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Ecological Life-history of *Lonicera japonica* Thunb.

Anna D. Leatherman
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To the Graduate Council:

I am submitting herewith a dissertation written by Anna D. Leatherman entitled "Ecological Life-history of *Lonicera japonica* Thunb.." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

Royal E. Shanks, Major Professor

We have read this dissertation and recommend its acceptance:

A. J. Sharp, James T. Tanner, Fred H. Norris, L. F. Seatz

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

August 11, 1955

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E. A. Waters
Dean of the Graduate School

ECOLOGICAL LIFE-HISTORY OF LONICERA JAPONICA THUNB.

A THESIS

Submitted to
The Graduate Council
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Doctor of Philosophy

by

Anna D. Leatherman

August 1955

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

INTRODUCTION

This study deals with the ecology of Lonicera japonica Thunb., a woody vine generally known as Japanese honeysuckle, which is regarded as a troublesome weed in southeastern United States. The investigator chose this species, because it could be studied in both southeastern United States and in southern California. Relatively few species can grow well in two areas whose climatic conditions and soils are so vastly different as they are in these two widely separated regions. Japanese honeysuckle, which grows profusely in southeastern United States, grows well under irrigation in southern California, but it does not become a pest.

There were two main objectives: first, to study the distribution, recognized variation, and economic importance of the species throughout the United States; and second, to make a detailed study of the ecological life-history of the vine. Information contributing to the first objective was secured chiefly by writing to botanists in every state in the United States, by reviewing the literature, by visiting nursery establishments, and by making observations in the field. Some field data were contributed by botanists from The University of Tennessee.

As an aid in accomplishing the second objective, outlines prepared by the British Ecological Society (1941, 1947), an outline for trees and shrubs (Pelton 1951), a paper on the ecological life cycle of seed plants (Pelton 1953), and an outline suggested for germination reports (D. B. Lawrence, et al. 1947) have been helpful.

The second objective required a review of the literature,

systematic field observations, and a series of greenhouse observations and measurements. The greenhouse observations and some field measurements were done at The University of Tennessee June 1952 to August 1953. Additional observations were made during the school years 1953-1955 at Upland College, Upland, California. The study of root development was made during the summer of 1954 at The University of Tennessee.

CLASSIFICATION

The genus Lonicera L., which belongs to the Caprifoliaceae, was named after Adam Lonitzer (Bailey 1933). This genus is composed of 180 species of erect or climbing shrubs (G. H. M. Lawrence 1951) and is widely distributed in the temperate zone of the northern hemisphere. It is represented as far south as Java and extends northward to the Arctic Circle; only twenty species occur in North and Central America, and the greatest concentration is in central and eastern Asia (Rehder 1903).

The name Lonicera japonica, proposed by Thunberg (1784), was accepted by Rehder (1903) in his synopsis of the genus. Japanese honeysuckle is the most appropriate English common name for this species, although it is sometimes also called Chinese honeysuckle (Britton and Brown 1936). Sui Kadsura (silver and gold) is the common name in the Japanese language. It is more often simply called honeysuckle in this country, a name which is also locally applied to other nectar-bearing flowers with long tubular corollas, such as Rhododendron roseum (Loisel.) Rehd. and Aquilegia canadensis L. (Fernald 1950), which belong to quite different families.

Japanese honeysuckle is a climbing plant which belongs to the phanerophytes in the life-form classification of Raunkiaer (1934). Braun-Blanquet (1932) placed honeysuckle in the subdivision Phanerophyta scandentia (lianas), which is based on a modification of Raunkiaer's (1905) earlier system. The habit of twining and trailing, often with

rooting at the nodes, is a distinctive character of the species.

The ovate or oblong leaves, 3 to 8 cm. or more long, are usually opposite; however, some stems have three leaves at a node. The margins of the leaves are usually entire, except for the basal leaves of shoots which are frequently lobed and infrequently toothed. The leaves have short petioles which are bent, and the upper surfaces of the leaves face the light. Japanese honeysuckle is evergreen in the southeast and is usually deciduous northward. Both the leaves and the stems are hairy. The fragrant flowers, white or occasionally pink at expansion, and yellow on the second day, are borne in pairs on the summit of solitary peduncles from the upper leaf axils. The fruits are subglobose to oval berries which are purple or black at maturity.

Three characters are the basis for assigning Lonicera japonica to the subgenus CHAMAECERASUS: "twining shrubs, leaves always distinct (not connate), the flowers in axillary pairs" (Rehder 1940). Japanese honeysuckle has been assigned to section NINTOOA on the basis of the following characters: "leaves usually evergreen or half-evergreen, calyx distinctly toothed, bracts usually subulate, corolla two-lipped with a slender tube, and fruit usually black" (Rehder 1940).

There are four horticultural varieties of Lonicera japonica Thunb. Lonicera japonica var. halliana (Dipp.) Nichols. is the common variety in the United States. It is often called Hall's honeysuckle (Armstrong Nurseries 1947). Mr. Masami Mizushima, Division of Botany, Research Institute for Natural Resources, Tokyo, Japan, has stated in correspondence that Lonicera japonica varies considerably and that the var. halliana is

merely a more vigorous variant. This variety differs from the original description of the species by Thunberg (1784) only in having the flowers white instead of red. Rehder (1903) recognized the var. halliana as nearest to the type of Lonicera japonica, with the exception that the flowers are usually white; however, both pink and white flowers have been observed on the same plant. Mrs. Misu Togasaki from Tokyo, Japan, has reported in correspondence the same color variations in Japan which have been observed in the United States.

Lonicera japonica var. chinensis (Wats.) Baker has red flowers, and the upper lip of the corolla is divided more than one-half; its leaves, which are red-purple when young, are nearly glabrous with some pubescence in the veins (Rehder 1940). The red flowers fit the original description of the type by Thunberg, but the glabrous leaves do not (Rehder 1903). Common synonyms for this variety are L. chinensis Wats. and L. flexuosa Ker, not Thunb. Other synonyms for this variety are recorded by Rehder (1903) and by Jackson (1946).

Lonicera japonica var. repens (Sieb.) Rehd. has white or purple-tinged flowers; the upper lip of the corolla is divided about one-third, and the limb is longer than the tube. The leaves are nearly glabrous; the basal ones may be lobed, and the veins are often purple (Rehder 1940). Rehder (1903) stated that most of the Japanese specimens which he saw belonged to the var. repens with short peduncles and a different leaf shape; however, the Japanese specimens had pubescence on both the upper and the lower leaf surfaces, at least when young, while the leaves are glabrous in the cultivated plants of var. repens. Common synonyms for

this variety are L. nigra Thunb., L. japonica var. flexuosa Nichols., L. flexuosa Thunb., and L. brachypoda DC. (Rehder 1940). Other less common synonyms for this variety are recorded by Rehder (1903) and by Jackson (1946).

A horticultural variant of Lonicera japonica var. repens is L. japonica var. aureo-reticulata (T. Moore) Nichols., which has yellow veins and smaller leaves. Mr. Masami Mizushima stated in correspondence that it has been discovered recently that the yellow veins in var. aureo-reticulata are caused by a virus. This variety is illustrated in color in "Illustrierte Garten-Zeitung" (Müller 1865). A common synonym for this variety is L. brachypoda var. reticulata Witte, and other less common synonyms are recorded by Rehder (1903) and by Jackson (1946).

Meehan (1888) reported that the characteristics which are supposed to separate L. japonica var. halliana from L. brachybotrya Asa Gray (another synonym for var. repens) and L. flexuosa Ker, not Thunb. (Loddiges 1825) can be found in different stages on the same plant. Rehder (1903) concluded that the species is variable and that, although the extreme forms seem distinct, there are no constant characters to satisfactorily separate the two forms which were described as separate species by Thunberg (1784).

Sax and Kribs (1930) reported that there are no known hybrids between subgenera of the genus Lonicera or between species of different sections of the genus and were able to obtain no seeds when such crosses were attempted. Rehder (1903) stated that there had been reported only one hybrid in the wild state in subgenus CHAMAECERASUS (Lonicera nigra x

xylosteum Bruegger), and he considered this a doubtful one. Many hybrids have appeared in botanical gardens and nurseries where species of *Lonicera* were growing close together; however, even in botanical gardens, only a few hybrids have been recorded in subgenus CHAMAECERASUS and none in section NINTOOA (Rehder 1903).

Sax and Kribs (1930), from observations of pollen mother cells and of the root tips of young plants, reported that Japanese honeysuckle has nine pairs of chromosomes. Most of the other species of *Lonicera* which were examined by Sax and Kribs also had nine pairs of chromosomes. There are only three species of *Lonicera* in section NINTOOA which are polyploids (Ammal and Saunders 1952).

The diploid number of eighteen chromosomes in *Lonicera japonica* was confirmed by observations of sections from the root tips of cuttings at The University of Tennessee. No evidence of polyploidy was observed in preparations from a number of plants.

SPREAD AND ECONOMIC IMPORTANCE

Lonicera japonica Thunb., native to China, Japan, and Formosa (Bor and Raizada 1943), was introduced somewhere into the United States in 1806. Horticultural variants were introduced from 1825 until 1860 (Rehder 1940). Before the Civil War, Japanese honeysuckle was a favorite ornamental due to its fragrant flowers (Andrews 1919). It went west with the early settlers and prospectors, as evidenced by its present-day persistence around early mining camps in Arizona. It is still prized as an ornamental in California (Figure 1), where it is one of the standard vines used to cover fences in the lowland sections.

Japanese honeysuckle had evidently become a weed before botanists were aware of the weedy character of the species. Neither Gray (1884, 1889) nor Chapman (1897) included it in their floras. Small and Vail (1892) observed Japanese honeysuckle in southwestern Virginia, near Abingdon, at an altitude of 1950 ft. and on limestone ledges along the Holston River at 2100 ft. They wrote:

> The range of this much neglected species now extends from New York to North Carolina and across the mountains into West Virginia. It has probably escaped from cultivation and become naturalized in many parts of New England and the territory west of the mountains, but at present we have no record as to its occurrence there.

Small (1897) received a specimen of Japanese honeysuckle from Florida, and he noted that it was spreading rapidly. R. M. Harper (1900) recorded that the vine was abundant near Athens, Georgia. Rehder (1904) observed honeysuckle as a common escape along the Connecticut coast and at Essex, Massachusetts, far from homesites.

Japanese honeysuckle was introduced into North Carolina many years ago as a stabilizer of road banks. It has not been used there in erosion control plantings in recent years. It is still used extensively for erosion control in some of the eastern states, and it has been planted to a limited extent in other states (Table I). In recent years most botanists and foresters have not recommended the use of Japanese honeysuckle as an erosion control plant, since it often spreads from the roads to the farmers' fields. O. A. Kimmel, Supervisor of the State Soil Conservation Commission in Pennsylvania, stated in correspondence that erosion occurs under the vines if growth has been poor.

The fruit and leaves of Japanese honeysuckle are included in the diet of songbirds, game birds, and game mammals (Martin, et al. 1951). The fruit has almost as great a percentage of crude protein and a greater percentage of fat than corn kernels and timothy hay; however, the leaves have a lesser percentage of both (Handley 1945). County agents in North Carolina and in South Carolina have reported in correspondence that beef cattle browse during the winter months on honeysuckle more than on any other woodland plant.

Japanese honeysuckle provides excellent cover for rabbits, cotton rats, other small mammals, bobwhites, and wild turkeys (Rainey 1949). It is considered important for the promotion of wildlife programs in several states (Table I).

The Cherokee Indians use the stems of Japanese honeysuckle to make baskets and trays (Leftwich 1952). Bees and other honey-gathering insects visit the flowers.

TABLE I

REPORTS OF ECONOMIC IMPORTANCE
OF JAPANESE HONEYSUCKLE

	Extensive Use for Erosion Control	Limited Use for Erosion Control	Important for Wildlife
East Central States			
Kansas		x	
Missouri	x		
Illinois (southern)		x	
Indiana (southern)		x	
Ohio (southern)		x	
Kentucky		x	
Tennessee			x
Middle Atlantic States			
North Carolina		x	
Virginia	x		x
West Virginia	x		
Maryland	x		x
Delaware			x
Pennsylvania	x		x
New Jersey	x		
Northeastern States			
New York	x		
Connecticut	x		
Rhode Island	x		
Massachusetts	x		

Twining over other vegetation is the only bad character of Japanese honeysuckle (Möller 1901). Remnants of the native flora have been entirely eliminated in numerous local places due to the spread of the vine, and it is regarded by some as one of the most troublesome weeds in the United States (Fogg 1945).

GEOGRAPHIC DISTRIBUTION

Habitat Character

Climatic Relationships

Japanese honeysuckle, an introduced plant, has escaped from cultivation and has become naturalized through most of the Deciduous Forest and Southeastern Evergreen Forest regions of the United States (Braun 1950), as shown in Figure 2, which also shows the approximate climatic limits of the species. The states where honeysuckle has become naturalized are chiefly south of the 30° normal January isotherm, and honeysuckle has not been reported as an escape south of the line where, under normal conditions, only 5 per cent of the January nights are lower than 32° F. It is also evident that Japanese honeysuckle has become naturalized chiefly in states east and south of the 40 in. mean annual precipitation limit.

The naturalized range of Japanese honeysuckle is closely correlated with the humid continental climate with warm summers (Daf) and the humid sub-tropical climate with no dry season (Caf). There are also records of a few escapes in the humid continental climate with cool summers (Dbf). The islands of Japan are in the Dbf climate in the north and in the Caf climate in the south (Trewartha 1943).

Thornthwaite's climatic system (1931) has been chosen to facilitate a more detailed analysis of the climatic distribution of Japanese honeysuckle in the United States. Nine stations where Japanese honeysuckle is a pest were selected. The thermal efficiency index (T-E),

based on the sum of monthly values from temperature data, and the precipitation-effectiveness (P-E) index, based on the sum of the monthly values read from a nomogram (Thornthwaite 1931), were computed. The index values were then plotted on a graph (Figure 3). (The terms "Modified 1931 System" were used on the graph, since the term "megathermal" introduced in a later classification (Thornthwaite 1948) was substituted for "tropical.") Index values used in plotting are indicated in Table II; the minimum temperature and the length of the growing season for each station are included. All of the stations where honeysuckle is a pest, with the exception of Charleston, South Carolina, are in the BrB'b climatic type. Charleston, which is in the CrB'b climate, is close to the mesothermal forest climate boundary.

The T-E and P-E indexes were also computed for eleven stations where honeysuckle has escaped and is not a pest. Six of these stations are in the microthermal forest climate. Columbia, Missouri, which is in the BrB'c type, is close to the microthermal forest climate. Three stations are located where the rainfall is seasonal. Honeysuckle has not been reported as a pest in Tallahassee, Florida, which is in the mesothermal forest climate.

The T-E and P-E indexes were likewise computed for eleven stations where honeysuckle is used as an ornamental and has not escaped. Five of these stations are in the microthermal forest climate, and six of them are in either grassland or steppe climates.

