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Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey

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FRYE, RICHARD J., II, and JAMES A. QUINN. (Dept. Bot., Rutgers Univ., Piscataway, N.J. 08854). Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. Bull. Torrey Bot. Club 106: 334–345. 1979.—The woody vegetation of a previously studied 60-yr-old successional forest on a floodplain of the Raritan River in New Jersey was analyzed for rate of forest development in relation to site characteristics. Environmental factors including texture, chemical characteristics, and moisture of the surface 15 cm of soil; soil horizonation; depth of the water table; and frequency of flooding were analyzed along an elevational gradient. A rather abrupt change in soil texture and chemical characteristics, especially exchangeable cations, occurred at approximately 3.35 m above mean sea level. Corresponding to this textural and chemical discontinuity was a change in depth of the water table. Comparisons of woody species composition above and below 3.35 m showed consistent differences, with the higher area having greater species richness, species diversity (H′), equitability (J′), basal areas of trees, and total cover of shrubs. Comparisons of the rate of forest development on the high area of the floodplain with that of nearby upland sites indicated that development occurs more rapidly on the floodplain. With respect to trees ($\geq$ 2.54 cm dbh), at stages of approximately 21 to 25, 40, and 60 years, the floodplain showed greater species diversity, equitability, basal area, mean stem diameter, and tree height. The floodplain study area passed from a thicket to a structurally complex forest stage between 40 and 60 years in development.

River floodplains usually contain variable physical environments. Soil type, frequency of inundation, drainage, and aeration often change considerably over short distances parallel and/or perpendicular to a river bed. Oosting (1942) pointed out, in a study conducted in North Carolina, that "slight variations in topography and drainage have pronounced effects upon moisture conditions in bottomlands," and that bottomlands are ". . . often made up of mixtures of species whose relationships are decidedly confusing."

Illichevsky (1933) listed species which are restricted to regularly flooded or to higher ground along various rivers in the Soviet Union. More recently Zelen'ko (1969), Arsenov (1970), and Arsenov and Sviridov (1970), in discussing the effects of hydrologic conditions upon vegetation, presented species according to the length of flood period they withstand and described zones of vegetation related to this flood tolerance and the expected period of flooding for the zone. Bell (1974) demonstrated a continual change in species composition along an elevational gradient of the Sangamon River in Illinois, which he suggested was a response to the decreased flood frequency with increasing elevation. In contrast, Robertson, Weaver, and Cavanaugh (1978) found that a site-inundation, soil drainage-aeration complex gradient, rather than an elevational gradient, accounted for most of the species distributional patterns on a Mississippi River floodplain.

The Raritan River and its tributaries drain nearly 2,862 km^2 of central New Jersey, including three of the state's four geologic provinces (Vermeule 1894). The river's various branches flow over 11 different substrate types before reaching Raritan Landing. This diversity of substrates creates a complex sediment load which has been differentially deposited at various elevations and distances from the present river bed. A detailed description of the

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geology of the river basin was presented by Wistendahl (1958).

Raritan floodplains have been extensively surveyed by Buell and Wistendahl (1955) and Wistendahl (1958). Buell and Wistendahl found, in examining four stands of relatively mature forest, that all showed common features, but compositional differences existed which appeared related to habitat differences. In describing a successional sequence, Wistendahl (1958) analyzed fields of three ages, 8, 21, and 36 years, along a section of the river designated as Raritan Landing. He stated that succession occurs rapidly but that quantitative comparisons to other floodplain studies were not possible due to a lack of comparable data. However, Wistendahl (1958) noted that succession on the floodplain appeared to be more rapid than on nearby upland fields of the New Jersey Piedmont.

Our research, initiated in 1972, had several objectives: 1) to make quantitative comparisons of environmental factors among the different floodplain habitats; 2) to determine if environmentally-determined compositional differences exist in the successional forest similar to those described for more mature forests by Buell and Wistendahl (1955); 3) to determine what changes have occurred during the 20 years of subsequent development of the young forest analyzed by Wistendahl; and 4) to make qualitative and quantitative comparisons to upland successional trends described by Bard (1952).

Materials and methods. DESCRIPTION AND HISTORY OF THE STUDY AREA. The site studied by Wistendahl (1958), part of the former Raritan Landing area, is located in Johnson Park of the Middlesex County Parks System (40°31′30″N, 74°28′50″W). It extends approximately 1.6 km upstream of the Landing Lane bridge of New Brunswick, New Jersey. According to Biel (1958) the region is characterized by a Continental climate. The average growing season ($\geq$ 43°F or 6.1 C) is 240 days, and the mean yearly temperature is 53.2°F (11.8 C). Precipitation averages approximately 110 cm annually and is rather evenly distributed with 7.0 to 9.9 cm each month, except for July and August which average 12.1 and 11.7 cm (climatological standard normals based on the period 1941–1970).

