The successional convergence of vegetation from grassland and bare soil on the Piedmont of New Jersey

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Monte, Judith Ann (Dept. of Geography, Louisiana State University, Baton Rouge, La.) The successional convergence of vegetation from grassland and bare soil on the Piedmont of New Jersey. William L. Hutcheson Memorial Forest Bull. 3:3-13. 1973. The rate and character of successional convergence between grassland and bare soil was studied by means of yearly sampling on permanent plots in two pairs of fields which have similar physiographic and soil conditions but different origins. The fields had been planted in *Dactylis glomerata*; one field of each pair was plowed, and all fields were then abandoned. Data were collected for seven and nine years for each pair of fields respectively.

Analysis of the data was conducted in three parts. Dissimilarity values were calculated using Bray and Curtis' Index; Whittaker's Dominance-Diversity curves were drawn for all fields; and Shannon-Wiener diversity values were calculated. The successional convergence between hay and plowed fields has been substantiated in all aspects of this study.

Introduction

It has been suggested that vegetational succession is directional developing toward one climax type. The extreme concept is that all successions in a climatic area, regardless of site, are in the process of change and that the direction of change tends toward one climax (monoclimax) (Clements, 1916). Clements was concerned more with process than with actual accomplishment of climax. Others (Tansley, 1935) who are perhaps more realistic and less inclined to academic concepts recognize that successions of various origins on the same physiographic and soil situations not only demonstrate the process of directional change but can and do develop toward relatively uniform "edaphic" climaxes. Thus, a hay field and a plowed field on comparable sites should ultimately be expected to show convergence to a similar type of vegetation. This study is an investigation of two pairs of fields to determine the rate and character of successional convergence of vegetation from grassland and from bare soil.

Unique to this study is the fact that data were collected for consecutive years (seven and nine in this case, for each of the pairs of fields, respectively) on permanent quadrats in the same fields. Thus, the data provide a reasonably precise picture of the early stages of old field succession.

Papers on old field succession are numerous in the literature, taking into account three different approaches. Most of the studies are descriptions of the vegetation in fields of various stages of succession, some consider the functional characteristics of the communities, and others attempt to describe the processes of succession.

Previous to this study, only Bard (1952) had studied old field succession on the Piedmont of New Jersey. She described the Hutcheson Memorial Forest, a forest over 250 years old, as approximating climax. By studying nearby fields (within a five-mile radius) of various ages, she was able to investigate the major changes which take place in the vegetation and soil during succession.

Hutcheson Memorial Forest, originally known as Mettler's Woods, is a mature (over 250 years old) oak forest (Buell, 1957) of 65 acres located just east of East Millstone on the Piedmont in Central New Jersey. Adjacent to the woods are fields totaling some 71 acres which are part of the tract (Buell, 1957; Monk, 1958). These fields, which were the major concern of this study, are covered with low-growing vegetation characteristic of farmland in the early stages of abandonment.

The gently rolling topography of the Piedmont is underlain by Triassic red shale of the Brunswick formation (Kummel, 1940). These shales weather to soils known as the Penn catena, which is moderately fertile, shallow, generally well drained, loamy, and sometimes slightly droughty (Tedrow, 1963).

According to Ugolini's (1964) study of the Hutcheson Memorial Forest, there are only slight differences in soil texture and depth between the fields chosen for this study, and thus, the fields may be considered to have similar soil conditions.

New Jersey has humid subtropical summers and mild winters. The Piedmont receives 44 to 48 inches of precipitation annually which is distributed evenly throughout the year. Despite this ample amount of precipitation, periods of drought are not uncommon (Dunlap, 1959). Severe summer droughts which occurred in 1962, 1963, 1965 and 1966 are pertinent to this study.

Methods

Selection of the Fields

Two pairs of field units on which data had been collected annually were available for the study (Figure 1). One field of each pair of fields was plowed just prior to the initiation of the records and the other was left as an orchard grass (*Dactylis glomerata*) meadow, with no further harvesting taking place.

The pair on which the longest record was available (nine years) was designated as E1 and E2. On both fields orchard grass had been planted and harvested for hay in 1961. This was the only harvest. Field unit E2 was plowed in June of 1962, while E1 remained an orchard grass field.

The other pair, designated C6 and C7 for which seven years of data were available, was also planted to orchard grass in 1961, but the fields were harvested for hay

1973. William L. Hutcheson Memorial Forest Bulletin 3(1):3-13.

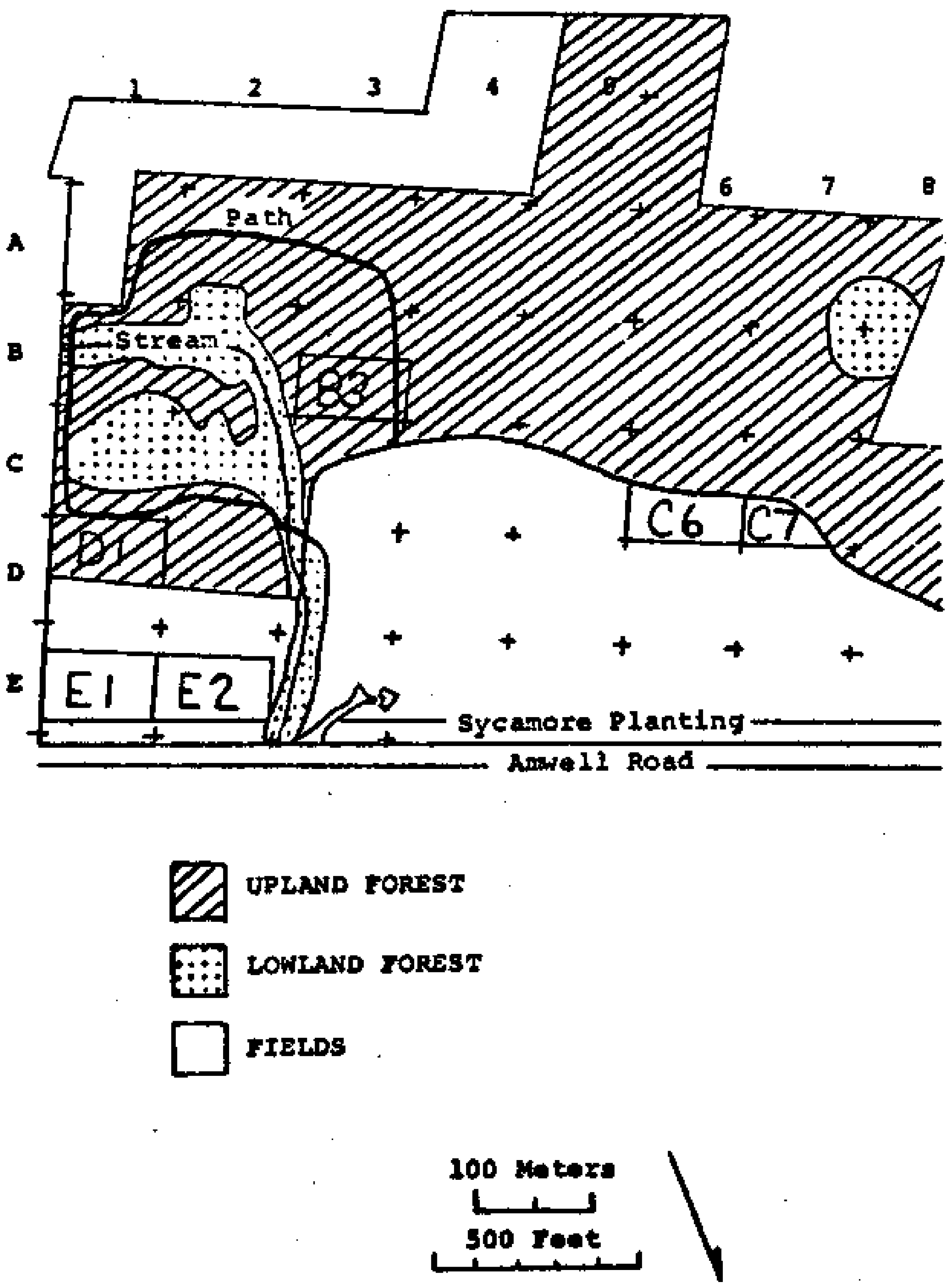


Figure 1. The position of the fields and the two forested areas sampled at Hutcheson Memorial Forest.

through 1963, after which they were abandoned from agricultural use. C7 was plowed in April 1964, thus, starting succession from bare soil in that field, while C6 remained in orchard grass.

Thus, the two pairs of fields have somewhat comparable histories, separated only by a two-year time span, allowing for: (1) comparisons within pairs, i.e., between C6 and C7, and between E1 and E2 for a consecutive number of years (seven and nine, respectively); and (2) for comparisons between pairs (representing a maximum of seven years of abandonment).

Vegetation Measurements

The area sampled in each field measured approximately 50 by 100 meters and contained 48 systematically placed permanent quadrats. The quadrats measured 1/2 x 2 m and were spaced eight meters apart along five lines of ten quadrats each, except for the fifth line which contained only eight quadrats.

Data were collected during late July through early August for seven and nine successive years for the C and E field, respectively, except for 1966 when data for fields C6 and E1 were not recorded. Percent cover of each species per quadrat was visually determined and recorded. The cover often totaled more than 100% due to overlap of the foliage of the species and particularly as a result of layering in the herbaceous community.

In addition to the above procedures, the vegetation on two areas in the forest, designated D1 and B3 on the map (Figure 1), was sampled using a quadrat system similar to the one used in sampling the fields. Cover data were recorded for the summer of 1970 only. The data included cover values for all layers of the forest. This was done following the same procedures as used in the field studies.

We sampled field E2 twice on the same day in the summer of 1970. For the second sampling the quadrats were arranged so that they were halfway between the original quadrats and perpendicular to them. Cover data were recorded as previously.

By sampling the forest in two places and by sampling a field twice with two different sets of quadrats, I hoped to obtain information with which I could better interpret the meaning of the Dissimilarity Indices which were calculated to compare the fields. The forest data would tell me something about how different two parts could be of a natural community which have had a long period of time to develop relatively free of human disturbance. The duplicate field sampling was to give me some basis for knowing the degree of difference that could result from the replicate sampling of the same field with the same number of quadrats (48).

Nomenclature follows Gray's Manual of Botany (Fernald, 1950) except for the Compositae, in which it follows Gleason and Cronquist (1963).

I wish to express appreciation to Dr. T. G. Siccama for his helpful advice on some aspects of the paper and to Dr. J. A. Small and Drs. M. F. and H. F. Buell for use of data collected on the fields.

Vegetation Analyses

Mean cover values derived from the data were used in the following three ways:

1. To compare the fields, dissimilarity values were calculated using the formula employed by Bray and Curtis (1957). This formula is a mathematical expression which attempts to show the similarity or dissimilarity between stands by taking into consideration the quantitative values of the species (in this instance, mean cover values) which the stands have in common and dividing that by the sum of the quantitative values of all the species for each of the stands. The actual formula for the Index of Dissimilarity is:

$$C = \frac{2w}{a + b}$$

$$ID = 100 - C$$

where: w = the sum of the quantitative values of the species shared by the stands; a = the sum of all values of the species for the first stand; b = the sum of all values of the species for the second stand.

2. Natural communities are mixtures of species which are unequally successful (Whittaker, 1965). In a given

community, one or a few species, the dominants, overshadow all others and may strongly affect the environment of the other species. The community also includes species which are of intermediate abundance or rare, and it is the number of these species which primarily determines the community's diversity. Taking this approach to the expression of diversity, Whittaker's Dominance-Diversity Curves were constructed from the field data.

By using some importance value, such as productivity, biomass, basal area, cover (mean cover was used in this study), etc., for the species, and plotting them against a species sequence, we get a curve which forms a continuous progression from dominants through intermediates to insignificant species. It was on this basis that Whittaker (1965) developed the family of curves for the plant communities in the Great Smoky Mountains. He found that the communities of the greatest diversity had sigmoid curves which fit the logarithmic series of Fisher, Corbet, and Williams (1943).

3. Finally, Shannon-Wiener Diversity Indices (Cox, 1967) were calculated for each of the fields in an effort to express mathematically that which the Whittaker Curves attempt to indicate graphically. The Shannon-Wiener Index gives a much better representation of the diversity of the fields because it attempts to describe the average degree of uncertainty of occurrence of a particular species at a certain point. This uncertainty increases both as Species Richness (the number of species) increases and as Evenness (the equal distribution of individuals among the species) increases. The formula used for calculating diversity is:

$$H' = 3.3219\left(\log_{10}N - \frac{1}{N}\Sigma n_i \log_{10} n_i\right)$$

where: N = total number of individuals of all species.
n_i = number of individuals of the i^{th} species.

To measure the Evenness of a field, we take the ratio of the observed diversity to the maximum diversity possible for the same number of species (Pielou, 1969). The formula for Evenness is:

$$J' = \frac{H'}{H'\max}$$

where: H' = diversity; $H'\max = \text{Log}_2 S$; S = the number of species in the field.