Nagasaki, mentioned by Thunberg (1784) as the type locality of the species, is the only Japanese city which was plotted, and it is in the

TABLE II

INDEX VALUES USED IN PLOTTING STATIONS IN FIGURE 3, WITH CLIMATIC PROVINCES INDICATED; MINIMUM TEMPERATURE AND LENGTH OF GROWING SEASON INCLUDED

Honeysuckle Stations	Mini um Tempera- ture (F.)	Length of Growing Sea- son in Days	Thornthwaite 1931 System P-E Index	T-E Index	Climatic Province
A pest					
Norfolk, Va.	2	242	72.0	82.2	BrB'b
Wil ington, N. C.	5	246	72.0	93.3	BrB'b
Charleston, S. C.	7	285	58.7	100.8	CrB'b
Savannah, Ga.	8	273	65.0	104.2	BrB'b
Birmingham, Ala.	-10	240	96.9	94.5	BrB'b
New Orleans, La.	7	292	87.9	111.5	BrB'b
Houston, Texas	5	301	83.6	110.9	BrB'b
Cairo, Ill.	-16	217	81.7	78.0	BrB'b
Knoxville, Tenn.	-16	217	90.3	78.4	BrB'b
Escaped, but not a pest					
Hartford, Conn.	-24	182	113.7	55.7	BrC'c
Ithaca, N. Y.	-24	158	88.4	50.6	BrC'c
Pittsburgh, Pa.	-20	183	82.6	62.2	BrC'c
Wooster, Ohio	-24	152	98.1	54.7	BrC'c
Lafayette, Ind.	-33	168	92.1	60.5	BrC'c
Columbia, Mo.	-26	189	75.5	68.1	BrB'c

TABLE II

INDEX VALUES USED IN PLOTTING STATIONS IN FIGURE 3, WITH CLIMATIC PROVINCES INDICATED; MINIMUM TEMPERATURE AND LENGTH OF GROWING SEASON INCLUDED (CONTINUED)

Honeysuckle Stations	Minimum Temperature (F.)	Length of Growing Season in Days	Thornthwaite 1931 System P-E Index	T-E Index	Climatic Province
Escaped, but not a pest					
Topeka, Kan.	-25	195	62.9	66.3	CrB'a
Tucson, Ariz.	6	245	15.4	104.3	EdB'b
San Bernardino, Calif.	17	253	28.8	93.2	DdB'b
Portland, Oregon	-2	263	96.5	63.0	BrC'b
Tallahassee, Fla.	-2	282	80.1	107.1	BrB'b
Ornamental; has not escaped					
Boston, Mass.	-18	199	101.0	54.5	BrC'c
Concord, N. H.	-32	153	96.6	46.9	BrC'c
Detroit, Mich.	-24	177	72.0	53.4	BrC'c
Madison, Wis.	-29	171	64.6	50.9	BrC'c
Des Moines, Iowa	-30	175	58.9	59.0	CrB'c
Oklahoma City, Okla.	-17	224	48.5	82.1	CrB'b
Lincoln, Neb.	-29	180	46.7	61.8	CdC'c
Denver, Colo.	-29	171	25.1	54.6	DdC'c
Salt Lake City, Utah	-20	192	37.8	59.4	CdC'c

TABLE II

INDEX VALUES USED IN PLOTTING STATIONS IN FIGURE 3, WITH CLIMATIC PROVINCES INDICATED; MINIMUM TEMPERATURE AND LENGTH OF GROWING SEASON INCLUDED (CONCLUDED)

Honeysuckle Stations	Minimum Temperature (F.)	Length of Growing Season in Days	Thornthwaite 1931 System		
			P-E Index	T-E Index	Climatic Province
Ornamental; has not escaped					
Spokane, Wash.	-30	184	39.7	50.2	CdC'c
Urbana, Ill.	-25	180	76.8	60.2	BrC'c
Japanese Station					
Nagasaki	22	245	130.9	84.7	ArB'b

ArB'b climatic type. The climate of Nagasaki, except for the greater annual rainfall, is similar to that in the United States where honeysuckle is a pest, between Latitudes 31 and 38°.

Japanese honeysuckle is scarce in the mountainous sections of eastern United States. It is very rare above 1200 ft. in Pennsylvania and in New York and does not escape at the higher elevations northward. However, R. G. Brown stated in correspondence that honeysuckle grows well at one station in Garrett County, Maryland, at 2500 ft. B. W. Wells observed Japanese honeysuckle at an elevation of 5000 ft. in the Pisgah Mountains in North Carolina. The vine is very abundant at an elevation of 2800 ft. in the Ouachita Mountains in Arkansas. It has been collected at Ramsey Canyon in the Huachuca Mountains at an elevation of 8406 ft. and at Douglas, Arizona, at an elevation of 8623 ft. (Kearney and Peebles 1951). Water is plentiful in the two canyons in which these collections were made; however, the surrounding country is semi-desert.

Soil Factors

Japanese honeysuckle grows on many different kinds of soils in the United States; however, the best growth has been observed on well-drained forest soils. In general, as has been reported by E. T. Wherry in correspondence, honeysuckle escapes from cultivation and spreads most rapidly when the soils are rich in minerals and circumneutral (pH 6.1-7.9) in reaction, spreads slowly in subacid (pH 5.1-6.0) soils and does not spread in mediacid (pH 4.1-5.0) soils. It has also been reported that honeysuckle has never been observed climbing over *Kalmia latifolia*

L. and *Vaccinium* spp., which are abundant in mediacid soils. Honeysuckle has escaped from cultivation and grows well under irrigation in the alkaline soils near Tucson, Arizona.

Honeysuckle is a pest chiefly in the states where red and yellow podzolic soils are characteristic. These soils have good structure, but they are generally low in minerals and in organic matter. It appears that other favorable factors, such as the longer growing season and less severe competition, more than compensate for the lower concentrations of essential minerals.

B. B. McInteer reported in correspondence that the best growth of honeysuckle in Kentucky has been observed on limestone soils. B. C. Tharp stated in correspondence that honeysuckle is locally a pest on black limestone soils near Houston, Texas.

Japanese honeysuckle is sparsely distributed on the coarse, white sandy soil of the sand hills in the southern half of the Coastal Plain of North Carolina and in small portions of Georgia, Alabama, northern Florida, Mississippi, and Louisiana. Xeric conditions frequently exist on these coarser sands due to a high rate of evaporation and excessive drainage, and they are aggravated by the heating of the soil which is a result of the low water content; the coarse sands are low in nitrogen and in other essential minerals, and root growth is slow (Wells and Shunk 1931). A species as mesic as Japanese honeysuckle can not grow well under these conditions. Seedlings may not survive the first growing season, since their roots are normally not extensive enough to utilize water at deeper levels in the soil.

Growth in Different Types of Habitats

During the summer of 1952 the growth of greenhouse-reared cuttings was compared with that of cuttings in different types of habitats at a series of altitudes in the Great Smoky Mountains. The stations chosen for the transplants were near those used in the Smoky Mountain Snowfall Study reported elsewhere (Shanks 1954). Weather records were available from January 1946 until March 1951.

Woody cuttings were planted in "vita band" pots in a fertile greenhouse soil. Ten cuttings of the same age were oven-dried to provide an estimate of the average dry weight of the shoots and roots at the time of planting, 0.137 and 0.009 grams, respectively.

On August 4 ten rooted cuttings were transplanted to each of three different types of habitats (open, deciduous forest, and evergreen forest) at each of four altitudes: 1500 ft., 3500 ft., 5200 ft., and 6000 ft. The cuttings were planted in two rows; five plants were put in each row at one foot intervals. They were dug out on October 30 and were taken back to the greenhouse for further analysis and comparison with the ten cuttings which grew in the greenhouse during the same period.

A comparison of the number of cuttings which survived in the three types of habitats at different altitudes is indicated in Table III. Although 85 and 75 per cent of the cuttings survived in the deciduous and in the evergreen forests, respectively, growth was poor in both types of habitats. There was much insect damage at three altitudes in the deciduous forests. The best growth occurred in the open habitats at

TABLE III

THE NUMBER OF LONICERA JAPONICA CUTTINGS WHICH SURVIVED AT DIFFERENT ALTITUDES AND IN DIFFERENT TYPES OF HABITATS IN THE GREAT SMOKY MOUNTAINS DURING AUGUST, SEPTEMBER, AND OCTOBER 1952; TEN CUTTINGS PLANTED IN EACH HABITAT AT EACH ALTITUDE

Altitude in Ft.	Open Habitat	Deciduous Forest	Evergreen Forest
1500	5 (Insect damage)	9 (Leaves chewed by insects and rodents)	6 (Slight growth)
3500	0	8 (Poor growth; insect damage)	5 (Slight growth; shaded by Rhododendron)
5200	10 (Many leaves had dropped off four plants; good shoot and root growth)	9 (Slight growth)	9 (Plants fresh and green; some shoot and root growth)
6000	10 (Good shoot and root growth)	8 (Evidence of trail clearing; insect damage)	10 (Plants fresh and green; some shoot growth; slight root growth)

6000 ft. and at 5200 ft. The light intensity was highest in the open habitats (Table IV), and more food was apparently manufactured than in the deciduous and in the evergreen forests where the light intensity was low. Moisture relations were more favorable at the higher altitudes (Table V). The soils ranged in pH from 4.0 to 5.6, and organic matter content varied greatly (Table IV), but any influence these factors might have had was obscured by the stronger limitations imposed by light and moisture deficiencies.

The cuttings which remained in the greenhouse grew more than those which were transplanted to the mountain habitats. The average shoot and root weight (based on the dry weights) of the greenhouse-reared cuttings was 1.15 and 0.4 grams, respectively, with a shoot-root ratio of 2.84. A comparison of the shoot-root ratios between the cuttings which grew in the greenhouse and those transplanted to different types of habitats and at different altitudes in the Great Smoky Mountains is shown graphically in Figures 4, 5, and 6.

Although there were consistent slight differences in the shoot-root ratios of Japanese honeysuckle transplants in the different types of habitats and at different altitudes in the Great Smoky Mountains, the differences were not statistically significant. The greatest contrast occurred between greenhouse-reared cuttings and the mountain transplants.

Community Relationships

Japanese honeysuckle is a pioneer plant in southeastern United States in that it can spread rapidly onto bare areas by layering.

TABLE IV

ANALYSIS OF HABITAT DIFFERENCES IN RELATION TO SHOOT AND ROOT GROWTH OF JAPANESE HONEYSUCKLE CUTTINGS AT DIFFERENT ALTITUDES AND IN DIFFERENT TYPES OF HABITATS IN THE GREAT SMOKY MOUNTAINS DURING AUGUST, SEPTEMBER, AND OCTOBER 1952

Altitude in Ft.	Soil Temperature (F.) Aug. 14	Light Intensity in f. c. Aug. 14	pH	Organic Matter, Weight Per Cent	Soil Moisture, Weight Per Cent Oct. 30	Average Shoot Weight in Grams	Average Root Weight in Grams	Average Shoot-Root Ratios
				OPEN HABITAT				
1500	61	6000	5.3	8.6	7.9	0.19	0.11	1.7
3500	60	6500	4.7	6.7	8.2	----	----	----
5200	61	6000	5.3	2.9	6.1	0.48	0.35	1.4
6000	57	9000	4.4	1.8	6.0	0.63	0.42	1.5
				DECIDUOUS FOREST				
1500	61	250	4.6	15.2	14.7	0.29	0.19	1.5
3500	58	460	4.5	78.7	93.6	0.19	0.13	1.5
5200	53	800	4.6	24.2	44.7	0.27	0.12	2.3
6000	53	410	4.0	65.2	131.8	0.38	0.11	3.5

TABLE IV

ANALYSIS OF HABITAT DIFFERENCES IN RELATION TO SHOOT AND ROOT GROWTH OF JAPANESE HONEYSUCKLE CUTTINGS AT DIFFERENT ALTITUDES AND IN DIFFERENT TYPES OF HABITATS IN THE GREAT SMOKY MOUNTAINS DURING AUGUST, SEPTEMBER, AND OCTOBER 1952 (CONCLUDED)

Altitude in Ft.	Soil Temperature (F.) Aug. 14	Light Intensity in f. c. Aug. 14	pH	Organic Matter, Weight Per Cent	Soil Moisture, Weight Per Cent Oct. 30	Average Shoot Weight in Grams	Average Root Weight in Grams	Average Shoot-Root Ratios
				EVERGREEN FOREST				
1500	61	125	5.6	20.7	27.2	0.25	0.14	1.8
3500	58	125	4.0	84.0	136.7	0.25	0.12	2.1
3500	58	40	4.0	84.0	136.7	—	—	—
5200	50	650	4.2	88.7	141.7	0.33	0.20	1.7
6000	50	500	4.3	34.4	64.8	0.33	0.13	2.5

TABLE V

VARIATIONS IN THE GREAT SMOKY MOUNTAINS IN TEMPERATURE, PRECIPITATION, AND EFFECTIVENESS OF MOISTURE WITH ALTITUDE DURING AUGUST, SEPTEMBER, AND OCTOBER (AVERAGES COMPUTED FROM DATA COMPILED BY R. E. SHANKS)

	1460'	3800'	5200'	6000'
Mean temperature (F.)	65.5	60.4	57.7	54.8
Mean precipitation in inches (5 year period)	4.40	5.61	5.99	7.99
Mean precipitation in inches (25 year period)	3.87	—	—	6.29
Heat index	7.34	5.04	4.71	4.02
P-E in inches	3.37	2.84	2.86	2.71
Potential evapo-transpiration in inches	32.22	26.58	24.03	21.04

Certain herbs such as Solanum carolinense L., Asclepias tuberosa L., Sorgum halepense (L.), Pers., Sonchus oleraceus L., Ambrosia artemisiifolia L., A. trifida L., Daucus carota L., Melilotus alba Desr., and Erigeron spp. are also frequent pioneers on the same sites as honeysuckle. Liriodendron tulipifera L., Sassafras albidum (Nutt.) Nees, Rhus typhina L., Rubus occidentalis L., and Campsis radicans (L.) Seem. are the more common pioneer woody species which invade road-cuts and abandoned fields at approximately the same time as honeysuckle.

Seedlings of honeysuckle are pioneers in crevices of stone walls (Figure 7) and of rocks, especially limestone. In such habitats colonization by honeysuckle may be slow, due to extremely variable moisture and soil conditions. As the roots of the honeysuckle penetrate deeper, more water percolates through the crevices and the chemical processes of oxidation, hydration, and carbonation are accelerated. Soil moisture conditions improve with the development of shade and the gradual accumulation of organic material.

Seedlings of honeysuckle are also pioneers on road-cuts, in abandoned fields, along fences, in openings of woodlots, and in other disturbed areas to which birds transport seeds, provided there is sufficient moisture for germination and survival.

Honeysuckle remains on roadside banks, where it is sometimes planted to control erosion, and does not invade woodlands along the northern fringe of its geographic range. There portions of the stems frequently freeze back, and thus colonies of honeysuckle do not spread so widely as they do southward.

In the southeastern United States there are relatively few deciduous and pine woodlots with entirely closed canopies. Openings of various sizes often exist, due either to recent cutting of the trees or to the falling of old trees during wind storms. Certain herbs such as *Carex* spp., *Panicum* spp., *Solidago* spp., *Aster* spp., *Prunella vulgaris* L., as well as most of the herbaceous pioneers mentioned previously, frequently invade these well-lighted openings soon after disturbance. Japanese honeysuckle and other lianas as *Parthenocissus quinquefolia* (L.) Planch., *Rhus radicans* L., *Vitis labrusca* L., *Clematis virginiana* L., *Smilax rotundifolia* L., and *S. glauca* Walt. invade woodlots at approximately the same time or soon after the herbaceous species. Honeysuckle invades practically any opening where there is sufficient moisture. Seeds of honeysuckle may germinate, or the vine may spread into the openings by layering. Seedlings of many of the shrubs and trees become established more slowly than honeysuckle.

