A SAMPLE OF THE VEGETATION IN THE LAKE GEORGE DRAINAGE BASIN.

Part III: Estimates of Biomass and Production in the Canopy Vegetation.

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A SAMPLE OF THE VEGETATION IN THE LAKE GEORGE DRAINAGE BASIN

Part III: Estimates of Biomass and Production in the Canopy Vegetation

A final technical report for Union Carbide Subcontract No. 3566 for the Eastern Deciduous Forest Biome, IBP, Lake George Site

by

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PREFACE

The purpose of this report is to summarize estimates of biomass and net production for the tree layer in representative stands from the Lake George drainage basin. Interpretations of major trends are given, but lack of support precluded a more detailed presentation at this time.

Future analyses of these data are planned, particularly as they relate to understory, shrub, and ground layer characteristics. Highlights were presented at the 1972 AIBS-ESA meetings in Minneapolis.

Finally, several limitations of our biomass-production estimates should be kept in mind. They are for above ground portions of trees (stems $\geq$ 10.2 cm, dbh) only and are based on regression relations derived at Hubbard Brook, N. H. by R. H. Whittaker. Naturally, their applicability to Lake George stands is open to question. Other possible errors involved in using these regressions are discussed in the report.

For these reasons our figures should be considered as tentative estimates obtained by using the most appropriate predicting equations currently available. Future development of regressions for Lake George or similar locales may lead to revised biomass-production estimates that are more accurate.

ABSTRACT

Biomass and net production of the tree layer (stems $\geq$ 10.2 cm, dbh) were estimated for 79 stands in the Lake George drainage basin by dimension analysis. Typical biomass and production ranges (100-300, x 10^3 kg/ha; 5-11 x 10^3 kg/ha/yr) were comparable to estimates for similar communities elsewhere. Since site factors were masked by past disturbance, biomass and production were largely a function of successional status. They increased linearly throughout the range sampled, except for a plateau at 80 yrs on coarse textured sites. Biomass and production in conifer and angiosperm dominated stands of comparable site and successional status did not differ appreciably.

INTRODUCTION

Documentation of biomass and production throughout the biosphere is a major objective of the International Biological Program. Although gross patterns have been delineated (e.g. Golley, 1972; Jordan, 1971; Leith, 1964/1965; Odum, 1971; Rodin and Bazilivetch, 1968; Whittaker, 1970; Woodwell, 1970), biome-wide and localized trends are as yet poorly defined.

Man is the major determinant of biomass and production in the Deciduous Forest Biome. Effects of human related disturbance are difficult to assess and do not always result in a predictable reduction in biomass and production. For example, severe logging may reduce biomass and production, but selective cutting may diminish biomass and increase production. Other man-related stresses such as pollutants, grazing, trampling, etc. may have similar effects. Although perturbations may stimulate production on a short term basis, they may adversely effect ecosystem fitness (ability to maintain high levels of gross production indefinitely). Little is known about long range effects of man's activities on ecosystem function.

Biomass and production are closely related to successional status. Practically all evidence indicates that biomass increases monotonically with succession. Data on production relations are less well established but generally suggest that gross production is maximized and net ecosystem production is minimized during succession. Net primary production is believed to be greatest during intermediate stages.

Thus, any attempt to trace biome-wide trends in biomass and production must consider the preceding factors in addition to obvious productivity influences such as solar radiation, water, nutrients, etc. Biomass and production variations in the Lake George drainage basin are primarily a function of past disturbance, (expressed as current successional status) rather than environmental factors per se.

Our 100-stand sample, which includes 75 randomly selected locales, is well representative of major site types and community variants found in the study area (Nicholson et al, 1971). As such, it depicts the range, variability, and spatial patterns of biomass-production found in a typically disturbed portion of the Eastern Deciduous Forest.

METHODS

Biomass and production of the tree layer (stems $\geq$ 10.2 cm, dbh) were estimated using dimension analysis (Whittaker and Woodwell, 1968). Details of the field sampling procedure are given in Nicholson et al (1971).

Two sets of regression equations developed by R. H. Whittaker (unpublished data) from Hubbard Brook, N. H. were employed:

$$\log_{10} Y = 1.19153 + 2.5246 \log_{10} X, \qquad (1)$$

$$\log_{10} Y = .89907 + 2.1199 \log_{10} X, \qquad (2)$$

for biomass and production of conifers, and

$$\log_{10} Y = 2.0918 + 2.4716 \log_{10} X, \qquad (3)$$

$$\log_{10} Y = 1.4094 + 2.0572 \log_{10} X, \qquad (4)$$

for hardwood biomass and production, respectively, in which Y = estimated biomass or production per tree in grams and X = tree diameter at breast height in centimeters.

Biomass and production of stands were determined by summing individual estimates for trees and expressing results on an area basis. Errors involved in the use of these regressions are discussed later in the paper.

Successional status of communities was determined from tree age and historical information. Tree ages were estimated from increment borings (most stands) or by a size-age regression derived for hardwoods. Historical information came from several sources: (1) land acquisition records (N.Y.S. Conservation Department and other owners), (2) old vegetation maps (cited in Nicholson et al, 1971), (3) interviews with long time residents, and (4) field evidence such as charcoal, stumps, etc.

RESULTS

Estimates of above ground biomass and net production for the tree layer (stems $\geq$ 10.2 cm, dbh) in the Lake George stands are listed in Table 1. Stand locations are given in Fig. 1. Mean biomass (207 t/ha = 10^3 km/ha) and production (8.2 t/ha/yr = 10^3 km/ha/yr) in 60 randomly selected forest stands from the south basin were within 1% of means for 12 randomly selected north basin stands (206 t/ha, 8.1 t/ha/yr). Differences between east and west sides of the drainage basin were also small, being within 20%.

Localized portions of the drainage basin exhibited notable contrasts in biomass and production, however. In particular, biomass and production of centrally located stands tended to be greater and less variable than elsewhere. Also, stands with maximum biomass and production tended to be near the lake; 8 of the leading 10 were within 0.5 km.

Although biomass and production were poorly correlated with environmental factors such as altitude, slope, and slope aspect, they were closely related to successional status. Relationships for different stand combinations are given in Figs. 2-13 (see also Table 2).

When all stands were compared (Figs. 2, 3) biomass was well fitted to the linear model (r = .805) as was production, which was described slightly better by a parabola (r = .867). The closeness of the relationships are not surprising in that biomass and production were a function of tree sizes while successional status was partially so.

Effects of site on successional trends in biomass and production were considered by examining fine and coarse textured stands separately. Fine textured soils included those classified as "very stony" and finer in soil surveys (Feuer and Johnsgard, 1956; Maine, 1968; Maine and Holmes, 1969). This breakdown resulted in nearly equal numbers of stands in both groups--41 coarse, and 40 fine. Successional trends in the two site groups are shown in Figs. 4-5 for biomass and production, respectively. Trends on fine textured sites better approximated the linear model than those on coarse sites (r = .785, .890 vs. r = .757, .570), suggesting that biomass and production level off sooner on coarse sites. The apparent tendency for biomass to plateau early in succession (40-60 yrs) could be related to difficulties in establishing true successional status of these stands, or a real trend caused by temporary stagnation in biomass accumulation. The occurrence of this lag on both fine and coarse sites (Fig. 4) and otherwise broad overlap in biomass and production throughout succession on the two site types (except in oldest stands) suggests that site factors are relatively unimportant in our sample.

Since different regression equations were used to estimate biomass and production of conifers (Equations 1, 2) and angiosperm species (Equations 3, 4) successional trends in stands dominated by these tree types were also examined separately by site type. Results for biomass are given in Figs. 6-9 and for production in Figs. 10-13. Although sample size and successional spread were less than desirable in some cases, they are sufficient to reveal general trends. Conifer dominated stands tended to have greater biomass than angiosperm stands of comparable age, but there was much overlap. This trend was most apparent in older stands on fine textured sites but barely apparent in young stands on coarse sites (Figs. 6, 8). Production estimates overlapped closely in most cases (Figs. 10-13), there being a slight tendency for angiosperm stands to exceed conifer stands of equivalent successional status. Finally, production and biomass of stands on fine sites corresponded to stand ages in a more regular way than did those on coarse sites.

DISCUSSION

Above Ground Tree Biomass:

Above ground (AG) tree biomass estimated for the Lake George stands (207 t/ha) are within the range others have reported for similar communities elsewhere. Ovington (1965) stated that 112-141 t/ha and 122-140 t/ha were typical for tree biomass in temperate deciduous and coniferous forests, respectively. Rodin and Bazilivetch (1968) gave 150-300 and 50-350 t/ha as common ranges for total organic matter in deciduous and coniferous/mixed atands. Deduction of the usual contribution of non tree components (30-50%, in their tables) reduces these ranges to 75-210 and 25-245 t/ha, respectively. Whittaker (1966) found a wider biomass range in the Great Smcky Mountain forest communities he studied, 86-500 t/ha for hardwoods, 130-180 t/ha for pine, and 170-600 t/ha for hemlock. The variation reflects topographic and altitudinal extremes included in his sample.

Biomass estimates from more homogeneous areas are less variable. For example, Long Island oak-pine communities Whittaker and Woodwell (1968) studied ranged from 92-191 t/ha. Two independent studies of Minnesota oak forests yielded similar results: 164 t/ha (Ovington, Heitkamp, and Lawrence, 1963), and 124 t/ha (Reiners, 1972).