Results

The trend toward convergence between plowed and hay fields was substantiated in this study on the basis of Dissimilarity Values, Whittaker Dominance-Diversity Curves, and Shannon-Wiener Diversity Indices. These three sets of calculations all indicated an increasing similarity between the two different types of fields.

Figure 2 (using Dissimilarity Indices) shows the convergence which is occurring between the hay and plowed fields. Fields C6 (hay) and C7 (plowed) were 86% different (assuming we can refer to the coefficient of Dissimilarity as expressing a percentage difference between communities) after the first year of abandonment. After seven years they were only 38% different. Fields E1 (hay) and E2 (plowed) were 96% different the first year, 63% different the seventh year, and 38% different by the ninth year.

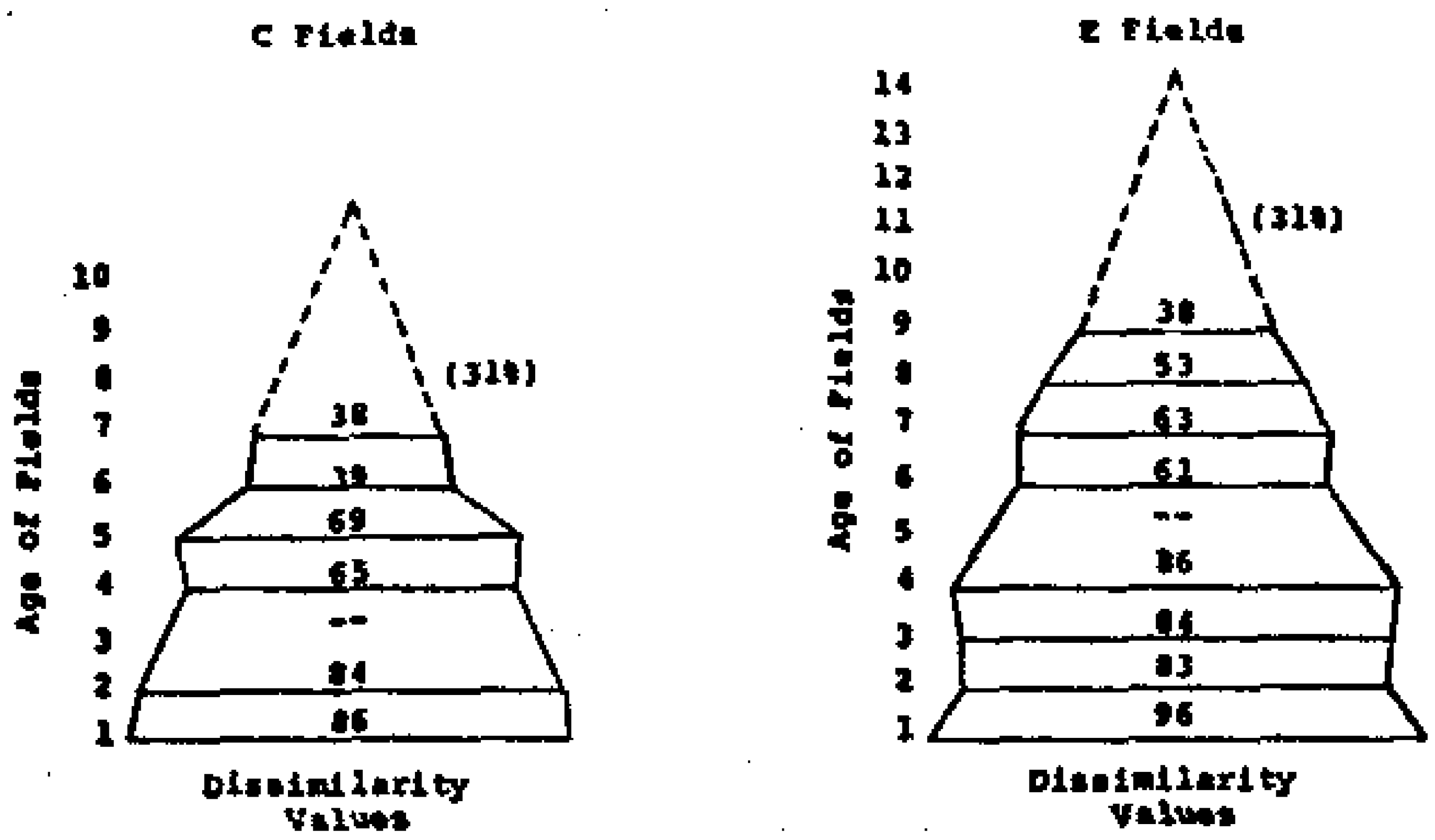


Figure 2. The convergence between hay and plowed fields, expressed as decreasing dissimilarity values through time. The dashed lines represent projections of convergence into the future, with 31% dissimilarity marked as the time when the hay and plowed fields may be considered to be essentially alike, i.e., 8 years after abandonment in the C fields and 11 years after abandonment in the E fields.

The significance of these values is best understood when we consider that: (1) when two "similar" areas of the forest were compared, they were found to be 31% different; and (2) when the same field was sampled twice, a 16% difference was found representing the difference due to sample error alone. Table 1 lists the plants and cover percentages found in both the first and second samplings of field E2 1970. The differences between these two show how close the two samples estimate each species (the greater the difference in mean cover, the more variation in sampling).

Tables 2 and 3 show the dominant species by year for each field, thus reflecting the annual successional changes in field composition. In field C6, *Dactylis glomerata* maintained dominance until 1969 when *Agropyron repens* replaced it as the leading dominant with a mean cover of 48%. Other important species included *Oxalis stricta, Chrysanthemum leucanthemum, Solanum carolinense,* and *Aster pilosus*. The first two years of abandonment found field C7 with a dominance of *Ambrosia artemisiifolia*. By the third year *Agropyron repens* was the leading dominant with a mean cover of 42%, increasing to 81% in 1968, and decreasing to 27% but still holding dominance in 1970. *Convolvulus sepium* was also quite abundant in 1968-1970.

Dactylis glomerata actually increased its coverage and thus dominance in field E1 from 1962 to 1967. In 1967 it covered 76% of the field, but decreased to 22% in 1968 and to less than 7% after that. E2 was covered with *Digitaria sanguinalis* (88% mean cover) the first year. *Rumex acetosella, Linaria vulgaris, Aster vimineus,* and *Hieracium pratense* made up the leading dominants during the following years. The interesting point here is that

Table 1. The list of plants resulting from two successive samplings designated field E2(1) and E2(2), respectively, 1970, showing the mean cover for each plant in each field and the amount of cover which they have in common. The difference between mean cover is also given.

Species	Mean cover Field E2(1)	Mean cover Field E2(2)	Mean cover Shared	Mean cover Difference
Abutilon theophrasti	—	0.22	—	0.22
Acalypha gracilens	0.002	—	—	0.002
Acalypha rhomboidea	0.16	0.18	0.16	0.02
Acer negundo	0.27	0.31	0.27	0.04
Achillea millefolium	6.54	4.81	4.81	1.73
Allium vineale	0.16	0.12	0.12	0.04
Ambrosia artemisiifolia	—	0.02	—	0.02
Apocynum cannabinum	0.52	0.20	0.20	0.32
Aster ericoides	3.90	3.54	3.54	0.36
Aster pilosus	17.90	21.14	17.90	3.24
Aster simplex	0.2	0.67	0.2	0.47
Aster vimineus	3.68	5.58	3.68	1.90
Barbarea vulgaris	0.10	0.16	0.10	0.06
Centaurea dubia	2.81	0.18	0.18	2.63
Cerastium vulgatum	—	0.16	—	0.16
Chrysanthemum leucanthemum	2.56	1.68	1.68	0.88
Cirsium arvense	0.02	—	—	0.02
Cirsium discolor	0.14	0.02	0.02	0.12
Convolvulus sepium	2.87	2.81	2.81	0.06
Cornus florida	—	0.002	—	0.002
Cyperaceae	—	0.002	—	0.002
Dactylis glomerata	0.45	0.79	0.45	0.34
Daucus carota	6.85	7.45	6.85	0.60
Dianthus armeria	0.52	0.27	0.27	0.25
Erechtites hieracifolia	—	0.002	—	0.002
Erigeron annuus	0.87	1.14	0.87	0.27
Fragaria virginiana	4.93	4.47	4.47	0.46
Hieracium florentinum	4.66	1.27	1.27	3.39
Hieracium pratense	26.14	27.33	26.14	1.19
Juniperus virginiana	0.56	0.08	0.08	0.48
Lactuca canadensis	0.04	—	—	0.04
Lepidium campestre	—	0.14	—	0.14
Linaria vulgaris	0.85	0.91	0.85	0.06
Lobelia inflata	0.10	0.02	0.02	0.08
Lonicera japonica	11.43	7.41	7.41	4.02
Lychnis alba	0.43	0.10	0.10	0.33
Oenothera biennis	1.43	1.45	1.43	0.02
Oxalis stricta	0.52	0.70	0.52	0.18
Penstemon hirsutus	0.04	—	—	0.04
Physalis subglabrata	0.04	0.02	0.02	0.02
Plantago lanceolata	2.89	2.52	2.52	0.37
Plantago rugelii	0.37	0.20	0.20	0.17
Poa compressa	0.10	—	—	0.10
Poa pratensis	4.08	8.20	4.08	4.12
Polygonum convolvulus	—	0.002	—	0.002
Potentilla canadensis	1.97	—	—	1.97
Potentilla recta	0.25	0.22	0.22	0.03
Prunus serotina	0.06	—	—	0.06
Pyrus malus	—	0.41	—	0.41
Raphanus raphanistrum	—	0.02	—	0.02
Rhus glabra	0.60	2.60	0.60	2.00
Rhus radicans	0.14	0.39	0.14	0.25
Rosa multiflora	2.81	0.25	0.25	2.56
Rubus allegheniensis	—	0.02	—	0.02
Rubus flagellaris	0.08	0.10	0.08	0.02
Rumex acetosella	0.93	1.06	0.93	0.13
Solanum carolinense	1.06	1.58	1.06	0.52
Solidago graminifolia	0.43	0.39	0.39	0.04
Solidago juncea	1.20	1.43	1.20	0.23
Solidago nemoralis	0.93	1.54	0.93	0.61
Taraxacum officinale	0.06	0.08	0.06	0.02
Trifolium hybridum	0.04	0.12	0.04	0.08
Trifolium pratense	0.002	0.06	0.002	0.058
Verbascum blattaria	0.35	0.45	0.35	0.10
Vicia villosa	2.18	0.62	0.62	1.56
Totals	122.22	117.62	100.09	

whereas these hay and plowed fields contained almost completely different dominant species during the first years of succession, by 1970 the C fields shared four out of the five most abundant species, representing over 80% mean cover, and the E fields shared five out of the eight most abundant species, representing over 60% mean cover. Visual inspection of the overall appearance of the fields at this point in time showed the E fields to look very much alike, and the same was true of the C fields. However, the C and E fields appeared quite distinct from each other.

Regression analysis of the dissimilarity values, comparing C6 with C7 and E1 with E2, shows that the C and E fields are changing at different rates (figure 3), the rate of convergence between hay and plowed fields being faster in the C fields than in the E fields. Using 31% as an estimate of dissimilarity that one might expect between two areas with the same history, the fields would assume

Table 2. The dominant species of fields C6 and C7. The shared species are shown in bold face type.

Year	C6 (Hay) Mean cover	C6 (Hay) Species	C7 (Plowed) Mean cover	C7 (Plowed) Species
1964	87	*Dactylis glomerata*	54	*Ambrosia artemisiifolia*
	9	*Agropyron repens*	31	*Raphanus raphanistrum*
	5	*Plantago rugelii*	11	*Chenopodium album*
	5	*Oxalis stricta*	10	*Plantago rugelii*
	3	*Barbarea vulgaris*	7	*Acalypha rhomboidea*
1965	47	*Dactylis glomerata*	60	*Ambrosia artemisiifolia*
	10	**Agropyron repens**	22	*Barbarea vulgaris*
	4	*Raphanus raphanistrum*	14	*Plantago rugelii*
	2	*Rumex acetosella*	5	*Oxalis stricta*
	2	*Chrysanthemum leuc.*	5	**Agropyron repens**
1966			42	*Agropyron repens*
			18	*Barbarea vulgaris*
			12	*Plantago rugelii*
			10	*Dactylis glomerata*
			9	*Lychnis alba*
1967	87	**Dactylis glomerata**	47	**Agropyron repens**
	5	**Agropyron repens**	26	**Dactylis glomerata**
	5	*Lotus corniculatus*	11	*Erigeron annuus*
	5	*Chrysanthemum leuc.*	9	*Oxalis stricta*
	4	*Rumex acetosella*	8	*Plantago rugelii*
1968	39	*Dactylis glomerata*	81	**Agropyron repens**
	13	**Agropyron repens**	14	*Convolvulus sepium*
	11	**Oxalis stricta**	8	**Oxalis stricta**
	8	*Raphanus raphanistrum*	5	*Linaria vulgaris*
	7	*Rumex acetosella*	4	*Solanum carolinense*
1969	48	**Agropyron repens**	61	**Agropyron repens**
	15	*Chrysanthemum leuc.*	24	*Convolvulus sepium*
	8	**Oxalis stricta**	11	*Hieracium pratense*
	8	*Rumex acetosella*	10	**Oxalis stricta**
	5	*Barbarea vulgaris*	7	*Solanum carolinense*
1970	50	**Agropyron repens**	27	**Agropyron repens**
	13	**Solanum carolinense**	18	**Convolvulus sepium**
	11	**Aster pilosus**	17	**Aster pilosus**
	9	*Rumex acetosella*	10	**Solanum carolinense**
	8	**Convolvulus sepium**	8	*Hieracium pratense*

likeness in 8 and 11 years after abandonment, respectively.