The growth of honeysuckle shoots is initiated before deciduous trees produce leaves. Stem elongation is rapid, and the vine climbs upon any tree which is readily available, sometimes to a height of twenty feet (Figure 8). Honeysuckle often climbs upon slender saplings and eventually bends them to the ground. The leaves of these saplings thus are placed under unfavorable light conditions, and some saplings die.

In some cases bark and xylem grow out over spirals of honeysuckle stems (Figure 9), which twine about the trunks and branches of trees. Individuals of the following species, *Prunus persica* (L.) Batsch, *P. serotina* Ehrh., *Ailanthus altissima* (Mill.) Swingle, *Acer rubrum* L.,

Cornus florida L., and Robinia pseudo-acacia L. have been noted as completely dead (Figure 10), or with some dead branches. Swollen areas of the host stem were observed above the constricting honeysuckle stems. Death or impaired growth of the trees was undoubtedly related to interruption of the translocation of food to the roots.

In some secondary deciduous and pine woodlots in southeastern United States, Japanese honeysuckle contributes to the groundcover, with a coverage ranging from 10 to 65 per cent. It is often abundant in areas where there is no canopy and in partially shaded areas, especially where there is little competition from other plants. Moisture conditions improve, and honeysuckle contributes shade under which shade tolerant tree seedlings can grow, especially in the drier types of woodlands. Honeysuckle is abundant during the shrub and small tree stages of secondary succession. Less honeysuckle is present as the canopy begins to close, and light intensity at ground level decreases. Japanese honeysuckle does not grow well as the forest approaches climax conditions. It has not been observed as a groundcover in portions of woodlands where mature trees are growing close together. No Japanese honeysuckle is present in certain mature oak-hickory, oak-chestnut, and pine forests in southeastern United States.

In the Piedmont, North Carolina, Japanese honeysuckle is long persistent in secondary succession, in bottomland pine forests and in river bottom forests of river birch, ash, elm, and sycamore (Oosting 1942). Table VI is a comparison of the density and frequency of Japanese honeysuckle in pine forests and in river birch forests of different ages.

TABLE VI

DENSITY AND FREQUENCY OF JAPANESE HONEYSUCKLE IN THE PIEDMONT, NORTH CAROLINA (DATA COMPILED FROM TABLES 4, 5, 9, AND 23, OOSTING 1942)

Forest Type	Age of Stand in Years	Density	Frequency in Per Cent
Pine	15	116.3	80
Pine	18	383.1	70
Pine	22	104.4	40
Pine	31	46.4	20
Pine	34	229.4	80
Pine	45	475.6	90
Pine	90	—	—
River birch	6	14.5	20
River birch	14	667.2	90
River birch	36	696.9	100
Postclimax	—	156.8	50

The vine is present in practically every age class in these two forest types. In some of the sycamore forests, ash and elm saplings grew more rapidly than honeysuckle and became dominant in the understory.

Oosting (1942) has observed honeysuckle in seven out of eleven primary bottomland habitats in the Piedmont, North Carolina. The invasion of honeysuckle on flood plains is much later in succession than that on secondary sites and occurs as the dominant trees approach maturity. *Salix nigra* Marsh. was the dominant tree in five of these communities, with a range in age between forty-five and fifty-two years. River birch and elm, respectively, were the dominants in the other two communities which honeysuckle had invaded. The understory was composed of various combinations of elm, ash, sycamore, red maple, red gum, persimmon, red mulberry, and flowering dogwood. Shrubs and lianas were the same species as those which had invaded secondary bottomland communities. Herbaceous species were rare, possibly due to the enormous masses of honeysuckle.

Honeysuckle seldom invades low delta areas in Mississippi; however, it is abundant on the banks of drainage ditches where the soil material is piled up several feet above the ditches.

Lonicera japonica usually occurs along country roadsides in Japan in relatively moist sites and is sometimes twined about shrubs and bamboo-grass. The vine cannot compete successfully with cultivated crop plants. It does not become a pest on continuously cultivated lands, and it has not been reported to be a pest in Japan.

Nature of Range Limits

In Massachusetts and in portions of New York, the tops of Japanese honeysuckle freeze back nearly every winter. The tops also freeze occasionally (approximately once in four years) in portions of Pennsylvania, Ohio, Indiana, Illinois, Michigan, and Wisconsin. The growing season ranges from 135 to 171 days at the stations where the tops freeze (Table VII), and Japanese honeysuckle is not a pest under these conditions. A few escapes have been recorded (Figure 11) near the approximate climatic limits of honeysuckle. The growing season is longer (ranging from 217 to 301 days), and honeysuckle rarely freezes at stations where it is a pest (Table II). It has become a pest in certain states due to the length of the growing season and the infrequent freezing back of the shoots.

Japanese honeysuckle is not recorded as an escape in south-central Florida and southward in the sub-tropical portion of Florida. There are many marshes, swamps, bogs, ponds, and lakes in the flat areas along the coast. The flatwoods are poorly drained and the water table is near the surface. Conditions are edaphically unfavorable for seed germination and seedling establishment over much of that area, and it is probable that climatic conditions are unfavorable to the breaking of seed dormancy.

Japanese honeysuckle is used as an ornamental in sections of Iowa and Oklahoma; however, it does not escape into the prairie. Very few shrubs invade the prairie, since the soil is occupied with fibrous roots of grasses and forbs. The native prairie plants utilize the water in the

TABLE VII

LENGTH OF GROWING SEASON AND MINIMUM TEMPERATURES AT STATIONS WHERE THE TOPS OF JAPANESE HONEYSUCKLE FREEZE

State	County	Station	Length of Growing Season in Days	Minimum Temperature (F.)
Massachusetts	Plymouth	Middleboro	135	-26
New York	Chemung	Elmira	153	-24
Pennsylvania	Westmoreland	Derry	146	-29
Ohio	Wayne	Wooster	152	-24
Indiana	Tippecanoe	Lafayette	168	-33
Illinois	Douglas	Tuscola	168	-25
Michigan[a]	Ingham	Lansing	158	-26
Wisconsin[a]	Dane	Madison	171	-29

[a]Japanese honeysuckle does not escape from cultivation in these two states.

first six inches of soil, and seedlings of invaders rarely become established (Weaver 1954).

Japanese honeysuckle is sparsely distributed in Texas and occurs chiefly along river bottoms in the eastern quarter of the state. L. H. Shinners reported in correspondence that honeysuckle does not invade woodlands in Texas unless there has been severe disturbance by man or by livestock. It sometimes becomes a pest locally and has been reported as such near Houston. It is widely cultivated in Dallas and seldom escapes, possibly due to the high average temperatures during June, July, and August (82.8° F.) and the summer drought. A large portion of the residential area of Dallas is built on heavy prairie clay soil, and honeysuckle does not grow well on this type of soil.

Sometimes Japanese honeysuckle escapes in southern California (Keck 1926) and in other irrigated states, but it has not become a pest under irrigation. Seeds might occasionally germinate in a favorable habitat, but the root system of seedlings would not be well-developed by the end of the first growing season due to the seasonal shortage of rainfall, and death by desiccation would result.

ECOLOGICAL LIFE-HISTORY

Seed Stage

Dispersal

The fruit of Japanese honeysuckle is a black or purple subglobose berry. In a sample of 200 fruits from Pennsylvania, the seeds ranged from one to sixteen per berry with an average of 5.9 ± 0.4. (The $\pm$ symbol refers to the standard error in this manuscript.)

Wild turkeys, bobwhites, mockingbirds, white-throated sparrows, white-crowned sparrows, slate-colored juncos, robins, purple finches, goldfinches, bluebirds, pine grosbeaks, and hermit thrushes eat the fruit of Japanese honeysuckle (Martin, *et al*. 1951; Handley 1945). House finches have been observed eating the fruit of honeysuckle in California. Food records at the Patuxent Research Refuge show that 0.5 per cent of the food in the stomachs of 114 robins, captured between December and February, was Japanese honeysuckle fruit (Handley 1945). Workers at the Patuxent Research Refuge mentioned that bobwhites and other gallinaceous birds utilize the pulp of Japanese honeysuckle fruit, and the seeds pass through the digestive tract and are excreted.

Evidence indicates that Japanese honeysuckle seeds are widely dispersed by birds. H. M. Butterfield, Department of Agriculture, University of California, stated in correspondence that he has often found honeysuckle seedlings in his garden and that the seeds were scattered by birds. C. A. Brown, Louisiana State University, reported in correspondence that he did not observe Japanese honeysuckle in his shrub border until

birds had come to his house which was built in an open field. Only a few mammals, such as cottontail rabbits and wood rats in California, eat the fruit of Japanese honeysuckle (Martin, et al. 1951), and some seeds may be dispersed by them. Japanese honeysuckle is widely distributed in the United States, and it would be difficult to explain its rapid extension into new areas if birds did not disseminate the seeds. The fruit which is not eaten by animals usually remains on the vines and falls during the spring months after the pedicels decay.

Dormancy

Seven species of *Lonicera* (not including *L. japonica*), upon which germination data have been reported, all had either dormant embryos or impermeable seed coats or both (U. S. Forest Service 1948).

Two lots of seed from the same parent plant were checked for permeability to water. The first lot, checked soon after extraction in December 1952, gained 44 per cent in weight during the first two hours of soaking in water, and an additional 8 per cent during the next two hours, after which no further increase in weight occurred. The second lot had been stored four months in stoppered bottles at approximately 70° F., before they were checked in April 1955. This second lot gained 26 per cent in weight during the first two hours of soaking, and attained a maximum increase of 47 per cent by 38 hours. Thus it appears likely that seeds of Japanese honeysuckle do not have impervious seed coats.

In many species of *Lonicera*, the embryo enters a period of dormancy immediately following its formation. Dormancy may be broken, according to the United States Forest Service (1948), by stratification of

seeds in a moist medium in a refrigerator at approximately 41° F. for sixty days. Fifteen hundred Japanese honeysuckle seeds were stored in moist sphagnum in a refrigerator in a temperature range between 43 and 46° F. Some of these stratified seeds, removed from the refrigerator after thirty and forty-five days, respectively, did not germinate when placed on moist filter paper in Petri dishes in a temperature range between 60 and 75° F. Neither did they germinate when planted in soil in the same temperature range. Seeds which were stored dry in stoppered bottles for thirty days and forty-five days, respectively, did not germinate either. While the seeds were under refrigeration, 30 per cent of the hypocotyls had emerged from the seed coats. Thus dormancy of the stratified seeds was broken by the end of sixty days.

Dormancy may be broken in the soil without previous stratification of seeds in the refrigerator. Japanese honeysuckle seeds, previously stored dry in stoppered bottles for thirty days at approximately 70° F., were planted at a depth of 4 mm. in soil near the greenhouse on January 3, 1953. The air temperature ranged from near freezing when the seeds were planted to the fifties when the first germination was observed, and to the sixties in April, with extreme values of 26 and 84° F. The soil temperature ranged between 38 and 60° F. during January and February. The average monthly precipitation from January 1 to April 30 was 4.9 inches. The earliest germination in the field was observed on March 3. The peak of germination near the greenhouse occurred between March 26 and March 31; the latest germination in the field was observed on April 20. Evidently germination in nature normally occurs in the spring

following the dispersal of the seeds, as in other species of Lonicera (U. S. Forest Service 1948).

Seedling Stage

Germination

Several types of planting media were used in the germination trials in the greenhouse. Sterilized soil, made up of seven parts of clay to three parts of sand, with added organic matter and added 4-12-4 fertilizer (one teaspoon per quart of soil mixture), was used in most of the flats. Fine sand was used in one lot and sphagnum in another. Four hundred seeds made up each lot, and all seeds were planted at a depth of 4 mm. Seeds previously stratified for sixty days in moist sphagnum and in sand, respectively, were planted in flats in the greenhouse on March 5, 1953. The seeds planted near the greenhouse on January 3, 1953, and those planted in the field at Upland on January 3, 1954, were not stratified in the refrigerator before planting.

Seeds of Japanese honeysuckle germinated well in the greenhouse March 8-April 8, 1953. The nocturnal soil temperatures ranged between 45 and 60° F., and the diurnal soil temperatures ranged between 60 and 75° F. during this same period. Honeysuckle seeds germinated well in the field at Upland, March 6-April 15, 1954. The minimum soil temperature during the period between planting of the seeds and germination was 36° F., and the maximum was 71° F. One lot of 400 seeds, previously stratified for four months in a refrigerator in a temperature range between 30

and 35° F., was planted in a flat and kept under a constant temperature of 77° F. Open pans of water were placed in the oven to keep the atmosphere moist. Only 2 per cent of this lot germinated. A constant temperature of 77° F. may be unfavorable to germination in Japanese honeysuckle. The Boyce Thompson Institute for Plant Research reported in correspondence that no germination occurred in *Lonicera tatarica* L. at a constant temperature of 77° F., but the seeds germinated well at a daily alternating temperature of 59 to 77° F.

A series of germination trials is reported in Table VIII. The highest percentage of germination (63 per cent) occurred in seeds of Lot 1. This was significantly different at the 1 per cent level from the percentage of germination (53 per cent) of Lot 7. The differences in the percentages of germination of Lots 1 and 7 may have been due to the different planting media used (Table VIII). Germination percentages of 55 and 10 per cent, respectively, occurred in seeds of Lots 2 and 3. These were significantly different at the 1 per cent level. Sterilized soil was used in Lot 2 and fine sand in Lot 3. The low germination percentage in Lot 3 was attributed to low moisture retention of the sand. Germination percentages of 55 and 1 per cent, respectively, occurred in seeds of Lots 2 (planted in sterilized soil) and 4 (planted in sphagnum). These were significantly different at the 1 per cent level. Blue-green molds covered the sphagnum several days after the seeds were planted. As the sphagnum was poorly aerated, the lack of oxygen may have inhibited the growth of seedlings beyond the emergence of the hypocotyl. The differences between percentages of germination in Lots 2 and 5, which were

TABLE VIII

GERMINATION OF SEEDS UNDER DIFFERENT TREATMENTS, MARCH 8-APRIL 8, 1953, EACH PERCENTAGE BASED ON FOUR HUNDRED SEEDS; GERMINATION COUNT TAKEN AT THE END OF FOUR WEEKS

Lot Number	Stratification Treatment in Days	Stratification Medium	Storage Temperature of Seeds (F.)	Planting Medium	Location	Per Cent Germination
1.	None	None	38-60 Planted Jan. 3; soil temperature	Stony clay fill	Near U. T. greenhouse	63
2.	Sixty	Moist sphagnum	43-46	Sterilized soil	Flats in greenhouse	55
3.	Sixty	Moist sphagnum	43-46	Sand	Flats in greenhouse	10
4.	Sixty	Moist sphagnum	43-46	Moist sphagnum	Flats in greenhouse	1
5.	Sixty	Sand	43-46	Sterilized soil	Flats in greenhouse	43
6.	Sixty; scarification	Sand; sandpaper	43-46	Sterilized soil	Flats in greenhouse	20
7.	None	None	36-71 Planted Jan. 3; soil temperature	Noncalcic brown soil	Near Upland College (1954)	53

55 and 43 per cent, respectively, were significant at the 1 per cent level. Moist sphagnum used in Lot 2 was apparently a better stratification medium than sand. Germination percentages of 43 and 20 per cent, respectively, occurred in seeds of Lots 5 and 6. These were significantly different at the 1 per cent level. Some of the embryos may have been injured by scarification of the seeds in Lot 6.

