

## 短 報

## Primary Productivity Changes for a Fifteen-Year Period in a Natural Beech (*Fagus crenata*) Forest in the Naeba Mountains \*

Yoshitaka KAKUBARI \*\*

### I. Introduction

Primary production studies of natural Japanese beech (*Fagus crenata*) forests were started in the 1960's, and the study in the Naeba Mountains by a Niigata University group was chosen as one of the supporting programs of the Japanese IBP/PT (International Biological Program/Productivity of Terrestrial community) Subcommittee (YAMADA and MARUYAMA, 1962; MARUYAMA, 1971, 1977; KAKUBARI, 1977, 1987). Beech plantations are not common in this country, also were dealt with by TADAKI *et al.* (1969). This paper introduces the distribution of primary productivity along an altitudinal gradient by the use of data of fifteen years, from 1970 to 1984.

### II. Study Site and Methods

The Naeba Mountains are located at about 36° 51' N and about 138° 41' E in the southern part of Niigata Prefecture.

On the northern slopes of the Naeba Mountains, beech forests are distributed over a range of altitude between 550 m and 1,550 m, corresponding to a range of warmth index 45~85 (KIRA, 1949). Bed-rock in the study area is predominantly andesite and basalt, on which the brown forest soil of a moderately moist type has formed.

Eight permanent plots ranging from 800 m<sup>2</sup> to 2,200 m<sup>2</sup> were established in 1970 as shown in Table 1. Plots 1, 7, and 8 were close to the lower and the upper limits, respectively, of beech forests in this area.

At 700 m in altitude, the deep winter snow accumulation (3~4 m in depth) was observed to remain until mid-May; beech leaves began to flush in late April or early May, and the start of the autumn-coloring of leaves took place in late October. Corresponding seasons at 1,500 m were early June (snow melting), late May~early June (leaf flush), and early October (leaf coloring). The duration of the growing period was estimated to be 183 days at 550 m, 173 days at 700 m, 161 days at 900 m, 153 days at 1,100m, 139 days at 1,300 m, and 127 days at 1,500 m.

All living trees on the plots (DBH > 4.5 cm) were numbered, and the positions of stem bases and crown projections were mapped. Each tree was marked with a band of red around the stem at breast height (130 cm), and their DBHs, aboveground heights, and species were recorded. Trees which died during one year and those which newly-reached the size of 4.5 cm DBH in the same year were recorded each autumn.

The upper layer of the canopies of the eight plots consisted mainly of beech with occasional mixtures of a small number of such species as *Quercus mongolica* var. *grosseserrata*, *Magnolia obovata*, *Kalopanax septemlobus*, *Betula grossa*, and *B. ermanii*. The second layer, about 5 m tall, contained *Acer palmatum*, *A. rufinerve*, *A. sieboldianum*, *Acanthopanax sciadophylloides*, *Fraxinus mandshurica*, *Magnolia salicifolia*, and so forth. The mean tree height decreased with increasing altitude at a rate of 30~60% per 800 m.

### III. Tree Mortality and Stem Diameter Increment, 1970~1984

The number of living trees on all plots totaled 698 at the first census in 1970. During the fifteen years, until the fall of 1984, 167 trees were found as standing dead or windfall trees caused by a heavy storm in 1982, whereas 13 stems newly-entered the tree class having a DBH of over 4.5 cm. The total number thus became

\* 角張嘉孝：苗場山ブナ林における15年間の一次生産量の変化

\*\* Fac. of Agric., Univ. of Shizuoka, Shizuoka 422 静岡大学農学部

544 in November 1984 (Table 2).

#### IV. Estimation of Biomass and Biomass Increment

Based on the allometric correlation between various tree dimensions and  $D^2H$  (SATOO, 1962), the stand biomass was estimated. The allometric equation was:

$$\log Y = h \log (D^2H) + K. \quad (1)$$

The dry weights of stems, branches and leaves and the stem-wood volume and leaf area per tree were taken as the dependent variable ( $Y$ ). The values of the two coefficients in the equation used in the calculation,  $h$  and  $K$ , are shown in Table 3.

