

Secondary Succession: Composition of the Vegetation and Primary Production  
in the Field-to-Forest at Brookhaven, Long Island, N. Y.\*

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Abstract. Natural communities respond to disruption through a series of changes in plant and animal communities that are broadly predictable. The field-to-forest sere of central Long Island follows the pattern set forth earlier for the Piedmont of North Carolina and for New Jersey. The communities of herbs that occur in the years immediately after abandonment are followed by an *Andropogon* stage which is replaced before the 20th year by pine forest. The pine is replaced in the next 25 years by oak-pine, which in the normal course is followed by oak-hickory. With repeated burning the oak-pine stage in various combinations of oaks and pine may be maintained indefinitely. Diversity, measured as number of species per unit land area, increased in this sere through the 3-5th years after abandonment <sup>to a maximum</sup>, dropped, and rose again in the later forest stages. Exotics were a conspicuous part of the communities of the earlier stages but their importance diminished as succession progressed and their contribution to net production was zero beyond the 20th year. The removal of exotics would probably not have changed the pattern of diversity appreciably. Net primary production increased with succession in this sere with major changes occurring as life-forms of the dominants shifted to woody plants. The peak net production was in the most mature forest, about  $1200 \text{ g/m}^2/\text{yr}$ . Root/shoot ratios declined from 4-5 in the early stages of succession to 0.3-0.5 with later stages. The standing crop of organic matter <sup>including humus</sup> <sub>^</sub> throughout the sere was about 15 times the net production, indicating a half-time of residence for all organic matter throughout the sere of about 10 years.

## INTRODUCTION

Natural communities respond to disruption through a series of changes in plant and animal populations that are broadly predictable. These changes extend beyond simple shifts in the sizes of populations to changes in species composition, in the physiognomy of the community, in net productivity, in soil structure and soil chemistry. They extend also to changes in the inventory of nutrients required to support the net production. It has become almost axiomatic that these changes are concomitant, progressive, and developmental as opposed to retrogressive or degenerative, (Clements 1928, Margalef 1963, Odum 1969, 1971), although there is abundant evidence that under certain circumstances biotic and nutrient impoverishment of the site may occur (Woodwell 1970, Whittaker and Woodwell 1971). The developmental changes following severe but discrete disturbance are sufficiently repetitive and predictable to be recognized as "succession" and the entire sequence of communities that leads to the most mature vegetation of a region is what Clements (1928) called a unit succession or "sere".

Although succession is one of the most vital of the basic trends of nature, second in importance perhaps only to evolution, detailed descriptions of seres are few enough that there remains substantial question as to whether intuitively attractive theories of succession such as that outlined by Margalef (1963) are supported in fact. If clear answers are ever available, they will come through study of complete seres, an undertaking that is complex and difficult.

One such sere is that of the Eastern Deciduous Forest of North America (Braun 1950) of which the succession from field to the oak-pine forests of central Long Island is one phase. This sere is short, floristically simple, and an attractive subject for a detailed examination of the basic principles of succession. The sere has, moreover, been the subject of studies of the effects of ionizing radiation which showed that the earliest stages of succession are very much more resistant to radiation damage than later forest stages (Woodwell 1967, Woodwell and Oosting 1965, Holt and Bottino 1972, Woodwell and Rebeck 1967, Woodwell and Marples 1968, and Woodwell and Whittaker 1968).

The objective of the work reported in this paper was a quantitative description of the field-to-forest sere of the sandy glacial outwash soils of central Long Island. The initial objectives of the work were restricted to floristics, diversity of plants, standing crop, and net production along the sere. Later reports will cover metabolism and nutrient budgets.

The broad outline of the field-to-forest sere of the Eastern Deciduous Forest was set forth most lucidly by H. J. Oosting and his students (Oosting 1942, 1958, Keever 1950) for the Piedmont of North Carolina. Other studies set forth the mechanisms controlling segments of the succession (Bormann 1953, Bordeau 1954, Billings 1938). The Piedmont at the time of these studies was recovering from the effects of a long-continued and especially exhaustive agriculture and large areas were in varying stages of secondary

succession. The successional patterns documented in detail for the Piedmont are recognized as broadly applicable throughout the forested regions of the temperate zone.

Succession in the Piedmont of North Carolina normally includes a rapidly changing sequence of dominance from grasses and herb ssuch as Digitaria sanguinalis and Erigeron canadensis through the first year after abandonment from agriculture to Aster ericoides and Ambrosia artemisiifolia after two years. In the third year and subsequently Andropogon virginicus and other species including A. ternarius and A. elliotii are overwhelmingly dominant. The Andropogon community may be long-lived but normally by the fifth year seedlings of Pinus taeda (loblolly pine) are conspicuous and by the 11th year the trees may be 8-15 feet in height. The pine stands are ultimately replaced by hardwoods whose seedlings appear in the sere as early as the 11th year. Liquidambar styraciflua, a successional tree, becomes a conspicuous understory tree during the third decade of succession with *Carya* spp. and upland oaks. After seventy-five years, at least on certain sites, the pine is still dominant, although there is an understory of hardwoods (Oosting 1942). In subsequent decades the succession moves toward an oak-hickory climax throughout most of the region. B. W. Wells, however, believed there would ultimately be a transition to beech-maple (Wells 1928) but there is very little evidence to support this contention and the transition seems improbable. Elsewhere, of course, the forest climax may be substantially different (Braun 1950).

Other seres of the eastern seaboard of temperate North America follow a similar pattern, although the rate of succession may vary appreciably (Evans and Dahl 1955, Blizzard 1931). On lands at the Savannah River Plant in South Carolina for instance an *Andropogon* stage is long lived and invasion by pine is very slow, apparently because of the remoteness of seed sources (Odum 1960, Golley and Gentry 1966, Golley 1965). The field-to-forest sere of New Jersey is similar in physiognomy, in genera, and to a lesser extent in species (Bard 1952, Harshberger 1916, Small et al. 1971). Eastward the flora becomes more impoverished but the sere for central Long Island retains basic similarity to the sere of the North Carolina Piedmont (Conard 1935, Woodwell and Oosting 1965) and to the other seres for the Eastern Deciduous Forest. Differences among the seres occur as a result of several factors but the most important general influence is differences in the ranges of species. The sere becomes simplified northward and eastward with impoverishment of the flora. Succession is slower where soils are poor and appears to be slower in the north (Bard 1952).

These studies and others that preceded them (Cowles 1899, 1901, Harper 1918, Cooper 1926, Clements 1928) have established the floristic pattern and physiognomy of succession in the temperate zone of North America. More recent emphasis on floristic diversity and primary production as fundamental interpretive functions of ecosystems has led to the attractive hypothesis that diversity and net production increase throughout succession to climax. The history of this hypothesis is long and complex, steeped as it

is in the evolutionary considerations that have been the root of most theory in ecology. One of the most articulate formulations of the hypothesis was set forth by Margalef (1963, 1968), but data to test it were then and remain now scant. What limited data are applicable (Loucks 1970, Auclair and Goff 1971) suggest that diversity and production vary along succession and that the climax or the more stable communities late in the sere are not necessarily either the most diverse or most productive. The question of the significance of changes in diversity and production along successional gradients remains one of the most central and puzzling problems of ecology resolution of which may never be achieved in a completely satisfactory way. The search for insight seems certain to reveal details of some of the most fundamental aspects of the evolution of communities.