Flooding occurs nearly every year, but is extremely variable. A maximum number of 16 floods have been recorded in one year, but frequently a much lower number occur, and sometimes none. The seasonal flood distribution does not correspond to peak rainfall. For 1903 to 1955, the greatest number of flood days occurred in March with the least in May through August (Wistendahl 1958).

Vermeule (1936) stated that the Raritan Landing area was occupied by dams, mills, wharves, and warehouses from 1750 to approximately 1875, when the warehouses were destroyed. The land then became pasture. Wistendahl (1958) found portions of the tract in various stages of succession. While his 8- and 21-yr fields have become recreation areas, his 36-yr field remains undisturbed. (This 36-yr field will hereafter be referred to as a 40-yr field since tree corings indicate that tree invasion occurred 40 to 42 years prior to Wistendahl's study).

The site of our research lies between 1.2 and 1.6 km upstream of Landing Lane bridge on the north bank of the river. It includes Wistendahl's 40-yr field and the lower ground adjacent to it. The site is bounded to the east by a drainage ditch and to the west by a younger forest.

VEGETATION SAMPLING. During 1972 and 1973, four transects of contiguous, nested quadrats were established from random starting points along the river bank, and run perpendicular to the river. The transects consisted of from 12 to 16 10 $\times$ 20 m quadrats for measuring trees ($\geq$ 2.54 cm dbh). Nested in each tree quadrat was a 2 $\times$ 20 m quadrat for saplings ($\geq$ 0.3 m height and $<$ 2.54 cm dbh). Four $\frac{1}{2} \times 2$ m seedlings ($<$ 0.3 m height) quadrats were placed in each sapling quadrat. Shrubs and lianas were measured by cover intercept along a 20 m tape stretched through the center of each 2 $\times$ 20 m quadrat. In all, 57 large quadrats were employed. Nomenclature follows Gleason and Cronquist (1963). Previous research (Wistendahl 1958) had indicated the difficulty of distinguishing *Fraxinus americana* and *F. pennsylvanica* due to their apparent gene exchange within the study area. Our observations substantiated this difficulty; thus all ash individuals were counted as *F.* spp. Voucher specimens have been deposited in the Chrysler Herbarium, Rutgers University.

Relative importance values were determined for tree-size members of each species following the method of Curtis and McIntosh (1950). Importance of shrubs and lianas was determined by relative cover. Sapling and seedling importance values were determined by relative density in each case. Species diversity was computed using the Shannon index of general diversity (H′) according to the formula found in Odum (1971): $H' = -\Sigma(n_i/N) \log (n_i/N)$, where n_i = importance value for each species and N = total of all importance values. Tree diversity and shrub and liana diversity were calculated separately. The equitability index (J′), $J' = H'/\log S$ where H′ = the Shannon index and S = the number of species in the sample (Pielou 1975), was calculated for each determination of H′.

Floodplain data for ages 21 and 40 years (Wistendahl 1955) and upland data for ages 25, 40, and 60 years (Bard 1952) were converted to importance values and used for comparisons. Importance value curves for all areas were constructed following Whittaker (1965).

ENVIRONMENTAL MEASUREMENTS. The elevation of a central point in each 10 × 20 m quadrat was determined using a surveyor's transit. All elevations were established relative to a USGS bench mark in Johnson Park. The height of the water table from June 26 through October 26, 1972, was monitored using piezometer tubes positioned at various distances from the river along two of the vegetational transects. Five tubes were used in each transect. Each tube was constructed of 5 cm internal diameter steel pipe, 1.2 m long, and lined with diametrically opposed holes at 10 cm intervals along the pipe's length.

Moisture content of the surface 15 cm of soil was determined during 1972 from June 26 to October 26, and during 1973 from March 28 to June 20. Four locations were chosen on each of three transects to encompass a wide range of elevation. Along two transects, they corresponded to locations of piezometer tubes and, along the third, to similar distances from the river. Thirty-five measurements were made for the first two transects, but only 24 for the third. Samples were taken from the surface 7 cm and from the 7 to 15 cm depth, placed in 85 g soil cans, and sealed. In the laboratory, samples were wet weighed, dried at 105 C for 24 hours, and dry weighed. Moisture percentages were calculated relative to dry weight, averaged for the two depths, and presented as moisture content of the surface 15 cm.

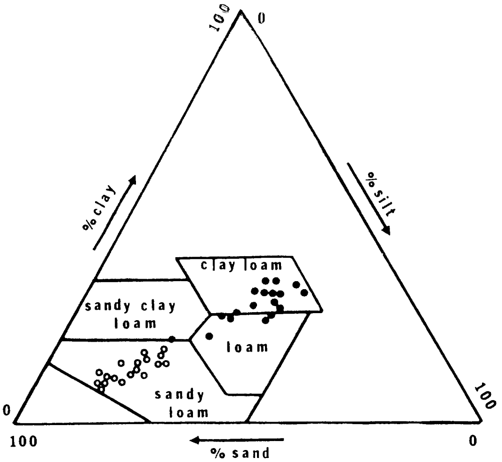

Fig. 1. Soil textural triangle with circle indicating intersection of percent sand, silt, and clay for 36 surficial soil samples from the floodplain. Open circles represent "high area" (> 3.35 m above sea level) samples, closed circles represent "low area" samples.