Stages in the germination of Japanese honeysuckle are illustrated in Figure 12. Observable germination begins with the emergence of the hypocotyl from the seed coat and is epigeous. The cotyledons are pulled upward through the soil by the extension of the hypocotyl. The primary root is approximately 2 or 3 cm. long at the time when the seed coat drops off the expanded cotyledons. The seed coat sticks to the cotyledons for several days before it is shed; in some cases the seed coats remain on the cotyledons, and the seedlings are "coatbound."

Establishment

A seedling becomes established as soon as the food reserve in the seed has been utilized and the process of photosynthesis has begun (Pelton 1953). The small amount of endosperm tissue in the seed of Japanese honeysuckle has disappeared by the time the cotyledons are expanded. The time from germination to establishment is short in this species. The cotyledons are green at the time of expansion, and thus food manufacture may begin in them.

A record was kept of some of the changes which occur in Japanese honeysuckle seedlings during the first two months. The median dates of

the developmental events have been recorded in Table IX. The plumule was observed five days after the cotyledons had expanded, and the first pair of leaves above the cotyledons was seen three days later. The decussate arrangement of the leaves could be observed in seedlings (Figure 13); this is not always evident in older plants. The seedling leaves were entire; no lobing was observed during the first season. The first branch was observed at the age of six weeks.

Seedlings died from various causes during the period of observation which followed germination. About 3 per cent of the seedlings which germinated in the greenhouse became chlorotic and died; 2 per cent were coatbound; 5 per cent died after they were not watered for four days, and a few of the seedlings were attacked by damping-off fungi soon after germination. The seedlings which grew in the field were not chlorotic. Two per cent of these seedlings did not become established due to defoliation of the cotyledons and leaves by insect larvae. Approximately 50 per cent of honeysuckle plants which grew in the field were used for various measurements, and 30 per cent died from drought during the first year. Approximately 18 per cent were still alive at the age of seventeen months when this phase of the observations was terminated and the plants destroyed.

<u>Development of the Seedling</u>

The development of the shoot is more rapid than that of the root during the early stages (Figure 12). The average shoot and root lengths of seedlings of different ages, after growth under different light conditions, are indicated in Table X. The average shoot-root ratios, based

TABLE IX

PHENOLOGY OF GERMINATION AND DEVELOPMENT OF SEEDLINGS OF LOT 2; MEDIAN DATES OF THE DEVELOPMENTAL EVENTS

Year	Month	Day	Event
1952	Nov.	11	Fruit collected in Pennsylvania; seeds extracted and stored in stoppered bottles at 70° F.
1953	Jan.	3	Seeds stratified in moist sphagnum; stored sixty days at a temperature of 43-46° F.
1953	Mar.	5	Dormancy broken; emergence of hypocotyl from 30% of seeds stratified in moist sphagnum
1953	Mar.	5	Seeds planted in sterilized soil in the greenhouse at a depth of 4 mm.
1953	Mar.	15	Cotyledons observed; seed coat attached to end of cotyledons
1953	Mar.	17	Seed coats dropped off; cotyledons dark green; root tip brown
1953	Mar.	19	Observed seedlings 3 mm. in length bend toward the light
1953	Mar.	20	Plumule observed
1953	Mar.	23	First leaves above the cotyledons expanded
1953	Mar.	30	Second pair of leaves above the cotyledons expanded
1953	Mar.- April	23 4	Peak of germination
1953	April	10	Third pair of leaves above the cotyledons

TABLE IX

PHENOLOGY OF GERMINATION AND DEVELOPMENT OF SEEDLINGS OF LOT 2; MEDIAN DATES OF THE DEVELOPMENTAL EVENTS (CONCLUDED)

Year	Month	Day	Event
1953	April	16	Fourth pair of leaves above the cotyledons
1953	April	25	First branch observed; branch was in the axil of one of the cotyledons
1953	April	27	Last observed germination of seeds stratified sixty days in moist sphagnum
1953	April	27	Cotyledons withered
1953	April	29	Cotyledons dropped off
1953	April	30	Fifth pair of leaves on unbranched seedlings
1953	May	12	Seedlings are woody at the base

TABLE X

COMPARISON BETWEEN SHOOT AND ROOT IN SEEDLINGS OF DIFFERENT AGES, AFTER GROWTH UNDER DIFFERENT LIGHT CONDITIONS; TEN PLANTS USED IN EACH GROUP

	Age in Days	Average Number Leaves	Average Shoot Length in cm.	Average Root Length in cm.	Average Shoot Weight in mg. (Dry)	Average Root Weight in mg. (Dry)	Average S/R Ratios
Greenhouse	25	4	3.0	2.0	18.3	6.6	2.8
Full sun	52	8	6.2	9.1	37.0	10.1	3.7
25% of full sun	52	10	9.7	7.7	41.1	6.4	6.4
5% of full sun	52	10	10.6	6.8	32.8	5.2	6.3

on the dry weight, are also indicated. They vary from 2.8 in 25-day-old greenhouse-reared seedlings to 6.4 in 52-day-old seedlings in 25 per cent of full sun. The appearance of the shoot and root of five-month-old seedlings is illustrated in Figure 14.

A series of seedlings was reared in a sandy loam with added organic matter and added commercial fertilizer, and another series in fine sand. The shoots of the plants in the sandy loam averaged 30 cm. in length at the age of five months, and those in fine sand averaged only 9 cm. The seedlings which were reared in the sandy loam had more branches and leaves than those which grew in fine sand. Comparative growth of seedlings from each series is illustrated in Figure 15.

A study of seedling survival under southern California climatic conditions was initiated at Upland on December 23, 1953. Fifty seeds were planted in each of two plots at a depth of 5 mm. Ten Japanese honeysuckle seedlings became established in these two plots by April 10. By May 25 the last of the seedlings had died from drought. These observations are consistent with the previous inference that Japanese honeysuckle seedlings would not survive the first growing season near Upland except under irrigation.

Mature Stage

Characteristics of the Shoot

Japanese honeysuckle is either a slender, woody, high-twining perennial or a trailing shrub with densely-tangled pubescent stems generally reddish brown in color. The young branches are herbaceous but

become woody later. The outer bark of woody stems is light brown and corky with scattered hairs. The bark on older stems is shredded and peels off readily. Annual rings are prominent, and the maximum age of stems noted by the author was twelve years. Food is stored in the outer cells of the pith cylinder (Mayberry 1935). The pith in young stems is composed of large cells with very thin walls. The thin walls soon break down, and no pith is present in mature stems.

F. B. Kulfinski, graduate student of Iowa State College, reported in correspondence that he had observed a relationship between the early-season growth of Japanese honeysuckle and the temperature when growth began. By the insertion of maximum-minimum thermometers in the litter layer of a 30-year-old red maple forest in Piscatawaytown, New Jersey, he observed that the range in temperature was between 34 and 48° F. when stem elongation began during the second week in March. He also reported that the period of stem growth in east central New Jersey during 1951 was 124 days. During this period the length of stems in five honeysuckle vines ranged from 16 to 160 cm., with an average stem elongation of 75±8.1 cm.

The length of stems attained in fifteen well-rooted potted cuttings during a five-month period of greenhouse culture ranged from 105 to 226 cm., and the average growth in length was 163±6.5 cm. The diameter of the stems ranged from 1.5 to 3.0 mm., averaging 2.0±0.08. The average dry weight per stem was 3.9±0.3 grams. The average number of leaves per stem was 57.3±3.9, with an average dry weight of 1.7±0.2 grams. The average number of branches per stem was 2.0±0.6. Apical dominance of the terminal

bud was pronounced, and branches were few unless the terminal bud had been cut off. The length of the branches ranged from 2 to 60 cm., averaging 12±4 cm., with an average number of leaves per branch of 19±8.

The buds of Japanese honeysuckle are dormant during the dry season in southern California. New growth begins approximately two weeks after the first torrential precipitation, and consequently the time when growth is initiated at Upland may vary from November until February. There was little growth in Tennessee in 1952 from July until December. New growth began during the middle of January in 1953 and was observed periodically after rainy days and warm temperatures. The first new shoots which are produced in spring have lobed leaves. The leaves which expand later in the season are entire.

The leathery leaves of mature Japanese honeysuckles are evergreen where the vine grows as a groundcover in lowland sites as far north as Connecticut, Rhode Island, and Ohio; the leaves remain on the vines only until the end of January in the less protected habitats northward. The leaves of honeysuckle are partially evergreen in Kansas but are usually shed by the end of January. In southern California many honeysuckle leaves became yellow during months of drought and were shed during October and November in 1953. No such seasonal pattern of leaf-fall was observed in the southeast, and the vine is generally evergreen from Maryland southward.

There is much variation in the size, shape, and weight of leaves which grow in different habitats. The leaves occurring on colonies in

full sunlight are shorter in length and narrower, as well as thicker and heavier, than the ones on portions of plants which are heavily shaded. The following averages are based on 100 leaves in each group. The average leaf surface of full sun leaves is 7.8 ± 0.7 cm.^{2} while that of shade leaves is 10.7 ± 0.6 cm.^{2}. The average dry weights of a sun and a shade leaf are 0.063 and 0.031 grams, respectively.

The upper epidermis is heavily cutinized on mature sun and shade leaves. There are no stomates on the upper epidermis. The average number of stomates per mm.^{2} of leaf surface on the lower epidermis of sun leaves is 404 ± 34, while the average number on shade leaves is 226 ± 32. Mayberry (1935) recorded an average of 204 stomates per mm.^{2} of leaf surface; he did not state whether he observed sun or shade leaves.

Using a modification of the technique described by Loomis and Shull (1937), certain average rates of transpiration in Japanese honeysuckle were determined at Upland. A 12 per cent cobalt chloride solution was used. Samples were secured from 7:30 A. M. until 5:30 P. M. from March 18 to April 8, 1955, in a temperature range between 58 and 85° F. They were obtained from well-watered plants in full sun, from plants in full sun which had not been watered for four days, and from well-watered plants in the shade. One hundred thirty samples were secured from the upper surface of the leaf and 330 samples from the lower surface.

The average rate of transpiration from the upper surface of the leaf was 0.051 ± 0.013 grams of water/hr./dm.^{2}, with an average rate from the lower surface of 1.649 ± 0.536 grams of water/hr./dm.^{2}. Curtis and

Clark (1950) state that transpiration rates of 1 to 2 grams of water/hr./$dm.^2$ of leaf area (one surface) would be high for most plants. The rate of transpiration from the upper surface per average honeysuckle leaf (9 $cm.^2$ on one surface) was 0.459 grams of water/hr., with a rate from the lower surface of 14.841 grams of water/hr.

The transpiration rate was also determined in August 1953 by the cut-twig method (Lilly 1951). The results were quite variable, but the average rate from seven samples was 15.8 grams of water/hr./leaf, as compared to 15.3 grams of water/hr./leaf by the cobalt chloride method.

In an effort to determine the rate of photosynthesis under field conditions, certain measurements were made according to a modification of the matched-leaf method of Denny (1930). A preliminary run using sets of 125 matched leaves from cuttings in each of two different light intensities was made to establish procedure and variability.

A photosynthesis measurement was made on July 27, 1953, at Knoxville, using four five-month-old potted honeysuckle plants under each of two different light intensities: full sun and 25 per cent of full sun. (The Weston Illumination Meter, Model 603, was used to determine the different light intensities wherever such measurements were made.) The samples in this case consisted of 240 matched pairs of leaves from each light intensity. At 5:30 A. M. sixty leaves were cut off from each plant and oven-dried for twenty-four hours. At 3:30 P. M. the matching leaves were cut and similarly oven-dried. Dry weight differences between morning and afternoon sets provided a basis for estimates of dry weight increase during the day, and this was regarded as an approximate measure of apparent

photosynthesis. Corrections for loss in weight due to respiration and translocation were not made. Dry weight increase was 8.3±1.2 per cent in full sun (C=30 per cent; the symbol C refers to the coefficient of variation when used in this manuscript) and 6.5±1.8 per cent in 25 per cent of full sun (C=55 per cent).

Cuttings were used in a second photosynthesis measurement on August 10, 1953. The same procedure was used which had been established in preliminary measurements. The cuttings were placed under each of three different light intensities: full sun, 25 per cent of full sun, and 5 per cent of full sun. The samples consisted of 125 matched pairs of leaves from each light intensity. Dry weight increase was 10.2±0.9 per cent in full sun (C=22 per cent), 6.5±2.3 per cent in 25 per cent of full sun (C=24 per cent), and 2.9±2.0 per cent in 5 per cent of full sun (C=167 per cent).

A third photosynthesis measurement was determined on March 31, 1955, near Upland College. The same procedure was followed as before, but intact plants were used instead of cuttings. One colony grew in full sun, while the other one was in a shaded habitat in a light intensity averaging 25 per cent of full sun. The samples consisted of 125 matched pairs of leaves. Dry weight increase was 9.9±1.2 per cent in full sun (C=27 per cent) and 7.9±1.6 per cent in 25 per cent of full sun (C=20 per cent).

Dry weight increases in the three photosynthesis measurements showed satisfactory agreement both in full sun and in 25 per cent of full sun. Dry weight differences between full sun and 5 per cent of full sun

were significant at the 5 per cent level, but the differences between full sun and 25 per cent of full sun were not statistically significant. Degree of reduction of photosynthesis by shading is generally consistent in the three measurements.

To provide a series of uniform plants for further study, fifty rooted Japanese honeysuckle cuttings were transferred to "vita band" pots. Ten of them were planted in each of five plots near the greenhouse. Shelters covered with different numbers of layers of cheesecloth were placed over four of the plots (Figure 16). The light intensities did not remain uniform and were reduced approximately 5 per cent under each shelter by the end of 100 days, due to dirt which collected in the cheesecloth. The cuttings remained in the soil 160 days. Comparative growth under different light intensities is illustrated in Figure 17. The number of plants surviving under each light intensity, the average height per plant, and the average shoot-root ratio are indicated in Table XI. The maximum length of shoots occurred in plants which grew under 25 per cent of full sun and the minimum under 5 per cent of full sun. Shade plants are characteristically taller than those of the same species in full sun, unless the light intensity is so low that little food is made. Plants which develop in partial shade typically have a higher shoot-root ratio than those of the same species in full sun (Meyer and Anderson 1952). The average shoot-root ratio of cuttings which grew in 25 per cent of full sun was 6.3, with an average of 3.4 in full sun.

The average dry weight of both shoot and root from each light

TABLE XI

COMPARISON OF RESULTS OBTAINED WHEN TEN ROOTED CUTTINGS WERE REARED OUT-OF-DOORS 160 DAYS (OCTOBER 19, 1952-APRIL 7, 1953) UNDER EACH DIFFERENT LIGHT INTENSITY

	Percentage of Full Sun				
	100	50	25	10	5
	Numbers of Layers of Cheesecloth				
	0	2	4	14	22
Number of plants surviving	7	8	8	5	1
Average number of nodes per plant	33.1	20.0	24.1	4.4	—
Average length in millimeters of the two longest internodes	62.8	55.2	70.7	1.9	—
Average height in centimeters	35.8	40.0	50.7	16.2	—
Average ratio of leaf width to length	0.6	0.6	0.78	—	—
Average shoot-root ratio, based on dry weight	3.4	3.0	6.3	4.6	4

intensity is indicated in Table XII. The shoot and root weights under full sun, 25 per cent of full sun, and 5 per cent of full sun were consistent with the results obtained in the photosynthesis measurements. The greatest apparent photosynthesis occurred in full sun, and the cuttings which grew in full sun weighed the most. Apparent photosynthesis in 5 per cent of full sun was low, and the cuttings did not grow well under this light intensity, as is indicated by the low survival rate.