The calculation of biomass was made for two different times, the spring of 1970 and the fall of 1984, on the assumptions, 1) that the allometric correlations of Table 3 did not change with time, 2) that trees of species other than beech also satisfied the same allometric relationship, 3) that tree-height curves did not

change during the period concerned, and 4) that root biomass was equal to 20% of the aboveground wood biomass. Because Plot 1 (550 m) lacked destructive sampling data obtained at the same levels of altitude, the calculations for this plot were made tentatively using the coefficients for 700 m.

The estimated biomasses in the spring of 1970 ranged from  $180 \text{ t} \cdot \text{ha}^{-1}$  at 1,500 m (Plot 7 in Table 4) to  $420 \text{ t} \cdot \text{ha}^{-1}$  at 900 m (Plot 4 in Table 4), being more or less similar between 700 m and 1,100 m but much smaller at higher altitudes. Except for a somewhat doubtful, smaller value at 550 m, that biomass de-

Table 1. Physiographical features of eight permanent plots along the altitudinal gradient

| Plots | Altitudes (m) | Plot sizes (m <sup>2</sup> ) | Starts of survey | Slopes (degree) |
|-------|---------------|------------------------------|------------------|-----------------|
| 1     | 550           | 2000                         | 14 May 1970      | 0               |
| 2     | 700           | 2200                         | 15 May 1970      | 10              |
| 3     | 700           | 2000                         | 24 May 1970      | 7               |
| 4     | 900           | 2000                         | 11 July 1970     | 7               |
| 5     | 1100          | 800                          | 10 July 1970     | 15              |
| 6     | 1300          | 2000                         | 14 June 1970     | 7               |
| 7     | 1500          | 1000                         | 13 June 1970     | 8               |
| 8     | 1500          | 1400                         | 9 July 1970      | 8               |

Table 2. Frequency distribution of DBH increments of all 531 trees which survived during the fifteen years on eight permanent plots

| Class of DBH increment (cm) | -1 | 0 | 1   | 2   | 3  | 4  | 5  | 6  | 7 | 8 | 9 | 10 | 11 | Total |
|-----------------------------|----|---|-----|-----|----|----|----|----|---|---|---|----|----|-------|
| No. of trees                | 1  | 3 | 198 | 106 | 82 | 69 | 44 | 13 | 9 | 2 | 3 | 0  | 1  | 531   |

Table 3. Coefficient ( $h$  and  $K$ ) of Eq. (1) used for the calculation of aboveground biomass at different altitudes

| Altitudes (m) | Dependent variables |                                |                  |                |                              |        | Sources |
|---------------|---------------------|--------------------------------|------------------|----------------|------------------------------|--------|---------|
|               | Stem wts. (kg)      | Stem volumes (m <sup>3</sup> ) | Branch wts. (kg) | Leaf wts. (kg) | Leaf areas (m <sup>2</sup> ) |        |         |
| 700           | $h$                 | 0.933                          | 0.940            | 1.066          | 0.791                        | 0.699  | * 1     |
|               | $K$                 | -1.401                         | -1.170           | -2.736         | -2.708                       | -0.852 |         |
| 900           | $h$                 | 0.890                          | 0.900            | 1.044          | 0.707                        | 0.594  | * 2     |
|               | $K$                 | -1.214                         | -1.005           | -2.347         | -2.133                       | -0.466 |         |
| 1100          | $h$                 | 0.931                          | 0.940            | 1.365          | 0.720                        | 0.709  | * 3     |
|               | $K$                 | -1.395                         | -1.189           | -3.842         | -2.402                       | -1.152 |         |
| 1300          | $h$                 | 0.915                          | 0.904            | 1.000          | 0.671                        | 0.629  | * 4     |
|               | $K$                 | -1.277                         | -1.050           | -2.250         | -2.015                       | -0.684 |         |
| 1500          | $h$                 | 0.904                          | 0.912            | 0.945          | 0.683                        | 0.656  | * 5     |
|               | $K$                 | -1.330                         | -1.081           | -2.098         | -2.152                       | -0.793 |         |

\*1, KAKUBARI *et al.* (1970); \*2, MARUYAMA and YAMADA (unpublished); \*3, KAKUBARI (unpublished);

\*4, YAMADA and MARUYAMA (1962); \*5, MARUYAMA *et al.* (1970).

