Diversity and Succession. Diversity (number of species) on any trophic level climbs steadily through the seral stages (Whittaker, 1953, 1963, 1966; Connell and Orias, 1964; Odum, 1969; Wilson, 1969), depending on increased number of niches as a result of increased biomass and stratification (Odum, 1969). Auclair and Goff (1971) have postulated that this is true for the more xeric or lowland areas in the western great lakes region, but that developing communities in mesic areas experience a slowly declining number of species after an early peak.

Quality of species change more rapidly than do the totals of gross or net primary production; often whole species arrays change without affecting total productivity (Odum, 1960; Golley, 1965).

Changes in This Study

In the current study, net primary productivity of the community increased with the addition of teasel flowering stalks. I would expect this new level of site productivity to drop and level off in time as the new pool of underground nutrients is reduced to a steady state level and at some value relative to the decomposition rate of the new teasel litter. The new value will probably be higher than that of the check community because there will probably be more nutrients cycling in the teasel community; that is, the new nutrients tapped by the teasel flowering stalks will be potentially available to all of the plant species on the site as the nutrients are released from the decomposing litter.

At the end of the first three years of this study, teasel and Agropyron were co-dominants. Shifts in species dominance may occur as the teasel population exhausts its exclusive source of nutrients. This latter factor is somewhat related to a similar situation that occurs when prairie soil is broken and planted in alfalfa. The alfalfa grows taproots up to 30 feet long and gives high yields for 3 to 4 years; however, subsequent yields are much lower because of depletion of water and nutrients at those depths (Kiesselbach, Russel, and Anderson, 1929).