In order to determine whether the relative length of day and night would affect the growth of Japanese honeysuckle, photoperiodic observations were made from January 3 until April 3, 1953. The length of the light period was increased to a daily total of sixteen hours for part of the plants by adding artificial illumination from 5:00 P. M. until 11:00 P. M. The light period was shortened to nine hours for other plants by covering them with black cloth from 5:00 P. M. until 8:00 A. M. daily. The honeysuckle cuttings were kept in water under long-day and short-day conditions, respectively, and were transferred to pots after roots formed. Seven cuttings were used under each photoperiod. Vegetative growth was more rapid, the internodes grew longer, and the plants were taller under long-day conditions (Figure 18). Bonner and Galston (1952) point out that the internodes of stems do not elongate and that root growth is often less when long-day plants are reared under short-day conditions. The average dry weight of shoot and root was greater under the long-day than under the short-day. The differences in the rate of growth and in the greater dry weight of the plants which grew under long-day conditions are probably the result of differences in total photosynthesis. There

TABLE XII

COMPARISON OF THE AVERAGE DRY WEIGHT OF SHOOTS AND ROOTS (OBTAINED FROM CUTTINGS WHICH GREW UNDER DIFFERENT LIGHT INTENSITIES) WITH THE APPARENT PHOTOSYNTHESIS RESULTS

Per Cent of Sun	Layers of Cheesecloth	Number Plants Surviving	Average Shoot Weight in Grams	Average Root Weight in Grams	Apparent Photosynthesis in Per Cent
100	0	7	1.86±0.20	0.55±0.06	10.2±0.9
50	2	8	1.20±0.31	0.36±0.08	
25	4	8	1.29±0.32	0.20±0.12	6.5±2.3
10	14	5	0.23±0.05	0.05±0.003	
5	22	1	0.2	0.05	2.9±2.0

was little difference between the lots in the average number of nodes per plant (Table XIII).

Characteristics of the Root

The root system of Japanese honeysuckle is usually shallow, typically growing to a depth between 15 and 30 cm. in moist soil. Branch roots may sometimes extend laterally for a distance ranging between 2 and 2.5 m. The extensive root system, which may attain a depth of 1 m. in drier soils, is an important factor in the drought resistance of the species and its survival on certain sites.

The root system of a 17-month-old Japanese honeysuckle plant is illustrated in Figure 19. Eight roots from the same series of honeysuckle plants, which grew near the greenhouse in stony clay-fill soil without definite profile, were excavated according to methods which were used by Weaver (1919). The depth to which these roots penetrated the soil ranged from 15 to 50 cm., averaging 29.8 ± 5.1 cm. The spread of the root ranged from 5 to 25 cm., with an average of 12.1 ± 0.8 cm. The dry weights of the roots ranged from 3.8 to 20.2 grams, averaging 8.5 ± 1.9 grams.

The main branches of the fibrous root system were thick, straw-colored, crooked, and tough. They ranged in diameter from 4 to 10 mm. and tapered toward the tip. The thick branches were covered with cork which could be peeled off. There were many smaller branches 1 mm. or less in diameter. There were also many shorter branches, and they did not follow the regular pattern of branching which characterized the main divisions of the root. Mycorrhiza were not observed in any of the stages

TABLE XIII

COMPARISON OF VEGETATIVE GROWTH IN JAPANESE HONEYSUCKLE UNDER LONG-DAY (16 HOURS) AND SHORT-DAY (9 HOURS); SEVEN PLANTS USED FOR EACH PHOTOPERIOD

	Long-day	Short-day
Average length of the two longest internodes in millimeters	82.70	31.00
Average number of nodes per plant	31.20	32.80
Average length of a plant in centimeters	74.00	26.40
Average shoot weight in grams (dry weight)	1.64	1.03
Average root weight in grams (dry weight)	0.34	0.26
Shoot-root ratio, based on dry weight	4.82	3.96

of root development which were examined.

Vegetative Growth and Colony Formation

Nurserymen often propagate Japanese honeysuckle by the use of firm wood cuttings or of semi-mature shoots of the current season's growth (Sheat 1948). The following section deals with a discussion of vegetative propagation for the most part in which cuttings are used as experimental material. There is no evidence that colonies have escaped from cultivation into new areas solely from the rooting of pieces of stem, especially if the escaped colonies are at a great distance from other honeysuckle colonies. However, vegetative growth is rapid after cuttings have rooted. The writer planted rooted honeysuckle cuttings in a bare area in the field at Upland. After two years individual stems had grown to a length of 3 m. in rocky soil without definite profile. This colony spread widely by layering. Growth of the colony was vigorous, and flowers were produced when the colony was two years old.

During the summer of 1952 herbaceous cuttings were propagated in the greenhouse. The sample size ranged between fifty and sixty in each of the first series of vegetative plantings. The following results were obtained with herbaceous cuttings with three pairs of leaves: 62 per cent rooted in aerated water, 66 per cent in vermiculite, and 69 per cent in sand. Only 12.7 per cent rooted when the leaves were cut off and the terminal bud was left on the cuttings. When two leaves and the terminal bud remained on the cuttings, 40 per cent rooted.

Twenty-five samples were used in each propagation trial in the

second series. Even three-inch pieces of stems with one node each rooted in a moist chamber. Only 17.6 per cent of the herbaceous and 28.0 per cent of the woody stem pieces rooted when the leaves were cut off. Herbaceous cuttings with three pairs of leaves were placed in a moist chamber, with 32 per cent rooting. Woody cuttings with three pairs of leaves cut off were also placed in a moist chamber, with 72 per cent rooting. New leaves grew before roots were formed on some of the cuttings, while the roots were produced before the leaves expanded on others. This growth is evidence that much food is stored in woody stems. A larger percentage of herbaceous cuttings rooted when leaves were left on the cuttings. The leaves may be cut off the woody cuttings, since food is stored in the stem.

Two distinct types of adventitious roots form in Japanese honeysuckle. The one type arises from the pericyclic region and develops from preformed meristematic root initials (Sandison 1934). This type usually arises at nodes, occasionally at internodes. The second type, called wound roots by Eames and MacDaniels (1947), forms at the end of a cutting after callus tissue is produced from meristematic cells in the cambium. Both kinds of adventitious roots were observed in the propagation of cuttings.

The average length of the roots on six-month-old greenhouse-reared cuttings was 47.4 ± 1.9 cm., and the average spread of the roots was 15.2 ± 0.9 cm. The average diameter of the main roots was 2.7 ± 0.3 mm. The average number of main root branches was 6.7 ± 1.1, and the average dry weight of the roots was 2.4 ± 0.2 grams.

Sixteen roots of honeysuckle were planted during 1953, of which 25 per cent produced new shoots. Abundant food is stored in the thick branches of the root in well-established vines. Leasure (1950) mentioned the fact that repeated sprayings are necessary if the root system is to be killed by starvation, since new shoots develop after the above-ground parts have died.

Japanese honeysuckle can spread vegetatively by creeping stems which root freely at the nodes (Figure 20). Extensive low colonies are formed by this method, especially where there is no support upon which honeysuckle can climb. Individual stems of honeysuckle have been observed which attained a length of 10 m. where the vine spread over bare areas by layering. Colonies have also been observed in which growth was poor, but they occurred where environmental conditions were unfavorable, as in heavily shaded habitats or in soils evidently deficient in water or in minerals.

The age of a colony can be approximated by cutting off sections of older stems near the ground and counting the annual rings. The age of twelve stem sections from an old honeysuckle colony near Knoxville ranged between five and twelve years, with a range in the diameter of stems between 1 and 2 cm. Seventeen stem sections from another near-by colony had a range between four and nine years, with a range in the diameter of stems between 1 and 1.5 cm. Andrews (1919) reported a single stem which was 18 cm. in diameter which must have been considerably older than any examined by the writer.

Since the oldest stems do not typically support much of the weight

of the plant, they are not as subject to mechanical damage and breakage as are the stems of tree species. When this circumstance is combined with the abundant layering, the vines have an almost indeterminate life span.

Reproductive Development

Floral Development and Pollination

In eastern United States the flowering period of Japanese honeysuckle may occur from late April to July and occasionally until November (Fernald 1950). There is an abundance of flowers from May until July in Tennessee. The earliest flowers were observed on May 1 in Knoxville and on April 25 in Upland. Flowers have been observed in September in both cities. From these observations and from herbarium records, the length of day during which Japanese honeysuckle blooms ranges between twelve and fifteen hours. No specific length of day appears to be required for flower bud initiation in this species.

The first floral buds were observed approximately one month before the expansion of the flowers. One peduncle which bears two foliaceous bracts is borne in the axil of each leaf of a reproductive branch. The paired, sessile, club-shaped, floral buds are covered with glandular hairs and are above the bracts. The flower buds are green when young. They become lighter in color at maturity and are white just before expansion. The floral buds appear on the current year's growth. The ones nearest the base of the current year's growth expand first. The flowers

continue to bloom at nodes nearer the tip of the branch as the season advances. New vegetative growth may occur at the tip of the branch after floral buds have differentiated. Flower buds have occasionally been observed on this late-season vegetative growth.

Kemp (1924) noted that the flowers opened toward evening, while Steyermark (1940) observed that the expanded flower remained white or rosy-tinted only one day after opening, turned yellow on the second day, and withered by the third day. These two observations were confirmed by the writer. The tube of the corolla did not contain any nectar at the time of the expansion of the flower. Approximately one-half of the length of the corolla tube contained nectar by the time the flower had changed to yellow.

The limb of the corolla is two-lipped and glandular-pubescent on the outside. The tube is about 2 cm. long and is longer than the re-curved lips. The five stamens are attached to the corolla tube. The solitary pistil is usually composed of three carpels; sometimes there are only two. The five sepals are fused with the inferior ovary. The stamens and pistil are exserted, with the stamens usually longer than the pistil at anthesis. The anthers dehisce and are covered with sticky pollen grains soon after the expansion of the flower. The approximate number of pollen grains per anther ranged between 650 and 850 in twenty-five observations. Pollen grains were mounted in white Karo and were from 48 to 50 μ in diameter in polar view. The stigma is glandular-pubescent and appears receptive even after anthers from the same flower have withered.

Cross-pollination occurs in Japanese honeysuckle. The species is pollinated by insects and by hummingbirds. The following insect pollinators were observed near Knoxville: HYMENOPTERA--*Apis mellifera* L., *Bombus* spp., and hornets, and LEPIDOPTERA--a hawkmoth. Two additional pollinating agents were observed in Upland: Anna's hummingbird and DIPTERA--syrphid flies.

Development of Fruit and Seeds

After the corolla tube drops off, the ovary gradually becomes larger until the fruit is mature. The fruit is green and hard during the period of development. The fleshy pulp of the purple or black berry is soft at maturity. Each fruit is about 5 or 6 mm. in diameter. Fruit of the genus *Lonicera* contains saponin and has emetic and cathartic effects (Kearney and Peebles 1951).

Approximately sixty days elapse between the abscission of the corolla and the maturation of the fruit. The fruit ripens during the short-days of September to December. There does not appear to be any definite temperature requirement for the maturation of the berries. The fruit matures in Pennsylvania when the temperatures are relatively cold. It becomes mature in southern California when the days are relatively hot and the nights are relatively cold.

In 1953 eleven flower-bearing branches, from honeysuckle climbing over a fence (Figure 21) near the Cherokee Farm of The University of Tennessee, were measured. The average length of the branches from the base to the tip was 30.6±4.9 cm., with an average diameter per branch of

2.4±0.1 mm. The average number of floral buds per branch was 27.3±5.0, and the average number of large green fruits per branch was 15.4±2.2. In this sample 56 per cent of the flower buds from the eleven branches produced fruit. Forty-one flower-bearing branches, selected from two different colonies, were analyzed in the same manner at Upland. The average length of the flower-bearing branches was 36±3.0 cm., with an average diameter per branch of 1.7±0.06 mm. The average number of flower buds per branch was 22.2±1.3, with an average number of mature fruits per branch of 12.6±0.9. In Upland 57 per cent of the floral buds from the forty-one branches produced mature fruit. This compared favorably with the percentage of fruit which set in the Tennessee colony. A larger percentage of fruit had begun to develop at Upland, but some fruit dropped off before maturity. Japanese honeysuckle blooms profusely in full sun, and fruit production is heavy.

The seeds are dark brown or black at maturity and range in length from 2 to 3 mm. They are ovate or oblong and are concave on the inner surface. The seeds are flattened and have three ridges on the back. The average weight per seed from fruits collected in Pennsylvania was 3.8 mg. in a sample size of 800. Mature seeds upon extraction had a moisture content of 10 per cent.

Not all of the seeds in each mature fruit were potentially capable of germination. One hundred seeds were opened soon after they were extracted from the berries. Approximately 10 per cent of the seeds which were of normal size did not contain embryos; 5 per cent of the smaller seeds did not contain embryos either. The "potential germination

percentage" (D. B. Lawrence, *et al*. 1947) was approximately 85 per cent.

CONTROL

Plants often become serious weeds when introduced into habitats which do not have the natural checks characteristic of their native environment. Japanese honeysuckle is not reported to be a pest in Japan. It became a pest in the United States in the century after its introduction as an ornamental, encountering no serious obstacle to its spread until it approached its climatic limits.

Climatic extremes tend to interfere with the growth of Japanese honeysuckle north of the 30° January isotherm, as previously pointed out, and thus prevent the species from becoming weedy northward. Observations in the Knoxville area indicate that stems and leaves may be killed (Figure 22) by temperatures in a range between 10 and 15° F., if preceded by a warm period with mean temperatures in a range between 60 and 70° F., as occurred in March 1955. Honeysuckle was observed to be resistant to wind damage in storms with velocities up to 100 m. p. h. The flexible stems usually do not break when heavily covered with snow or ice.

Few insect pests have been reported on honeysuckle in the United States; however, several hornworm larvae (Sphingidae) were observed eating the leaves. A hornworm larva was placed in a rearing cage, and the adult was later identified as *Haemorrhagia diffinis* Boisduval (bumblebee hawkmoth). Comstock (1950) mentioned that hornworm larvae of this species feed on bush honeysuckle (*Diervilla*) and on snowberry (*Symphoricarpos*), which are in the same family as Japanese honeysuckle. The hornworm larvae were never observed on honeysuckle in large numbers.

A larva (Hesperiidae) was seen in a folded leaf of Lonicera japonica var. chinensis. Since this kind of larva would come out of the leaf at intervals and eat leaves for one year before entering the next stage of metamorphosis, it was not placed in a rearing cage. There were not enough larvae to do much damage. During the summer of 1954 snails ate the leaves of seedlings of L. japonica var. chinensis and did much damage.

No disease-producing organisms were observed on Japanese honeysuckle by the writer. However, several have been reported in the literature. Wescott (1950) reported the following disease-producing organisms on Lonicera japonica: Corticium koleroga (Cke.) v. Hohn, Phoma mariae G. W. Clinton, and Erysiphe polygoni DC. Seymour (1929) listed ten species of fungi which have been observed on Japanese honeysuckle. Dr. K. Hisauchi reported in correspondence that Pseudomonas tumefaciens (S. and T.) Duggar, Polyporus dichrous Fr., Rhytisma lonicericola Henn., and Systrema natans Theiss. have been observed on Lonicera japonica in Japan, and that none of these organisms have had serious effects on the vine in Japan.