## METHODS

### Selection of Stands

Secondary seres, especially in their early stages, are subject to wide variations in floristics, dominance and diversity, and the patterns observed in a single field of a hectare or less may be heavily biased by "chance". This means that it is especially important in describing the pattern of old-field succession to incorporate either systematic studies of many stands or to draw on comprehensive experience with local successions in interpreting individual patterns. Most of the stands examined in this study were prepared specifically for the work. The region provides at present very limited opportunity for examination of other stands representative of

the early stages of succession; there are many stands characteristic of later stages.

A series of old fields was obtained on the Brookhaven National Laboratory site by abandonment of corn (Zea mays) culture over six successive years. The fields were about 1/4 hectare each and adjacent to one another on level land in the section of the site known as "The Farm". The area was probably in agriculture during the last century; more recently it has been used by the Biology Department for field studies. The soil is Sassafras sandy loam (Lounsbury et al. 1928).

Two abandoned fields supporting young stands of pitch pines were sampled as stands of intermediate age. The most mature forest stand was the control area of the Irradiated Forest (Woowell and Rebeck 1967, Whittaker and Woodwell 1968, 1969). This forest is sprout-growth white oak, scarlet oak, and pitch pine (Hawley and Hawes 1912). At the time of study it was between 55 and 60 years of age. The previous disturbance was probably severe and repeated fire. The land had never been in agriculture. No abandoned agricultural land of appropriate age is available in the immediate area.

Sampling of all stands except the forest, which has been sampled previously, was during the summers of 1969-70. Species' lists were compiled for each stand. Voucher specimens of higher plants were placed in the Herbarium at Brookhaven National Laboratory. Nomenclature of plants follows Fernald (1950) with secondary reliance on Gleason and Cronquist (1963) for recognition of exotics.

### Minimal Area

The size of the sample needed to describe a community varies not only with the structure of the community but also with the configuration of the plots and the purpose of the sampling. For most common descriptive purposes in studies of vegetation a sample large enough to include an estimated 90% of the species has usually been considered adequate (Oosting 1958). A graph of numbers of species against cumulative area sampled (species-area curve) in herbaceous vegetations, including old-field communities, usually shows a pronounced flattening when the total area reaches 10-100 m<sup>2</sup>, although there are not many direct appraisals available (Cain 1938, Cain and Castro 1959, Evans and Dahl 1955, Woodwell and Oosting 1963, Vestal 1949). The total area sampled in most quadrat-based studies of floristics where plots are used such as those of Oosting (1942) usually fall within this 10-100 m<sup>2</sup> range whether an analysis of the species-area relationship has been made or not.

The intensity of sampling for dominance, net production, or standing crop depends on the degree of resolution required. If net production of the plant community is the principal objective and a standard error of  $\pm 10\%$  is acceptable, there is little point in a sampling intensity that provides a standard error of the mean of  $\pm 10\%$  for the 4th most important species of  $\pm 10\%$ .

In this work where a principal objective was a comparison of diversity and production throughout the sere separate <sup>sampling</sup> programs were used as outlined below.

### Diversity

Tests of the relationship between the total area sampled by small plots and the total number of species encountered showed that there was a small but steady increase in the numbers of species as <sup>the area sampled increased</sup> to 300-400 m<sup>2</sup> when the total numbers of species in 1-year, 6-year, and 16-year fields were 37, 42 and 44. Increasing the area to 1000-2000 m<sup>2</sup> increased the 1-year-field's total to 39, the 6-year-field's total to 48, and added no new species to the total for the 16-year field. While it is clearly possible to describe communities on the basis of diversity and abundance data from a total area of not more than 100 m<sup>2</sup>, experience shows that an appraisal of diversity gains from tabulations based on 1/10 hectare or larger plots as opposed to series of smaller plots, however arranged. In the analyses of diversity in this work, tabulations of higher plant species were made over each entire field (i.e. a 100% sample).

### Biomass and net production

Estimates of standing crop and net production of herbs were based on the harvest technique (Woodwell and Whittaker 1968, Odum 1960, Malone 1968). Shoots were harvested in ten 1/4 x 1 meter plots arranged in rectangular grids. The configuration of plots was the same in all harvests, but plots were offset so that different but adjacent areas were harvested in successive samples. Harvesting was at monthly intervals to assure an estimate of maximum standing crop. Shoots of herbaceous species were clipped at ground level and placed in cold storage until they could be sorted by species.

Standing dead material was included in the current year's production if unweathered. The separation of weathered and unweathered material was not usually difficult. Peak standing crops of individual species (oven dry weights) were summed to obtain estimates of net shoot production for the community. Such estimates are of course minimal estimates of net productivity. Current twigs and leaves of shrubs were clipped in late summer, dried and weighed.

Root standing crops were also estimated by the harvest technique, although the sampling was much more difficult and the estimates less reliable than for shoots. A sample consisted of five cores, eight centimeters in diameter, and twenty centimeters long. The root sample was taken from each plot at the earliest and latest shoot harvests. Roots and large particulate detritus were removed from mineral matter by wet-sieving and flotation. Separation by species was not possible, nor was any attempt made to separate live and dead material. Detritus other than that clearly originating from roots was negligible. Small roots and root-hairs were included as "organic matter" determined by loss on ignition at 500<sup>o</sup> C.

Estimates of organic matter in the soils of the mature forest were based on values given by Reiners (1965) and Horrill and Woodwell (1973). All estimates of soil organic matter refer to the upper 20 centimeters of soil and are therefore conservative estimates of total soil organic content.

Estimates of the standing crop and net production of trees were obtained using regressions of tree dimensions on dbh (Whittaker and Woodwell 1968). Data on tree populations in the intermediate aged stand were obtained from a 1/10 ha plot.

Caloric equivalents of tissues are summarized in Table 1. Caloric content of shrub tissues were assumed to be equivalent to those of the oaks.

## RESULTS AND DISCUSSION

### Floristics

The sere that is characteristic of abandoned agricultural land in central Long Island follows the widely-recognized transition from dominance in the first year by such hardy exotic herbs as Digitaria sanguinalis, an annual, to a sometimes long-lived and surprisingly stable community in which grasses dominate. In the field that we sampled grasses had from 25% to more than 40% of the net shoot production (Table 2). While Andropogon is often a conspicuous member of the grass-stage community it does not dominate in all fields or in all segments of any field. Its net shoot production was  $36 \text{ g/m}^2$  in the 15th year of the sere we examined. The grass community is replaced by Pinus rigida and ultimately by oak-hickory forest. The late successional forest over most of central Long Island has dominance shared by Quercus alba, Quercus coccinea and Pinus rigida. Most such stands have been burned at least once. Original upland forests were probably oak-hickory with oak-chestnut on the moister, richer sites (Braun 1950). Chestnut (Castanea dentata) sprouts are still common. The most mature upland forests are not oak-hickory, but no such stand was sampled in this work.

The sere is complex, both in numbers of species and in floristic structure, especially during the early stages. In this study 154 species were encountered (Table 2) throughout the sere to the oak-pine stage. The

largest numbers of species occurred in the 3rd to 5th years after abandonment (Fig. 1). In the year of abandonment there were 19 species; in the fifth year after abandonment, there were 64 species. By the time the pine stage was well developed, diversity had dropped to 29 species, approximately the same as in the forest. Annuals dominated the first stages of succession, <sup>but</sup> were replaced by biennial and perennial herbs within the first 3 years following abandonment (Table 2).

#### Dominance and Shoot Production

Dominance as indicated by net shoot production (maximum standing crop in the communities of herbs) is shown in Table 2 for all species except the minor species of the oak-pine forest which were encountered by Whittaker and Woodwell (1969), and the grasses of low net production which were not identified in the two youngest fields.