Tree biomass in most of our hardwood communities was 100-300 t/ha. The range is high compared with Ovington's but low compared with Whittaker's. If the Lake George stands are better developed than Ovington's from Europe but inferior to the Smokies' stands such discrepancies are explainable.

Biomass in conifer-dominated stands, typically 100-350 t/ha, also compares favorably with other estimates. Ours exceed younger European plantations, approximate communities of similar status, but are below Whittaker's (1966) high estimates.

Above Ground Net Production:

Production estimates for stands also compare favorably with other studies. Mean estimated production (8.2 ± 2.7 t/ha/yr) agrees with total AG production in the Minnesota oak forests (8.2 t/ha/yr, Ovington, Heitkamp, and Lawrence, 1963; 8.9 t/ha/yr, Reiners, 1972), but is lower than Whittaker's estimates for trees in the Smokies' hardwood forests (5.4-24.1 t/ha/yr). Only a few of our older communities (115+ yrs) had production estimates exceeding 14 t/ha/yr. Production in most coniferous stands (4-12 t/ha/yr) closely approximated the range Whittaker (1966) found in the Smokies (4.2-13.3 t/ha/yr).

Accuracy of Estimates:

Estimates of biomass and production by dimension analysis are prone to many error sources (Madgwick, 1970; Satoo, 1966; Kira and Shidei, 1967; Atiwill and Ovington, 1968). Three such factors may seriously limit accuracy of our estimates: (1) regressions used originated from another locale (Hubbard Brook, N. H.), (2) regressions were not always species-specific, and (3) size classes sampled deviated from sizes used to establish regressions. The effect of factor (1) on our estimates cannot be evaluated without size-weight data from Lake George.

Factor (2) may have profoundly affected estimates for coniferous species. Regressions derived for red spruce (*Picea rubens*) at 700-1000 m from Hubbard Brook were used for white pine (*Pinus Strobus*) and hemlock (*Tsuga canadensis*) at 100-400 m at Lake George. Based on climatic and species differences, the Hubbard Brook equations should underestimate weights at Lake George.

But the size discrepancy of the red spruce regressions (factor 3) would overestimate weights of larger trees. Regressions were based on stems 2.9-37.6 cm (mean = 14.5 cm, dbh) while 25-35 cm, dbh conifers were commonly encountered in samples. The net effect of these (and other) error sources on predicted weights are difficult to assess.

However it is safe to say that biomass-production estimates for angiosperms were much less affected by these kinds of errors. Although error due to factor (1) is still involved, the species (beech, sugar maple, and yellow birch) and sizes (mean = 24 cm, dbh) used to establish the Hubbard Brook regressions were quite comparable to our sample.

Nonetheless, uncertain applicability of the regressions to our sample area (factor 1) precludes computation of meaningful within-community error estimates at this time. Therefore, the estimates reported herein are best considered as being relative -- good indicators of biomass-production among the Lake George stands (with some reservations on angiosperm vs. conifer comparisons), not precise measures. Even if this were possible, only general comparisons could be made with other studies (as we have already done), because of effects of other variables, e.g. age (Ovington, 1962; Art and Marks, 1972), and site (Jordan, 1972), to mention a few.

Local Biomass-Production Trends:

The absence of meaningful basin-wide (north-south, east-west) biomass-production patterns demonstrates that factors of this scale are either not important or are superseded by others. A similar lack of correspondence between site (e.g. soil texture, altitude, slope, slope-aspect) and biomass-production suggests that these factors, too, are relatively unimportant.

Biomass-production patterns do correspond closely with past disturbance, however. Contrasts between stands from east and west sides of the basin in the central portion are related to historical events. Greater and less variable biomass-production of eastern vs. western stands is probably due to factors such as: (1) more uniform land-use history (larger ownership units) and (2) less frequent, less severe logging in eastern stands. The more subtle pattern of high biomass near the lake has a similar explanation -- old growth lakeside stands have been protected for aesthetic reasons while more distant stands have been logged whenever profitable.

That past forest exploitation is the major determinant of present biomass-production patterns is not so surprising; the close relationship between biomass and production and successional status is frequently emphasized. Although continued augmentation in biomass during succession is in agreement with past studies, such a trend for net production is not. Several authorities (e.g. Kira and Shidei, 1967; Rodin and Bazilivetch, 1968; Odum, 1969) state that net primary production is maximum in early succession. But most of their supporting evidence is from plantations, and successional trends in natural communities could differ. In one of the few studies which estimated gross and net production of all components Woodwell and Whittaker (1968) found that net production exceeded ecosystem respiration by 20%, although the community studied was not mature. Based on this and related studies, Whittaker (1970) suggests that net production is asymptotic with succession, not parabolic such as plantation data suggest.

However Loucks (1970) and Sharpe (unpublished data) both claimed that their data on natural seres showed well defined preclimax peaks in net production. According to Loucks, in the southern Wisconsin oak sere, both biomass and net production peaked at about 125 years. Sharpe found a much earlier production peak (20-30 yrs), but no well defined biomass peak using composite data for various aged upland oak forests. Results of these two studies partially concur with currently popular successional models on changes in net production (e.g. Odum, 1969) but contrast with predicted biomass trends and the net production model suggested by Whittaker (1970).

Our data, for the tree layer in over 70 representative communities, suggest that both biomass and production increase during the successional range sampled (~150 yrs), except in the oldest communities on coarse sites, where a plateauing occurs. While we expect that a similar leveling occurs on fine textured sites in older communities than we sampled, a late term reduction is also possible. If so, this would conform to Loucks' model, but not Sharpe's.

Only a gross underestimation of non-tree biomass and production in the youngest forest communities would bring out an early succession (20-30 yrs) production peak and negate the increase in biomass. But even if understory, shrub, and herb production were included, it is doubtful this would change the overall trend. Contribution of these components to total production has repeatedly been shown to be small in closed forest stands, i.e. ~5-10% (cf. Ovington, 1965; Whittaker, 1966; Rodin and Bazilivetch, 1968; Monk, Child, and Nicholson, 1970; Reiners, 1972), or 3-5 t/ha/yr or less in young open stands (e.g. Whittaker, 1966; Bazilivetch and Rodin, 1968). Since estimated production in our old growth stands (tree layer only) is usually at least twice this, adding non tree production to younger stands will not result in a well-defined early succession production peak unless estimates for older stands are much too high. Although this may be possible for conifers in some old-growth stands (because of limitations of regression equations discussed earlier), it is unlikely for angiosperm species, which account for the bulk of the data.

SUMMARY - CONCLUSIONS

Biomass and net production of trees (stems $\geq$ 10.2 cm, dbh) above ground were estimated for 79 forest communities in the Lake George drainage basin. Estimates were made by dimension analysis (Whittaker and Woodwell, 1968), i.e. stand species-dbh tallies were converted to biomass and production estimates using the most appropriate size-weight regression equations available.

Our biomass-production estimates are comparable to estimates others have made for similar temperate zone communities. Inter-community variations were more closely related to past disturbance, than gross environmental factors (e.g. location, soil texture, altitude, slope, and slope aspect). Both biomass and production corresponded closely to community age, increasing linearly with age over most of the successional range sampled (150 yrs).

Successional trends were remarkably similar on fine and coarse textured sites (Figs. 4-5), except for plateauing at 80 yrs on coarse sites. Differences between conifer and angiosperm dominated stands of equivalent age and texture class were also minimal (Figs. 6-13), there being a slight tendency for greater biomass in conifer stands and greater production in angiosperm stands.

Neither biomass nor net production showed well defined preclimax overshoots as others reported previously for plantations. Although our successional range may prevent a direct testing of Loucks' (1970) model, the close similarity of successional trends in biomass and production on fine and coarse-textured sites (Figs. 4-5) and early plateauing on coarse sites is suggestive of an asymptotic relationship as proposed by Whittaker (1970).

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Table 1: Above ground biomass and production of trees (stems $\geq$ 10.2 cm, dbh) in the Lake George drainage basin stands.