Table 4 shows the amount of change (expressed in dissimilarity values) which has taken place in each field from its first year of abandonment to the last year of sampling. Values are also given for the E (1968) fields. The change has been great in all of the fields, but in all cases the plowed fields show the greatest change. Also, it is interesting to note that the C fields show the most similar amount of change (their values are closer to each other), whereas the E fields differ extensively from each other.

It follows that a comparison between C6 and E1 (both hay fields) and a comparison between C7 and E2 (both plowed fields) need not necessarily be expected to yield low dissimilarity values at the same age. Results for the first and seventh years are given in Table 5. The one-year-old plowed fields were very different from each other (92% dissimilar), and even after seven years they were still 54% different. Even the hay fields, which with an almost complete dominance of *Dactylis glomerata* we would expect to have very low dissimilarity values, were 42% different at age one and 79% different at age seven. If these values seem surprising, we must remember that although the data represent the same age fields, they represent different chronological dates.

An extremely important factor influencing the first year's successional vegetation of the plowed fields was, I believe, the amount of precipitation received by these

Table 3. The dominant species of fields E1 and E2. The shared species are shown in bold face type.

	E1 (Hay)		E2 (Plowed)	
Year	Mean cover	Species	Mean cover	Species
1962	55	*Dactylis glomerata*	88	*Digitaria sanguinalis*
	20	*Plantago rugelii*	14	*Mollugo verticillata*
	13	*Plantago lanceolata*	5	*Portulaca oleracea*
	8	*Erigeron annuus*	4	*Cyperus* sp.
	2	*Daucus carota*	2	*Rumex acetosella*
1963	53	*Dactylis glomerata*	18	*Rumex acetosella*
	12	*Plantago rugelii*	10	*Chenopodium album*
	7	*Aster ericoides*	10	*Ambrosia artemisiifolia*
	6	*Erigeron annuus*	8	*Barbarea vulgaris*
	2	*Poa pratensis*	7	*Convolvulus sepium*
1964	72	*Dactylis glomerata*	40	**Rumex acetosella**
	10	*Daucus carota*	13	*Convolvulus sepium*
	6	*Plantago rugelii*	11	*Linaria vulgaris*
	4	**Rumex acetosella**	11	*Ambrosia artemisiifolia*
	4	*Aster ericoides*	11	*Trifolium hybridum*
1965	67	*Dactylis glomerata*	17	**Rumex acetosella**
	3	*Chrysantehmum leuc.*	14	*Linaria vulgaris*
	3	**Rumex acetosella**	11	*Erigeron annuus*
	2	*Aster ericoides*	4	*Convolvulus sepium*
	2	*Linaria vulgaris*	4	*Lychnis alba*
1966			18	*Linaria vulgaris*
			10	*Vicia villosa*
			8	*Daucus carota*
			8	*Lychnis alba*
			7	*Rumex acetosella*
1967	76	*Dactylis glomerata*	19	*Aster vimineus*
	13	*Aster ericoides*	19	*Ambrosia artemisiifolia*
	7	*Linaria vulgaris*	15	*Convolvulus sepium*
	7	*Poa pratensis*	11	*Aster pilosus*
	5	*Rumex acetosella*	11	*Erigeron annuus*
1968	22	*Dactylis glomerata*	19	*Aster vimineus*
	18	**Oenothera biennis**	8	**Oenothera biennis**
	11	*Linaria vulgaris*	8	*Chrysanthemum leuc.*
	8	*Poa compressa*	8	*Hieracium pratense*
	4	*Rumex acetosella*	6	*Erigeron annuus*
1969	23	*Linaria vulgaris*	23	*Hieracium pratense*
	14	**Oenothera biennis**	15	*Aster vimineus*
	12	*Rumex acetosella*	10	*Aster pilosus*
	12	**Chrysanthemum leuc.**	8	**Chrysanthemum leuc.**
	7	*Poa pratensis*	8	**Oenothera biennis**
1970	13	*Aster ericoides*	26	**Hieracium pratense**
	10	**Poa pratensis**	18	*Aster pilosus*
	9	**Lonicera japonica**	11	**Lonicera japonica**
	8	**Daucus carota**	7	**Daucus carota**
	8	*Potentilla canadensis*	7	*Achillea millefolium*
	6	**Fragaria virginiana**	5	**Fragaria virginiana**
	6	*Solidago juncea*	5	*Hieracium florentinum*
	6	**Hieracium pratense**	4	**Poa pratensis**

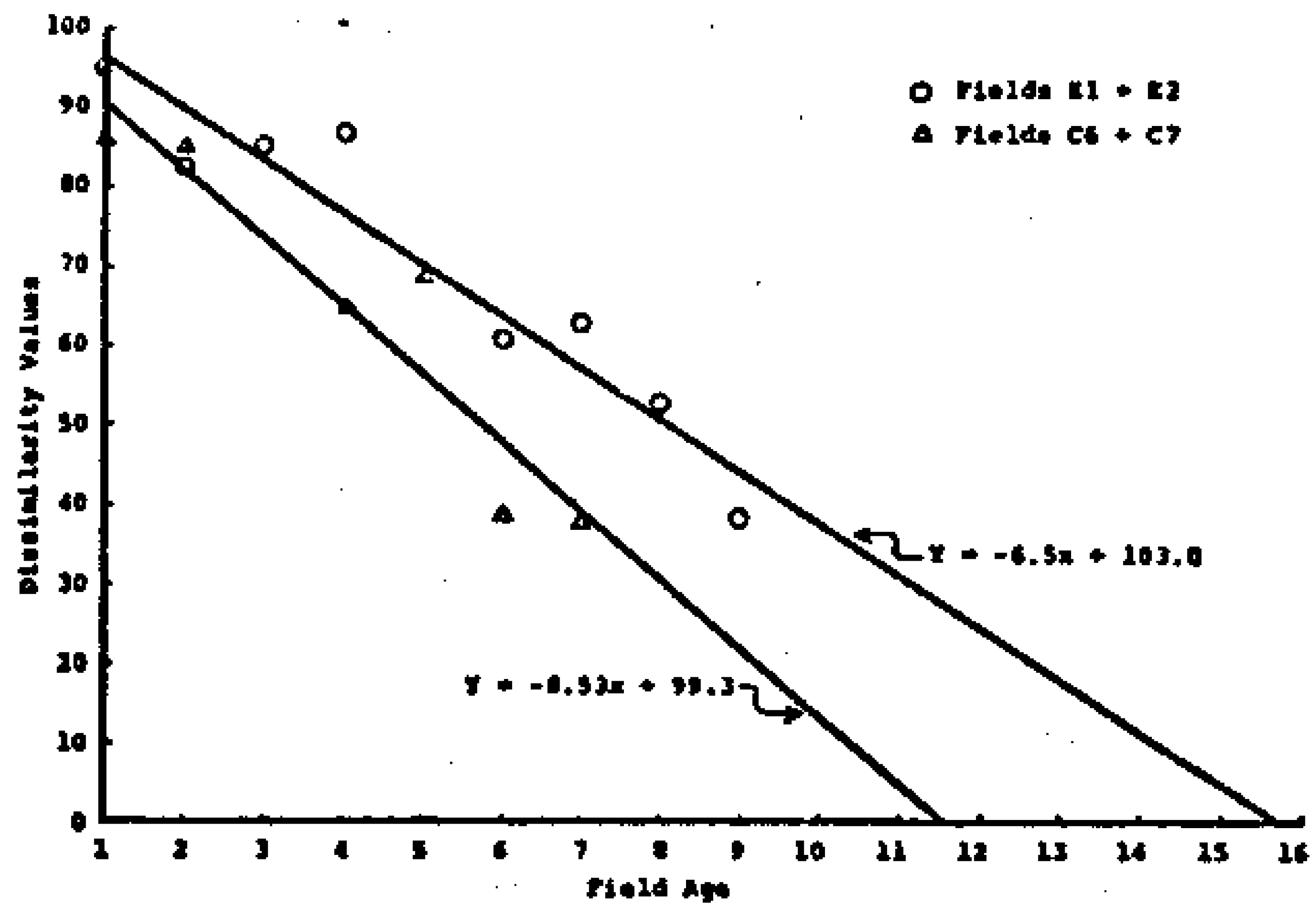


Figure 3. Regression analysis showing the rate of convergence of the C and E fields. The extension of these lines shows the C fields to become alike in 12 years and the E fields in 16 years.

Table 4. Dissimilarity values showing the degree of change occurring within each field by comparing the first and last year of each field, plus the first and seventh year of the E fields.

Fields	Years being compared	Number of years since abandonment	Dissimilarity
C6 (plowed)	1964-1970	7	78
C7 (hay)	1964-1970	7	85
E1 (hay)	1962-1968	7	69
E2 (plowed)	1962-1968	7	97
E1 (hay)	1962-1970	9	81
E2 (plowed)	1962-1970	9	97

Table 5. Dissimilarity values comparing two plowed fields of the same age and two hay fields of the same age.

Fields being compared	Field year	Age of fields	Dissimilarity value
C7-E2 (plowed)	1964-1962	1	92
	1970-1968	7	54
C6-E1 (hay)	1964-1962	1	42
	1970-1968	7	79

newly abandoned fields. As indicated earlier, 1962, the year in which the E fields were abandoned, was a fairly dry year, whereas 1964, the year in which the C fields were abandoned, was a moderately wet year. This influence can be seen, for example, in the distribution of *Digitaria sanguinalis*, *Ambrosia artemisiifolia*, and *Raphanus raphanistrum* for those years. In field E2 (1962), *Digitaria sanguinalis* had a mean cover of 88%, but dropped to 0% in E2 (1964) and to 3% in C7 (1964). Likewise, *Ambrosia artemisiifolia* and *Raphanus raphanistrum* were very abundant in 1964, but scarce in 1962. Thus, the success of particular species may be dependent upon their water requirements.

There were also several other factors involved here. Ugolini (1964) indicated minor differences in soil between the fields, implying soil differences as probable casuses for only slight changes in vegetation. No doubt, plant competition, germination requirements, and time of plowing were important also. (E2 was plowed in June 1962; C7 was plowed in April 1964.) And Wales (1969) describes what he calls "edge-effect." In this case, the north facing side of the forest acts as a barrier to winter winds, resulting in snow accumulation and, thus, greater soil moisture there. Also, the proximity of the fields to the forest provides for seed dispersal of forest species from the forest to the field. This phenomenon can be seen in the C fields, where such forest representative species as *Acer rubrum*, *Cornus florida*, and *Parthenocissus quinquefolia* were found.

If we next turn our attention to expressions of diversity, we see first that the construction of Dominance-Diversity curves (Whittaker, 1965) shows increasing diversity in each field, as the curves, through successive years, approach the sigmoid shape (Fisher et al. 1943). They also show a decrease in single species dominance with time (Figures 4, 5, 6, and 7).

When the 1964 Dominance-Diversity curves of C6 and C7 are compared, clear differences can be observed between them. The same is true for the 1962 curves of fields E1 and E2. However, comparisons between C6 and C7 (1970) curves show striking similarity. This is true of E1 and E2, for both 1968 and 1970 curves (Figures 4, 5, 6, and 7). The similarity of the curves supports the hypothesis of increasing similarity between hay and plowed fields.