Year-by-year shifts in dominance occurred during the first five years. In the year of abandonment Digitaria sanguinalis was commonly dominant, although Mollugo verticillata was widespread and conspicuous. Both species are annuals. The shoot production of these two species was about 85% of the total production of the field.

Dominance shifted in the first year after abandonment to Rumex acetosella and Erigeron canadensis. Erigeron, because of its superior height, assumed "aspect" dominance throughout the year although its productivity was less than 1/6 that of Rumex in this field. Several species of grasses were important; Agropyron repens was the most conspicuous and abundant (Table 2).

In the second year after abandonment several additional species contributed significantly to the total organic production. Erigeron, while still conspicuous as dead stems remaining from the previous year's bloom, dropped in productivity to about  $6 \text{ g/m}^2$ , approximately 1/5 of its production the previous year. Rumex acetosella remained as one of the three principal species with an above-ground production of almost  $100 \text{ g/m}^2$ . Solidago nemoralis was next in abundance with  $88 \text{ g/m}^2$ . It shared aspect dominance with S. juncea, S. tenuifolia-graminifolia (which could not be separately identified in the field), and with Aster ericoides.

During the third year after abandonment the tendency to divide dominance among an increasing number of species was accentuated. Except for Mollugo and Digitaria, which occurred only in the year of abandonment, dominants of the earlier communities were present, but with diminished abundance. Potentilla canadensis and Lespedeza capitata had the highest above-ground standing crop, but Solidago nemoralis, Panicum lanuginosum, Aster ericoides, Eupatorium hyssopifolium, Sisyrinchium arenicola and several species of grasses were conspicuous contributors to an increasingly diverse and productive community.

During the fourth year the trend toward increased partitioning of dominance proceeded further. The highest above-ground standing crop ( $73 \text{ g/m}^2$ ) was attributable to Lespedeza, but 12 species had peak standing crops in excess of  $10 \text{ g/m}^2$ . Principal among these were Solidago juncea, and S. tenuifolia-graminifolia with a combined total of  $95 \text{ g/m}^2$ . Potentilla canadensis had a

peak of  $27 \text{ g/m}^2$  and an increasing number of grasses contributed to total above-ground production of about  $400 \text{ g/m}^2$ .

By the fifth year dominance was shifting clearly toward the grasses with more than  $100 \text{ g/m}^2$  attributable to two species, Panicum commutatum and P. lanuginosum. The Solidago's were still abundant contributing collectively about  $100 \text{ g/m}^2$  of the peak shoot production. Shrubs were beginning to appear: Comptonia peregrina, for instance, had a peak production of about  $10 \text{ g/m}^2$  in the fifth year of abandonment.

The fifteenth-year community was a young stand of Pinus rigida in a Festuca rubra-Andropogon virginicus field. The Pinus production was  $124 \text{ g/m}^2$ , nearly 1.3 of the total production. Andropogon, Festuca, and the remaining grasses (Table 2) contributed nearly 40% of the production. By the 20th year the pine stand was well developed with Pinus rigida contributing  $640 \text{ g}$  of shoot growth/ $\text{m}^2$ . The canopy was closed, herbs and grasses were largely reduced to trace production. The moss, Polytrichum commune, was conspicuous and contributed appreciably to net production of ground cover.

The most mature stand included in Table 2 is the oak-pine stand studied earlier (Whittaker and Woodwell 1968). The data are based on five 0.1 ha plots representative of the oak-pine forests of central Long Island. Most such stands have been burned; some have been pastured at one time. No such stand available to this study had originated following cultivation. The greatest shoot production in the forest was attributable to Quercus coccinea, about  $400 \text{ g/m}^2$ . Q. alba production was 230, and Pinus rigida,  $120 \text{ g/m}^2$ . Shrub and herb production was trivial by comparison.

### Diversity

The number of species per unit area of land is the most direct, simple and broadly useful definition of diversity as the term is applied in ecology. The definition is practical in study of terrestrial plant populations where the sampling can easily be related to an area. It is less practical in studies of insect and other populations where there may be uncertainty as to the area sampled. In such sampling the ratio of the number of species to the total number of individuals in the sample becomes a reasonable criterion of diversity. Some of the more complicated indices of diversity that have been developed in recent years (Auclair and Goff 1971, Pielou 1966, MacArthur 1965) take into consideration the effect of the abundance of a species on diversity and change the simple definition toward one more heavily influenced by practical limitations imposed by sampling techniques. This generally applies to information theory indices as well, despite the clarity of the objective of extracting additional information as to the structure of the populations from the basic data on diversity and abundance. We prefer to follow the simpler definition of diversity as the number of species per unit area.

Highest diversity occurred during the 3rd-5th years after abandonment (Fig. 1). During these years the 1/4 ha fields contained 50-60 or more species. Diversity reached a minimum in the pine forest stage and rose to 34 in the late successional oak-pine forest.

Exotics have an important role in the early stages of succession but their importance declines abruptly within a few years. Exotics declined

from 60% to about 27% of the flora within the first three years (Table 2). Exotics participated in the 15th year community but were absent in the later stages examined in this study. The trend toward diminished importance of exotics as succession progresses is more conspicuous when net production is considered. Nearly 90% of the net production was due to exotics in the year of abandonment (Fig. 2). This dropped to 50% in the second year, and to less than 10% by the fifth year.

The high diversity observed in the 3rd to 5th years after abandonment was due in part (27-34%) to exotics. It seems probable that a peak in higher plant diversity would have occurred during this time if exotics had not <sup>been</sup> present. If we assume that the absence of exotics would not result in the addition of indigenous species <sup>the</sup> to a sere, there would be more than 40 indigenous species during the 5th year of succession and highest diversity would be in this year. Diversity apparently does not increase regularly in this sere as succession progresses but reaches a peak early in the sere, declines and rises subsequently through the late successional oak-pine stage, but does not achieve the peak it reached earlier.

#### Biomass

Shoots. The use of maximum standing crop as the best measure of net production of herbs means that our estimates of net production and standing crop coincide in the early stages of succession when the community was dominated by annuals, but diverge later in succession as perennial plants became dominants. As woody plants increased in abundance, biomass

rose rapidly to several kilograms/m<sup>2</sup> (Table 3). The increase was irregular: a peak of shoot biomass exceeding 300 g/m<sup>2</sup> occurred in this sere in the first year after abandonment. It dropped to 200-300 grams through the 5th year when invasion by shrubs became significant, and increased regularly thereafter to more than 8000 g/m<sup>2</sup> in the late successional oak-pine forest. A shoot biomass in excess of 12,000 g/m<sup>2</sup> seems probable in the larger statures oak-hickory/oak-chestnut climax forest of central Long Island.

Roots. Measurements of root production and standing crop are always less precise than measurements of shoots. In this work the problem was complicated during the early years of succession by the persistence of large particulate organic matter, mostly roots, from the crop. By the third year (2nd year after abandonment) the new roots predominated. Total mass approached 700 g/m<sup>2</sup>, more than 3 times the mass of the shoots in that stage (Table 3). The mass increased to 900 g/m<sup>2</sup> by the 4th and 5th years after abandonment, and rose further in the later forest stages to 3600 g/m<sup>2</sup>.