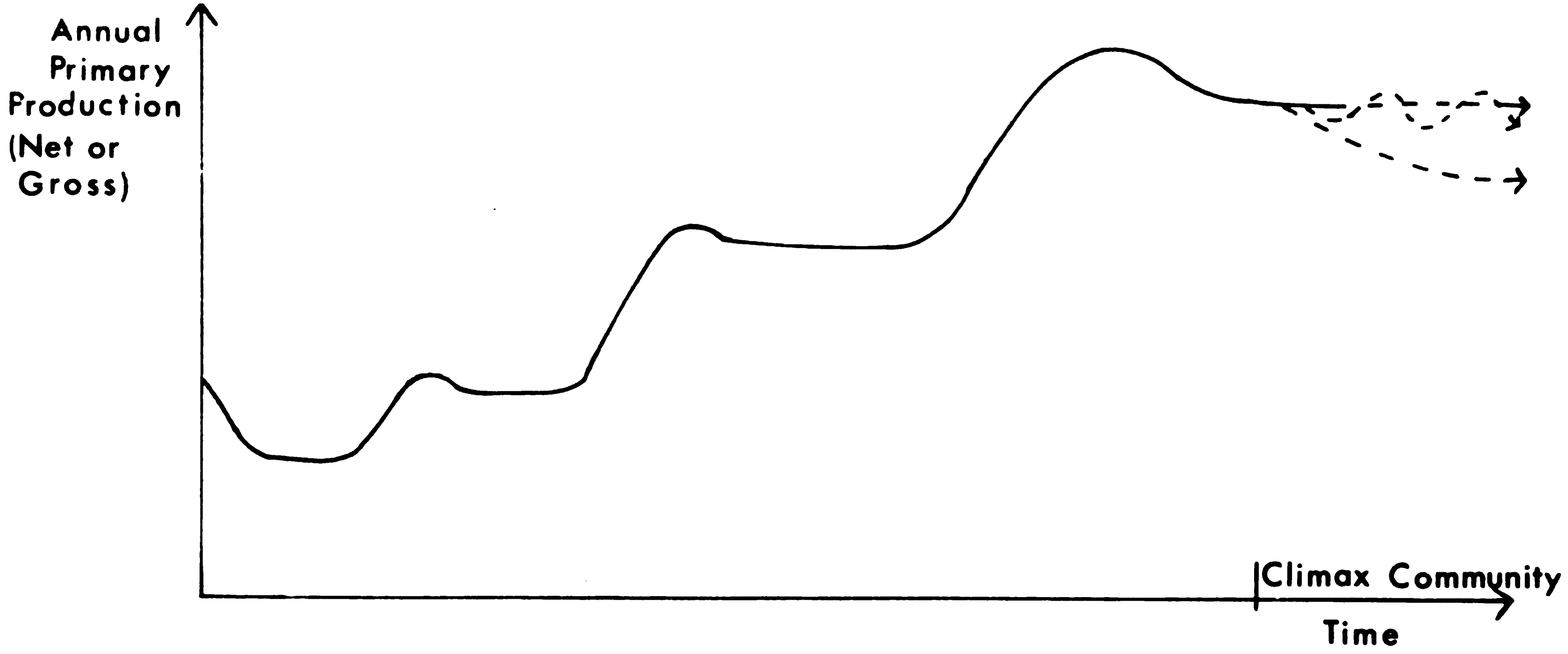
General Model

Assuming diversity (number of species) to be increasing in a relatively constant manner and primary productivity to be increasing in steps and plateaus during terrestrial succession, I propose that each step in the productivity curve shows a peak and subsequent decline before leveling off on some new higher plateau (Figure 22). The peaks in Figure 22 could represent the invasion by perennial grasses, then shrubs, then trees. Any new life form that is able to survive and also tap some new resource will cause a sudden increase in total productivity; this will peak and then level off as part of the biomass of the new invader enters the decomposer pool.

The time period for each plateau and the distance between plateaus is more predictable in earlier stages, then progressively less so since many variables determine the survival of the increasing number of species. Some of these variables include the availability of propagules (Bazzaz, 1968), which may be related to size of the area (Golley, 1965; Davis, 1968), allelochemic effects of intermediate successional species (Rice, et al., 1960), timing

FIGURE 22

Annual Primary Production During Secondary Terrestrial Succession of a Plant Community.



Terrestrial Succession

FIGURE 22

of life cycles (Keever, 1950), and different growth rates (Bard, 1952).

As each new life form invades, the fate of the forms originally present is not known. The teasel introduction study showed they are unaffected, at least initially. Eventually the earlier forms probably do decrease in productivity. This would help to explain the measurements in climax forest communities where the tree canopy productivity is greater than that of the shrub layer which in turn is greater than that of the herbaceous layer (Whittaker, 1966).

Again, the life form of the plant seems to be important in describing one level of community development. Within each growth form, species composition may change more than once. An example of species change within a growth form may be found in the data of Cantlon _et al._ (unpubl.) where _Poa_ sp. (bluegrass) replaces _Agropyron repens_ (quackgrass) after _Rhus typhina_ (staghorn sumac) enters the plant community.

Natural selection may be said to be operating on the species level and on a higher level, between whole groups of populations, selecting for various strategies which allow more efficient environmental exploitation which then results in increased total productivity on the site. This strengthens the concept of a community as an integrated whole and not merely an assemblage of individuals or even taxonomic species.

III. The Relationship Between Productivity and Diversity

A commonly-held notion is that productivity and diversity are negatively related in communities. This notion has gained some support from information on yield-diversity relationships in agricultural crops, from nutrient enrichment studies, and from a misunderstanding of Margalef's use of the term productivity. On the other hand, Whittaker (1966, 1969) finds no correlation between net or gross primary productivity and diversity of communities. Further, comparisons of climax communities on a world-wide basis, the results of this teasel introduction study, and Patten's (1962) phytoplankton community show a positive correlation between net primary productivity (biomass accumulation) and diversity (number of species).

I submit that general statements about the productivity-diversity relationship (henceforth called the P-D relationship) can be made only within defined limits and that there is only an indirect relationship between the two in any case.

The Negative Relationship

Some support for the notion of a negative relationship between productivity and diversity has been gained from the vast amounts of information on yield-diversity relationships in agricultural crops or weeds (Harper, 1967b). (See Reviews in deWitt, 1960; Donald, 1963; Whittington and O'Brien, 1968; Loomis, Williams, and Hall, 1971.) Harper (1967b) describes diallel analysis where pairs of species are grown together and in mixed stands for analysis of productivity. He states that a rigid demonstration that "a mixture of plant species outyields pure stands seems not to have been made." However, in those few studies where there is an increase in yield in mixtures, various explanations have been given: the species were not synchronous in growth, reducing interference (Harper, 1967b), the species were of different growth habit (Baeumer and deWitt, 1968; Whittington and O'Brien, 1968), or the experiment was conducted for more than one growing season (Harper, 1961). The answer to the contradiction lies in the degree to which the forms have been mutually selected, that is, their "ecological combining ability" (Harper, 1964). The technique used in paired species studies are not likely to solve problems of the relationship between productivity and diversity in natural communities (Harper, 1964; MacIntosh, 1970; Scarisbrick and Ivins, 1970).