Japanese honeysuckle is a serious pest in the Middle Atlantic States only in areas which have been protected from periodic burning (Handley 1945). Although the stems and leaves are readily burned by fire, the roots and stem bases are not harmed. Fire alone will not check the growth of honeysuckle, but the vine can be kept in check where fire is accompanied by heavy browsing of livestock and deer. If honeysuckle grows along fences, livestock will browse enough of the vine to prevent its spreading

into the field (Warbach 1953).

Japanese honeysuckle is difficult to eradicate due to its extensive, well-developed root system. Carleton (1950) has found a combination of the herbicides 2,4-D and 2,4 5-T, mixed with diesel oil, effective in stopping the spread of honeysuckle from woodland borders. In Virginia (Hurt 1926) honeysuckle has been eradicated from apple orchards by spraying with a combination of waste engine oil and a lighter oil such as straw oil. For honeysuckle occurring in fields, Muenscher (1936) recommended mowing the vines, burning them, plowing the field, sowing an intertilled crop followed by an annual smother crop, and close pasturing with sheep or goats. J. K. Underwood, of the Tennessee Agricultural Experiment Station, stated that Esteron 44, Esteron 245, 2,4-D, and 2,4 5-T will prevent the translocation of food to the roots, if the sprays are applied at the right time, under the right conditions, and in the proper concentrations. No practical method of control has been found to eradicate Japanese honeysuckle where it has spread over large areas of low-value land.

SUMMARY

Lonicera japonica Thunb. (Japanese honeysuckle) is a woody vine which was introduced somewhere into the United States from eastern Asia in 1806. It was formerly a favorite garden plant in the southeast and is still a prized ornamental in states where it does not escape from cultivation. Its weedy tendencies were first noticed during the century after its introduction.

Japanese honeysuckle may be useful in the control of erosion, but it should be used with care as it may become a pest. Certain wild and domestic animals browse on honeysuckle, and some birds eat the fruit. Honeysuckle provides cover for game birds and small mammals. It is also a minor honey source, and is locally utilized in basket-making.

Honeysuckle has become naturalized principally in disturbed areas and is widespread through most of the Deciduous Forest and the Southeastern Evergreen Forest regions, and it is scarce or absent at higher altitudes in the northern part of its range. It has escaped from cultivation locally in irrigated areas in the western states. It often interferes with the growth and reproduction of native plants on favorable sites. It has escaped chiefly south of the 30° normal January isotherm, between Latitudes 31 and 38°. It has become established principally within the 40 in. mean annual precipitation limit.

Honeysuckle may grow on different kinds of soils, but it spreads most rapidly on well-drained, circumneutral, forest soils. It is sparsely distributed in the coarse, white sandy soils of the sand hills

in the southern half of the Coastal Plain of North Carolina.

The embryo enters a state of dormancy immediately following its formation. Dormancy may be broken by stratification for sixty days in moist sphagnum in a temperature range between 43 and 46° F. The seeds, mostly disseminated by birds, normally germinate during the spring following their dispersal. Death of seedlings is due chiefly to drought, defoliation by insects and snails, a chlorotic condition, and damping-off fungi.

The greatest dry weight increase in photosynthesis measurements occurred in full sunlight, with the lowest increase in 5 per cent of full sunlight.

Stem elongation in the spring season has been reported to begin in a temperature range between 34 and 48° F. Stems may elongate up to 1.5 m. during a five-month growing season in moist soils. Honeysuckle spreads vegetatively by layering and thus forms extensive low colonies. The oldest stems may attain a size up to 18 cm. in diameter. Since typically they do not support much of the weight of the plant, they are not as subject to mechanical breakage as are the stems of tree species. When this circumstance is combined with the abundant layering, the vines have an almost indeterminate life span.

The fibrous root system is usually shallow, typically growing to a depth between 15 and 30 cm. in moist soil. Branch roots may extend laterally for a distance of 2.5 m. The extensive root system, which may attain a depth of 1 m. in drier soils, is an important factor in the drought resistance of the species and its survival on certain sites.

Flowers expand when the length of day is from twelve to fifteen hours, and photoperiod does not appear to be a critical factor in flower bud initiation. The chief pollinating agents are hummingbirds and insects in the orders HYMENOPTERA, LEPIDOPTERA, and DIPTERA. Maturation of the berries occurs during the short days of September to December.

Stems and leaves may be killed by fire and herbicides, but sprouting frequently occurs from underground parts. Some insects and disease-producing organisms attack honeysuckle, but have apparently not seriously limited its spread in southeastern United States. Honeysuckle can be controlled if the land is useful for agriculture, but no practical method has been found to eradicate this vine in large areas of low-value land.

BIBLIOGRAPHY

BIBLIOGRAPHY

Ammal, E. K. J. and B. Saunders. 1952. Chromosome numbers in species of Lonicera. Kew Bulletin 4:539-541.

Andrews, E. F. 1919. The Japanese honeysuckle in the eastern United States. Torreya 19:37-43.

Armstrong Nurseries. 1947. Catalogue. Ontario, California.

Bailey, L. H. 1953. The standard cyclopedia of horticulture. Vol. II. The Macmillan Co. New York.

Bonner, J. and A. W. Galston. 1952. Principles of plant physiology. W. H. Freeman and Co. San Francisco.

Bor, N. L. and M. B. Raizada. 1943. Some beautiful Indian climbers and shrubs. Jour. Bombay Nat. Hist. Soc. 44:73-77.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co. Philadelphia.

Braun-Blanquet, J. 1932. Plant sociology. McGraw-Hill Book Co. New York.

British Ecological Society. 1941. Biological flora of the British Isles. Schedule for contributors. Jour. Ecol. 29:358-360.

______. 1947. Biological flora of the British Isles. Revised schedule for contributors. Jour. Ecol. 34:202-204.

Britton, N. L. and A. Brown. 1936. An illustrated flora of the northern United States, Canada, and the British possessions. 2nd Ed. Vol. III. Lancaster Press, Inc. Lancaster, Pa.

Carleton, M. 1950. Kill that tough brush this winter. Country Gentleman 120:22, 58.

Chapman, A. W. 1897. Flora of the southern United States. 3rd Ed. American Book Co. New York.

Comstock, J. H. 1950. An introduction to entomology. 9th Ed. Comstock Pub. Co. Ithaca, New York.

Curtis, O. F. and D. G. Clark. 1950. An introduction to plant physiology. McGraw-Hill Book Co., Inc. New York.

Denny, F. E. 1930. Twin-leaf method of studying changes in leaves. Amer. Jour. Bot. 17:818-841.

Eames, A. J. and L. H. MacDaniels. 1947. An introduction to plant anatomy. 2nd Ed. McGraw-Hill Book Co. New York.

Fernald, M. L. 1950. Gray's manual of botany. 8th Ed. American Book Co. Atlanta.

Fogg, J. M., Jr. 1945. Weeds of lawn and garden. University of Pennsylvania Press. Philadelphia.

Gray, A. 1884. Synoptical flora of North America. Vol. I. Smithsonian Institution. Washington.

______. 1889. Manual of the botany of the northern United States. 6th Ed. American Book Co. New York.

Handley, C. O. 1945. Japanese honeysuckle in wildlife management. Jour. Wildlife Management 9:261-264.

Harper, R. M. 1900. Notes on the flora of middle Georgia. Bull. Torrey Bot. Club 27:321-341.

Hurt, R. H. 1926. Honeysuckle eradication in Virginia apple orchards. Va. Agric. Exp. Sta. Bull. 244:3-8.

Jackson, B. D. 1946. Index Kewensis. Part III. Clarendon Press. Oxford, England.

Kearney, T. H., R. H. Peebles, and collaborators. 1951. Arizona flora. University of California Press. Los Angeles.

Keck, D. D. 1926. Lonicera and Symphoricarpos in southern California. Bull. Southern Calif. Acad. Sci. 25:66-73.

Kemp, E. L. 1924. Some observations on Lonicera japonica Thunb. Torreya 24:103-104.

Lawrence, D. B., E. G. Lawrence, and A. L. Seim. 1947. Data essential to completeness of reports on seed germination of native plants. Ecol. 28:76-78.

Lawrence, G. H. M. 1951. Taxonomy of vascular plants. The Macmillan Co. New York.

Leasure, J. K. 1950. Some common weeds and their control. Univ. of Tenn. Agric. Exp. Sta. Bull. 213.

Leftwich, R. L. 1952. Arts and crafts of the Cherokee today. Western Carolina Teachers College Bull. 29:1-12.

Lilly, C. J. 1951. A study of the cut-twig method for measuring transpiration. M. S. Thesis, University of Tennessee. Knoxville.

Loddiges, C. and Sons. 1825. The Botanical Cabinet 11:1937. C. Loddiges and Sons. Hackney, near London.

Loomis, W. E. and C. A. Shull. 1937. Methods in plant physiology. McGraw-Hill Book Co. New York.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants. McGraw-Hill Book Co. New York.

Mayberry, M. W. 1935. Comparative anatomical research within the genus Lonicera. Univ. Kansas Sci. Bull. 22:27-53.

Meehan, T. 1888. Contributions to the life histories of plants, No. II. Proceedings of the Academy of Natural Sciences of Philadelphia. Philadelphia.

Meyer, B. S. and D. B. Anderson. 1952. Plant physiology. 2nd Ed. D. Van Nostrand Co., Inc. New York.

Möller-Erfurt, L. 1901. Möllers' Deutsche Gärtner-Zeitung 16:609-610.

Muenscher, W. C. 1936. Weeds. The Macmillan Co. New York.

Müller, K. 1865. Illustrierte Garten Zeitung. Vol. 9. C. Schweizerbart'sche Verlagshandlung und Druckerei. Stuttgart.

Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Amer. Midl. Nat. 28:1-126.

Pelton, J. 1951. Outline for ecological life history studies in trees, shrubs, and stem succulents. Ecology 32:334-343.

______. 1953. Ecological life cycle of seed plants. Ecology 34:619-628.

Rainey, R. S. 1949. Honeysuckle--friend or foe. Va. Wildlife 10:8, 9, 26.

Raunkiaer, C. 1905. Types biologiques pour la géographie botanique. Bull. Acad. Roy. Sci. Denmark 5.

______. 1934. The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer. Clarendon Press. London.

Rehder, A. 1903. Synopsis of the genus Lonicera. Rep. Missouri Bot. Gard. 14:27-232.

______. 1904. Preliminary lists of New England plants. Rhodora 6: 54-61.

______. 1940. Manual of cultivated trees and shrubs. 2nd Ed. The Macmillan Co. New York.

Sandison, S. 1934. The rooting of cuttings of Lonicera japonica: a preliminary account. New Phytologist 33:211-217.

Sax, K. and D. A. Kribs. 1930. Chromosomes and phylogeny in Caprifoliaceae. Jour. Arn. Arboretum 11:147-153.

Seymour, A. B. 1929. Host index of the fungi of North America. Harvard University Press. Cambridge, Mass.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecol. 35: 354-361.

Sheat, W. G. 1948. Propagation of trees, shrubs, and conifers. Macmillan and Co., Limited. London.

Small, J. K. and A. M. Vail. 1892. Report on the botanical exploration of southwestern Virginia during the season of 1892. Memoirs of the Torrey Bot. Club 4:93-201.

Small, J. K. 1897. Studies in the botany of the southeastern United States. Bull. Torrey Bot. Club 24:487-496.

Steyermark, J. A. 1940. Spring flora of Missouri. Missouri Botanical Garden. St. Louis.

Thornthwaite, C. E. 1931. The climates of North America according to a new classification. Geog. Review 21:633-655.

______. 1948. An approach toward a rational classification of climate. Geog. Review 38:54-94.

Thunberg, C. P. 1784 (Reprint 1933). Flora Japonica. In Bibliopolio I. G. Mulleriano. Lipsiae.

Trewartha, G. T. 1943. An introduction to weather and climate. 2nd Ed. McGraw-Hill Book Co. New York.

United States Forest Service. 1948. Woody plant seed manual. U. S. Dept. Agric. Misc. Pub. 654.

Visher, S. S. 1954. Climatic atlas of the United States. Harvard University Press. Cambridge.

Warbach, O. 1953. Control of Japanese honeysuckle in wildlife borders. Jour. Wildlife Management 17:301-304.

Weaver, J. E. 1919. The ecological relations of roots. Carnegie Inst. Wash. Pub. 286.

______. 1954. North American prairie. Johnsen Publishing Co. Lincoln, Nebraska.

Wells, B. W. and I. V. Shunk. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina Coastal Plain: an ecological study. Ecol. Monogr. 1:465-520.

Wescott, C. 1950. Plant disease handbook. D. Van Nostrand Co., Inc. New York.

APPENDIX

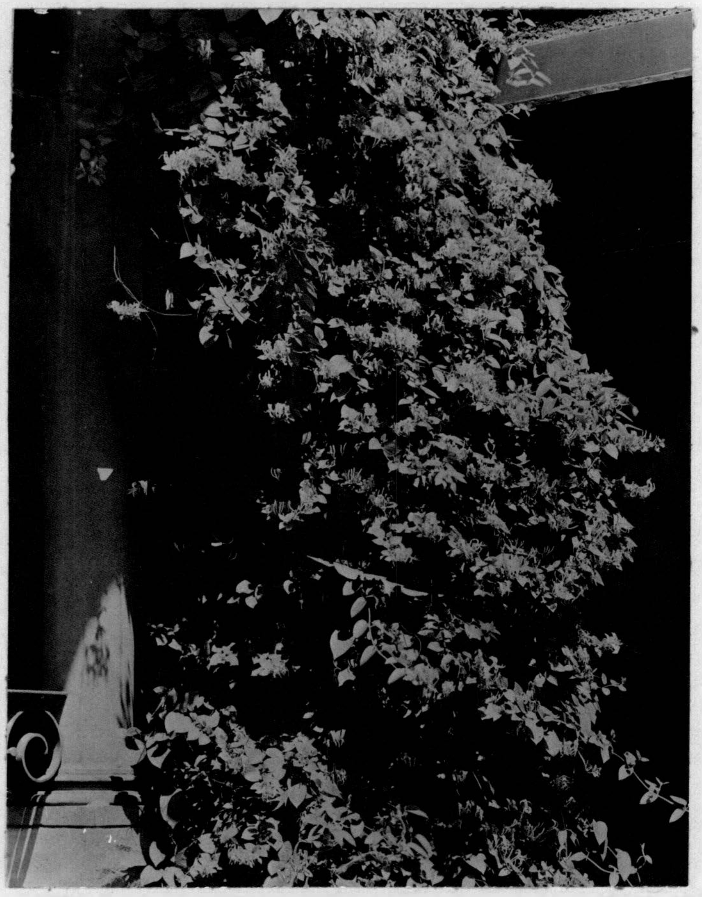

Figure 1. Japanese honeysuckle as a porch climber (Courtesy of Armstrong Nurseries, Ontario, California).