Textural analyses of soils were conducted using the hydrometer method outlined by Bouyoucos (1953). Thirty-six soil samples were collected from the surface 15 cm. The elevation was recorded for each sample according to the quadrat from which it came. Chemical analyses were conducted by the Soils Testing Laboratory, Rutgers University, on the following: cation exchange capacity, *p*H, and concentrations of Ca, K, Na, Mg, P, NH_4-N, and NO_3-N. Cation exchange capacity was determined by the ammonium acetate method (Schollenberger and Simon 1945), and techniques for determination of NH_4-N and NO_3-N followed those of Hanna and Purvis (1955). Soil *p*H was determined using a Photovolt model Digicord meter on a soil-water (1:1) suspension. Concentrations of Ca, K, Na, and Mg were determined by atomic absorption spectrophotometry. The cations were extracted using a 1 N solution of ammonium acetate. The concentration of P was obtained using the methods of Flannery and Markus (1970).

Four soil pits (1.2 × 0.6 × 1.2 m deep) were excavated. Visual analysis of pit walls was conducted, and soil samples were collected where soil texture or color appeared to change.

The Bound Brook gaging station located 9.5 km upstream had recorded stream discharge and elevation of flow for 32 years between 1903 and 1973. By measuring the elevation of several floods and lesser flows at the study site and using the Bound Brook discharge data, a table was constructed for the study site which predicted the elevation of flow for any given discharge. Flooding frequency was then determined for each elevational interval as the percentage of days with the equivalent discharge.

Results. ENVIRONMENTAL VARIABILITY ALONG THE VEGETATION TRANSECTS. The textural analyses of soils to a depth of 15 cm showed a rather abrupt change in surficial soil type at approximately 3.35 m above mean sea level. All soil samples collected above 3.35 m were sandy loams, while the majority of samples collected below 3.35 m were either clay loams or loams bordering on clay loams (Fig. 1). This textural discontinuity with its attendant internal drainage difference was chosen as a point of division for purposes of comparing vegetational composition in the floodplain forest, and the areas will hereafter be referred to as the "high" and "low" elevation areas.

The major soil textural types are not distributed similarly along the four vegetation and soil transects with respect to distance from the current river bed. It is evident from the elevational profiles of the four transects (Fig. 2) that transects 3 and 4 display sandy loam soils to a distance of approximately 130 m from the river. Transect 1 possesses sandy loam to only 60 m, and transect 2 has no sandy loam soil.

Surficial soil differences are somewhat indicative of differences among soil pit profiles. Profiles from 4.6 and 4.8 m elevations contain sandy loam to a depth of 10 to 15 cm and loamy sand to a depth exceeding 106 cm. Profiles from 3.1 and 3.3 m