When the changes in productivity and diversity are examined in nutrient enrichment experiments on communities, initial results show impoverished fauna and flora (Patrick, 1949; Williams, 1964; Hall, Cooper, and Werner, 1970; Stephenson, 1972). Productivity increases and diversity decreases; the result is a "bloom" and the effects are attributed to a release from competition with the fastest growing populations taking advantage of the new nutrient source. If one examines any available data from a later date in similar studies, he often finds that the productivity has peaked and leveled off and diversity climbs again. Thus, if one looks within one site or pond, the changes in productivity and diversity are inversely related during the recovery period after the experimental perturbation.

Margalef (1969) hypothesizes a negative correlation between productivity and diversity. It should be made clear that Margalef almost always uses the term "productivity" to mean the productivity to biomass ratio (P/B) and states so in the beginning of most of his papers (e.g., "Primary productivity per unit biomass will be named here productivity, gross or net," 1967, p. 260). He also has said that productivity, meaning net primary productivity _per se_, increases during succession, but that the ratio (P/B) of primary productivity to total biomass drops (Margalef, 1965, 1968). Indeed, his experimental aquatic microcosms in the laboratory do show a negative correlation between the P/B ratio and diversity (number of species).

Margalef rarely discusses net or gross primary productivity _per se_ and is more often concerned with the P/B ratio which he relates to community stability and efficient use of resources. Perhaps his system has a more or less constant rate of net or gross productivity since his laboratory aquatic systems are closed to the addition of organisms and/or nutrients from the outside. Frank (1968) states that P/B goes down if one assumed constant productivity throughout succession. However interesting, the validity of the diversity-stability hypothesis is not entirely evident from studies of plant communities (Loomis et al., 1971).

Some investigators have attempted to support Margalef's statements that productivity (meaning P/B) and diversity are negatively related by correlating diversity with primary productivity only (McNaughton, 1968; Hurd et al., 1971). Such a misapplication of Margalef's statements concerning the P/B and diversity relationship hinders the accuracy of interpretations of the investigators' results since they are not referring to the same "productivity."

Lack of Relationship

Whittaker (1966, 1969) states that he finds no relationship between gross or net primary productivity and diversity. Perhaps his results can be explained by considering scale; he is mainly comparing communities from site to site within one geographical, climatic zone, as opposed to successional or nutrient-augmentation studies on one site, or a world-wide comparison of biomes. Most likely the difference in productivity he observes is related to fertility of the various sites as well as the stage in succession. In pioneer stages of upland temperate forests, diversity has been shown to be higher in mesic (fertile) sites and lower at both ends of the "fertility" scale (Whittaker, 1960, 1965, 1966; Monk, 1966b, 1967; Auclair and Goff, 1971). Then as the various seres move toward climax communities, diversity peaks and drops on the mesic sites, but slowly rises to some leveling-off point in both the less fertile (xeric and lowland) sites (Auclair and Goff, 1971). An understanding of this reveals that diversity does not correlate with productivity in measurements across all these communities within one geographical region.

Ovington _et_ _al_. (1963) and Monk and McGinnis (1966) have examined productivity and diversity, respectively, in climax and successional communities and found no time-related general pattern. Ovington (1964), in a comparison of net annual primary productivity in three ecosystems, found no difference between a maize field and oak woodland; both produced less plant material than a nearby savanna ecosystem. Again, within one geographical region, comparisons among sites of various ages and management do not yield good correlations of diversity to productivity.

The Positive Relationship

Comparisons of climax communities made on a more worldwide scale tend to show a general increase in annual net or gross primary production toward the tropics (Ogawa, Yoda, and Kira, 1961; Bray and Gorham, 1964; Whittaker, 1966).

This is perhaps partially dependent on soil fertility (here, in terms of a faster turnover of nutrients due to higher temperatures over the entire year), though the productivity level varies greatly from region to region within a climatic area. The greater diversity (numbers of species) in the tropics is perhaps due to many factors, only one of which may be higher primary productivity (more resources to partition, MacArthur, 1969b), the others being lack of thermal seasonality (MacArthur, 1969b), faster turnover rates (Olson, 1963; Margalef, 1968), longer evolutionary time (Wilson, 1969), and longer food webs (Hutchinson, 1959). (See Odum, Cantlon, and Korniker, 1960 and Pianka, 1966b.)