Stand number	Biomass (kg/ha)	Production (kg/ha/yr)
GROUP I - RANDOM, SOUTH BASIN (n = 63):		
1	136,000	7,170
2	293,000	12,590
3	324,000	10,470
4	108,000	5,740
5	121,000	7,030
6	---	---
7	---	---
11	146,000	6,500
12	116,000	5,150
13	99,000	4,460
14	168,000	7,620
15	179,000	7,070
16	167,000	9,390
17	94,000	5,340
20	168,000	4,000
21	187,000	8,380
22	227,000	6,000
23	106,000	5,970
24	116,000	6,340
25	343,000	11,150
26	340,000	10,030
32	157,000	6,910
33	280,000	7,040
37	97,000	2,240
38	185,000	7,130
39	201,000	5,120
40	93,000	4,840
41	223,000	8,800
42	305,000	13,710
43	242,000	10,780
44	258,000	9,650
45	262,000	7,030
48	154,000	7,140
49	143,000	6,020
50	187,000	8,290

Table 1 (continued) - page 2

Stand number	Biomass (kg/ha)	Production (kg/ha/yr)
51	147,000	4,470
54	160,000	7,210
55	147,000	7,560
62	29,000	1,060
65	203,000	8,360
66	178,000	6,530
68	126,000	6,360
71	207,000	9,490
72	207,000	11,020
73	212,000	10,610
74	234,000	10,830
75	186,000	9,400
76	258,000	9,640
81	261,000	7,350
82	203,000	10,440
84	161,000	8,150
85	276,000	11,770
86	151,000	7,020
88	340,000	11,030
89	304,000	9,600
90	160,000	7,100
92	314,000	12,620
95	277,000	9,040
96	276,000	12,450
97	195,000	8,950
98	351,000	14,340
99	594,000	12,570
100	—	—
GROUP II - RANDOM, NORTH BASIN (n = 12):		
18	230,000	4,670
19	199,000	10,510
27	243,000	8,600
28	268,000	12,610
29	253,000	10,350
30	173,000	5,490
31	242,000	11,380
34	239,000	5,730
35	191,000	8,940
36	142,000	6,170
46	236,000	9,520
47	59,000	2,950

Table 1 (continued) - page 3

Stand number	Biomass (kg/ha)	Production (kg/ha/yr)
GROUP III - NON RANDOM (n = 25):		
8	---	---
9	---	---
10	184,000	3,630
52	96,000	3,680
53	365,000	15,900
56	181,000	5,510
57	---	---
58	---	---
59	---	---
60	---	---
61	21,000	1,390
63	---	---
64	---	---
67	509,000	15,250
69	---	---
70	---	---
77	---	---
78	---	---
79	---	---
80	---	---
83	---	---
87	---	---
91	487,000	11,190
93	---	---
94	---	---

Table 2: Key to symbols for dominant tree species in the Lake George stands.

Common Name	Scientific Name[1]	Symbol in Figs. (2-13)
1. Hemlock	*Tsuga canadensis* L.	triangle (△)
2. White Pine	*Pinus strobus* L.	inverted triangle (▽)
3. Large-tooth Aspen	*Populus grandidentata* Michx.	flag (▷)
4. Paper Birch	*Betula papyrifera* Marsh.	inverted dagger ( )
5. Beech	*Fagus grandifolia* Ehrh.	plus sign (-|-)
6. White Oak	*Q. alba* L.	large circle (◯)
7. Northern Red Oak	*Q. rubra* L. Var. *borealis* (Michx.f.) Farw.	square (□)
8. Black Oak	*Quercus velutina* Lam.	diamond (◇)
9. American Elm	*Ulmus americana* L.	asterisk (✳)
10. Sugar Maple	*Acer saccharum* Marsh.	small circle (○)
11. Red Maple	*Acer rubrum* L.	dagger ( )

[1] Nomenclature follows Fernald (1953).

Figure 1 - Location of randomly selected stands.

Figure 2 - Above ground tree biomass of stands (10^3 kg/ha) plotted against age. Fine textured sites indicated by solid symbols and coarse textured sites by open symbols.

Figure 3 - Above ground tree production of stands (10^3 kg/ha) plotted against age. Fine textured sites indicated by solid symbols and coarse textured sites by open symbols.

Figure 4 - Above ground tree biomass of stand groups (10^3 kg/ha) plotted against age. Solid plot is for coarse textured sites while docked plot is for fine. Error brackets indicate $\pm$ 1 standard error of means.

Figure 5 - Above ground tree production of stand groups (10^3 kg/ha) plotted against age. Solid plot is for coarse textured sites while docked plot is for fine. Error brackets indicate $\pm$ standard error of means.

Figure 6 - Above ground tree biomass of conifer dominated stands on fine textured sites (10^3 kg/ha) plotted against age.

Figure 7 - Above ground tree biomass of conifer dominated stands on coarse textured sites (10^3 kg/ha) plotted against age.

Figure 8 - Above ground tree biomass of angiosperm dominated stands on fine textured sites (10^3 kg/ha) plotted against age.

Figure 9 - Above ground tree biomass of angiosperm dominated stands on coarse textured sites (10^3 kg/ha) plotted against age.

Figure 10 - Above ground tree production of conifer dominated stands on fine textured sites (10^3 kg/ha/yr) plotted against age.

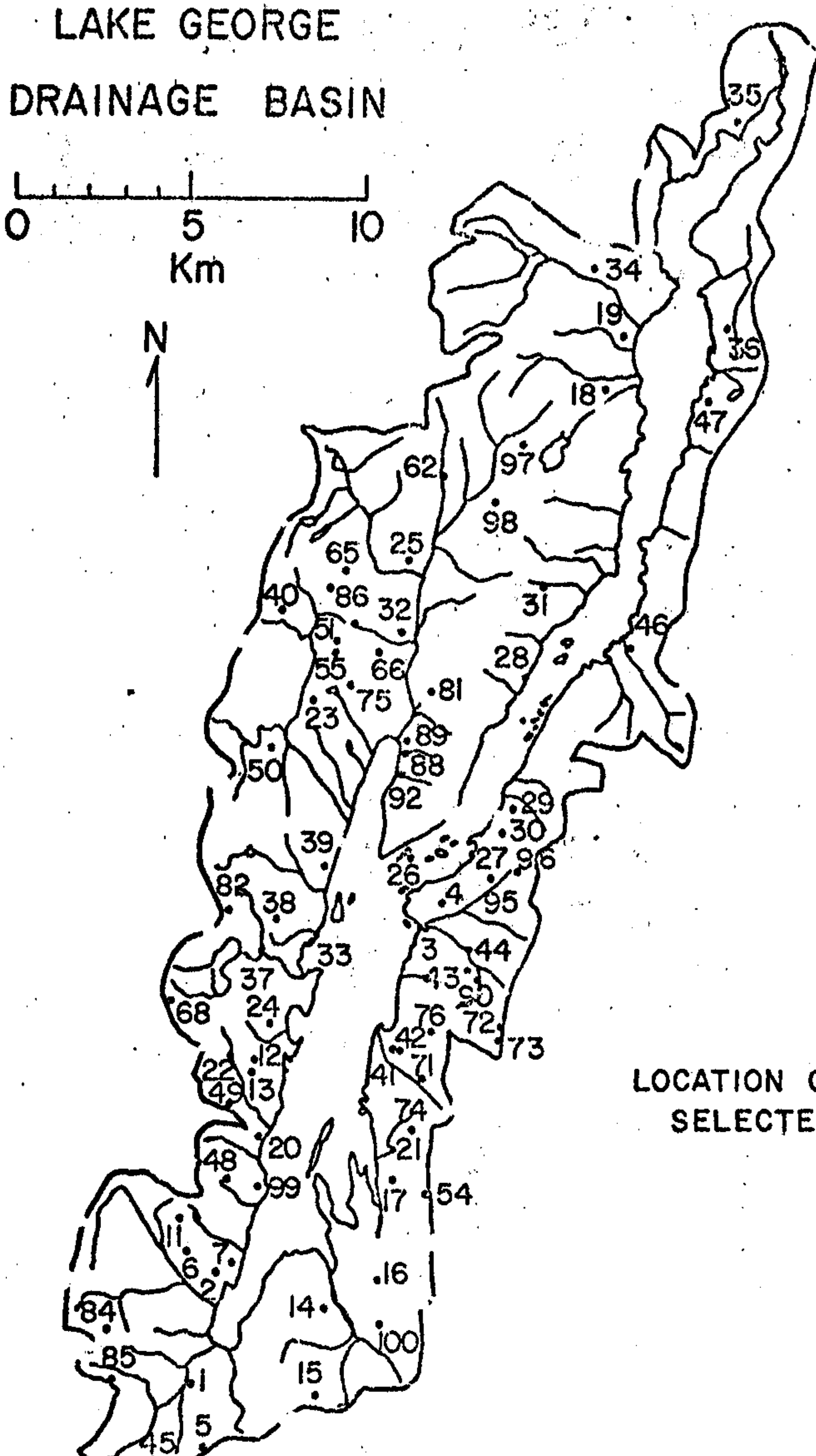
Figure 11 - Above ground tree production of conifer dominated stands on coarse textured sites (10^3 kg/ha/yr) plotted against age.

Figure 12 - Above ground tree production of angiosperm dominated stands on fine textured sites (10^3 kg/ha/yr) plotted against age.

Figure 13 - Above ground tree production of angiosperm dominated stands on coarse textured sites (10^3 kg/ha/yr) plotted against age.