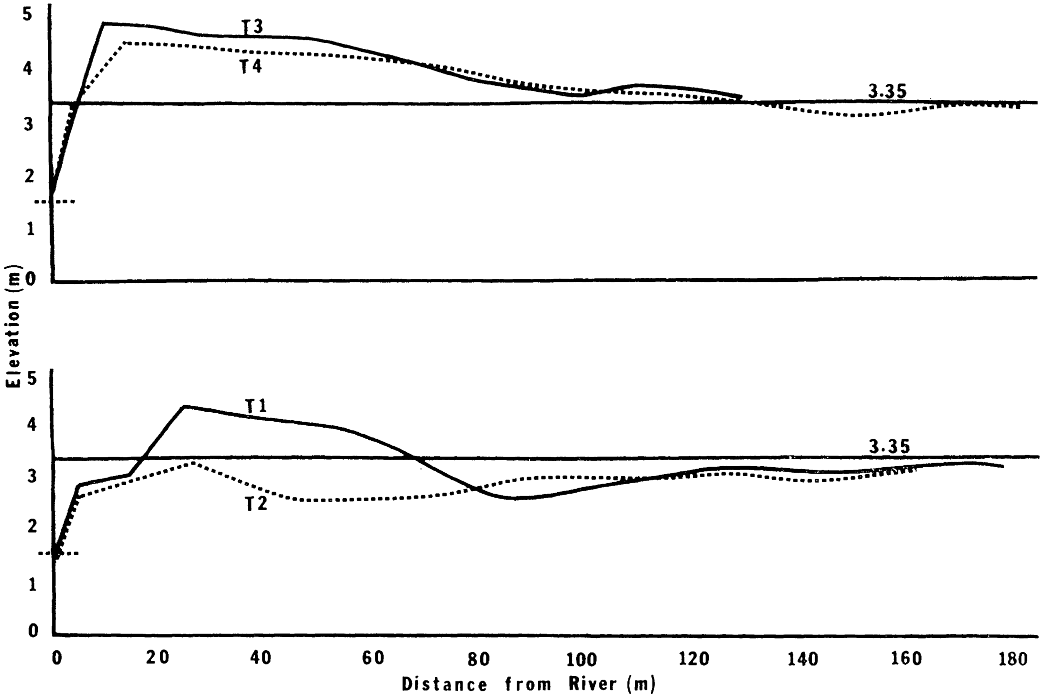

Fig. 2. Elevational profiles of the four vegetational transects at the floodplain. Dashed line at left indicates the average elevation of river flow during the period of the study. Areas > 3.35 m above sea level (high areas) have sandy loam soils, and areas < 3.35 m (low areas) have either clay loams or loams bordering on clay loams.

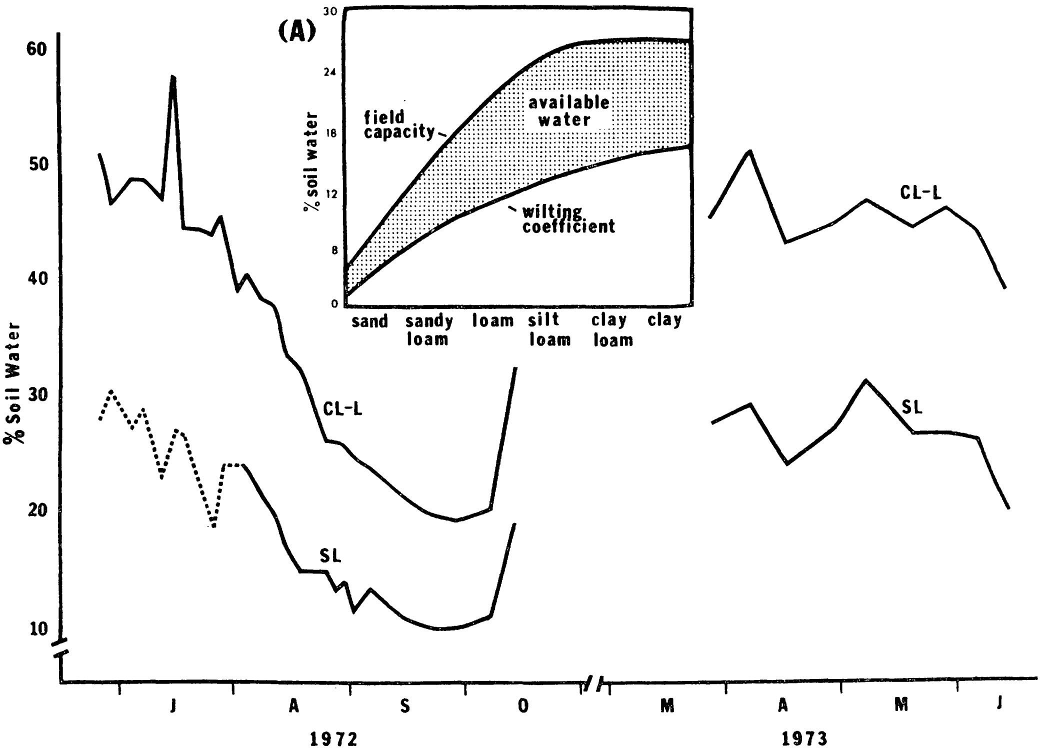

Fig. 3. Surficial soil moisture (% of dry weight) of soils in the high and low areas of the floodplain from June 1972 to June 1973. Solid lines represent the average of six samples, broken lines the average of two samples. CL-L were soils from the low area and clay loam or loam in texture. SL were soils from the high area and sandy loam in texture. (A) General relationship between soil moisture characteristics and soil texture (after Brady, 1972).

contain several depositional layers, all high in clay content. Both low area profiles show strong glei development (indicative of anaerobic conditions) at depths of approximately 30 cm.

Chemical analyses conducted on the surficial soil samples show a *p*H range of 4.0 to 4.5 for the high area and 4.1 to 5.1 for the low area. The mean cation exchange capacity of the high area is 7.46 me/100 g soil, while it is 15.28 in the low area. Total exchangeable cations averaged 2.32 me/100 g soil for the high area and 5.12 for the low area. No consistent differences were found for extractable P or NH_4-N and NO_3-N between the areas.

Moisture trends in the surface 15 cm of soil show that available soil water was consistently high in both areas (Fig. 3). Even though a prolonged drought occurred from August through September 1972, soils in both areas remained at moisture levels above their probable wilting coefficients. Moisture in both areas remained above probable field capacity throughout much of the summer prior to the drought.