The results of the teasel introduction study show both productivity and diversity increasing when teasel reaches the flowering stage. Diversity was increased by both teasel and "extra" annuals that invaded with teasel and annual production increased as a new source of nutrients enlarged the site's total potential for primary production. Though productivity and diversity measurements may be mathematically correlated positively, I am not prepared to state that productivity and diversity are positively related generally. Indeed, there is probably no direct relationship, only an indirect one such that (if we insist on correlating diversity and productivity) yields a positive correlation in some situations and a negative correlation in others.

In studies over time on one site the positive or negative correlations may merely reflect relative rates of change in diversity and productivity.

General Model

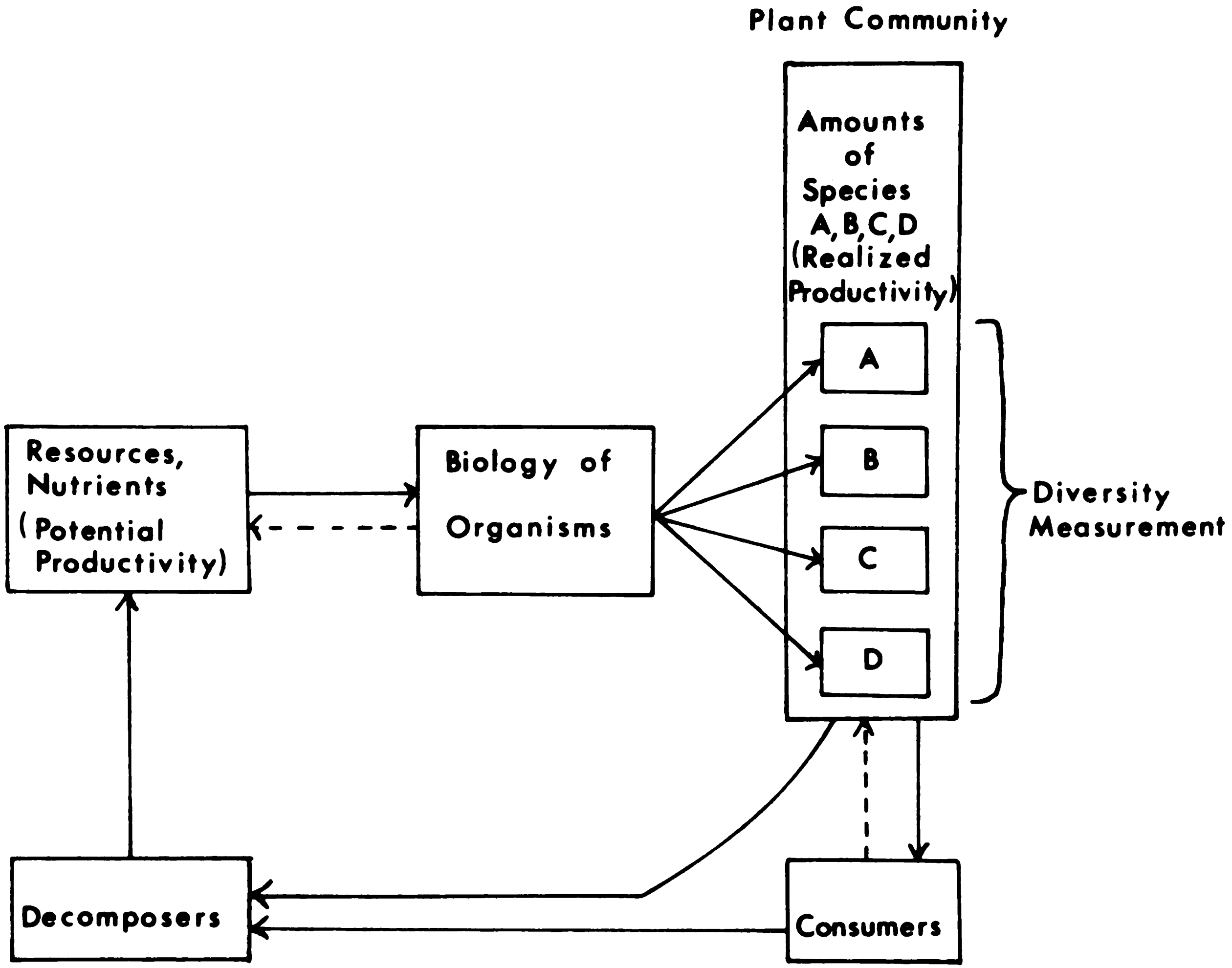
Many of the processes in a terrestrial community that determine productivity and diversity, and any subsequent relationship between the two, depend upon (1) the amount of available nutrients in the system (due to natural conditions in terms of amount of water, soil pH and composition, etc., as well as initially "loose" nutrients present because of artificial additions, fertilizer residues, initiation of succession, or a new source), (2) the turnover rate of the nutrients by decomposers, which in turn is regulated by moisture content and temperature conditions, and (3) the biology (physiology, life form, competitive abilities, etc.) of the available organisms, the outcome of whose interactions we record as diversity.