Figure 8 shows the convergence of Species Richness (the number of species in each field) between the hay and plowed fields. In 1970 the total number of species for C6

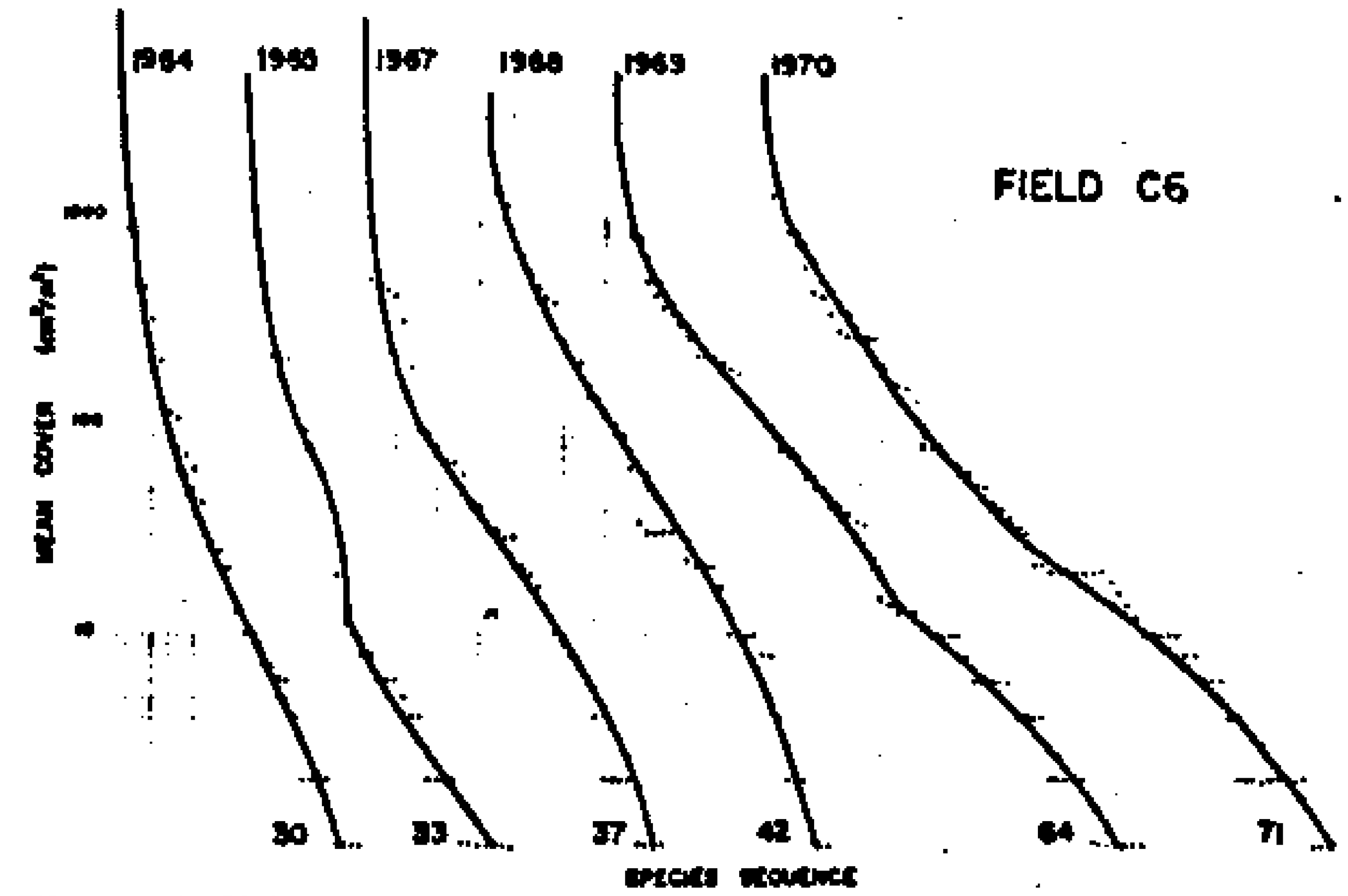


Figure 4. Whittaker's Dominance-Diversity curves for field C6 (hay). "Species sequence" refers to the sequence of cover values for the species occurring each year resulting in the curves. Numbers at base of each curve show the numbers of species occurring in the sampling that year.

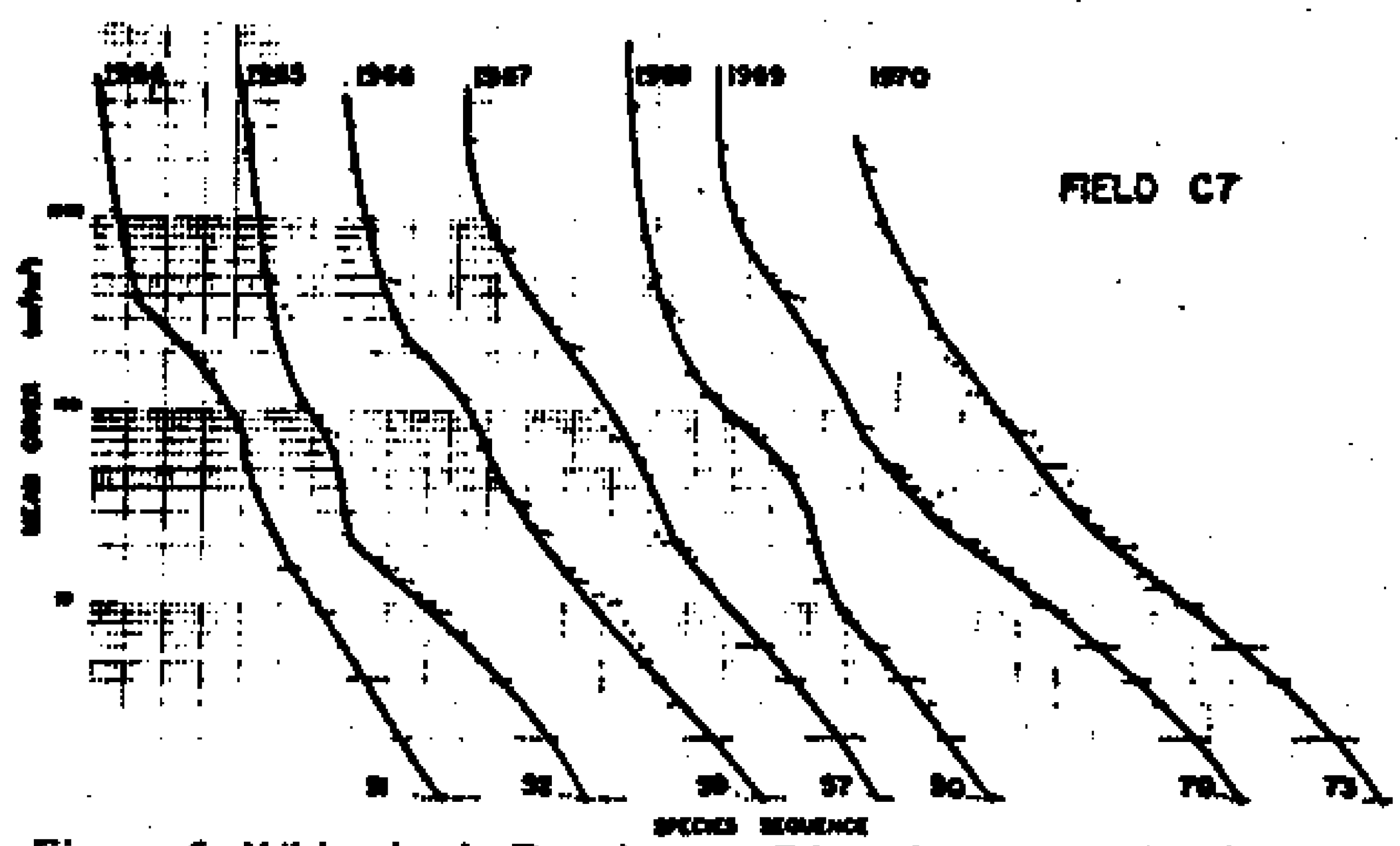


Figure 5. Whittaker's Dominance-Diversity curves for field C7 (plowed). For explanation see fig. 4.

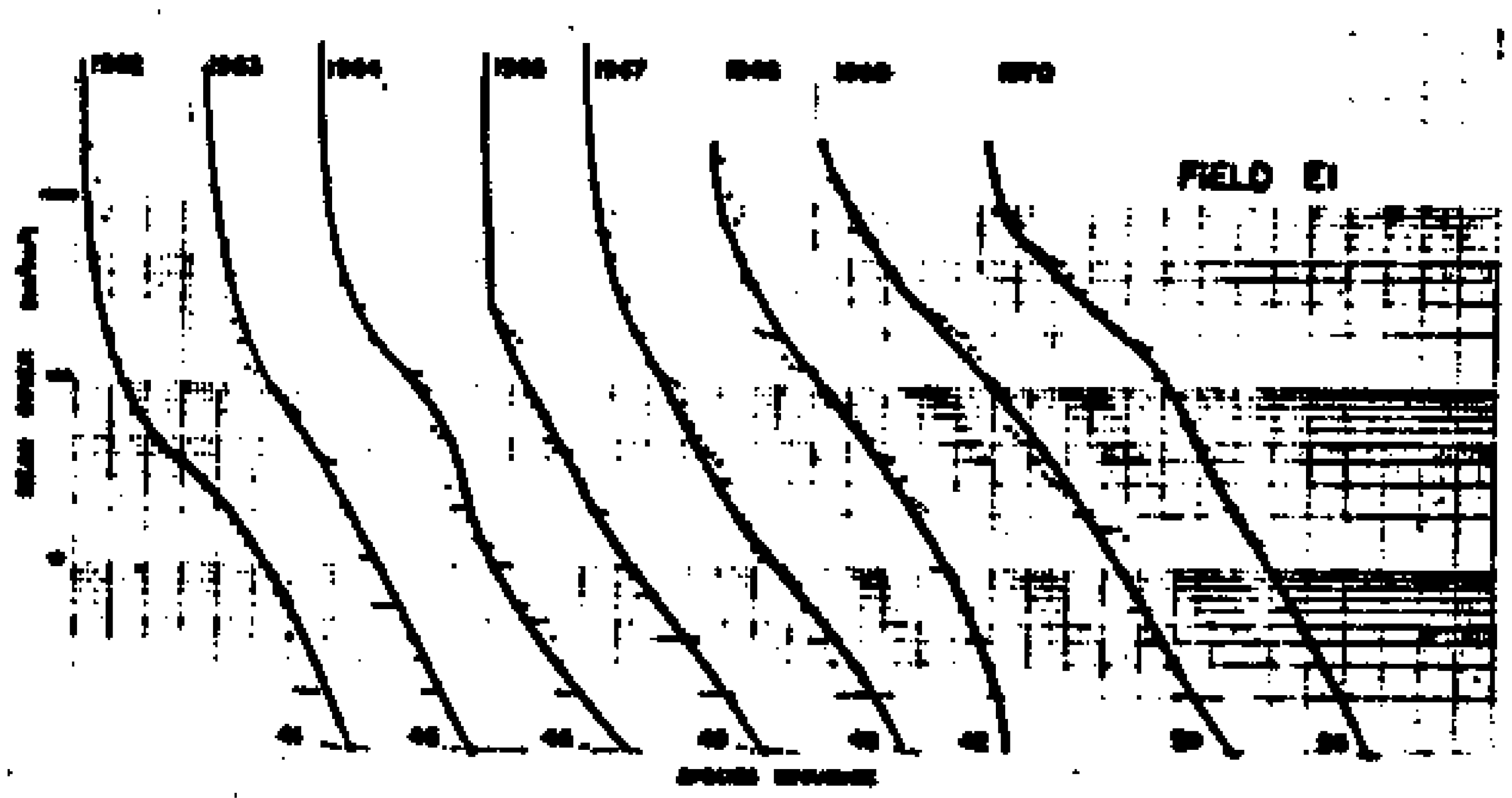


Figure 6. Whittaker's Dominance-Diversity Curves for field E1. (hay). For explanation see fig. 4.