The water table, recorded 36 times during the summer and autumn of 1972, varied slightly for the several locations, but was consistently higher than the average flow of the river (1.58 m) during the period. Throughout the low area, excluding the river bank, the water table was within 0.6 m of the soil surface for more than 50% of the recordings with only one exception. Only two piezometer tubes were located in the high area, but frequent soil corings were conducted to 0.9 m depth as a check. Neither in the tubes nor through corings was the water table ever encountered within 0.6 m of the surface in the high area.

The frequency of flooding by discharge class and the equivalent flooded elevations indicates that elevations below 3.35 m re-

Table 1. Relative density, frequency, dominance, and importance values for trees (≥ 2.54 cm dbh) in the high area. Based on 5,600 m^2. (Total density = 432; total basal area = 11.72 m^2.)

Species	Relative density (%)	Relative frequency (%)	Relative dominance (%)	Importance value (%)
Fraxinus spp.	22.5	13.9	42.8	26.4
Acer negundo	23.6	15.8	3.7	14.4
Quercus palustris	4.9	6.1	15.6	8.9
Sassafras albidum	7.6	7.3	6.4	7.1
Acer saccharinum	2.8	3.6	11.4	5.9
Ulmus americana	8.3	7.3	1.8	5.8
Tilia americana	6.0	7.3	2.9	5.4
Ailanthus altissima	3.5	4.2	5.6	4.4
Celtis occidentalis	2.8	4.9	1.9	3.2
Acer rubrum	2.8	4.9	1.5	3.1
Prunus serotina	3.5	4.2	0.7	2.8
Acer saccharum	2.6	4.2	1.0	2.6
Crataegus spp.	2.3	3.6	0.1	2.0
Cornus florida	1.9	3.6	0.3	1.9
Robinia pseudoacacia	1.6	1.8	1.5	1.6
Gleditsia triacanthos	0.5	0.6	1.6	0.9
Acer platanoides	0.5	1.2	0.7	0.8
Morus alba	0.7	1.2	0.1	0.7
Juglans nigra	0.5	1.2	0.1	0.6
Nyssa sylvatica	0.5	0.6	0.1	0.4
Ulmus rubra	0.2	0.6	0.1	0.3
Juniperus virginiana	0.2	0.6	0.1	0.3
Quercus bicolor	0.2	0.6	0.0	0.3
Carya cordiformis	0.2	0.6	0.0	0.3

ceive a wide range of flooding, varying from as many as 18 days to as few as 0.7 days during an average year (see Table 2 in Frye, 1975). Those portions subject to 18 days are temporary swamps and stream beds and as such are devoid of trees. The majority of the low area is subject to 11.5 or fewer days of inundation during an average year. Most of the high area is subject to considerably less than one day of flooding per year, and is never inundated during most years.

VEGETATION ON THE HIGH AND LOW ELEVATION AREAS. Twenty-eight of the 10 × 20 m quadrats occurred on the high and 29 on the low area. For purposes of equal-area

Table 2. Relative density, frequency, and dominance, and importance values for trees (≥ 2.54 cm dbh) in the low area. Based on 5,600 m^2. (Total density = 430; total basal area = 9.26 m^2.)

Species	Relative density (%)	Relative frequency (%)	Relative dominance (%)	Importance value (%)
Acer negundo	59.5	22.9	30.5	37.6
Fraxinus spp.	12.3	20.3	26.1	19.6
Quercus palustris	7.7	10.2	26.6	14.8
Ulmus americana	8.1	11.9	2.3	7.4
Tilia americana	2.6	5.1	4.9	4.2
Prunus serotina	2.3	6.8	0.9	3.3
Carya cordiformis	2.1	5.1	0.2	2.5
Gleditsia triacanthos	0.9	2.5	3.7	2.4
Acer saccharinum	0.9	4.2	1.6	2.2
Quercus bicolor	1.2	3.4	0.9	1.8
Crataegus spp.	0.7	2.5	0.4	1.2
Juglans nigra	0.5	1.7	0.8	1.0
Betula nigra	0.2	0.9	0.6	0.5
Juglans cinerea	0.2	0.9	0.5	0.5
Acer platanoides	0.2	0.9	0.0	0.4

Table 3. Comparison of woody species composition of the high and low areas. Tree reproduction includes trees 2.5 to 10.0 cm dbh, saplings, and seedlings.

Parameter	Trees[a]		Tree reproduction		Shrubs	
	High	Low	High	Low	High	Low
Species richness	24	16	22	14	14	9
Density/5,600 m²	432	430	272[b]	341[b]	—	—
Basal area (m²)	11.72	9.26	—	—	—	—
H′	2.52	1.95	2.20	1.40	2.10	1.60
J′ (%)	79	70	71	55	80	74
Sapling density/5,600 m²	—	—	8,200	2,600	—	—
Seedling density/5,600 m²	—	—	2,850	850	—	—
Total cover/560 m (m)	—	—	—	—	413	155

[a] All individuals of tree species ≥2.54 cm dbh.
[b] Density of trees 2.5 to 10.0 cm dbh.

comparison, one of the low area quadrats was randomly selected and its data excluded.