LAKE GEORGE

DRAINAGE BASIN



LOCATION OF RANDOMLY SELECTED STANDS

FIGURE 2

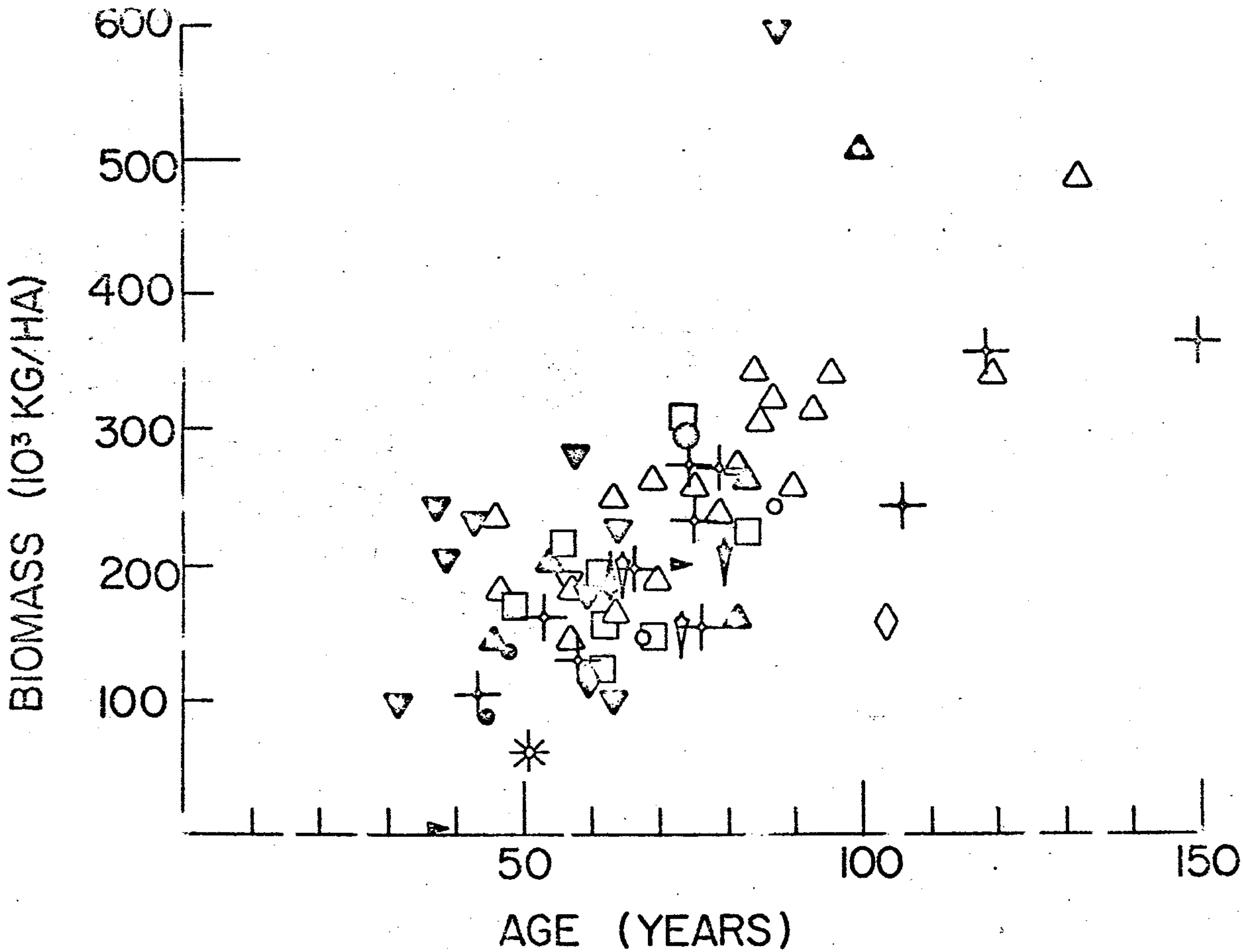


FIGURE 3