Root/Shoot ratio. The standing crop of roots exceeded the mass of shoots through the 15th year of the sere (Table 3). In the earlier stages of succession the mass of roots was commonly 2-4 times the mass of shoots. In the forest stages roots were 0.3 to 0.4 of the shoots, approximately what has been reported for other forest stands (Rodin and Basilevich 1967, Ovington 1965). The Brookhaven forest is unusual in having many trees that have developed from sprouts after fires and roots may be considerably older and disproportionately large by comparison to shoots (Whittaker and Woodwell 1968). In the more mature oak-chestnut or oak-hickory forest one would expect

roots to be a lower fraction of shoots, probably approaching the 20% observed in other similar stands (Ovington 1965). The pattern of increasing root/shoot ratios along the succession of the coastal plain of the southeastern United States reported previously by Monk (1966) does not apply in this sere.

Litter. The accumulation of litter followed a regular pattern with about  $200 \text{ g/m}^2$  present after the harvest of corn at the end of the year of abandonment, about half of that at the end of the following season, and generally increasing quantities thereafter (Table 3). By the 5th year there was standing crop of litter of  $400 \text{ g/m}^2$ . By the 20th year the standing crop was about  $1000 \text{ g/m}^2$  and in the 50th year, about  $1600 \text{ g}$  for leaves and small twigs alone (data for the forest from Woodwell and Marples 1968). Large branches and boles accounted for an additional  $\text{g/m}^2$ .

Soil Organic Matter. The total organic content of soil (including roots) varied surprisingly little through succession (Table 3). The lowest content ( $5500 \text{ g/m}^2$ ) occurred during the 3rd and 4th year after abandonment. The maximum ( $8600 \text{ g/m}^2$ ) was in the forest. The decline during the herbaceous plant stages of the first three years of the sere probably reflects the transition from dominance by successional species.

Total Organic Matter. The principal contributions to total organic content of the communities along the sere accrued from the woody plants. Prior to their ecesis, however, the major pool of organic matter was in the soil which contained through the herbaceous segment of the sere about 80% of the total. In the forest, of course, the fraction dropped, but still remained 36% of the total in the system.

Net Primary Production

Shoots. Shoot production, expressed as dry organic matter, increased along the sere from about  $130 \text{ g/m}^2$  in the year of abandonment to about  $400 \text{ g/m}^2$  in the first year after abandonment and remained approximately the same through the 15th year after abandonment. As the abundance of shrubs and young trees increased, net production also rose, reaching about  $860 \text{ g/m}^2$  in the late successional forest (Table 4 and Fig. 2).

These estimates are probably low. There were losses to decay and to herbivores that were not measured. It seems unlikely to us

that the losses were greater than 10% since herbivore consumption was not apparent and decaying organic matter was included in each estimate of standing crop of herbs.

Roots. Direct measurement of root production in such a sere is virtually impossible. Indirect measurements offer at best an indication of the magnitude of net production. In this work root production was estimated from measurements of standing crop of roots and from estimates of the amount of heterotrophic respiration in the A-horizon. The abundance of roots and large organic particles that were separable by flotation (see Methods) in the early stages of the sere is indicated in Fig. 2. There was an early decline to a minimum in the first sample of the third year after abandonment and a regular increase in later years. From the third year through the second sampling of the fifth year the average annual net increment of roots appears to have been about  $125 \text{ g/m}^2$ . The standing

crop increased from about  $500 \text{ g/m}^2$  to more than  $900 \text{ g/m}^2$  in this period. The annual increment of root standing crop is a contribution to net ecosystem production (Woodwell and Whittaker 1968) and not a direct estimate of net primary production. Net primary production exceeds it by the amount of heterotrophic respiration that consumes roots during the year.

Two estimates of heterotrophic respiration are available from these soils. Woodwell and Marples (1968) observed in the oak-pine forest that decay consumed about 10% of the organic matter of the A-horizon annually and data of Horrill and Woodwell (1973) indicate a similar rate of decay. If that rate applies to the increasing standing crop of roots in this sere, there would be  $\frac{125}{.9} = \sim 140 \text{ g of roots/m}^2$  available annually through the early years of the sere. Roots would constitute about  $\frac{140}{400 + 140} = 26\%$  of the net production or  $\frac{140}{400} = 35\%$  of the shoot production. Applying that ratio to the shoot production of the first two years yields the estimates of Table 4 for net production of roots during the first two years following abandonment.

Root/Shoot Ratios for Net Production. The ratio of root tissue to shoot tissue in the net production ranged in these estimates between about 0.3 and 0.4 (Table 4) with no consistent trend along the sere. The lowest estimate of roots as a fraction of shoots was in the pine stage (20th year after abandonment) when root production was 23% of shoot production; the highest were the 3rd, 4th and 50th years. The distribution of net primary production between roots and shoots appears to vary little along this sere with root production commonly about 30% of the net shoot production.

Root/NPP Ratios. The fraction of net primary production that is attributable to roots also varies little along the sere. The lowest fraction was in the pine stage where roots accounted for about 20% of the net primary production. The ratio was about 30% in the 3rd and 4th years and in the oak-pine forest. A mean for the sere of about 25% seems reasonable, confirming appraisals from other similar vegetations (Rodin and Basilevich 1967).

Total net production. Net production of the herbaceous plant communities of the early stages of succession was less than half that of the late successional forest and a third of that commonly recognized as representative of temperate zone forests. In the year of abandonment net production of old field herbs was  $170 \text{ g/m}^2$ ; production rose in the following years to about  $500 \text{ g/m}^2$ , a rate that persisted through the 15th year. In the 20th year it was  $830 \text{ g/m}^2$  and in the late successional forest of about 50 years',  $1200 \text{ g.m}^2$  (Table 3, Fig. 2). The data for the first two years after abandonment approximate closely the end-of-season crop of similar fields studied by Woodwell and Oosting (1965), but productivity in the control field of Woodwell and Oosting in 1969, eight years after abandonment was  $960 \text{ gm/m}^2$ , suggesting that variations in site quality may cause at least a two-fold variation in net primary productivity. The productivity of lowland systems is still higher, exceeding that of the oak-pine forest. Estimates of net primary productivity of a local fresh water marsh by a late-season harvest of standing crop indicate a minimum production of  $1300 \text{ g/m}^2/\text{year}$  for shoots alone. These data substantiate the more extensive work of Jervis (1969).

If root production is 35% of shoot production, total net production might be as much as  $1800 \text{ g/m}^2/\text{yr}$ , or 50% more than that of the forest. The standing crop of living matter in the marsh was about  $3600 \text{ g/m}^2$ , about 30% of that in the forest.

Organic Accumulation Ratios. Because net primary production is the source of all organic matter in the vegetation except those very small quantities that are brought in precipitation or from other sources, the ratio of the various organic pools to net production offers a series of indices of both structure and function of the vegetation. Most of these pools of carbon are larger than annual net production (Table 5) and the most convenient ratio is an expression of NPP as a fraction of the pool. The standing crop of higher plants by this index was 4.9 times the net production in the year of abandonment, dropped to about 1.7 times net production in the 2nd and 3rd years, and rose later in the sere to about 10 in the oak-pine forest. This ratio is substantially lower than that for other, larger stured forests (Whittaker and Woodwell 1971). The ratio would rise further in the more mature oak-hickory and oak-chestnut forests. The assumption also seems reasonable that if the standing crop of organic matter that remained from the agricultural crop could be separated with precision from the standing crop of the successional plants the ratio of standing crop (biomass) to net production in the first years of the sere would approach unity in these early years.