Figure 23 shows diagramatically the relationships among these important factors. Any change in the amount of any compartment (primary producers, consumers, decomposers, nutrient pool) or in flow rates, whether naturally or experimentally induced, will cause changes in the whole system; also, considerable time, on the order of years, is required for readjustment.

An experimental enrichment of a community directly manipulates the resources by artificially increasing the

FIGURE 23

Relationships in a Plant Community Among Resources, Plants, Consumers, and Decomposers, Relative to the Potential Productivity, Realized Productivity, and Indices of Diversity.



Relationship between Productivity and Diversity in a Plant Community.

FIGURE 23

amount of "loose" nutrients. If certain organisms are present that can take advantage of the increased nutrient pool by rapid rates of growth, they do so and increase greatly relative to those with slower growth rates: the result is lower diversity of the enriched community. The same sort of situation holds true in aquatic laboratory microcosms or terrestrial cropland after abandonment when the initial amount of available nutrients is quite high. In all the above cases, the initial increased amounts of biota move eventually into the decomposer compartment and the amount of nutrients in the system becomes dependent on the rate of release from the decomposers.

The role played by detritus in nutrient regeneration becomes more and more important through seral stages (Margalef, 1968; Odum, 1969). In a study of revegetation of ground by kudzu, Witkamp *et al*. (1966) found an increase in microbial activity over time up to "a fixed rate of breakdown for a given substrate . . . regardless of composition or density of the microflora." Olson (1963) estimates a matter of centuries for the decomposition rate in forests to reach 95% of its steady-state level; thus these communities continue to show an increase in primary productivity for that time. In the kudzu succession studies, large portions of the cycling minerals (84% nitrogen, 79% phosphorus) were locked up in litter and soil dead organic matter by the ninth year. Witkamp *et al*. (1966) attributed the leveling off of kudzu growth to stagnation of mineral cycles. Thus, the potential productivity of communities become dependent on the turnover of material within the system more than the standing crop of nutrients (Ketcham, 1961; Pomeroy, 1960, 1970; Olson, 1963; Westlake, 1963).

When teasel was added to the plant community a new source of nutrients was reached. Earlier I proposed a general terrestrial succession model which showed new life forms (shrubs, trees, etc.) tapping new pools of nutrients with increases in total amount in the living system. It is evident that some organisms might increase the resource (potential productivity) compartment.

A measure of diversity in the plant community reflects the result of the competition among organisms. Again, the plant biomass will eventually move into the decomposer compartment, often _via_ the consumers. The consumers may also influence diversity in the plant community by differential feeding or by increasing competition (Odum _et_ _al_., 1962; Harper, 1969).

Statements have been made that increased productivity is generated by increased dominance (McNaughton, 1968), and, alternately, that "species diversity increases productivity efficiency of the ecosystem while dominance makes the system stable, though less efficient for production" (Singh and Misra, 1968). Golley (1965) relates productivity and diversity directly with a "system of regulation of the production process through the diversity of the vegetation." Such statements of a direct causal relationship between productivity and diversity bypass either the very important decomposer role or fail to consider the "biology filter," and should be reconsidered.

Perhaps explanations of the productivity-diversity relationship take on a hierarchial framework. One level of potential primary production is set by the amount of light exposure and the temperature and moisture regimes (thus, by climate within a geographical area); another, lower, level is set by the amount of available nutrients in the system (fertility). A still lower level of realized production in each locality is determined by the biology of the organisms living there. A measure of diversity in the plant community then reflects the outcome of the competition among these organisms.

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