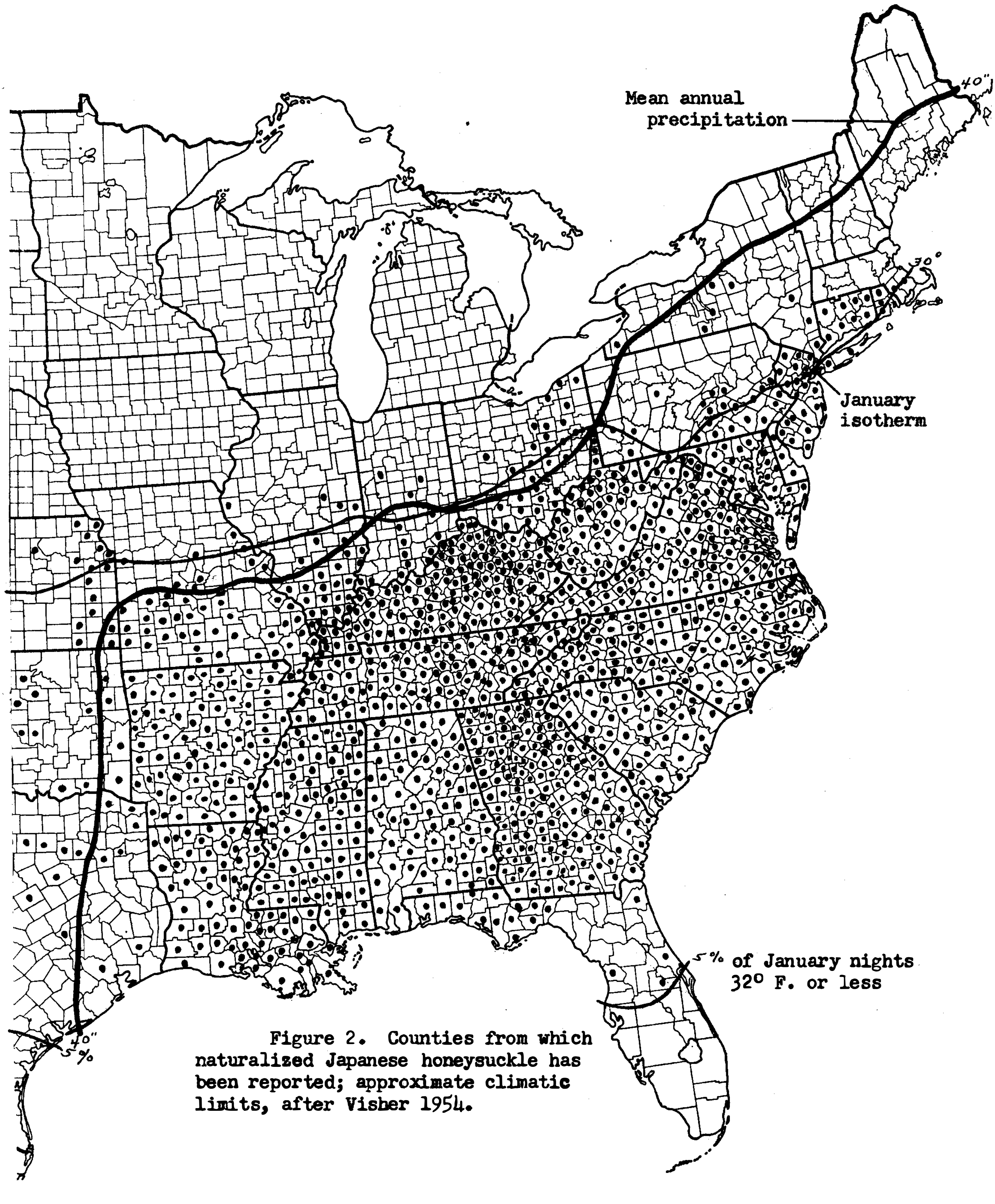

Figure 2. Counties from which naturalized Japanese honeysuckle has been reported; approximate climatic limits, after Visher 1954.

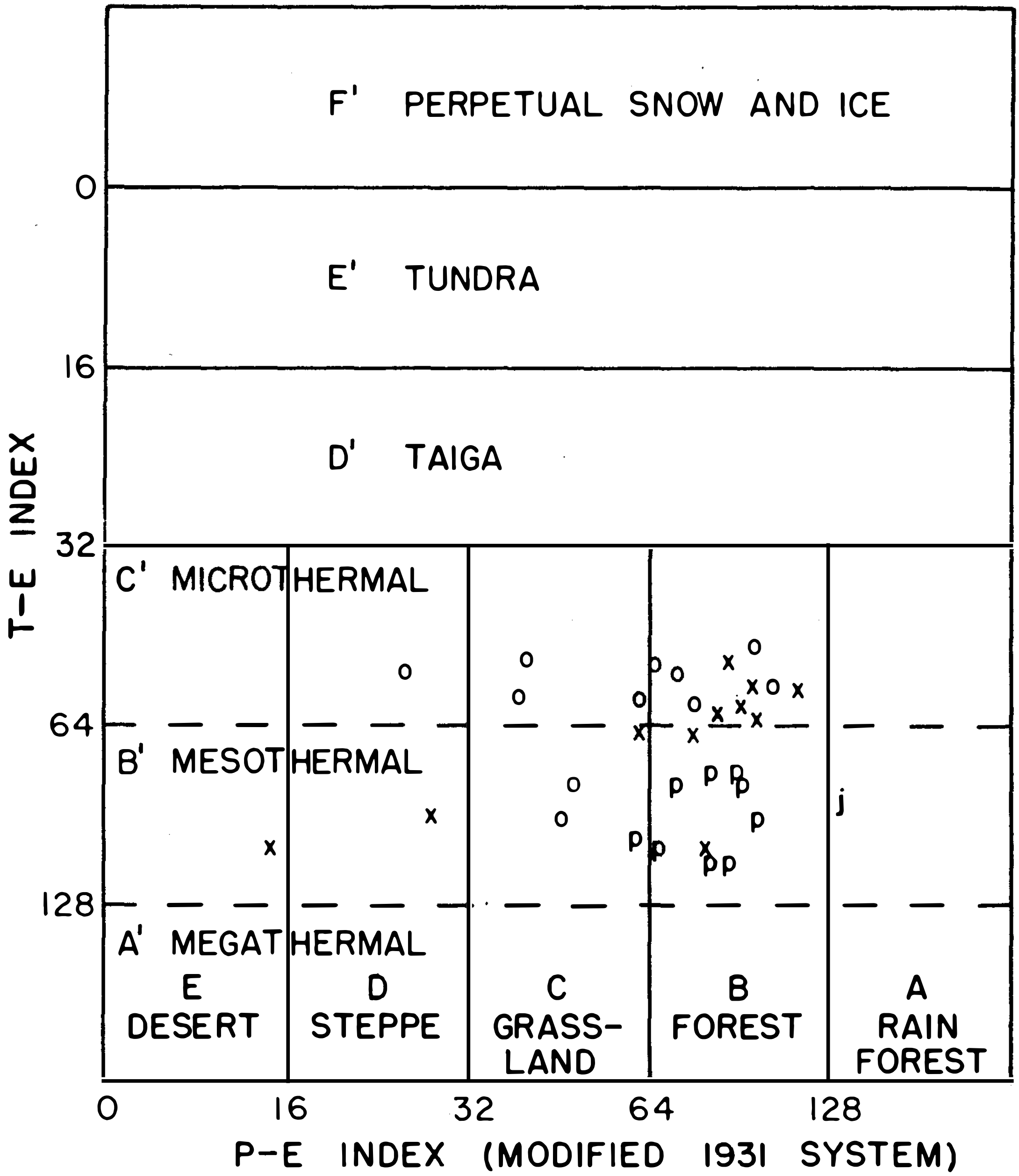

Figure 3. Graph showing the position of Japanese honeysuckle stations according to the 1931 system of Thornthwaite.

Symbols used:

- p Stations where honeysuckle is a pest.
- x Stations where honeysuckle has escaped but is not a pest.
- o Stations where honeysuckle is used as an ornamental but has not escaped.
- j Japanese station.

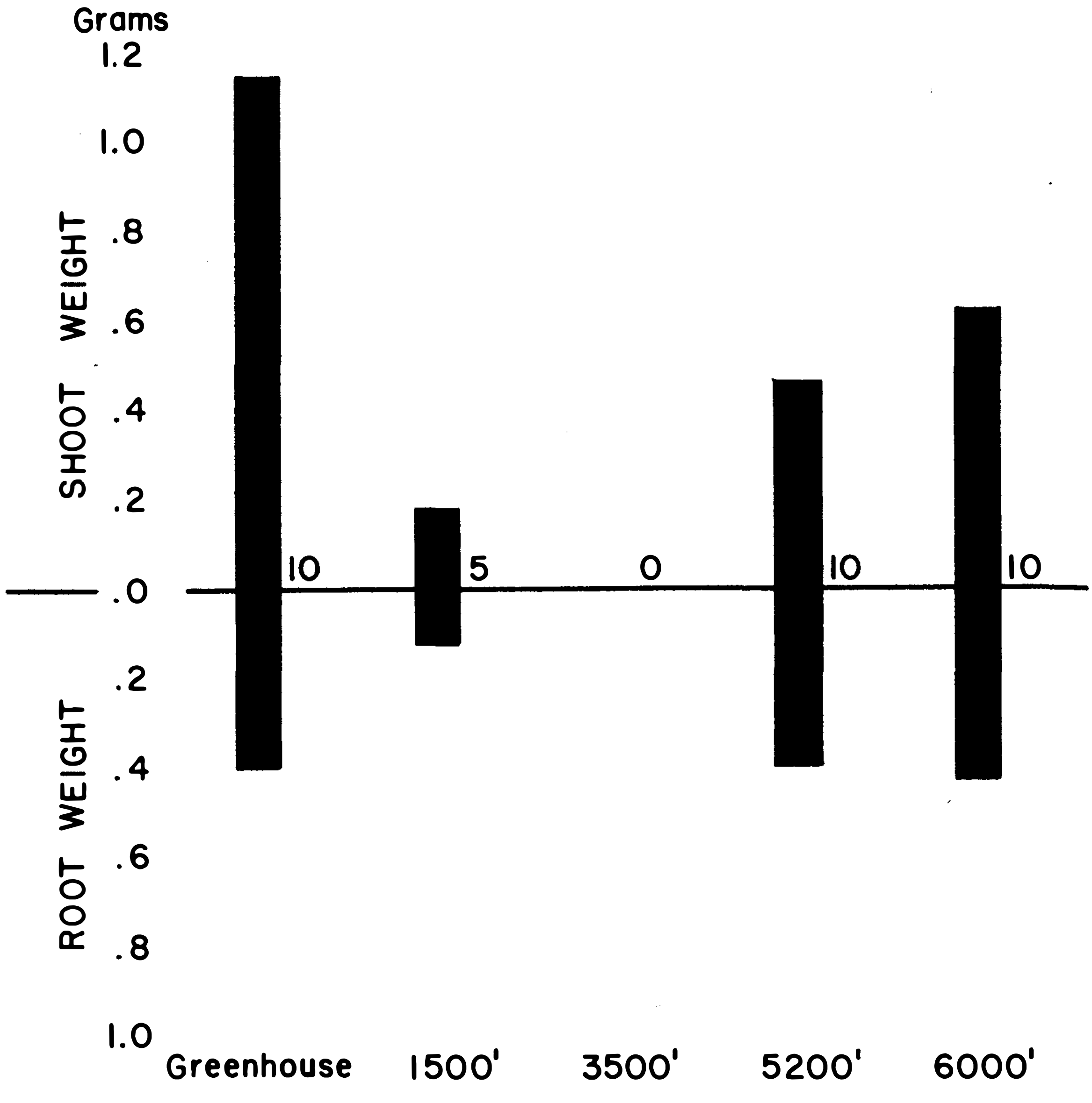

Figure 4. Comparison of average shoot and root weights of greenhouse-reared cuttings of Japanese honeysuckle with those transplanted to open habitats at different altitudes in the Great Smoky Mountains, August 4 to October 30, 1952; ten cuttings planted at each altitude, number surviving indicated.

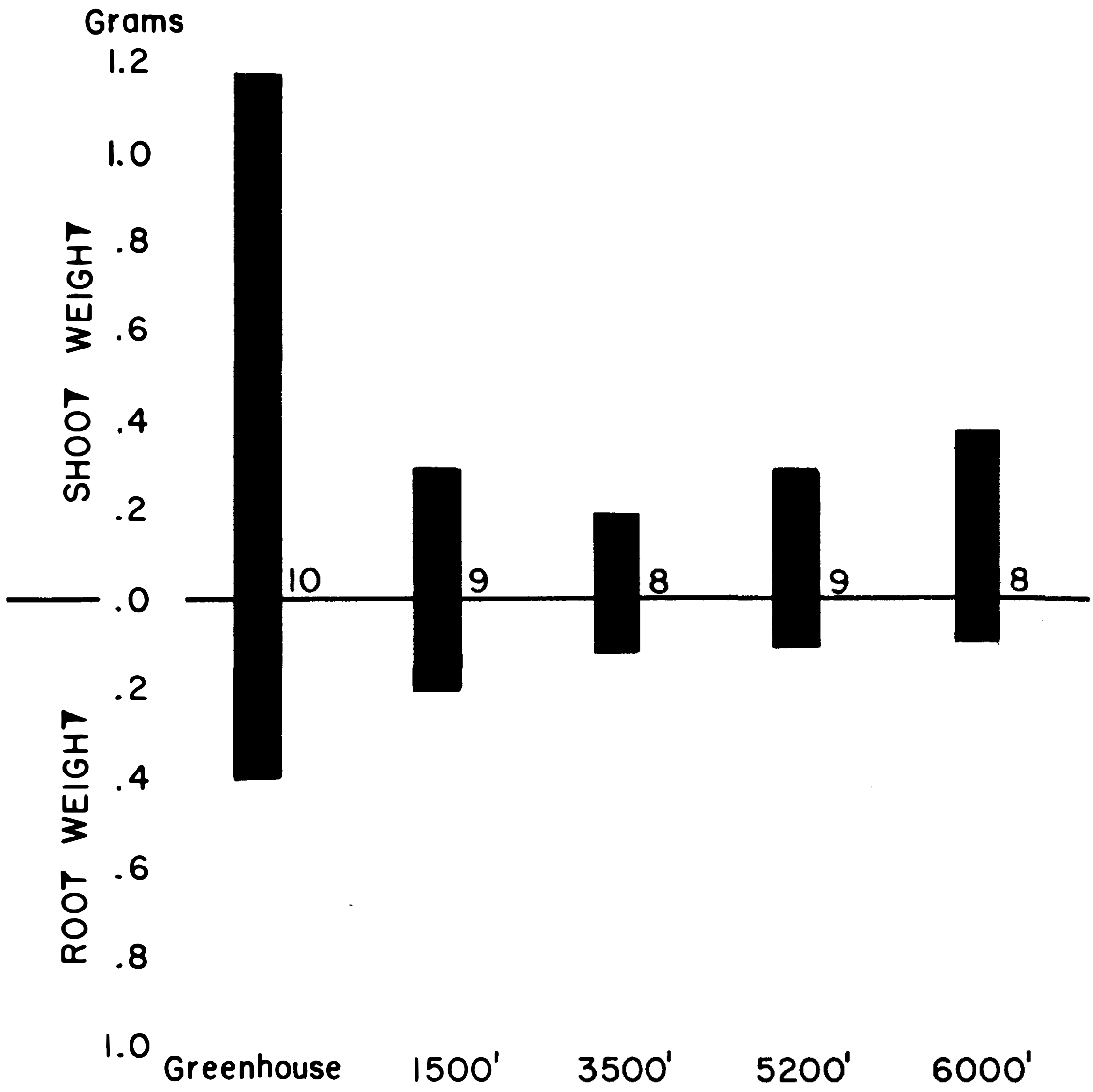

Figure 5. Comparison of average shoot and root weights of greenhouse-reared cuttings of Japanese honeysuckle with those transplanted to deciduous forests at different altitudes in the Great Smoky Mountains, August 4 to October 30, 1952; ten cuttings planted at each altitude, number surviving indicated.