Table 4. The estimated biomasses at two different times, spring of 1970 and fall of 1984\*

| Plots | Altitudes<br>(m) | Trees | Vs<br>(m <sup>3</sup> ·ha <sup>-1</sup> ) | Ys<br>(t·ha <sup>-1</sup> ) | Yb<br>(t·ha <sup>-1</sup> ) | Yr**<br>(t·ha <sup>-1</sup> ) | Yl<br>(t·ha <sup>-1</sup> ) | Total<br>(t·ha <sup>-1</sup> ) | U<br>(ha/ha) |
|-------|------------------|-------|-------------------------------------------|-----------------------------|-----------------------------|-------------------------------|-----------------------------|--------------------------------|--------------|
| 1     | 550              | 410   | 411.0                                     | 223.5                       | 45.0                        | 53.7                          | 2.3                         | 324.5                          | 4.5          |
|       |                  | 320   | 454.8                                     | 247.0                       | 51.1                        | 59.6                          | 2.5                         | 360.2                          | 4.7          |
| 2     | 700              | 341   | 460.5                                     | 249.6                       | 53.6                        | 69.2                          | 2.4                         | 374.8                          | 4.4          |
|       |                  | 286   | 425.5                                     | 230.5                       | 50.2                        | 55.2                          | 2.2                         | 338.1                          | 3.9          |
| 3     | 700              | 250   | 526.0                                     | 285.2                       | 60.8                        | 60.7                          | 2.8                         | 409.5                          | 5.0          |
|       |                  | 165   | 419.8                                     | 227.6                       | 48.6                        | 56.1                          | 2.2                         | 334.5                          | 3.9          |
| 4     | 900              | 705   | 445.5                                     | 245.9                       | 100.5                       | 69.3                          | 4.0                         | 419.7                          | 5.5          |
|       |                  | 565   | 476.4                                     | 263.1                       | 110.3                       | 74.7                          | 4.1                         | 452.2                          | 5.6          |
| 5     | 1100             | 1175  | 402.5                                     | 226.9                       | 105.7                       | 66.5                          | 2.3                         | 401.4                          | 3.6          |
|       |                  | 900   | 405.5                                     | 228.3                       | 111.6                       | 68.0                          | 2.3                         | 410.2                          | 3.6          |
| 6     | 1300             | 885   | 240.4                                     | 160.0                       | 41.9                        | 40.4                          | 2.4                         | 244.7                          | 3.3          |
|       |                  | 630   | 259.1                                     | 172.8                       | 45.9                        | 43.7                          | 2.4                         | 264.8                          | 3.4          |
| 7     | 1500             | 590   | 226.6                                     | 117.5                       | 30.7                        | 29.7                          | 1.8                         | 179.7                          | 3.2          |
|       |                  | 480   | 249.5                                     | 129.3                       | 34.0                        | 32.6                          | 2.0                         | 197.9                          | 3.4          |
| 8     | 1500             | 400   | 257.8                                     | 133.3                       | 35.4                        | 33.7                          | 1.9                         | 204.3                          | 3.3          |
|       |                  | 286   | 211.1                                     | 109.2                       | 29.0                        | 27.6                          | 1.6                         | 167.4                          | 2.7          |

\* Upper values mean the biomass in 1970 and the lower ones mean that in 1984, Vs, Volumes of stems ; Ys, Yields of stems ; Yb, Yields of branches ; Yl, Yields of leaves ; Yr, Yields of roots ; U, Leaf-area index ; Total, Ys+Yb+Yr+Yl. \*\* Root biomass was equal to 20% of aboveground wood biomass(Ys+Yb).

Table 5. Estimated rates of gross and net production in beech forests at different altitudes in the Naeba Mountains during the period in 1970~1984