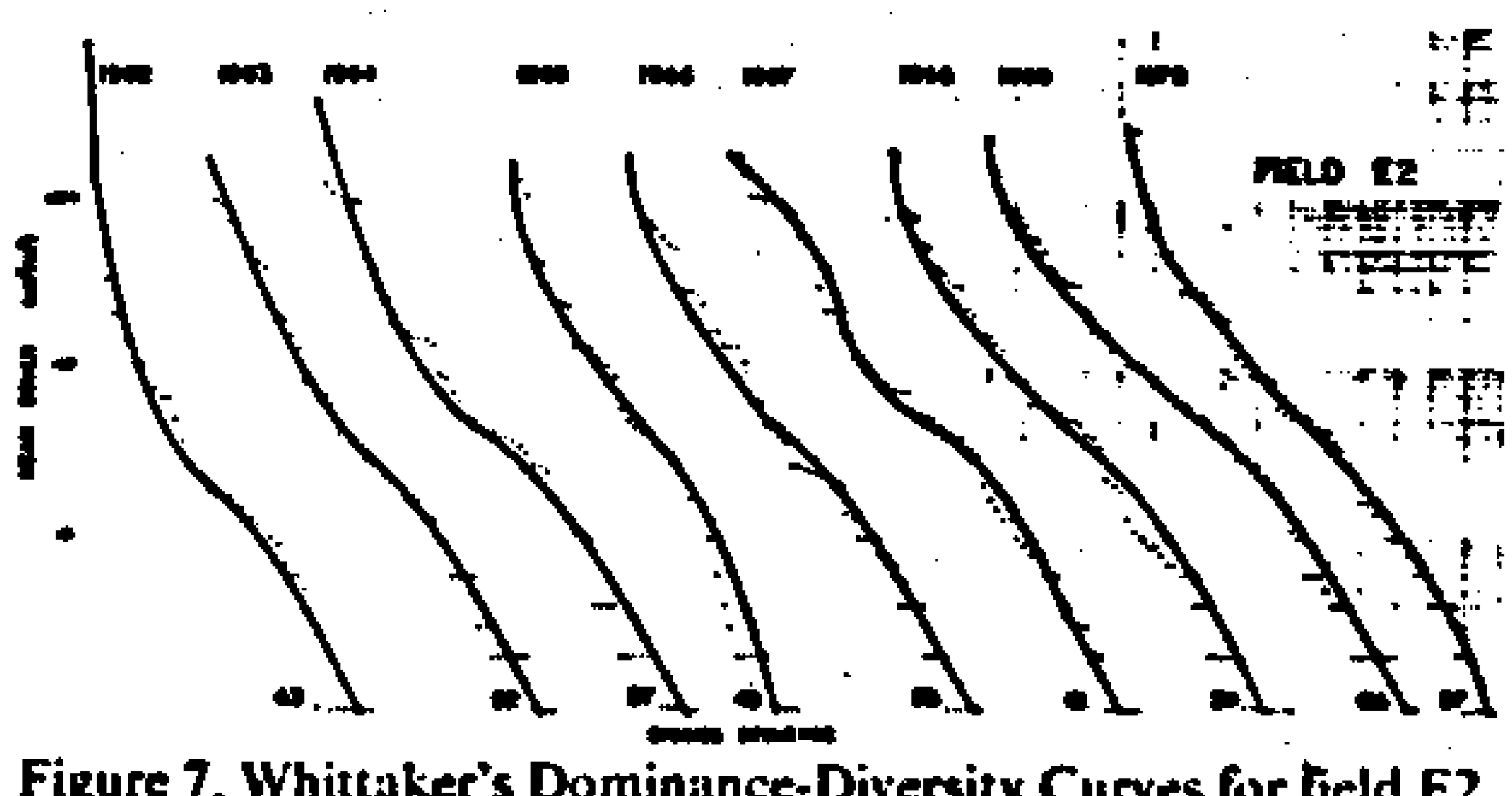


Figure 7. Whittaker's Dominance-Diversity Curves for field E2. (plowed). For explanation see fig. 4.

and C7 and for E1 and E2 were almost equal. The general trend was toward an increase in species number with the plowed fields (with one exception) always having the greater number of species.

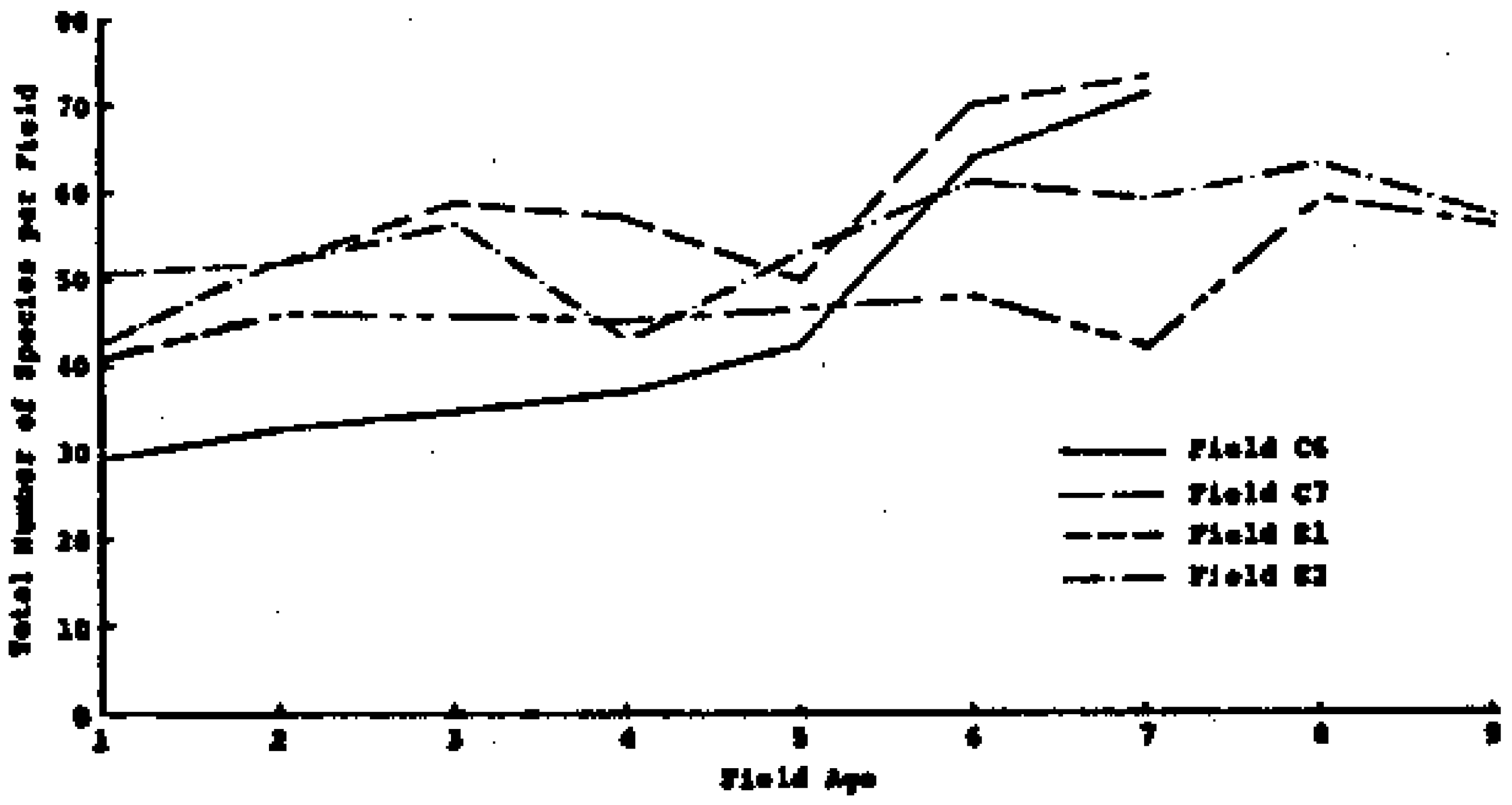
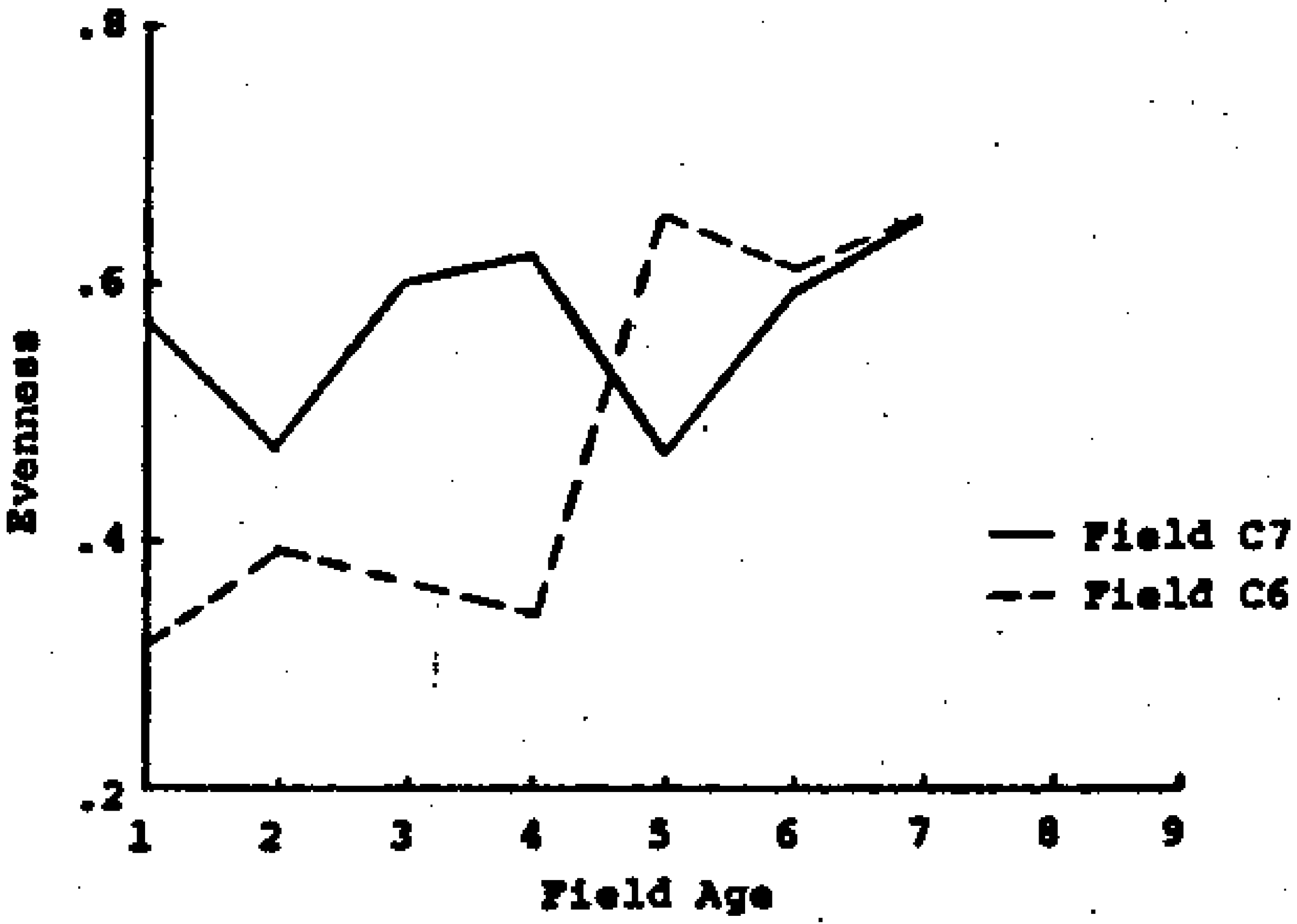


Figure 8. The convergence of Species Richness (the total number of species per field per year) between the hay (C6, E1) and plowed (C7, E2) fields. Since C6 was not sampled the third year and E1 the fifth year, the curves at these points are not comparable with the others.