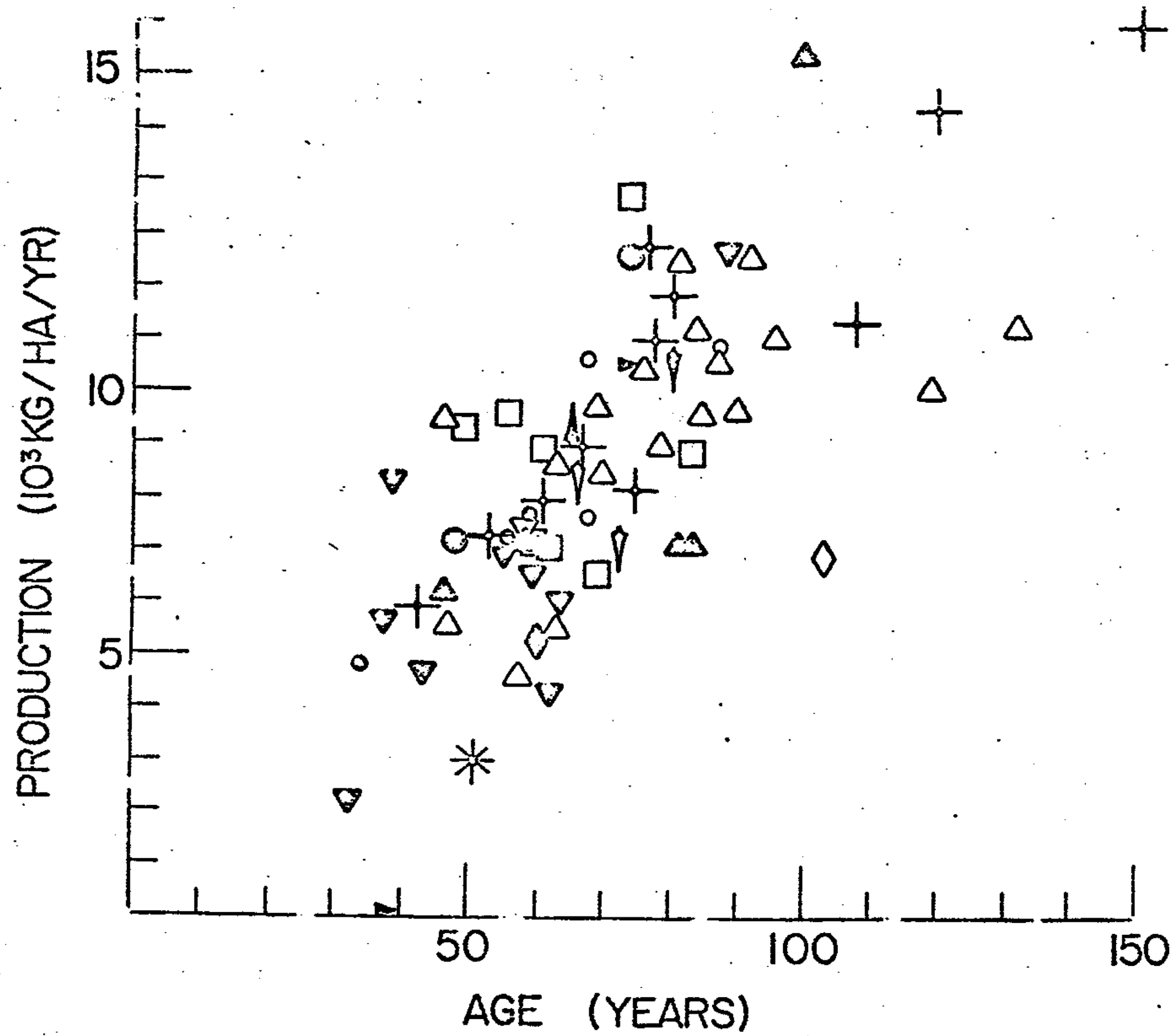


FIGURE 4

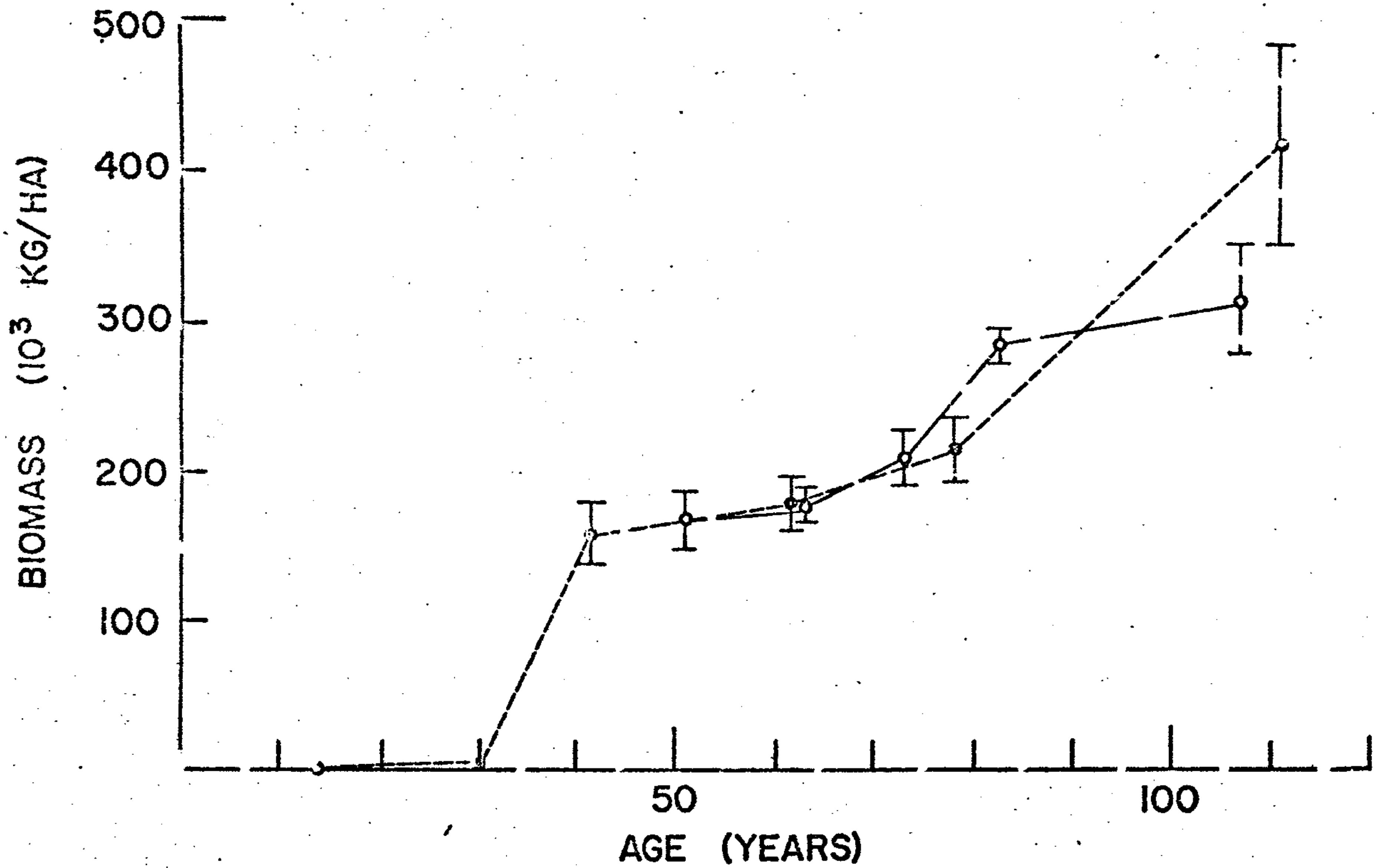
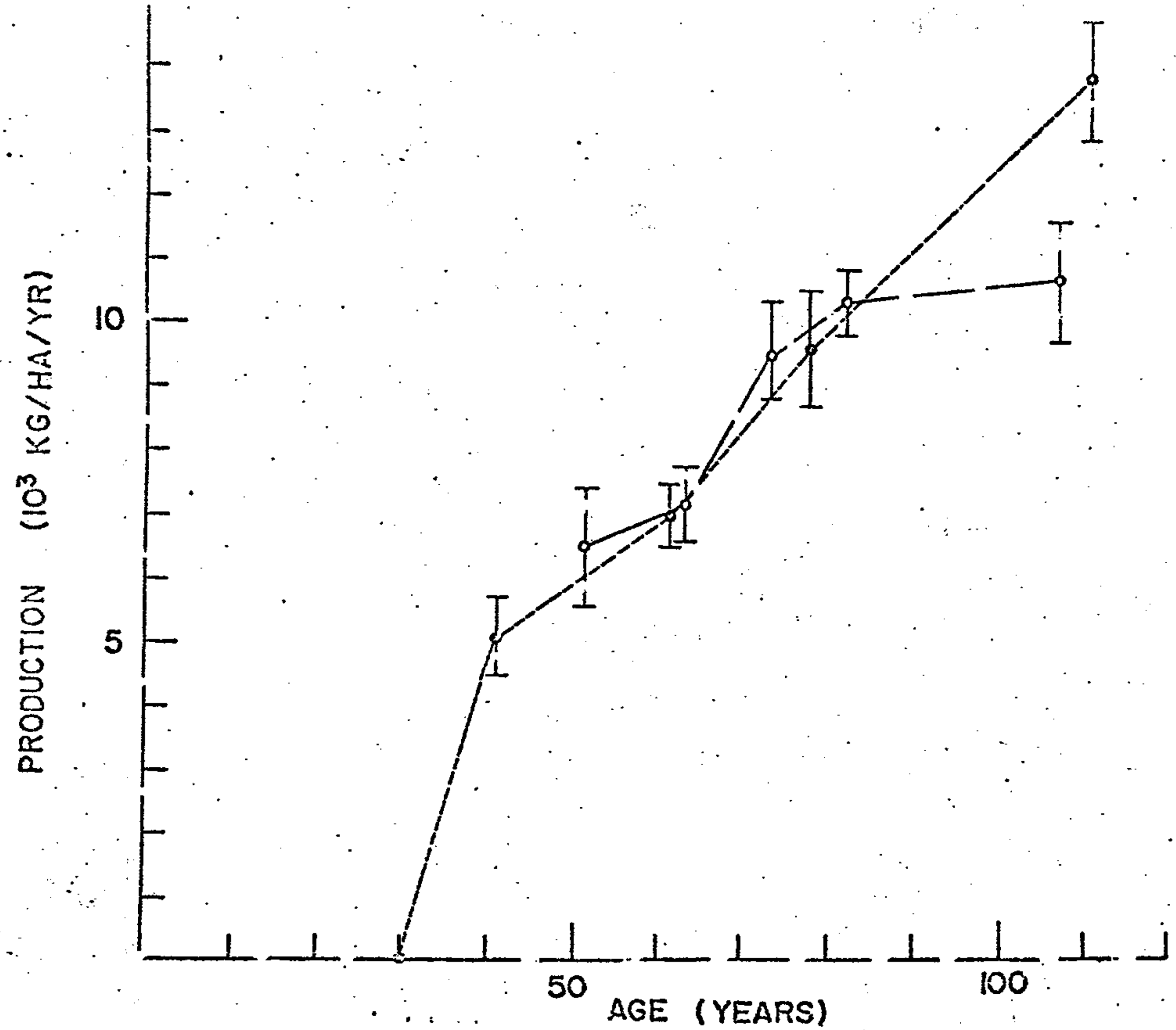