Tables 1 and 2 provide the tree species in order of importance for the high and low areas, respectively. The high area is richer in species, has higher diversity and equitability values, and greater total basal area (Table 3). Stem density is equal in the areas. The greater basal area of the high area is at least partially a function of the difference in the species composition of the locations; *Acer negundo,* with one of the smallest mean basal areas per stem of the species found on both locations, comprises 60% of the stems on the low area and only 24% on the high area.

Importance value curves (Fig. 4) for the areas illustrate the differences in relative importance of the various species, reflecting the higher equitability value for the high area, where more species share the intermediate position.

In the shrub and liana category, the high area is again richer in species, has a greater diversity and equitability, and a greater total cover (Tables 3 and 4).

Nearly all tree, shrub, and liana species found in the low area also occur in the high area, but additional species are found in the high area and the importance values of shared species vary considerably. Such tree species as *Sassafras albidum, Acer saccharum, Ailanthus altissima, Celtis occidentalis, Cornus florida, Robinia pseudoacacia,* and *Morus alba* were found on the high area and not on the low area. The importance value of *Fraxinus* spp. was greater on the high area than on the low area. *Acer negundo* and *Quercus palustris,* however, showed higher importance values on the low area. Shrub species *Lindera*

Table 4. Relative cover of shrub and liana species in the high and low areas. (Total cover/560 m: high, 413 m; low, 155 m.)

Species	Relative cover (%)	
	High area	Low area
Vitis spp.	31.1	33.5
Lonicera japonica	13.2	1.2
Lindera benzoin	10.7	—
Rhus radicans	10.3	12.1
Rubus allegheniensis	9.8	8.1
Cornus amomum	7.1	31.7
Parthenocissus quinquefolia	5.6	9.5
Staphylea trifolia	4.2	2.5
Viburnum prunifolium	4.1	1.0
Sambucus canadensis	1.8	0.4
Ligustrum vulgare	1.5	—
Cornus racemosa	0.5	—
Rosa sp.	0.1	—
Berberis thunbergii	0.1	—
Space (unoccupied)	42.5	74.0

benzoin, Ligustrum vulgare, Cornus racemosa, Rosa sp., and *Berberis thunbergii* were found only on the high area. The relative cover value of *Lonicera japonica* was greater on the high area while that of *Cornus amomum* was the greater on the low area.

Discussion. ENVIRONMENT-VEGETATION RELATIONSHIPS. The site of this study differs somewhat from the common concept of a floodplain. Surficial soils seemingly display the expected distribution, coarse textured soils on the area near the river and fine soils in the low area away from the river, but the soils do not show a gradient of textural change, rather they fall into two categories—sandy loam and clay loam. The high area nearer the river at the study site is much higher than upstream or downstream of the site, and is located along the inside of a bend in the river. It is probable that the soil was deposited during a previous period in the geologic history of the river. Flooding of the site now occurs initially through the low elevation area away from the river due to the lower near-stream area upstream of the site. The high area is thus flooded only rarely and remains as an island during most floods. Along one transect (T2 of Fig. 2) in which the near-stream area is low, flooding sometimes occurs in the near-stream area first, and it is there that surficial soils display a higher sand content than the majority of the low area samples.

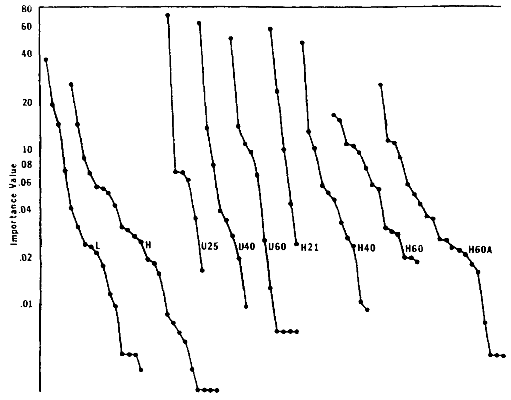

Fig. 4. Importance value curves. High (H) and low (L) areas of the floodplain based on 5,600 m² samples; upland (U) areas of ages 25, 40, and 60 years based on 2,500 m² samples; high areas of ages 21, 40, and 60 years based on 800 m² samples; high area 60A based on 2,500 m² sample. Each point on a curve represents the importance value for a species.