Litter was defined in this study as loose organic debris (including wood, twigs, bark and leaves) that is subject to cycles of wetting and has

not become incorporated into the normally continuously moist humus horizon. The amount of litter has been appraised previously for the forest by Woodwell and Marples (1968) who showed that the distribution of litter when wood is included is very irregular but that an average amount, not including wood, is probably about 1600 g of dry O.M./m<sup>2</sup>. The amount of litter along the sere ranged as might be expected from about 20% of the net primary production in the first year after abandonment to 1.2-1.3 times the net production in the later stages of the sere (Table 5). The data for the year of abandonment were heavily influenced by residues from the crop.

The litter is transformed into humus, which is a large pool of carbon in temperate zone forests. The ratio of humus to net primary production varied by more than a factor of two along the sere, if the high ratio of the year of abandonment is not included. The crop residues that caused the <sup>distortion of the</sup> ratio in the year of abandonment probably <sup>persisted</sup> through the second year after abandonment, distorting these ratios as well (Table 5). In the third year the ratio was 9.5. In the 4th, 5th and 15th year it was between 11 and 16. It dropped as net production rose in the forest stages of succession to about 7.

The ratio of total organic matter, including plants to NPP varied substantially less than the humus/NPP ratio. If we omit the high ratio, 48, for the year of abandonment, the ratio of total OM/NPP ranged between 12 and 19 throughout the sere with no consistent trend. It appears that in this sere of central Long Island there are substantial changes in net primary production and the distribution of organic matter between the higher plant populations, litter,

humus, and other soil organic matter, but that the ratio of total organic matter to net primary production approximates 15 throughout the sere. Such a relationship suggests that the removal of organic matter from a terrestrial ecosystem is a constant for the locale, no matter the form of the organic matter. If the standing crop that can be supported is 15 times the annual increment of new organic matter, the organic matter must disappear with a half-time of about 10 years.

Dominance and Diversity. One of the most direct techniques for examining the interaction of dominance and diversity is through graphs developed by R. H. Whittaker (1965) after Motomura (1932) in which he plotted net productivity as a measure of dominance on a logarithmic scale against species sequence on an arithmetic scale. Such curves tend toward two extreme forms: (1) the steep linear curves of a geometric series and (2) sigmoid curves. The steep linear curves are characteristic of communities in which dominance tends to be concentrated in a small number of species. Diversity is low. Communities with higher diversity tend to have sigmoid curves, although there is a wide range of possibilities for variation in form and slope. The flattening that makes them sigmoid indicates that increments of net production are approximately equally distributed among several species. Presumably the distribution of resources among species that are clumped in this way shows some degree of "equitability". Plants that form synusia such as the *Gaylussacia-Vaccinium* synusium of the oak-pine forest of eastern North America seem to contribute to this type of sigmoid flattening of the dominance-diversity curves (Whittaker and Woodwell 1969). Subdominants

of the forests studied by Reiners in the Anoka Sand Plain of Minnesota were similarly clustered (Reiners 1972).

The dominance-diversity curves of the field-to-forest sere of Long Island appear in Figure 3. They range from the steeply linear curves of a geometric progression in the early and late stages of succession to strongly sigmoid curves in the intermediate stages. The curve of the zero-year is steep and strongly linear; dominance is heavily concentrated in a few species and exotics play a prominent role in a community of low diversity. The curves become increasingly sigmoid through the 5th year, when dominance is held exclusively by indigenous species and diversity is high. In the 14th year the curve is still conspicuously sigmoid, although much steeper than in the 5th year. In later stages the dominants are trees, diversity is lower, and the distribution of net production again approaches the geometric series.

The clustering of species is conspicuous throughout the array of curves, but especially in the more diverse communities. It includes indigenous and exotic species apparently without pattern although in later years exotics move progressively toward the lower end of the curves. Exotics are not present in the forest stands.

The shift in form of the curves follows very closely the shift in diversity along the sere. Diversity is highest in the 5th year when the sigmoid shape is most pronounced. The tendency toward a geometric progression in the distribution of net production among species is strongest

in the zero year and in the stands in which trees are dominants. While the pattern is neither simple nor intuitively attractive from the standpoint of theory, it is revealing both of the pattern of succession in this vegetation and of the usefulness of the dominance-diversity curves in interpreting community structure. The array of curves supports R. H. Whittaker's earlier insights (Whittaker 1965) assigning the steeper, more nearly linear curves to communities characteristic of disturbed sites where dominance is concentrated in one or two aggressive species. Such sites frequently have a high representation of exotics. The community of the year of abandonment is a classic example in support of this set of conclusions.

The trend toward linearity in these curves later in succession is the result of the combination of reduced diversity and the assumption of dominance by a new life form, the trees. The displacement of the oak-pine forest by the more mature oak-hickory climax would be expected to result in a re-accentuation of the trend toward a sigmoid form in the dominance-diversity curves, but it seems doubtful that the forest stands would duplicate the diversity of the fifth-year field.

Efficiency of Energy Fixation. The thermodynamic efficiency of plant communities has been expressed in a wide variety of ways with numerical values for efficiency that are confusing if not downright misleading. The confusion arises from uncertainty as to the fraction of the solar spectrum that should be used, from the occasional use of short-term measurements of production in estimations of efficiency, from uncertainty as to the precision

of various measurements of productivity between terrestrial and aquatic systems, and from the intrinsic variability of nature. The most useful measurements of efficiency for the purposes of this study are based on local insolation, estimated from meteorological records at Brookhaven as 357 Langleys/day ( $1.3 \times 10^6$  kcal/m<sup>2</sup>/yr) and the net production. Insolation was measured over the years 1950-1958. Net production seems most useful because it is measurable; gross production can usually only be inferred by adding estimates of respiration. <sup>to net production</sup> Comparisons of the efficiency of net production along a sere reflect whatever differences there may be in net production because insolation is constant along the sere. Nonetheless, the efficiencies are of interest in appraising the function of natural vegetations.

Efficiency of net production in the field-to-forest sere at Brookhaven ranged between less than 0.1% in the year of abandonment to between 0.16 and 0.19% in the intermediate stages of succession to 0.3 to 0.4% in the later stages (Table 6). This pattern reflects the increase in net production from about 750 kcal/m<sup>2</sup>/yr in the year of abandonment through 2500 kcal/m<sup>2</sup>/yr in the 15th year after abandonment to 5600 kcal/m<sup>2</sup>/yr in the 50-year stand. If succession were allowed to continue through the oak-hickory stage, the larger stature of trees in these forests provides a basis for expecting a further increase in net production.

No Efficiency  
of energy fixation would increase proportionally, but probably would not exceed 1% under any circumstances. The efficiency of net production is sometimes

estimated on the basis of only that fraction of the solar spectrum that lies in the visible range between 4000 and 7000 Å. This is about 43% of the insolation. Restriction of the calculations to that segment of the spectrum would increase the apparent efficiency of energy fixation in net production to 0.91 for the oak-pine forest stage (Woodwell and Whittaker 1968). Efficiencies in this range are common for many natural vegetations (Whittaker and Likens 1973).

#### The sere as a unit

The field-to-forest sere at Brookhaven has been strongly modified in the past two centuries by man. The modifications have been two: changes in the species participating and changes in the physical and chemical conditions of the site. The changes in species include both additions to the flora and, to a much lesser extent, removals. Species added to the flora are hardy, widely distributed, weedy herbs that find a role only in the communities of the earliest years of the sere. The exotic herbs have a strong influence on the appearance, diversity, and productivity of the early communities of the sere. They appear to increase diversity and productivity, although there is no certain evidence as to the structure of the sere in the absence of the exotics. They seem to have no long-term effect. The species that drop out are a fewer. The principal loss has been the chestnut, Castanea dentata, formerly a species of richer upland soils. Chestnut sprouts persist today, giving uncertain confirmation to the distribution of the tree. The chestnut was probably not an important component

of the sere described in this work, restricted as it was to more mesic sites within the sandy outwash plains and to the richer soils of the uplands.