| Plots | Altitudes<br>(m) | Biomass<br>increments | LD  |     | NP  | LR   |     | Total<br>respirations | GP   |
|-------|------------------|-----------------------|-----|-----|-----|------|-----|-----------------------|------|
|       |                  |                       | W   | L   |     | W    | L   |                       |      |
| 1     | 550              | 2.4                   | 2.4 | 2.5 | 7.3 | 17.5 | 7.1 | 24.6                  | 31.9 |
| 2     | 700              | -1.8                  | 4.7 | 2.2 | 5.1 | 16.2 | 5.4 | 21.6                  | 26.7 |
| 3     | 700              | -5.6                  | 8.7 | 2.2 | 5.3 | 16.5 | 5.4 | 21.9 (21.8)           | 27.2 |
| 4     | 900              | 2.2                   | 1.8 | 4.1 | 8.1 | 20.4 | 6.7 | 27.1                  | 35.2 |
| 5     | 1100             | 0.6                   | 1.9 | 2.2 | 4.7 | 20.0 | 3.3 | 23.3                  | 28.0 |
| 6     | 1300             | 1.3                   | 0.8 | 2.4 | 3.7 | 12.9 | 3.1 | 16.0                  | 19.7 |
| 7     | 1500             | 1.2                   | 0.1 | 2.0 | 3.3 | 8.7  | 3.3 | 12.0                  | 15.3 |
| 8     | 1500             | -2.4                  | 3.6 | 1.6 | 2.8 | 8.1  | 2.0 | 10.1 (11.1)           | 12.9 |

Notes : Data are shown as dry weights(t·ha<sup>-1</sup>·y<sup>-1</sup>) ; LD, Loss by death ; NP, Net production (biomass increment+LD(W) + LD(L)) ; LR, Loss of respiration ; GP, Gross production (NP+total respiration) ; W, Wood ; L, Leaves.

Biomass increment means biomass differences of the yield of stems, branches and roots, for two different times, the spring of 1970 and the fall of 1984.

Numerals in parentheses indicate the average total respiration for altitudes indicated.

creased with increasing altitude was apparent. The difference in biomass of trees that survived throughout the fifteen years gives the biomass increment. Its rate was greater than 2.3(2.2~2.4)t·ha<sup>-1</sup>·y<sup>-1</sup> between 550 m and 900 m, but was less 1.3(1.2~1.3)t·ha<sup>-1</sup>·y<sup>-1</sup> above 1,300 m(refer to biomass increment in Table 5). The negative values of "Biomass increments" in Table 5 indicate the loss of stand biomass due to death and to windfall trees. Subtracting this loss and adding the biomass of newly-counted trees to the increment of the living tree biomass, the net increase in stand biomass was calculated as shown in Table 5. The rate of net biomass increase was the largest on Plot 1 at 550 m(2.4 t·ha<sup>-1</sup>·y<sup>-1</sup>), and generally was greater at lower altitude plots than at higher altitude plots.

## V. Loss of Organic Matter Due to Litter-Fall and Community Respiration ; Estimation of Litter-Fall

Leaf litter accounted for nearly 80% of the plots' means of total litter-fall rates ( $2.6\sim 5.0 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ ). This amounted to  $2.5\sim 3.5 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  in a previous report (KAKUBARI, 1977). The branch litter contributed about 20% ( $0.1\sim 2.0 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ ), and other fractions, except seeds, were negligibly small in amounts. Japanese beech forests tend to have a mast-year every 5~7 years (MAEDA, 1988). A considerable amount of masts was 2~5% of the total litter-fall. Annual mean litter-falls are shown under LD(L) of Table 5. Both leaf litter (LD (L)) and leaf biomass (Y1) had maximum values at 900 m (Plot 4). The amount of litter was likely to have a peak at 900 m, gradually decreasing toward both higher and lower altitudes.

## VI. Estimation of Community Respiration

The loss of organic matter by community respiration was calculated on the basis of some of the reports of the referenced researchers. The mean respiration rate in leaves ( $r$ :  $\text{mgCO}_2\cdot\text{dm}^{-2}\cdot\text{h}^{-1}$ ) as a function of temperature ( $T^\circ\text{C}$ ) was assumed to be according to NOMOTO (1964).

$$r = 0.15 \times 2.03^{T/10} \quad (2)$$

Combining this Eq.(2) with the estimates of leaf area indexes (U in Table 4) and monthly mean-temperatures of the plots, monthly amounts of leaf canopy respiration were computed. The mean respiration loss in woody organs was assumed simply to be equal to 0.049 of their biomass according to MARUYAMA *et al.* (1968).