Zelen'ko (1969), Arsenov (1970), Arsenov and Sviridov (1970), and Bell (1974) refer to areas where flood frequency is relatively high. Similarly, McDermott (1954), Hosner (1958, 1959), Hosner and Minckler (1960), Hosner and Boyce (1962), and Hook et al. (1970), who characterize the flooding tolerance of tree seedlings, all refer to extended periods of inundation. The Raritan River does not provide such frequent or extended periods of inundation at our study site. Even the lowest spot experiences a flooding frequency of under 5%. Bell (1974) did not encounter a species, among those found at his site, which was limited to areas where flood frequency was 5% or less. In fact, he found four relatively rare species located only where flooding occurred more than 5% of the time. Thus, on the Raritan floodplain, flooding *per se* probably exerts its effects mainly through physical damage. Plants in the low area are subject to considerable flotsam and may be pushed over or removed during heavy flooding, either by the flotsam or the water itself. High area plants show no such damage. Since the 5% or less flooding frequency is distributed throughout the year, much of the flooding occurs during the dormant period for deciduous plants and would have much less effect upon physiological processes. The most intense flooding occurs during late summer and fall and is associated with tropical storms. Such floods are usually of short duration, but their intensity may result in considerable physical damage, especially to seedlings, saplings, and shrubs.

The position of the water table appears more closely associated with vegetational differences than any other measured parameter. Most plants growing in the low area encountered standing water at less than 0.6 m from the surface between 53 and 75% of the period of record. The soils at shallow depths show glei, indicating a periodically higher water table and poor aeration. Wilde (1958) classified soils with similar water tables as shallow to mid glei soils and stated that such situations are unfavorable to deep-rooted species, are often of lowered productivity, and that roots in such soils are mainly limited to the shallow, well-aerated layer above the water

Table 5. Community parameters for trees ($\geq$2.54 cm dbh) on upland fields abandoned 25, 40, and 60 years previously (three fields and total sample of 2,500 m^2/age-group). Adapted from Bard (1952). Tree height is that of *Juniperus virginiana*, the most important species.

Parameter	25	40	60
Species richness	6	8	11
H′	0.98	1.25	1.57
J′ (%)	55	60	66
Density	77	103	383
Basal area (m^2)	0.142	0.301	1.238
Mean stem diameter (cm)	4.85	6.10	6.35
Tree height (m)	3–4	4–5	5–6

table. In the two soil pits in the low area, there was a high concentration of root area within the surface 0.3 m with the majority of large roots concentrated above the level of standing water.

In contrast, the high area is well-drained, and the water table was not encountered at depths less than 0.6 m. Seventy-two percent of the recordings at 3.9 m elevation did not locate the water table within the 1.2 m depth of the piezometer tube. No glei condition was found in the high area soil pits of 1.2 m in depth. Wilde (1958) considered such soils as deep glei soils. In these situations tree roots can develop in a sufficiently deep, well-aerated layer and receive additional moisture from the ground water. He stated that such situations are commonly associated with high productivity. Root area distribution in the high pits did not show the surface concentration found in the low area.

Surficial soil moisture within the low area may also influence species composition. Wiegand and Lemon (1958) found that at field capacity the concentration of O_2 at certain root surfaces was suboptimal for normal root respiration in clay soil but optimal in a sandy loam. The surface soils in the low area are mainly clay loams, and subsurface soils are even higher in clay content. Soils in both areas were at or above estimated field capacity for a large portion of the growing season (Fig. 3). Therefore, the combination of shallow water table and high surface moisture may limit the establishment of certain species not adapted to poorly drained soils, and reduce the competitive ability of species only marginally capable of surviving in such habitats. Also, the intensity of flooding through the low area may be an additional limiting factor since species respond unequally to physical damage. For example, *Acer negundo,* the species with the highest importance value in the low area, is able to withstand shallow water tables and responds to physical damage by sprouting. The differences in community structure and species composition between the areas is apparently a result of the differential success of the colonizing propagules of an initially similar group of species.

RATES OF SUCCESSIONAL FOREST DEVELOPMENT. Statements about succession on floodplains must take into account the different physical habitats. Since Wistendahl's (1955) discussion of succession was confined to the high, well-drained area, we will focus on qualitative and quantitative comparisons between nearby upland and high area floodplain successional trends, using data adapted from Bard (1952) and Wistendahl (1955) in addition to the data of this study.

Bard's data from upland sites indicate that only a slight change occurs in tree species richness from the 25- to the 60-yr fields (Table 5). This small change may be in part historical rather than of natural origin. The presence of an orchard in two of the old fields and an estate from which an exotic species escaped in a third account for most of the change in richness. During the 35 years, species diversity (H′) increased, due mainly to increased equitability. The number of trees increased slightly from 25 to 40 years but more than tripled from 40 to 60 years (Table 5). During the first period the mean stem diameter increased, but during the second it changed little. This may be explained, in part, by the large increase in the number of saplings reaching tree-size during the second period. These fields thus approached a thicket

Table 6. Community parameters for trees (≥ 2.54 cm dbh) on successional floodplain fields (21, 40, and 60 years) of the high area, based on 800 m^2 samples. Fields 21 and 40 adapted from Wistendahl (1955), field 60 from the current study. Tree height is that of *Fraxinus*, the most important species.