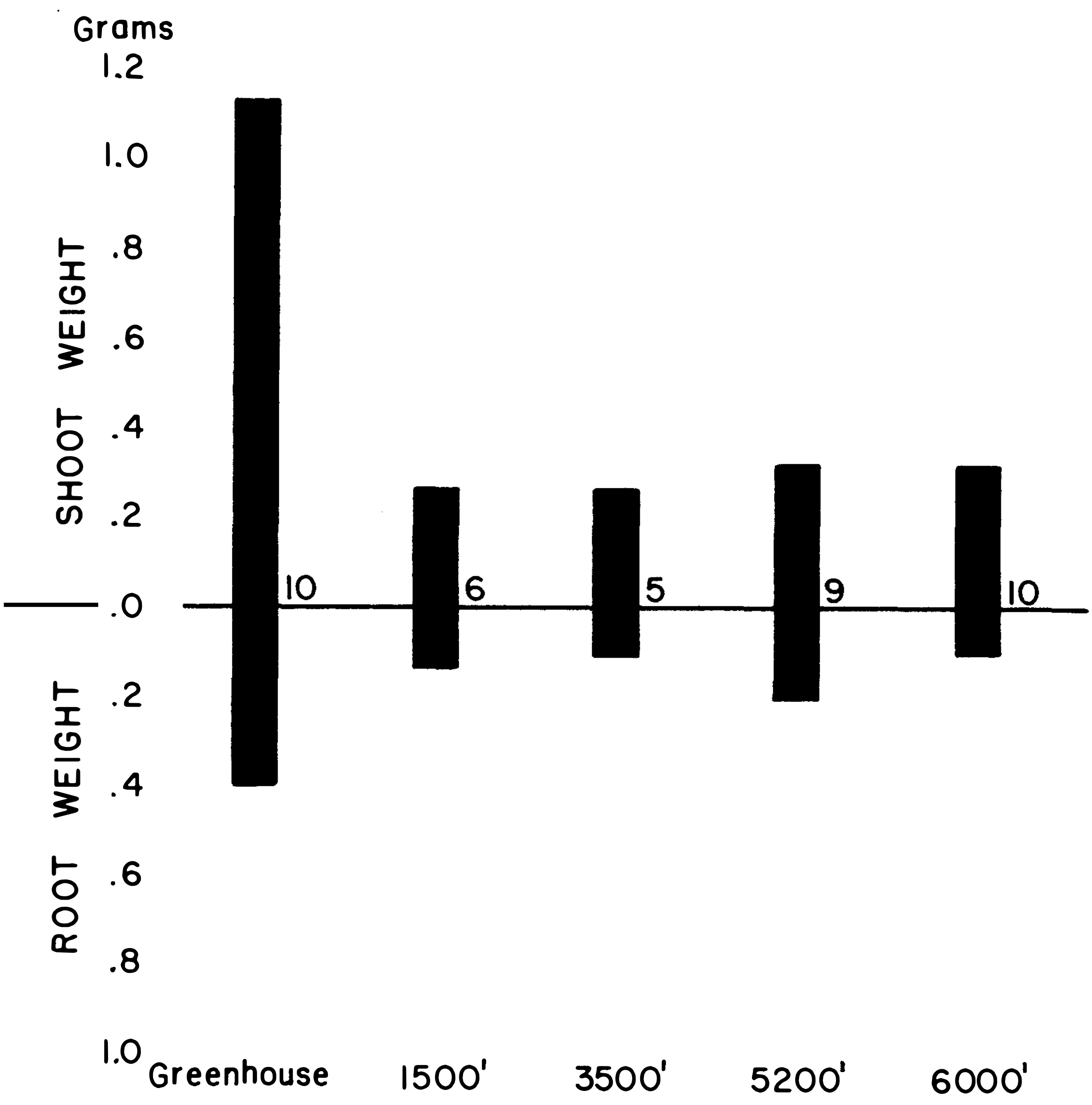

Figure 6. Comparison of average shoot and root weights of greenhouse-reared cuttings of Japanese honeysuckle with those transplanted to evergreen forests at different altitudes in the Great Smoky Mountains, August 4 to October 30, 1952; ten cuttings planted at each altitude, number surviving indicated.

Figure 7. Japanese honeysuckle upon a stone wall near Barbara Blount Hall, University of Tennessee.

Figure 8. Overgrowth of honeysuckle on a 20 ft. tall *Acer saccharinum* L.

Figure 9. Bark of Prunus serotina Ehrh. growing around twined honeysuckle stem. (Photo by Dorothy Crandall.)

Figure 10. Five-inch thick trunk of dead *Robinia pseudo-acacia* L. with encircling honeysuckle stems *completely buried* in the bark. (Photo by W. J. Cloyd.)

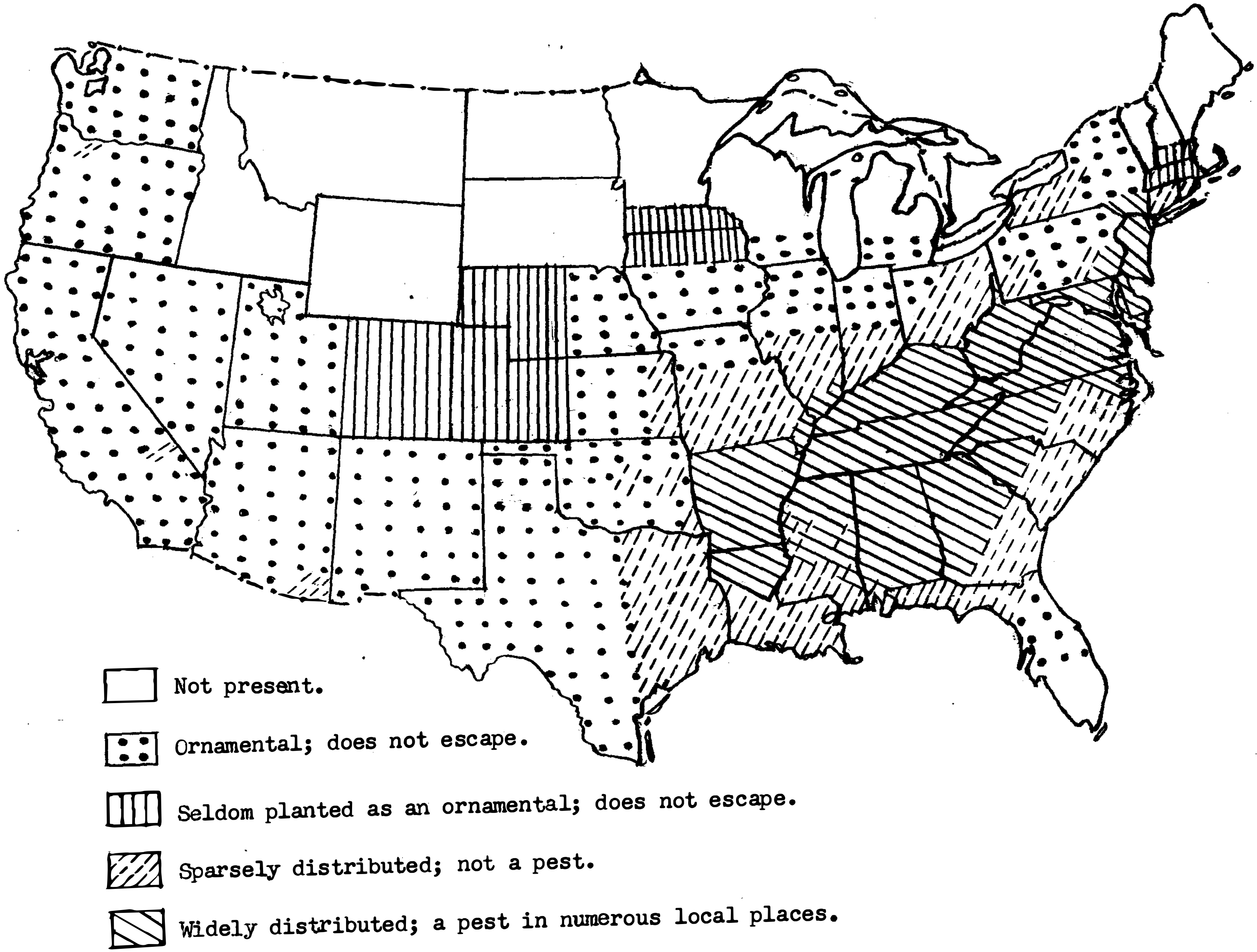

Figure 11. Reports of known ecological status of Japanese honeysuckle.

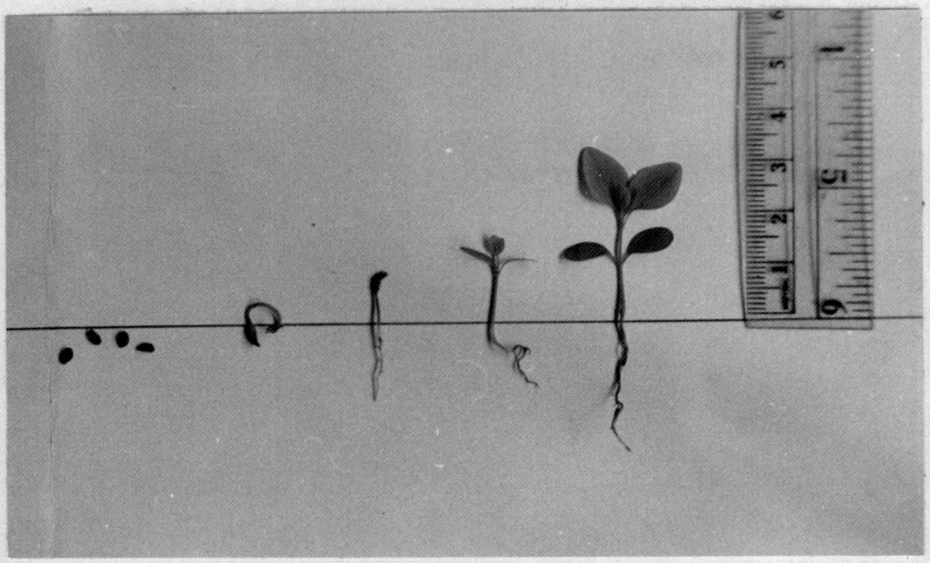

Figure 12. Stages in germination of Japanese honeysuckle.

Figure 13. Japanese honeysuckle seedlings.

Figure 14. Honeysuckle seedlings at the age of five months. Scale ½ natural size. (Photo by W. J. Cloyd.)

Figure 15. Plants of the same age, after having grown in different kinds of soil; the one to the left in a sandy loam with added organic matter and added commercial fertilizer, the one to the right in fine sand. Scale 1/3 natural size. (Photo by W. J. Cloyd.)

Figure 16. Shelters covered with cheesecloth.

Figure 17. A series of honeysuckle plants which grew under different light conditions; the light intensities were from left to right: 5 per cent, 10 per cent, 25 per cent, 50 per cent, and full sun.

Figure 18. Vegetative growth of Japanese honeysuckle under long-day (left) of 16 hours and under short-day (right) of 9 hours.

Figure 19. Root system of Japanese honeysuckle at seventeen months. Scale 1/3 natural size. (Photo by W. J. Cloyd.)

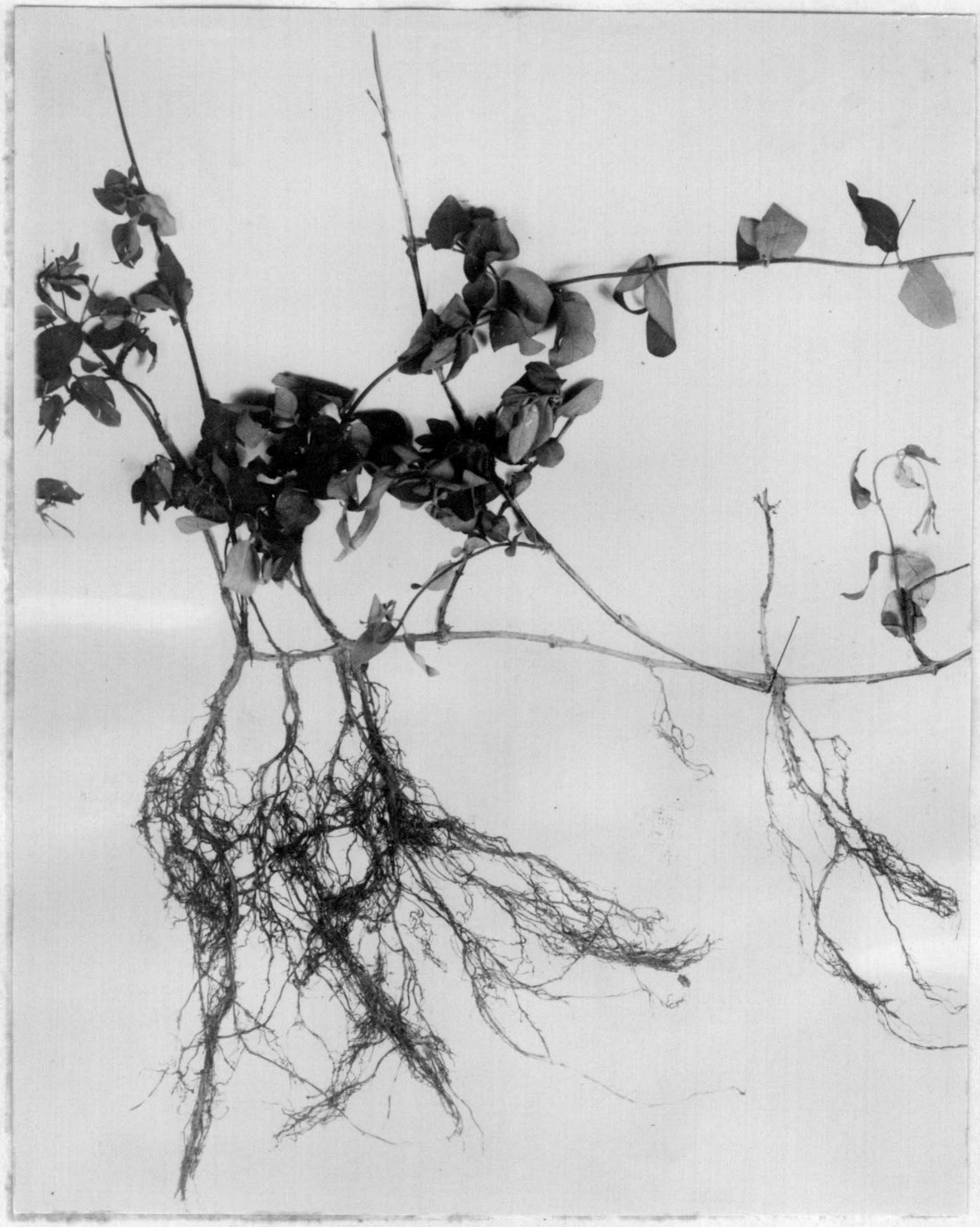

Figure 20. Stem of Japanese honeysuckle rooting at the nodes. Scale 1/3 natural size. (Photo by W. J. Cloyd.)

Figure 21. Honeysuckle near Cherokee Farm, University of Tennessee, completely covering the supporting fence.

Figure 22. July 1955 aspect of a dense tangle of honeysuckle stems near Knoxville; most of these stems were dead. (Photo by Dorothy Crandall.)