## VII. Altitudinal Changes in Production Rates

The rates of net production were approximated by the sum of the rates of net biomass increase and litter-fall, neglecting the consumption by grazing of herbivores. The litter-fall rates (KAKUBARI, 1977) at 550 m and 1,100 m were substituted by those at 700 m and 900 m, respectively, because they were not actually measured. The gross production rate was obtained by adding the rate of community respiration to that of net production. The results are summarized and are shown in Table 5 as average rates of gross and net productions during the period of 1970 to 1984.

All of the net production, community respiration and gross production tended to culminate at the middle altitudes around 900 m. Because each level of altitude was represented by one or two plots, the altitudinal trend in Table 5 may not be greatly reliable, but it is not unreasonable that a plant community should exhibit its maximum capacity near the center of its distribution range along a certain environmental gradient. The estimated net production was approximately  $3.1 (2.8\sim 3.3) \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  at 1,500 m and  $5.2 (5.1\sim 5.3) \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  at 700 m in Table 5, decreasing by about 40% with the increase of altitude to 800 m. The corresponding decrease in the community respiration rate was about 50% per 800 m increase in altitude from  $21.8 (21.6\sim 21.9) \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  at 700 m to  $11.1 (10.1\sim 12.0) \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  at 1,500 m as shown in Table 5.

## Acknowledgements

The author thanks Emeritus Professors T. SATOO and K. NEGISI of University of Tokyo for suggesting this study. He also thanks his colleagues of the Institutes of Silviculture at Tokyo and Niigata Universities for their help in the field work as well as the members of the Maebashi Regional Forest Office and the Muikamachi District Forest Office.

## Literature cited

- KAKUBARI, Y.: Distribution of primary productivity along the altitudinal gradient. *J. Int. Biol. Program Synth.* **16**: 201~212, 1977
- : Modelling the productive structure and function of natural forests of *Fagus crenata* at different altitudes in Naeba Mountains—An analysis of dry matter production with an eco-physiological computer simulation model based on an individual tree. *Bull. Tokyo Univ. For.* **76**: 107~162, 1987
- , MARUYAMA, K., and YAMADA, M.: Ecological studies on natural beech forest (21). A comparative study of

- biomass and productivity according to altitudes on beech forest. *Niigata Norin Kenkyu* 22: 43~55, 1970 (in Japanese with English Summary)
- KIRA, T.: Forest zones of Japan. Ringyo Gijutsu Kyoukai, Tokyo, Sapporo, 41pp, 1949 (in Japanese)
- MAEDA, T.: Studies on natural regeneration of beech (*Fagus crenata* BLUME). *Spec. Bull. Col. Agric. Utsunomiya Univ.* 46: 1~79, 1988 (in Japanese with English Summary)
- MARUYAMA, K.: Effect of altitude on dry matter production of primeval Japanese beech forest communities in Naeba Mountains. *Mem. Fac. Agric. Niigata Univ.* 9: 85~171, 1971
- : Beech forests in the Naeba Mountains. *J. Int. Biol. Program Synth.* 16: 186~212, 1977
- , YAMADA, M., and NAKAZAWA, T.: A tentative estimation of the gross photosynthetic production—Ecological studies on natural beech forest (17). *Trans. 79th Meet. Jpn. For. Soc.*: 286~288, 1968 (in Japanese)
- , KAKUBARI, Y., NAKADA, K., and YAMADA, M.: On the estimation of biomass and production of natural beech forest at its upper limit of distribution. Comparative study of primary productivity in forest ecosystems. *In* Progress report for 1969 (SHIDEI, T., ed.). 42~46, 1970 (in Japanese)
- NOMOTO, N.: Primary productivity of beech forest in Japan. *Jpn. J. Bot.* 18: 385~421, 1964
- SATOO, T.: Notes on KITTREDGE's method of estimation of amount of leaves of forest stand. *J. Jpn. For. Soc.* 44: 267~272, 1962
- TADAKI, Y., HATIYA, K., and TOCHIAKI, K.: Studies on the production structure of forest (XV). Primary productivity of *Fagus crenata* in plantation. *J. Jpn. For. Soc.* 51: 331~339, 1969 (in Japanese with English Summary)
- YAMADA, M. and MARUYAMA, K.: Quantitative ecological studies on natural beech forests. *Trans. 72nd Meet. Jpn. For. Soc.*: 245~248, 1962 (in Japanese)

(Received December 11, 1990)