Parameter	21	40	60
Species richness	5	11	14
H′	1.12	1.74	2.41
J′ (%)	70	72	91
Density/2,500 m^2	375	737	197
Basal area/2,500 m^2 (m^2)	0.947	6.584	4.241
Mean stem diameter (cm)	5.69	10.67	18.69
Tree height (m)	9–11	12–18	18–24

stage between 40 and 60 years after abandonment. Our observation of the 60-yr fields after 25 more years (1974) revealed that tree density remained very high and that the thicket stage had not been passed. Importance value curves of the 25-, 40-, and 60-yr fields illustrate that single species dominance, although lessened, is still evident at 60 years (Fig. 4). The heights of *Juniperus virginiana* did not exceed 6 m in the 60-yr fields.

Forest development occurred more rapidly on the high area of the floodplain than on the upland sites (Table 6). This is apparent in spite of the fact that the sample area was only 1/3 the sample area of the upland fields. We initially analyzed only 800 m^2 for our 60-yr stage so that our data would be comparable to those collected earlier by Wistendahl (1955). (As mentioned previously, our 60-yr field was a resample of Wistendahl's 40-yr field.) Considering these 800 m^2 samples, we note a marked increase in species diversity over the nearly 40-yr period as a result of both increased richness and equitability. Density increased to the 40-yr stage, when a nearly impenetrable thicket occurred, and dropped sharply at the 60-yr stage. Total basal area followed the same pattern. Basal area is considerably greater than on the upland at each stage on the floodplain site. Density is greater only on the two younger fields as the floodplain passes out of the thicket stage between 40 and 60 years. Although upland trees showed only a slight change in mean stem diameter as the thicket stage was approached, a corresponding slight change was not found for the floodplain trees. Mean stem diameter nearly doubled from the early to the advanced thicket stage on the floodplain. As the stand thinned out from 40 to 60 years, mean stem diameter again almost doubled. Heights of *Fraxinus* spp. were 3× as great as their upland counterparts (*Juniperus virginiana*) in each age-group, and as a result the overall community exhibited a greater structural diversity. Figure 4 illustrates the change in importance value curves between the thicket and post-thicket stages of the floodplain high area. A large decline occurs in the importance of ash while several intermediate species increase in importance.

Since comparisons of richness and diversity are best made on the basis of samples of equal area, we decided to utilize a 2,500 m^2 area of the 60-yr floodplain high area for comparison with the 60-yr upland values of Bard (1952) based on 2,500 m^2 (Table 5). This sample had individuals of 20 species, a density of 209 trees, an H′ of 2.63, and an equitability of 88%. Thus, on an equal-area basis, nearly twice the number of species were found in the floodplain forest as in the upland thicket. The importance value curve for this 2,500 m^2 high area floodplain sample illustrates that many more species are found in the intermediate importance range and that single species dominance is not as pronounced as on the upland sites (Fig. 4). Since 60-yr floodplain high area curves for 2,500 m^2 and 800 m^2 differ mainly in number of rare species, it is likely that the same would be true for comparable 40-yr curves. Comparison of the 40-yr curve for the floodplain with the upland sites shows a closer approximation to the upland 60-yr age-group. Thus, both habitats display similarly shaped curves during their thicket stage. The main difference is that the thicket appears earlier on the floodplain and passes more rapidly. A structurally complex forest develops much sooner on the floodplain high area than on nearby upland sites.

Succession on the low area floodplain site cannot be traced due to the absence of data on stages prior to the 60-yr stage. From the 60-yr data it appears probable that prior development was roughly similar to that in the high area. A more dense forest may have existed earlier, but the major species was probably *Acer negundo*. A lower mean height and a lower diversity than the high area was probably the situation. However, development of trees to forest status apparently occurred at about the same rate as on the high area.

Several environmental conditions which differ between the high area floodplain and the nearby upland sites might be proposed as factors contributing to the differences in successional trends. Floodplains are commonly considered to be highly fertile due to the frequent deposition of new soil from upstream sites; however, it was previously shown that the high area currently receives flood waters only rarely. Surficial soils of the high area display a slightly lower *p*H and cation exchange capacity than those upland soils studied by Bard (1952). Although the data are limited, they do suggest that the high area site is not significantly more fertile than upland sites. Since climatic differences are minimal due to the close proximity of the sites, macroclimate may be considered similar. Again due to absence of flooding and nearness of sites the seed input on the upland and floodplain sites may be largely the same. In fact, the only readily discernible differences between the locations are the depth and type of soils and the proximity to the water table. Soils of the upland fields are relatively shallow (ca 0.5 m) and may subject plants to water stress during prolonged dry periods. Conversely, we have found that soil moisture of the floodplain high area does not ordinarily drop to the wilting coefficient and that the water table lies within the reach of deeper-rooted species throughout the growing season.

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