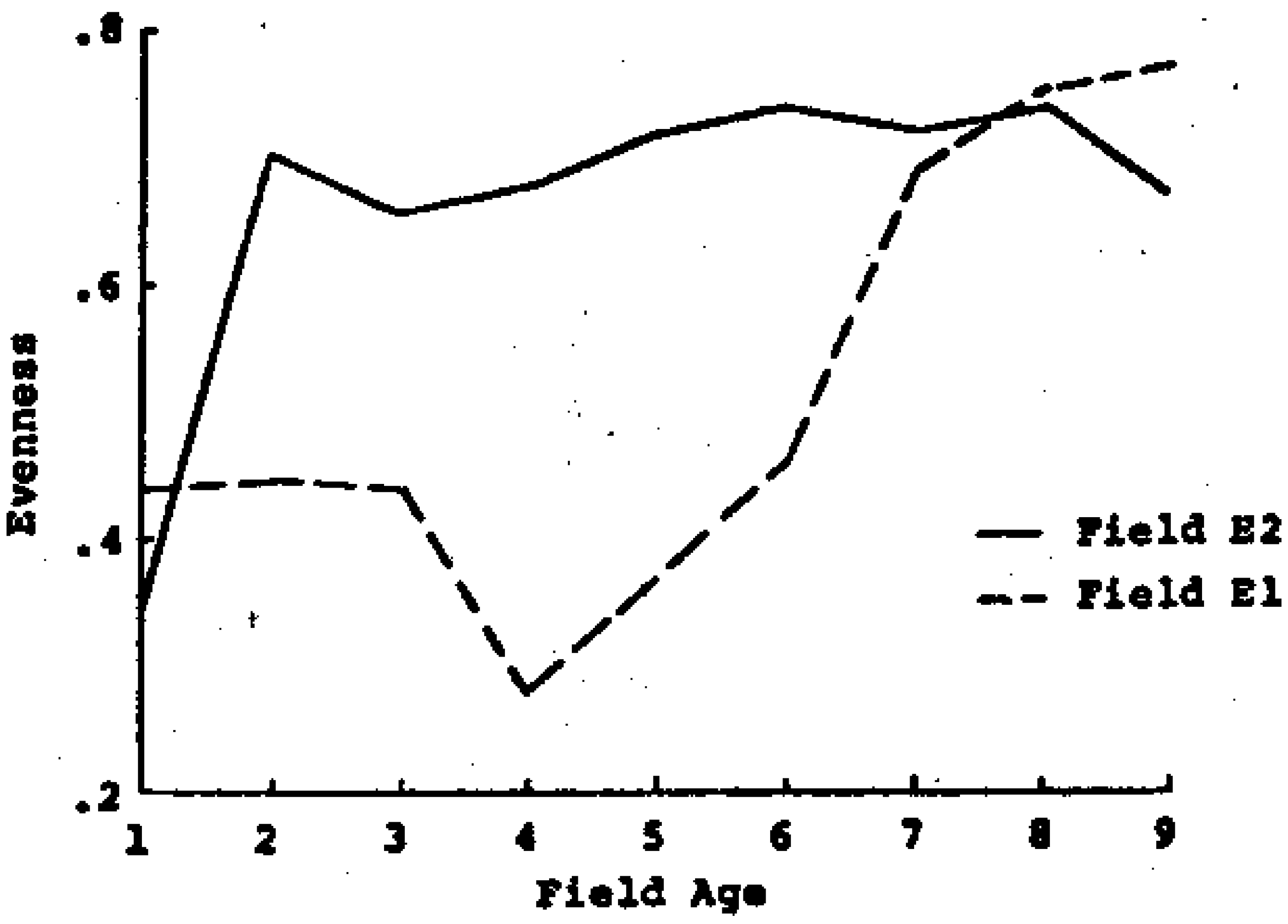


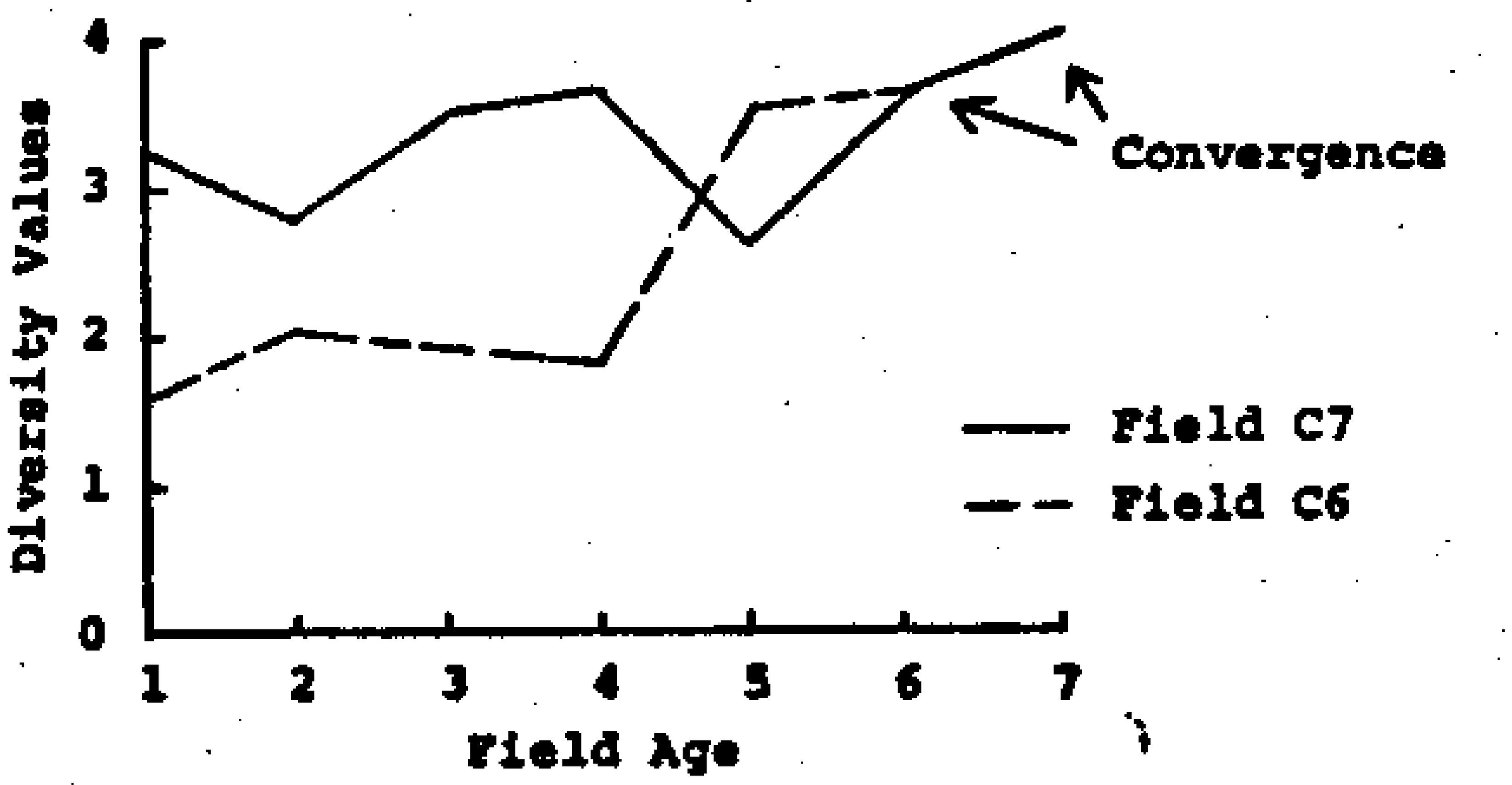
Figure 9. Diversity values for the C and E fields, showing the convergence of the hay (C6, E1) and plowed (C7, E2) fields through time.

Shannon-Wiener Diversity Indices were calculated for all four fields, the two forest areas, and the E2 (1970) second sampling. These are shown in Table 6. The significance of the diversity values is best understood when we consider that two "similar" areas of the forest had diversity values of 3.272 and 3.066, a difference of 0.21, and that two samplings of the same field yielded diversity values of 3.918 and 3.757, a difference of 0.16.

The overall trend was toward greater diversity with field age, confirming results found previously with the

Table 6. Shannon-Wiener Diversity Values.

Year	hay C6	plowed C7	hay E1	plowed E2	E2 (2nd)	forest (D1)	forest (B3)
1962			2.352	1.874			
1963			2.458	3.966			
1964	1.588	3.212	2.425	3.837			
1965	1.973	2.671	1.551	3.694			
1966	—	3.518	—	4.103			
1967	1.781	3.628	2.541	4.365			
1968	3.478	2.578	3.694	4.255			
1969	3.638	3.608	4.431	4.402			
1970	3.991	4.020	4.495	3.918	3.757	3.272	3.066



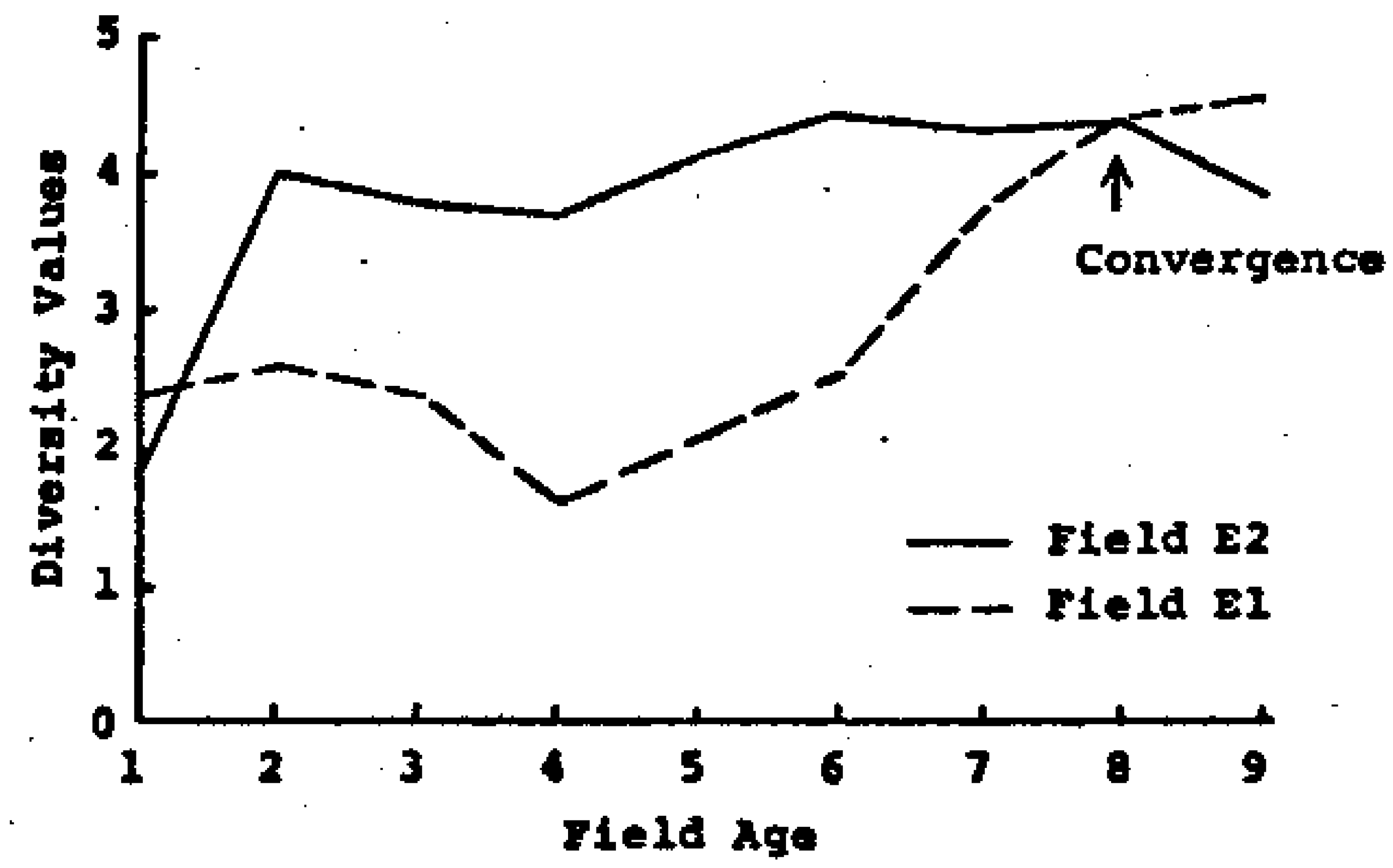


Figure 10. Evenness values for the C and E fields, showing the large increase in Evenness in the hay fields, four to five years after abandonment.

Whittaker curves and Species Richness. The plowed fields generally had the higher diversity values.

Diversity values for plowed and hay fields varied widely from each other during the first few years of succession, but converged to similar values in the last two years of study (Figure 9). Except for E2 (1962), the plowed fields maintained high diversity for most of the years with a range of 2.6 to 4.4, whereas the hay fields had a wider range of 1.6 to 4.5 indicating a greater amount of change. This great amount of change or large increase in diversity in the hay fields can be seen in Figure 9. It occurred in the C fields between four to five years after abandonment. and in the E fields between six to eight years after abandonment. I found that this change in diversity was due to Evenness rather than Species Richness. Figure 10 shows Evenness plotted against field age. The similarity of the Evenness graphs to the diversity graphs in Figure 9 indicates that diversity in these fields is best explained by Evenness rather than Species Richness. At the time of increase of diversity, increase in Species Richness was very small; the C fields increased by five species and E fields by 11 species.

Apparently the high dominance concentration of hay during the first four to five years of succession plays an important part in the development of vegetation on hay fields. Beckwith (1954) suggests that this is the time when a hay field starts to deterioriate, thus creating openings in the vegetation where the existing species might then multiply.

Discussion

The results of this study lend weight to the concept that successions in an area on comparable sites converge to a similar type of vegetation and that in New Jersey the rate of convergence is rapid. This is certainly true of two fields such as a hay field and a field starting out with bare soil. Such fields with similar physiographic and soil conditions may become essentially alike after as little as 8 to 11 years after abandonment.

The similarity in slopes (Figure 3), yet differences in dissimilarity values between the C and E fields, suggested that perhaps some other factors than those already considered were at work here (The slopes are not significantly different at the .05 level.) Beckwith (1954) states that

> hay lands differ sharply from cultivated . . . lands since by the time they are abandoned they have already been occupied by a heavy growth of perennial plants. Sometimes the growth has persisted for many years under annual mowing of hay. Nevertheless, during the years that crops are cut from hay fields various woody plants and other perennials are established that only become conspicuous after abandonment. For this reason it is necessary to begin the study of successional trends on these lands with the last year of plowing instead of the year of actual abandonment.

This idea suggests that the C6 (1964) field, which was planted in 1961 and harvested through 1963, but not abandoned until 1964, may represent a field which is older than one year and perhaps as old as three years.

Table 7. A comparison, using dissimilarity values, between field C6 (1964) and one-, two-, and three-year-old hay fields of field E1.

Field comparisons C6 (1964) with:	Dissimilarity values
E1 (1962)	42
E1 (1963)	39
E1 (1964)	27

With this in mind, I decided to compare (using dissimilarity values) field C6 (1964) to various age E1 fields to see whether field C6 most resembled a one-, two-, or three-year-old hay field which had not been subject to mowing. The results showed C6 (1964) to be most like E1 (1964) — a three-year-old unmowed hay field (Table 7).