The second type of change in physical and chemical conditions is less conspicuous, more difficult to establish as fact, but more important in bringing fundamental change to the sere. This is the set of changes brought by harvest of the original forest followed by increased frequency of fire. The original forest of the sand plains of central Long Island is not known with certainty. Relicts of oak-chestnut stands, now oak-hickory, remain on the Brookhaven Laboratory Site. The drier, sandier soils probably supported an oak-pine forest not greatly different in composition from the best developed of the oak-pine relicts of today. These stands merge to oak-hickory on the more mesic, richer sites. The oak-pine forest, however, has been degraded by repeated fires. It is a sprout-growth forest throughout its extent (Hawley and Hawes 1912), and in places has been replaced by nearly closed stands of bear oak (*Q. ilicifolia*). This change constitutes fire-caused regression (Clements 1928) and has not been considered in the sere we have discussed. There seems little question, however, that this regression results in a very long-lived, slowly-changing community that contains a lower inventory of nutrients (Woodwell and Whittaker 1967, 1973) than the more mature oak-pine forest. The site is impoverished in species, in net productivity, in nutrients, and in standing crop of organic matter. It is the next step in the impoverishment of the sere we have described.

Conclusions. 1) The field-to-forest sere of central Long Island, New York, was studied in detail over several years to determine its floristic composition and the patterns of change in diversity, dominance, and productivity from the time of abandonment of agriculture through the late successional oak-pine forest.

2) The sere follows the broad pattern set forth in detail previously for the North Carolina Piedmont and for New Jersey. In the year of abandonment Mollugo verticillata and Digitaria sanguinalis dominate. In the following year Rumex acetosella and Erigeron canadensis are dominants. In the second year after abandonment the community becomes more complex with Rumex, Solidago nemoralis, and Aster ericoides as conspicuous co-dominants. In following years the community shifts, first to a complex grass-sedge community, then, in the 15th year toward a pine (Pinus rigida) forest. By the 20th year the pine forest is well developed. Few such stands survive many years without burning. Burning results in the oak-pine forest that is common over large areas of central Long Island in which Q. alba, Q. coccinea, P. rigida are major components. Further development might lead to oak-hickory on the richer sites.

3) One hundred fifty-four species of higher plants were encountered. Diversity was measured as number of species per unit of area. It was greatest in the 3rd to 5th years after abandonment. It dropped in the pine stage and rose slightly through the oak-pine forest. The data supports broadly the theory that diversity increases with time in succession but it seems clear that the increase is neither simple nor universal.

4) Exotics contributed importantly to diversity and to the net production in the first five years of the sere but their subtraction from the total numbers of species leaves a peak of diversity in the 5th year.

5) Peak biomass among the herbaceous communities occurred in the first year after abandonment when shoot-standing crop exceeded  $300 \text{ g/m}^2$ . Standing crop dropped subsequently to  $200\text{-}300 \text{ g/m}^2$  through the 5th year when invasion by shrubs became appreciable. In the oak-pine forest standing crop of shoots was more than  $8000 \text{ g/m}^2$ .

6) Root standing crop was high. It approached  $700 \text{ g/m}^2$  in the 2nd year after abandonment and increased subsequently to more than  $900 \text{ g/m}^2$  in the 4th and 5th years. It was  $3600 \text{ g/m}^2$  in the oak-pine forest.

7) Root/shoot ratios declined with succession from 3-5 in the early stages to 0.3 - 0.5 in the forested stages.

8) The standing crop of litter was at a minimum one year after abandonment and rose subsequently to  $400 \text{ g/m}^2$  in the 5th year,  $1000 \text{ g/m}^2$  in the 20th year, and  $1600 \text{ g/m}^2$  in the late successional forest.

9) Total soil organic matter reached a minimum of  $5500 \text{ g/m}^2$  in the 3rd and 4th years after abandonment. The maximum was  $8600 \text{ g/m}^2$  in the forest.

10) Net primary production increased along the sere from about  $170 \text{ g/m}^2$  in the year of abandonment to about  $500 \text{ g/m}^2$  in the 1st through 15th years after abandonment. It rose subsequently to  $1200 \text{ g/m}^2$  in the forest.

11) The ratio of net primary production to total organic matter approximated 15 throughout the sere. This relationship means that the half-time of residence of organic matter at any point on the sere is about 10 years and the size of the organic pool at any site is a simple function of the net productivity.

12) Dominance-diversity curves for the sere pass through a transition from strongly linear on a semi-logarithmic scale in the early stages of the sere to the sigmoid curves characteristic of communities with high diversity and back to strongly linear in the forest stage. As exotics become less important in the sere, they slip toward the lower end of the curves. The pattern supports the hypothesis that communities of disturbed sites have the more nearly linear curves; the communities with higher diversity tend toward the sigmoid curves.

13) Thermodynamic efficiency of energy fixation follows the pattern of primary productivity along the sere. The efficiency of net production, based on insolation measured by an Eppley pyrhelimeter, increased from less than 0.1% to about 0.4% along the sere with the forest the most efficient. If the estimate is based solely on energy usable in photosynthesis, efficiency of net production increases to about 0.91% for the forest.

14) Diversity, productivity and thermodynamic efficiency are not correlated along this sere, although it is probably true that the most efficient use of the resources needed to support life on a continuing basis is offered by the forest.

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Table 1. Calorie equivalence of tissues used in estimating thermodynamic efficiency in the Brookhaven sere.

Tissues		Caloric Equivalence cal/g. o.d. wt.	Reference
Oak:	Stem Wood	4570	Ovington and Lawrence 1967 Reiners 1972
	Stem Bark	3710	
	Branches	4560	
	Twigs	4700	
	Roots	4680	
Pine:	Stem Wood	4780	Ovington 1961
	Branches	4890	
	Leaves	5090	
	Roots	4180	
Herbs:	Forest	4370	Ovington and Lawrence 1967
			Reiners 1972
			Ovington and Heitleamp 1960
Old Field			
	Shoots	4400	Kucera et al. 1967
	Roots	4210	Wiegert and Evans 1964
			Old 1969
			Golley 1960, 1965
			Van Hook 1971
			Malone 1968

Table 2. Net shoot production (gm/m<sup>2</sup>/yr) by species in the upland field-to-forest sere of central Long Island