FIGURE 5



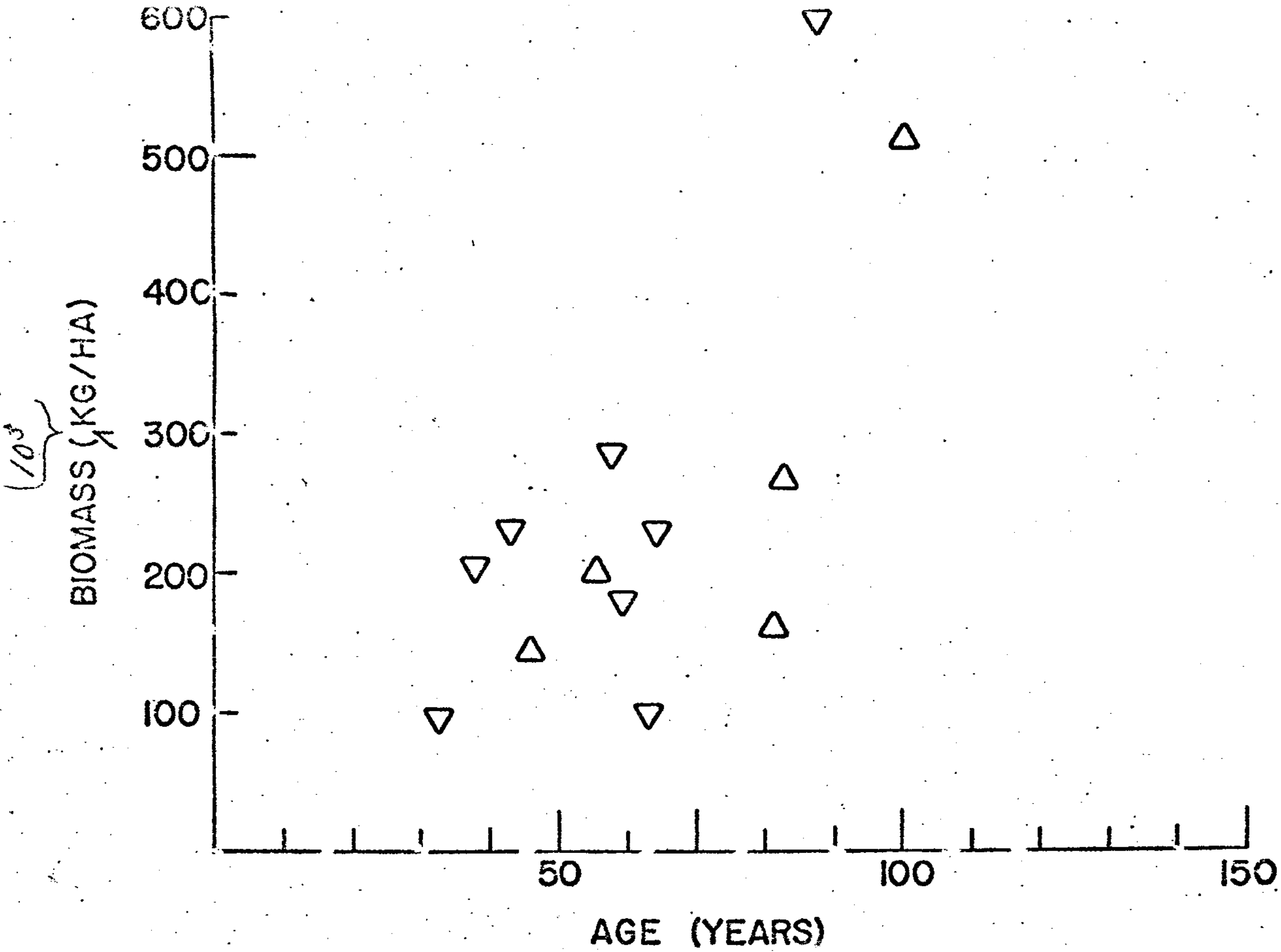


FIGURE 6

FIGURE 7

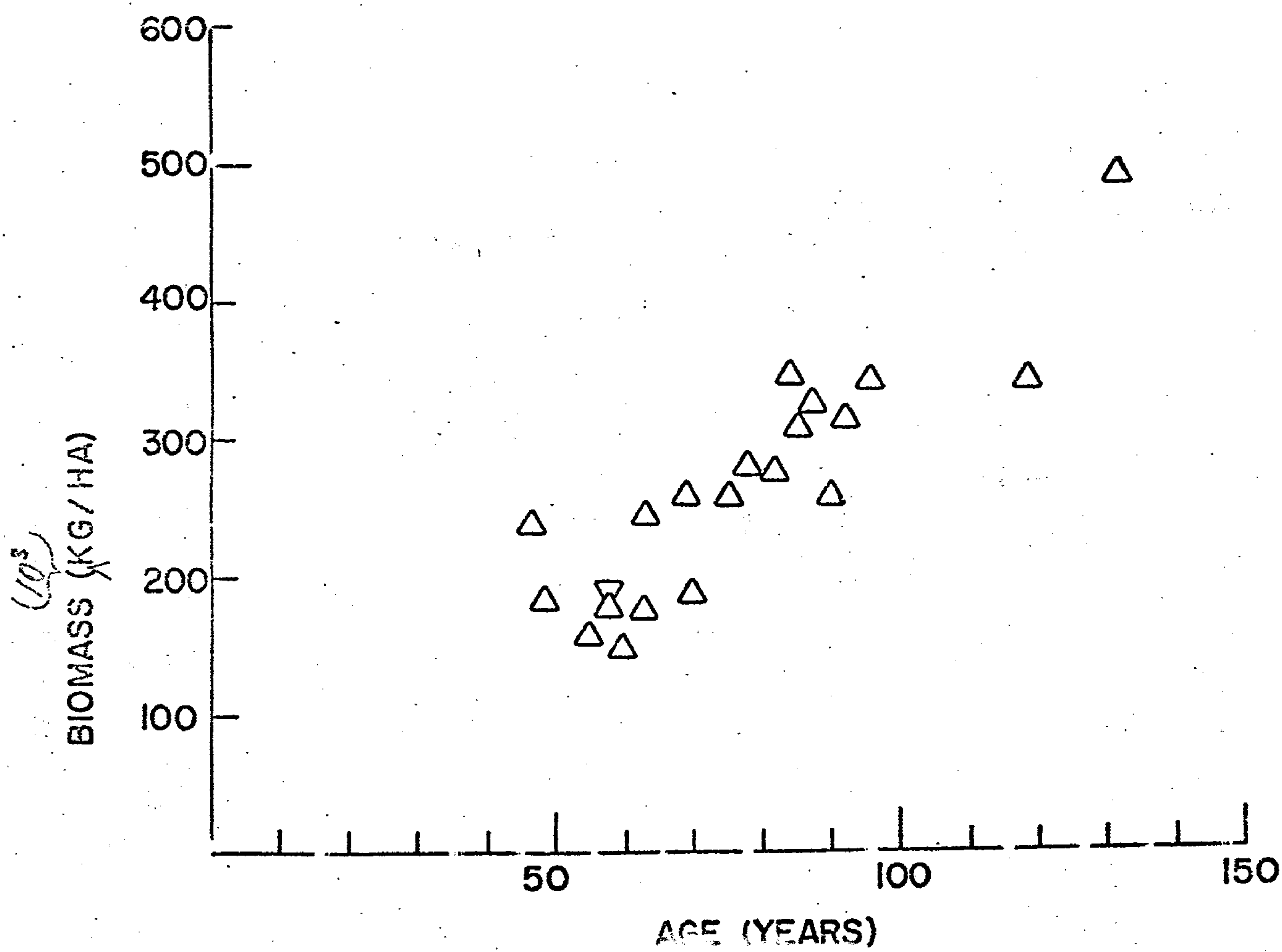
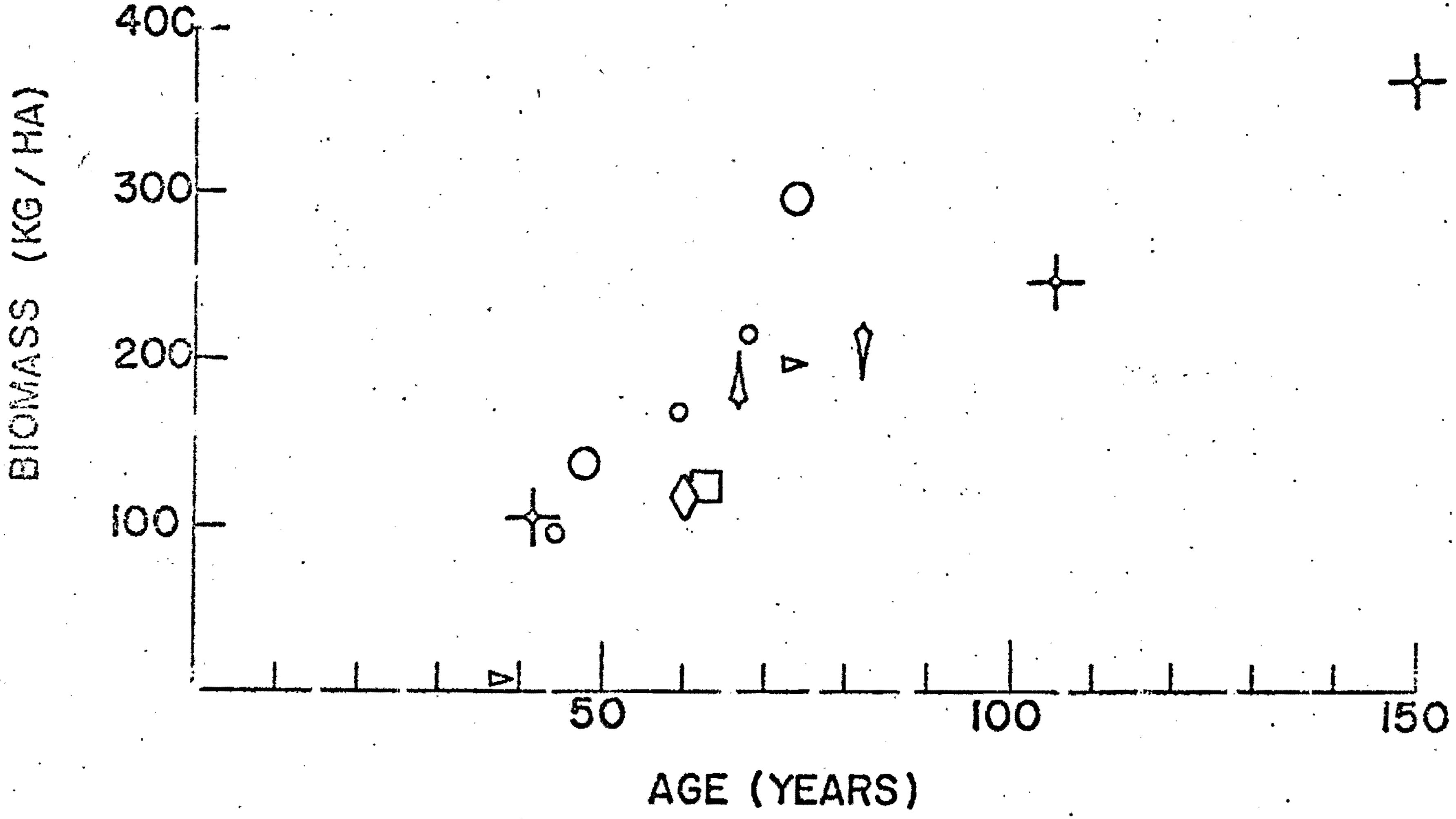