Thus, the data for the C fields in Figure 3 may actually represent a comparison between a hay and plowed field in which the hay field is two years older than the plowed field at each point along the graph. This would account for the faster rate of convergence and the smaller dissimilarity values found in the C fields as opposed to the E fields.

To test this idea further, I recalculated dissimilarity values for the E fields by making the E fields comparable on an age basis to the C fields. That is, using the E field data, I compared its three-year-old hay field to its one-year-old plowed field, etc. The values were then graphed, a regression line was drawn through the data, and the line was compared to the C field regression line (Figure 11). I found that the slopes were not significantly different ($P > .50$), suggesting similar rates of succession between both pairs of fields, but the dissimilarity values were significantly higher in the E fields (using the F test, $P < .05$).

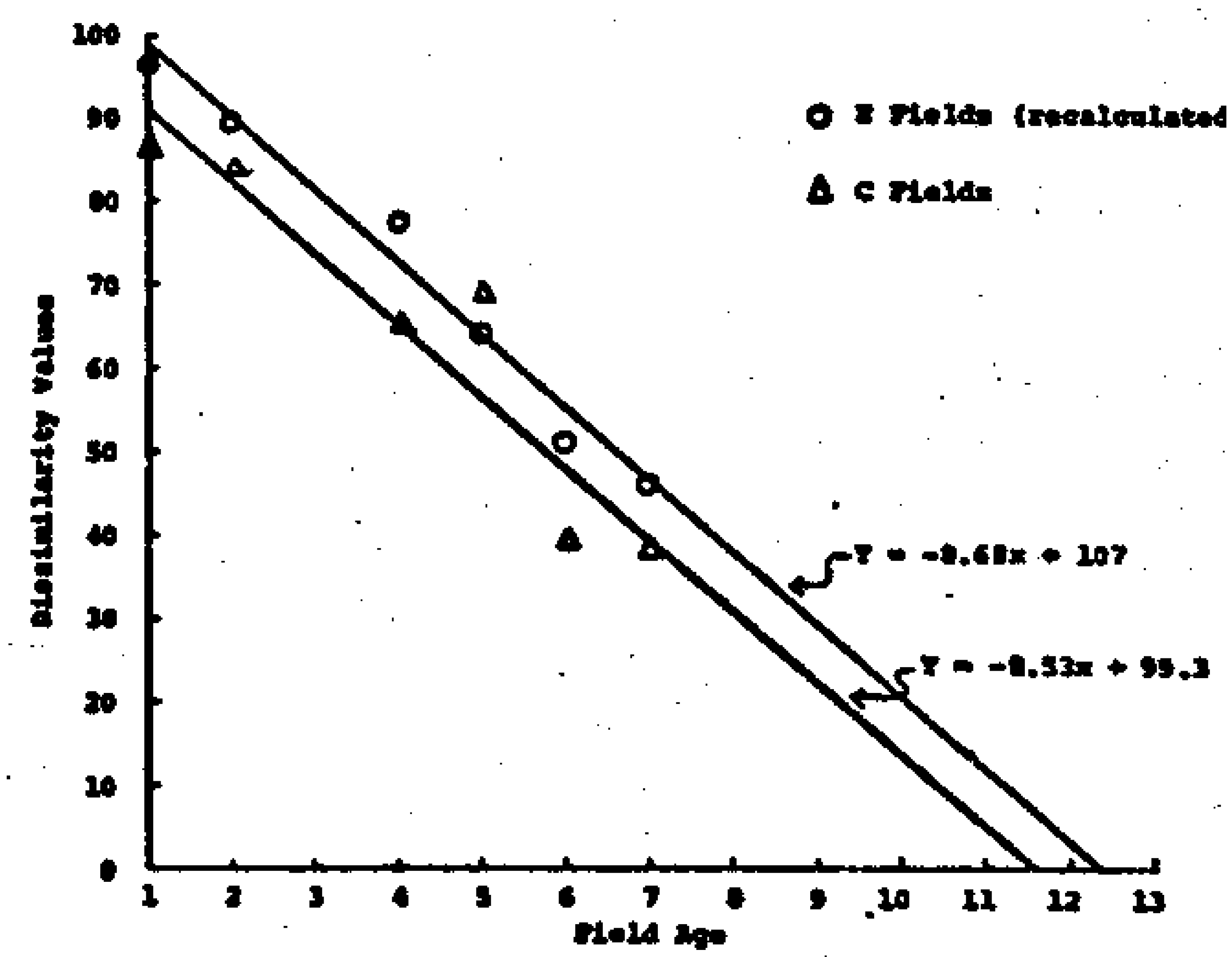


Figure 11. A comparison between the C and E fields in which the E field data have been made comparable to the C fields. The slopes are not significantly different at the .05 level; the dissimilarity values are significantly higher (.05 level) for the E fields.

Referring back to Figure 3, it would seem that the dissimilarity values calculated for the C fields may indeed represent a comparison between a hay and plowed field in which the hay field is two years older than the plowed field. If this is so, then the regression line drawn through these values does not represent a completely valid picture of the rate and character of successional convergence between hay and plowed fields at Hutcheson Memorial Forest. I therefore suggest instead that it is the E fields' data which represent the best estimate of successional convergence. Following this assumption, a 95% Confidence Interval for β (the true slope) was drawn around the E fields' regression line. If read at 31% dissimilarity, this interval ought to tell us the time period in which we might expect a hay and plowed field, on the average, to converge to similar vegetation 95% of the time. Figure 12 shows this to be expected within a minimum of 10 years and a maximum of 14 years after the time of last plowing.

Assuming that C6 (1964) represents a three-year-old hay field, we might then go back and look at the figures and tables which have been derived in the results portion of this paper to see if our interpretation of the results would change:

1. Figure 2. The older age of field C6 would explain the faster rate of convergence in the C fields as opposed to the E fields.
2. Tables 2 and 3. In this case, C6 (1964) would be compared to E1 (1964), C6 (1965) to E1 (1965), etc. An interesting point here is the amount of *Dactylis glomerata* in the hay fields, which shows the same trend in both fields of a decrease and then an increase, and finally a loss of dominance in 1968.
3. Table 4. In this table, C6 (1964-1970) would actually represent a three-year-old hay field being compared to a nine-year-old hay field, in which case we would expect the dissimilarity value to be smaller than that of a comparison between a one-year-old and a nine-year-old field. We find this to be true. Field C6 changed only 78%, while E1 changed 81%.
4. Table 5. The C6 and E1 dissimilarity values were recalculated. Table 8 shows that the fields started out much more alike (27% dissimilarity), and that they remained alike for a few years (about four to five years), after which time, according to Beckwith (1954), hay fields deteriorate and as a result openings are created for the establishment of many wild plants, both annuals or biennials and perennials. After seven years they had become 66% different, which may reflect microclimate, soil, plant competition, and other such differences between the fields.
5. Figure 8. Figure 13 shows the results from Figure 8 with the line for field C6 redrawn. Figure 13(B) shows field C6 to be following field E1's pattern in the number of species per year. The number of species increased greatly after seven years in both hay fields. It appears that in the next two years field C7 may converge with C6 as did E2 with E1 in 1970 (Figure 13(A)).
6. Figure 9. Figure 14 shows the results from Figure 9 with the data from field C6 redrawn. Figure 14(B) shows a similar pattern between the diversity lines of C6 and E1, especially between six to nine years after the last plowing. It appears that the C6 and C7 fields might converge at eight or nine years, after the last plowing (Figure 14(A)).
7. Figure 10. Figure 15 shows the data from the Evenness graphs, with the C6 data redrawn and compared to field E1. The greatest increase in Evenness occurred between six to seven years after the last plowing in both the fields. This time period is slightly greater than that suggested by Beckwith for the deterioration of a hay field. Thus, the above data seem to indicate that the C6 field had actually been undergoing succession

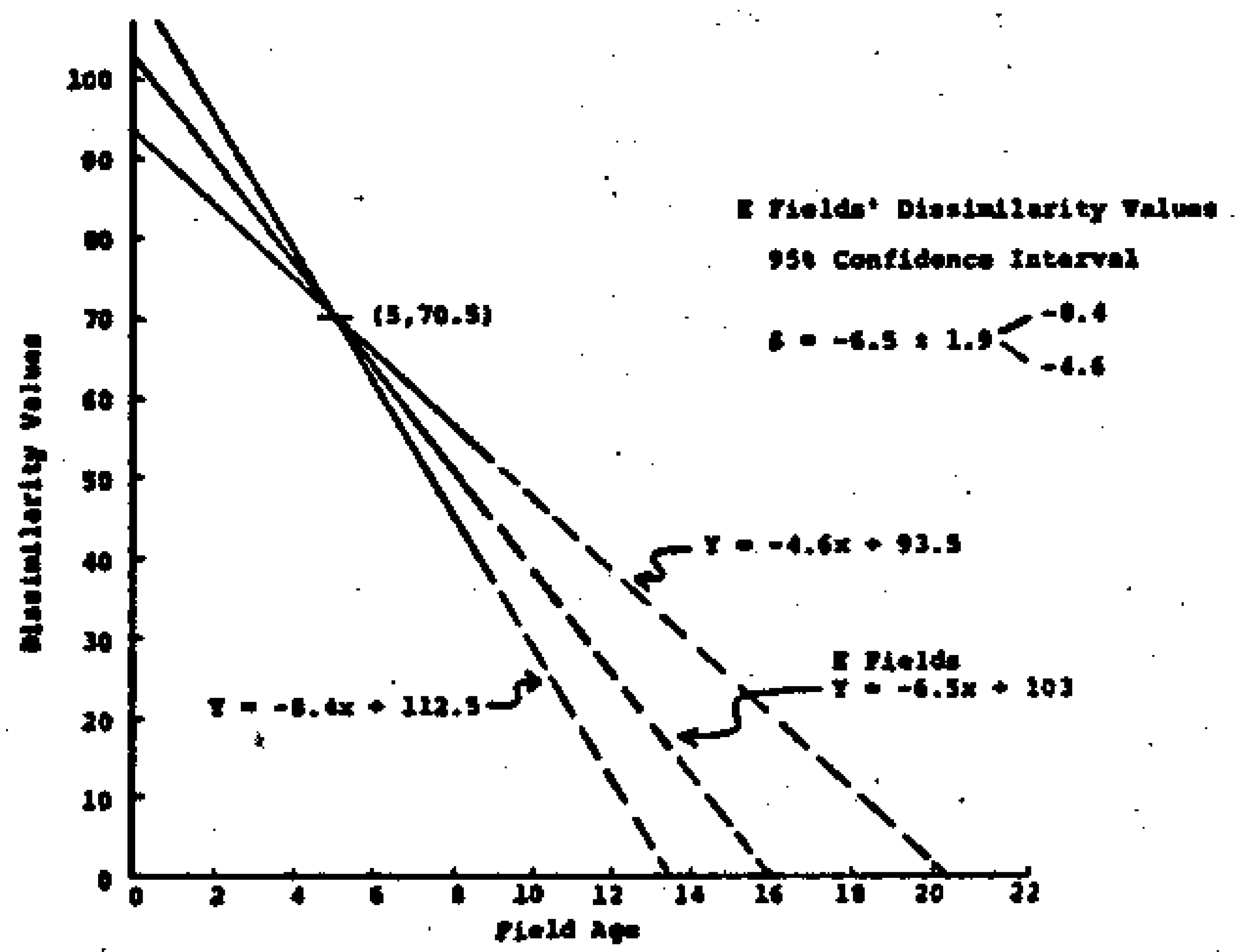


Figure 12. The 95% Confidence Interval for β (true slope), drawn around the E fields' regression line and read at 31% dissimilarity, shows the time period when we would expect convergence to similar vegetation in a hay and plowed field, i.e., between 10 and 14 years after the time of last plowing.

Table 8. Dissimilarity values comparing the two hay fields. Comparisons were made on years since abandonment and years since last plowing (fields C6 and E1).