Species <sup>1</sup>	Origin (N-natural E-exotics)	Age of Field (years)								
		0	1	2	3	4	5	15	20	43
<i>Mollugo verticillata</i>	E	43.0								
<i>Digitaria sanguinalis</i>	E	65.6								
<i>Rumex crispus</i>	E	0.2	t <sup>2</sup>							
<i>Setaria glauca</i>	E	t	t	0.7		t				
<i>Chenopodium album</i>	E	t	t				t			
<i>Ambrosia artemisiifolia</i>	N	t	0.5		0.1	0.2	t			
<i>Verbascum thapsus</i>	E	0.4	t	t	1.0	t	t			
<i>Solanum carolinense</i>	N	t	t	t	0.1	t	0.5	t		
<i>Agropyron repens</i>	N	t	15.7	8.1	1.9	22.4	13.5	0.9		
<i>Convolvulus sepium</i>	N	t			1.1	1.3	t	t		
<i>Solidago juncea</i>	N	2.1	2.4	30.2	2.7	44.2	50.7	10.6		
<i>Solidago tenuifolium</i> <sup>3</sup>	N	2.1	1.0	24.0	14.8	50.5	40.7	0.3	t	
<i>Hypericum perforatum</i>	E	t	0.7	6.4	7.8	0.2	0.2	t	t	
<i>Eupatorium hyssopifolium</i>	N	9.5	2.1	0.2	22.0	8.2	17.1	6.5	0.1	
<i>Rumex acetosella</i>	E	1.7	186	98.9	6.9	10.4	3.8	3.2	t	
<i>Oxalis stricta</i>	N	t	0.2	0.1	2.3	0.3	0.1	t		
<i>Solidago nemoralis</i>	N	0.5	3.3	88.1	35.9	12.3	21.0	2.7		
<i>Silene antirrhina</i>	N		t							
<i>Plantago aristata</i>	N		t							
<i>Lychnis alba</i>	E		t							
<i>Rosa sp.</i>	N		t							
<i>Erechtites hieracifolia</i>	N		t							
<i>Erigeron strigosus</i>	N		0.7							
<i>Trichostema dichotomum</i>	N		0.1							

<i>Poa pratensis</i>	E	0.4						
<i>Lepidium virginicum</i>	N	t	t					
<i>Trifolium repens</i>	E	t	0.4	t				
<i>Specularia perfoliata</i>	N	t	t	0.1				
<i>Lonicera japonica</i>	E	1.6			t			
<i>Gnaphalium obtusifolium</i>	N	0.1	0.6		0.1			
<i>Juncus tenuis</i>	N	t	11.6	14.0	6.9	3.9		
<i>Oenothera biennis</i>	N	t		t	t	t		
<i>Panicum commutatum</i>	N	4.1	1.4	0.2	10.8	74.7		
<i>Rudbeckia hirta</i>	N	t	1.1	0.2			0.2	
<i>Daucus carota</i>	E	t						t
<i>Panicum lanuginosum</i>	N	3.0	5.8	26.5	16.4	31.5	0.1	
<i>Erigeron canadensis</i>	N	33.5	5.8	1.9	1.0	4.3	t	
<i>Rubus flagellaris</i>	N	t		0.2	0.6	5.2	t	
<i>Anthoxanthum odoratum</i>	E	t						t
<i>Plantago lanceolata</i>	E	t	t	1.6	2.8	0.1	2.1	
<i>Potentilla recta</i>	E	t		t	t	t		
<i>Agrostis alba</i>	E	t	8.6	1.0	3.1	0.4	1.0	
<i>Poa compressa</i>	E	t	12.3	2.7	1.4	0.5	0.4	
<i>Hieracium pilosella</i>	E	0.4	2.2	6.1	4.2	1.4	14.2	
<i>Achillea millefolium</i>	N	0.8	0.8	16.4	0.1		2.9	
<i>Chrysanthemum leucanthemum</i>	E	0.7	2.1	0.8	1.4	1.5	4.1	
<i>Desmodium marilandicum</i>	N	1.2	0.1	0.4	12.5	2.5	55.6	
<i>Rhus copallina</i>	N	t			t	t	t	t
<i>Lespedeza capitata</i>	N	0.2	t	51.5	73.0	5.8	t	t
<i>Potentilla canadensis</i>	N	9.2	13.6	72.4	27.3	49.2	2.6	t
<i>Plantago major</i>	E		t					
<i>Viola sagittata</i>	N		t	0.2				

Potentilla norwegica	E	t	t				
Carex vulpinoides	N	t				0.6	
Carex Y	N	0.2	t	1.4		9.6	
Carex normalis	N	1.6	1.2	12.2		1.1	
Paspalum setacea	N	t	0.5	2.1		0.7	
Danthonia spicata	N	0.1	4.2	1.0		0.1	
Galium Aparine	N	t	t			0.1	
Sisyrinchium arenicola	N	0.6	14.8	3.8		2.7	
Aster ericoides	N	50.1	23.4			1.5	
Carex normalis <sup>4</sup>	N	1.8	2.2	2.2		1.4	
Carex festucacea	N	1.8	6.9	5.4		1.6	
Stellaria graminea	E	0.8	t	t		2.6	
Juncus trifidus	N	0.4	0.5	0.2		0.8	
Stachys hyssopifolia	N	0.8	2.5	2.5		1.7	t
Taraxacum officinalis	E	0.1	0.1	t		0.1	
Panicum polyanthes	N	1.0	6.5	13.4		2.6	0.2
Hieracium pratensae	E	0.5	1.3	1.2		3.6	3.6
Hieracium floribundum	E	t	1.0	0.8		0.2	1.6
Festuca rubra	N	t				68.0	
Andropogon virginicus	N	0.2	0.2	8.0		9.9	36.3 t
Trifolium arvensae	E	t	t				t
Trifolium pratensae	E		t				
Panicum depauperatum	N		0.5	1.9			
Solidago canadensis	N		0.6			t	
Vicia dasycarpa	E		7.6			1.0	
Vicia tetrasperma + V. cracca	E		0.2			0.5	t
Triodia flava	N		3.5	0.5		7.7	1.2
Potentilla argentea	E			t			

Agrostis hyemalis	N			t				
Carex annectens	N			t				
Rhynchospora sp.	N			t				
Polygala polygama	N			t				
Carex swanii	N			t	1.0			
Asclepius amplexicaulis	N			t	t			
Dianthus Armeria	E			0.2	0.2	t		
Comptonia peregrina	N			0.8	10.4	t		1.4
Trifolium agrarium	E				t			
Apocynum cannabinum	N				4.9			
Dactylis glomerata	E				1.0			
Penieum clandestrium	N				t			
Lysimachia quadrifolia	N				t			t
Prunys seretira	N				t			0.1
Fragaria virginiana	N				0.1	1.1	t	
Hypericum punctatum	N					t		
Rubus sp.	N					t		2.1
Myrica pensylvanica	N		0.2	0.6	5.2	t	1.1	0.8
Pinus rigida	N	t				124	640	123
Quercus velutina	N					t	t	46.3
Pyrola sp.	N						t	
Smilax sp.	N						t	
Betula sp.	N						t	
Acer rubrum	N		t	t			t	
Quercus coccinea	N						t	395
Quercus alba	N							0.3 231
Quercus il icifolia	N							0.3 2.8
Vaccinium vacillans	N						t	14.5

Vaccinium angustifolium	N							t	3.5
Gaylussacia baccata	N								33.3
Kalmia angustifolium	N								0.6
Pyrus arbutifolia	N								0.1
Gaultheria procumbens	N								0.9
Pteridium aquilin um	N								0.7
Carex pensylvanicum	N								0.5
Moss	N							27.2	
Miscellaneous forb species	N	2.8	4.2	5.6	1.1	3.2	6.8	6.9	0.4 0.1
Miscellaneous graminoid species	N	0.6	108.0	0.5	24.0	4.1	4.1	57.0	1.4 0.0
Miscellaneous shrub species	N								4.5
TOTAL		128	380	389	396	377	412	417	675 859

<sup>1</sup>Nomenclature follows Fernald (1950)

<sup>2</sup>"t" = trace (Less than 0.1 gm/m<sup>2</sup>/yr)

<sup>3</sup>Includes some Solidago graminifolia

<sup>4</sup>Includes some Carex festucacea

Table 3. Organic matter along the field-to-forest sere of central Long Island. Data are dry organic matter (in grams). Root/shoot ratios are for terminal standing crop.