FIGURE 8



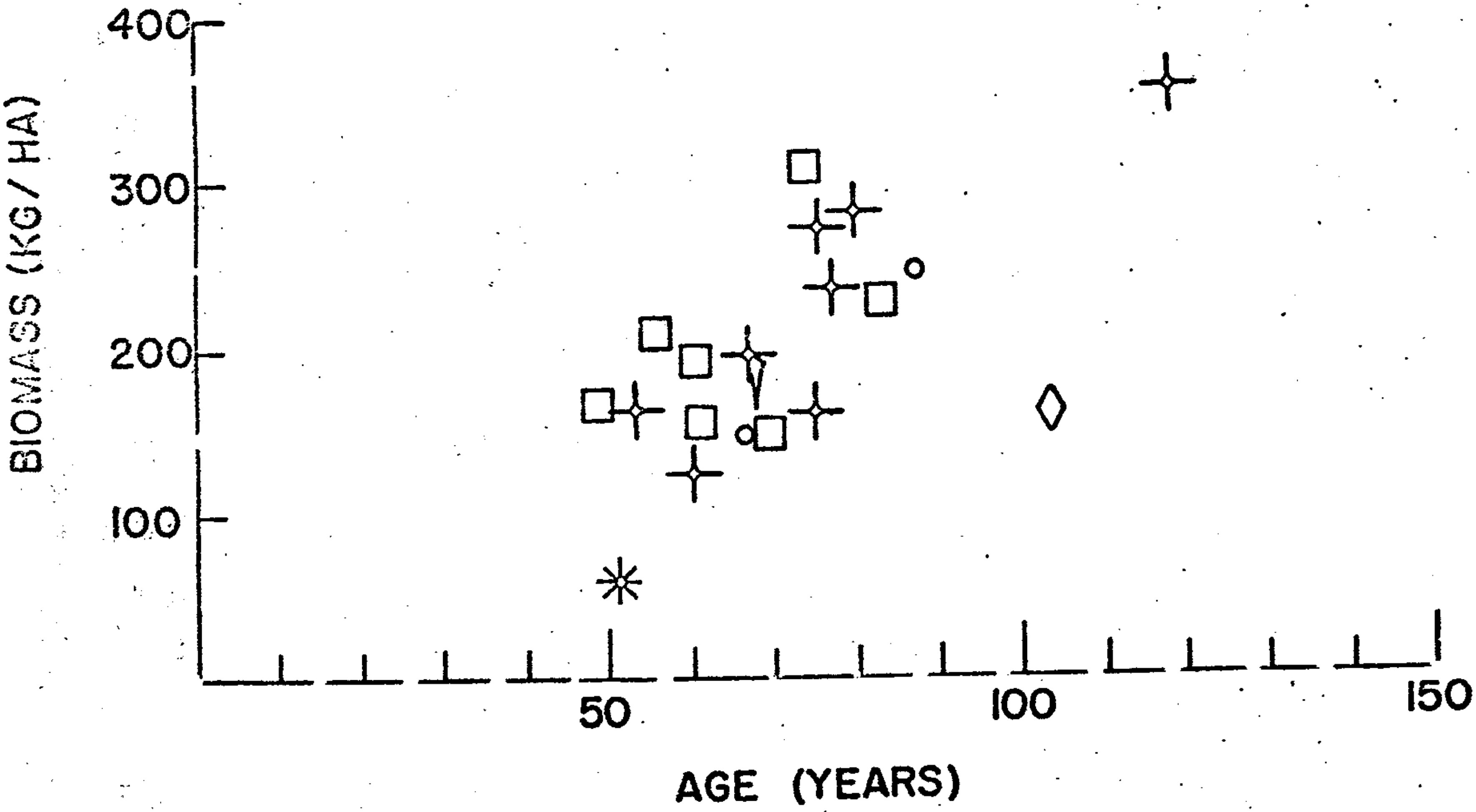


FIGURE 9

FIGURE 10

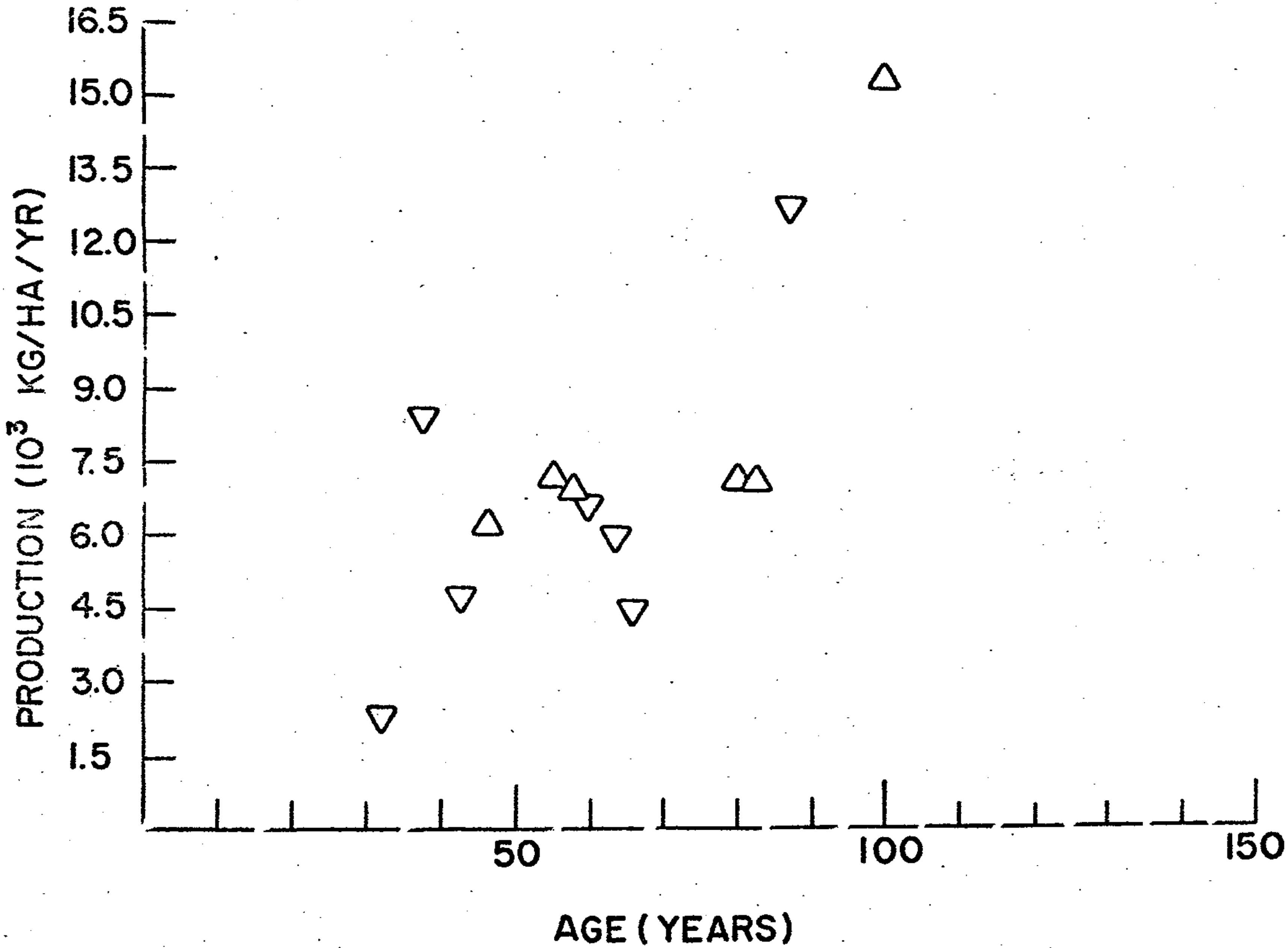
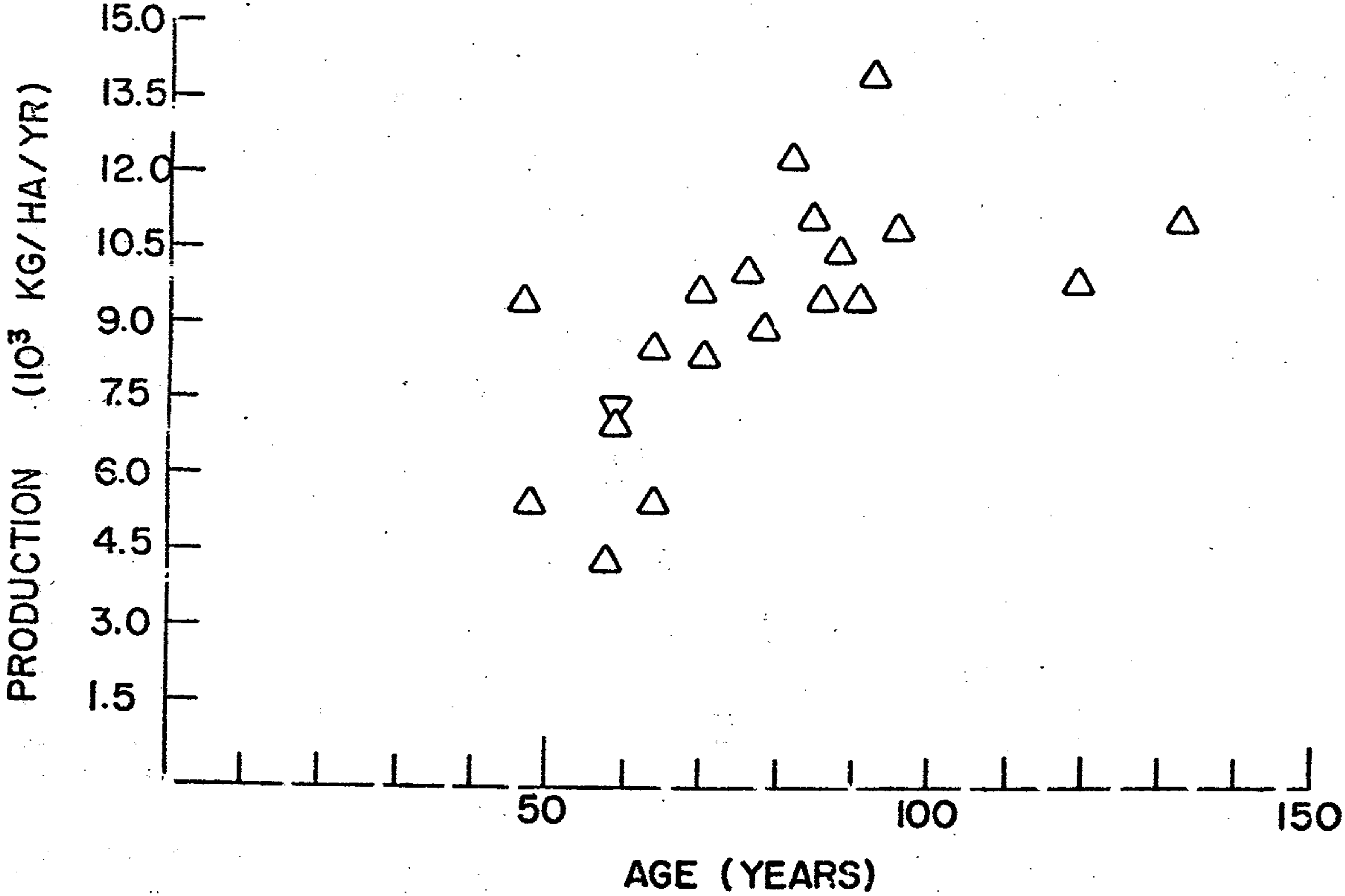