Fields	Years since abandonment	Dissimilarity values
C6 (1964)-E1 (1962)	1	42
C6 (1965)-E1 (1963)	2	38
C6 (1966)-E1 (1964)	3	—
C6 (1967)-E1 (1965)	4	24
C6 (1968)-E1 (1966)	5	—
C6 (1969)-E1 (1967)	6	81
C6 (1970)-E1 (1968)	7	79
	Years since last plowing	
C6 (1964)-E1 (1964)	3	27
C6 (1965)-E1 (1965)	4	32
C6 (1966)-E1 (1966)	5	—
C6 (1967)-E1 (1967)	6	26
C6 (1968)-E1 (1968)	7	60
C6 (1969)-E1 (1969)	8	65
C6 (1970)-E1 (1970)	9	66

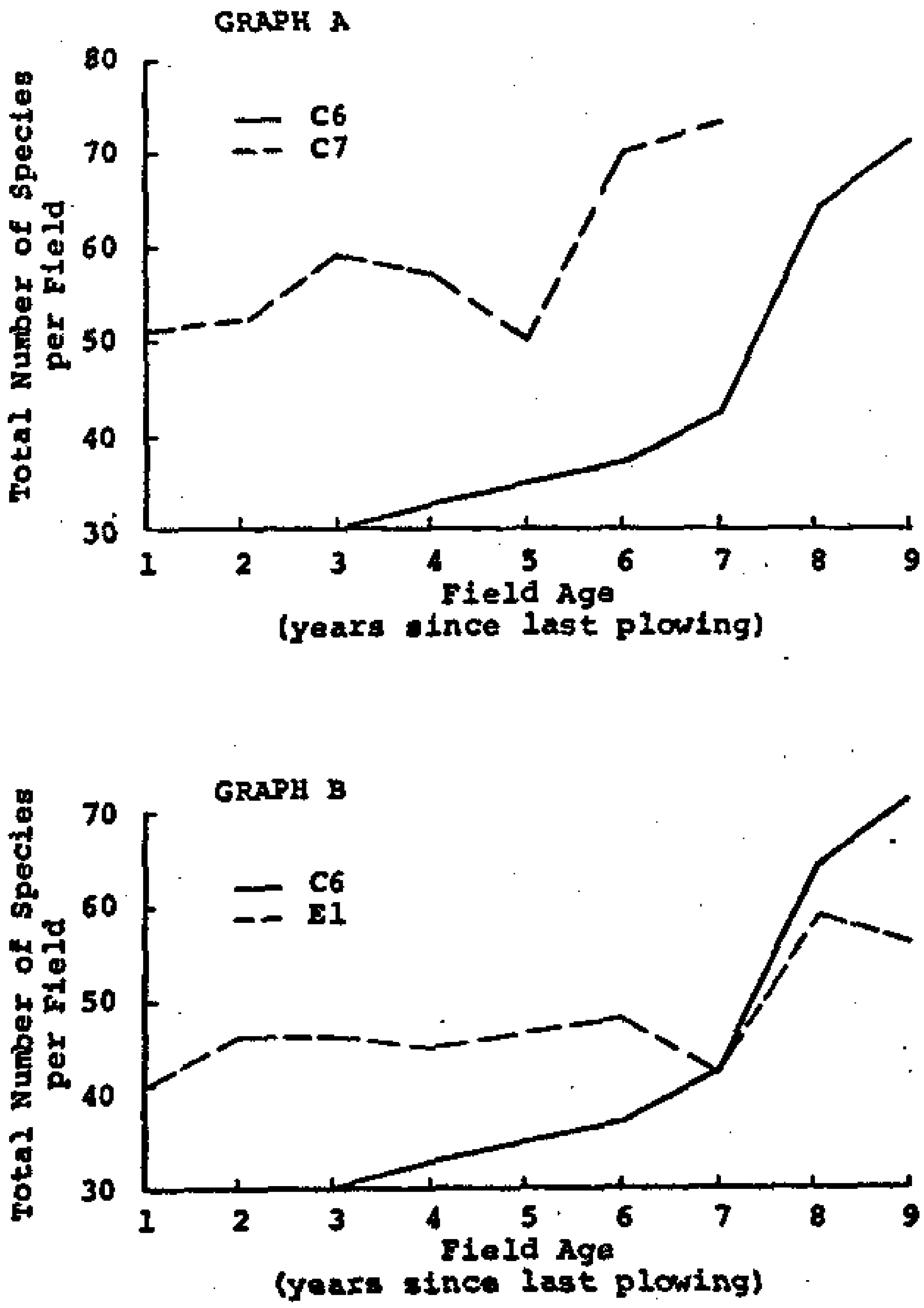


Figure 13. Species Richness (the number of species per field). C6 has been redrawn so that the data start from the time since last plowing rather than since abandonment. Graph A shows C6 (hay) compared to C7 (plowed): Graph B shows C6 compared to E1 (hay).

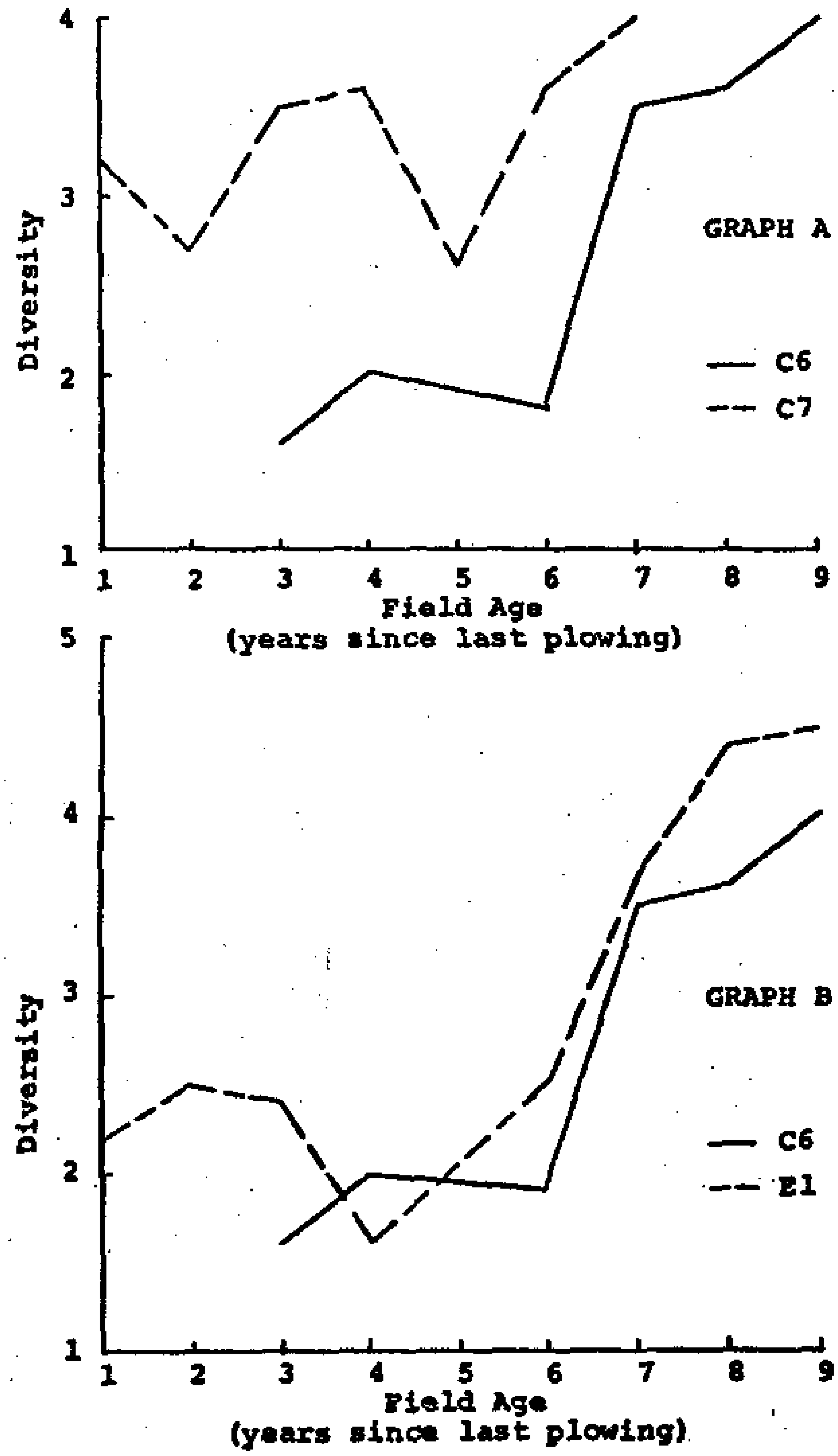


Figure 14. Diversity values for the C and E fields, with field C6 redrawn so that the data start from the time since the last plowing rather than since abandonment. Graph A shows C6 (hay) compared to C7 (plowed): Graph B shows C6 compared to E1 (hay).

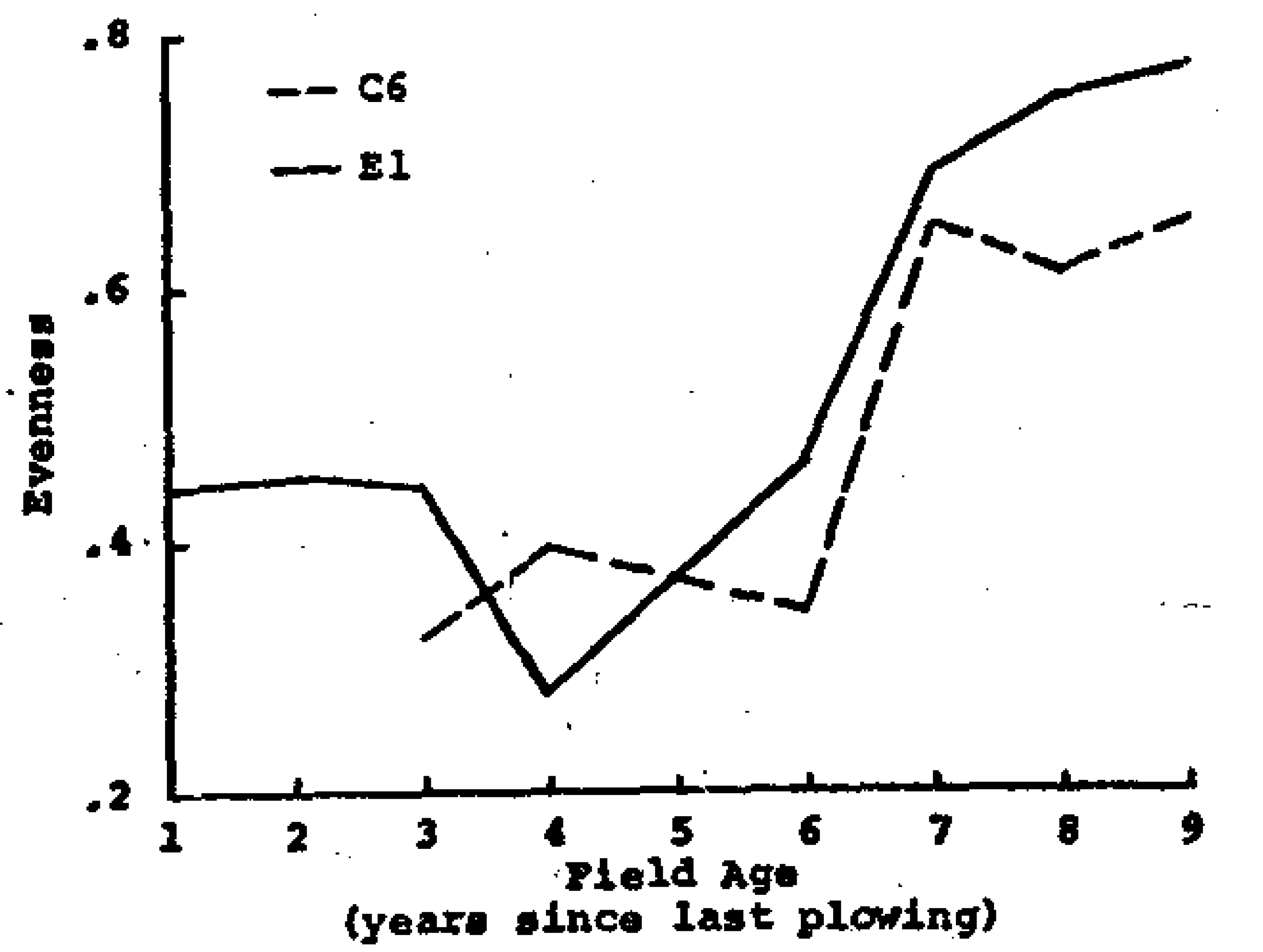


Figure 15. Evenness values for the C and E hay fields, with the data from field C6 redrawn, so that the data start from the time of last plowing rather than since abandonment.

during the years of hay harvesting, and that it may be considered three years old at the start of the sampling. This fact has helped to explain the faster convergence found between the C fields. In conclusion, we are led to rely on the E field data as the best estimate of successional convergence between a hay field and a plowed field on the Piedmont of New Jersey.

Based on the findings of this study, what then are the characteristics of vegetational change which we might anticipate in old abandoned fields? The increasing convergence of these fields through the years has been substantiated in all aspects of this study. One is tempted to conclude that, in general, old fields, regardless of origin, will show convergence during succession. Thus, we probably are safe in predicting decreasing dissimilarity values between fields which occupy similar locations, as succession progresses. Our data lead us to expect the number of species to increase in a field, and to become comparable in fields of the same age after a relatively few years. It is perhaps safe to anticipate that diversity will increase with succession up to a certain point, and regardless of origin will be comparable from field to field. However, as our forest data suggest, a decline in diversity may be anticipated in later successional stages. Although the species may vary from site to site, we would expect to find only one or two species in the young fields with high dominance, followed by increased evenness or a sharing of dominance by several species as the succession proceeds.

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