Component:	Age of Stand (yrs after abandonment)								
	0	1	2	3	4	5	15	20	~50
	$\text{g/m}^2$								
Shoots	130	330	210	260	280	260	840	4600	8200 <sup>1</sup>
Roots	700	990	670	690	900	920	1240	1400	3600 <sup>1</sup>
Root/shoots	5.4	3.3	3.2	2.7	3.2	3.5	1.5	0.30	0.44
Biomass: Higher Plants	830	1320	880	950	1180	1180	2080	6000	11800
Litter	200	110	180	260	360	400	380	970	1600 <sup>2</sup>
Humus + Soil O. M.	6900	6800	6800	5400	5600	8300	7000	5900	8600 <sup>3</sup>
Total O. M.	7930	8230	7860	6610	7140	9880	9460	12800	22000

<sup>1</sup>Whittaker and Woodwell 1969

<sup>2</sup>Woodwell and Marples 1968

<sup>3</sup>Reiners 1965 and Horrill and Woodwell 1973

Table 4. Net primary production (NPP) of the Brookhaven sere. Numbers in brackets ( ) estimated from Whittaker and Woodwell (1969) on the assumption that root/shoot ratio is 36% for oaks, 24% for Pinus rigida, and 120% for shrubs.

	0	1	2	3	4	5	15	20	~50
<u>Shoots:</u>									
Herbs	130	380	390	400	370	390	280	29	2
Shrubs	-	-	-	t	t	20	10	5	61
Trees	-	-	-	-	-	-	120	640	800
Total Shoots	130	380	390	400	370	410	410	674	863
<u>Roots:</u>									
Herbs	45	130	110	170	150	90	100	4	4
Shrubs	-	-	-	t	t	(24)	12	(6)	73
Trees	-	-	-	-	-	-	30	150	260
Total Roots	45	130	110	170	150	114	132	154	337
Total NPP	175	510	500	570	520	524	540	830	1200
Roots/Shoots	0.35	0.34	0.28	0.42	0.41	0.28	0.32	0.23	0.39
Roots/NPP	0.26	0.26	0.22	0.20	0.29	0.22	0.24	0.19	0.28

Table 5. Organic accumulation ratios for the Brookhaven sere.

	Age of Stand (yrs after abandonment)								
	0	1	2	3	4	5	15	20	~50
Biomass/NPP (Higher Plants)	4.7	2.6	1.8	1.7	2.3	2.2	3.9	7.2	9.8
Litter/NPP	1.1	0.22	0.36	0.46	0.69	0.76	0.70	1.2	1.3
Humus/NPP	39	13	14	9.5	11	16	13	7.1	7.2
Total OM/NPP	45	16	16	12	15	19	18	15	19

Table 6. Efficiency of net primary production along the field-to-forest sere at Brookhaven, New York. Annual insolation was  $1.3 \times 10^5$  Langley (357 Langley/day) or  $1.3 \times 10^6$  kcal/m<sup>2</sup>/year as measured at Brookhaven over nine years between 1950-1958. (BNL Met. Data).

	Year								
	0	1	2	3	4	5	15	20	50
NPP in kcal/m <sup>2</sup> = 1 yr.	750	2180	2140	2400	2260	2280	2500	3940	5600
Efficiency (Annual) in %	0.058	0.17	0.16	0.18	0.17	0.17	0.19	0.30	0.43

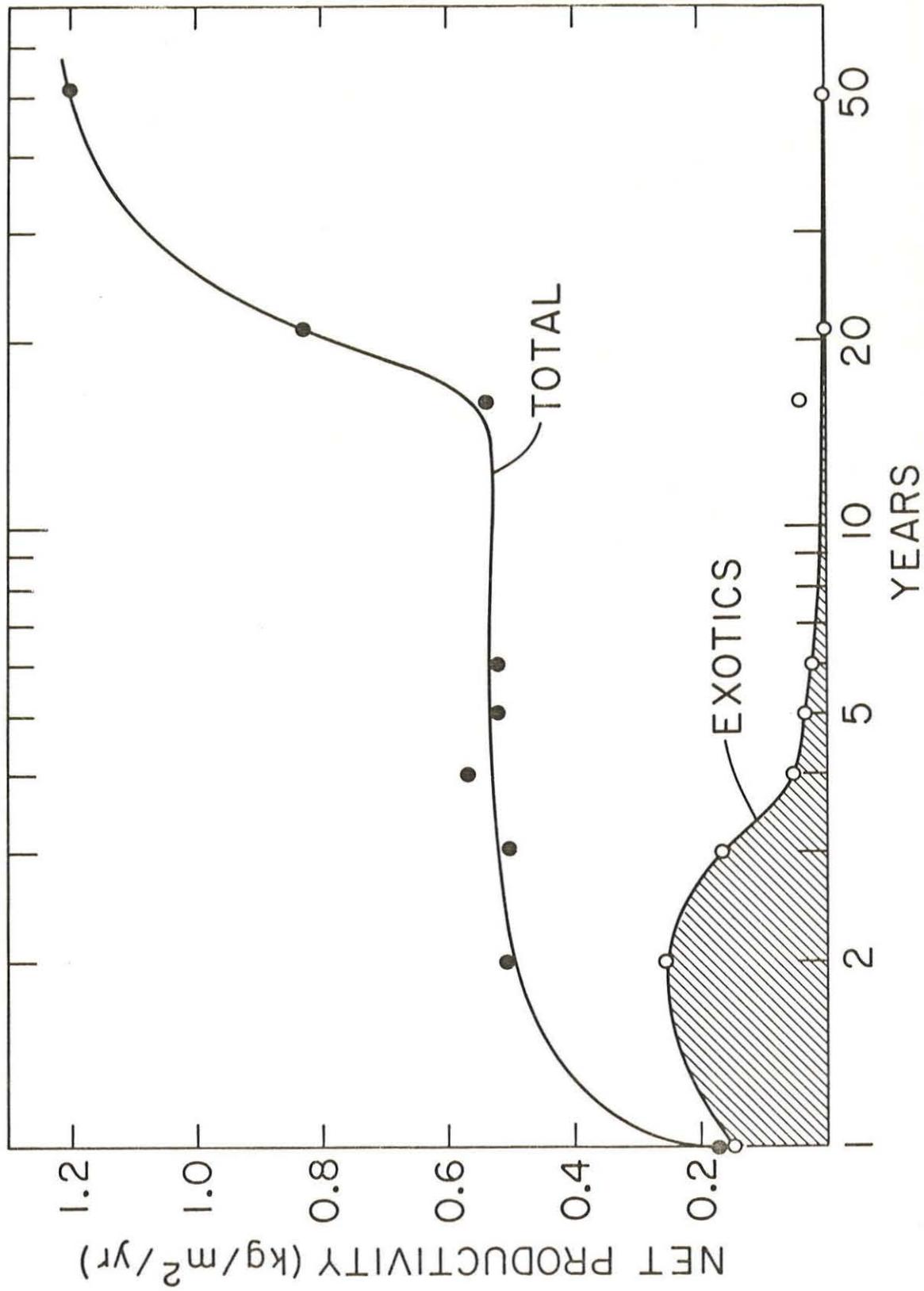


FIGURE 2

• Fig. 2 (Neg. # 6-503-73)