PRODUCTION (10^3 KG/HA/YR)
16.5
15.0
13.5
12.0
10.5
9.0
7.5
6.0
4.5
3.0
1.5
50
100
150
AGE (YEARS)

FIGURE 11


PRODUCTION (10³ KG/HA/YR)
15.0
13.5
12.0
10.5
9.0
7.5
6.0
4.5
3.0
1.5
50
100
150
AGE (YEARS)

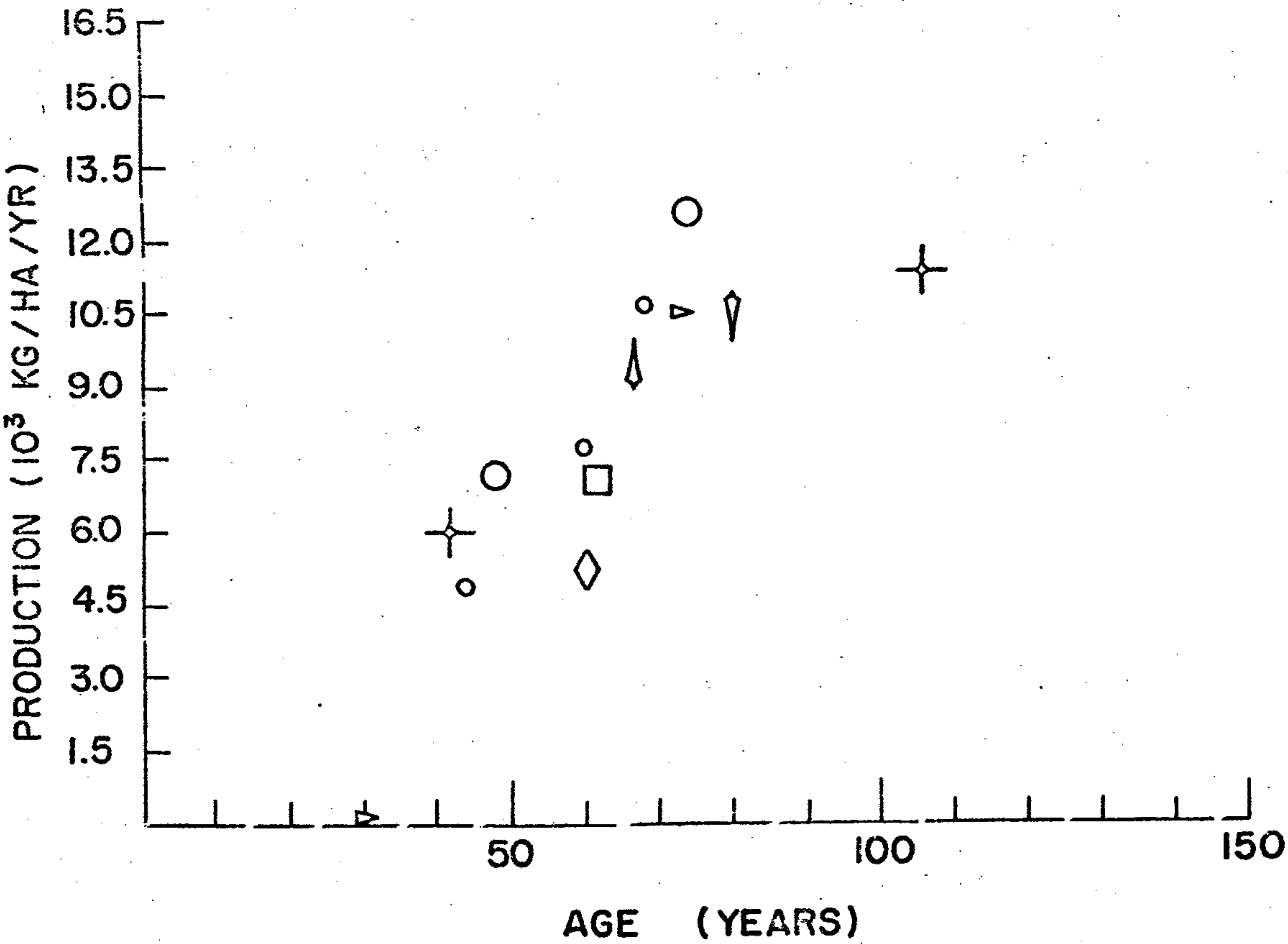
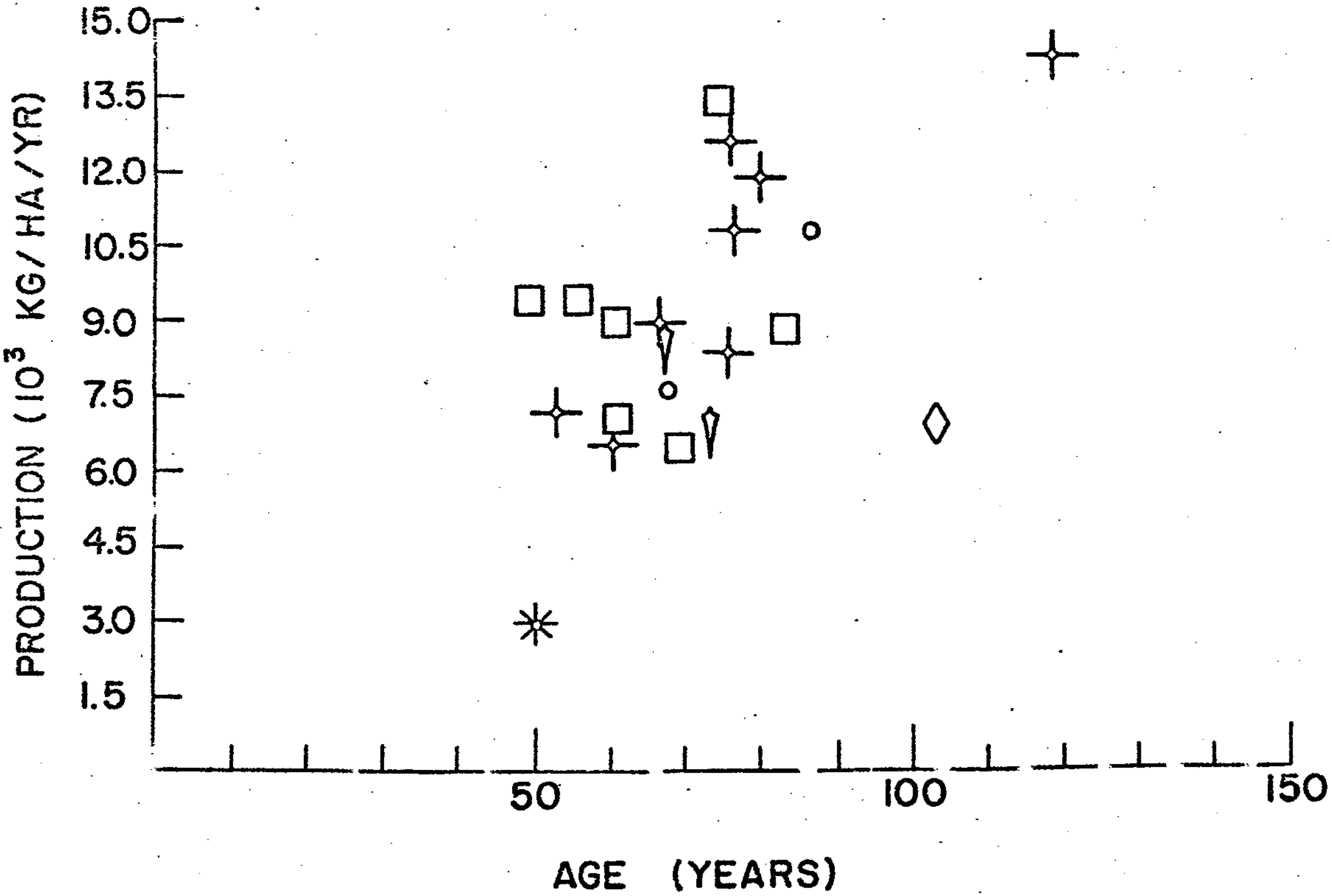

PRODUCTION (10^3 KG / HA / YR)
16.5
15.0
13.5
12.0
10.5
9.0
7.5
6.0
4.5
3.0
1.5
50
100
150
AGE (YEARS)

FIGURE 12

FIGURE 13



PRODUCTION (10^3 KG/HA/YR)
15.0
13.5
12.0
10.5
9.0
7.5
6.0
4.5
3.0
1.5
50
100
150
AGE (YEARS)