

Distribution of C₃ and C₄ Plants and Changes in Plant and Soil Carbon Isotope Ratios with Altitude in the Kirigamine Grassland, Japan

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Synopsis

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The aim of this study was to clarify how temperature underlines the proportion of C₃ and C₄ grasses along an altitudinal gradient in the Kirigamine grassland of central Japan. We investigated the altitudinal patterns of C₃ and C₄ plants in the Kirigamine grassland (1,500 to 1,920 m a.s.l.), and analyzed its relationship to temperature, topography and soil carbon and nitrogen contents based on field survey data of 1992 to 1995. The C₄-grass percentage (measured as % of total grass coverage or biomass) decreased and the C₃-grass percentage increased with altitude, indicating the existence of a transition between C₃ and C₄ grasses in the grassland. Seasonal changes in the proportion of C₄ and C₃ grasses of the C₃-C₄ transition indicated that there was a shift of productive activities from C₃ to C₄ grasses with increasing temperature. The significant correlation between percentage of C₄ and C₃ grasses and temperature-related factors suggests that temperature is of primary importance in determining the proportions of C₄ and C₃ grasses along the altitudinal gradient. Precipitation, soil C and N contents, and topographical factors (slope inclination and aspect) showed less influence on the transition in the grassland. On the other hand, the C₃-C₄ balance point (C₃ and C₄ grasses each constituting 50% coverage) in the Kirigamine grassland had a mean August (the warmest month) minimum temperature of 13°C, which was in rough agreement with the balance point in other temperate regions but higher than that of tropical regions. This suggests that C₄ plants require warmer summer for distribution to higher latitudes.

We measured carbon isotope ratios ($\delta^{13}\text{C}$) of vegetation and found that the values decreased with increasing altitude, and indicating the transition from C₄ to C₃ grasses with increasing altitude as well. Moreover, we clarify the changes in altitudinal pattern of C₃ and C₄ plants in past

vegetation of the Kirigamine grassland, based on the changes in carbon isotope ratios of present vegetation and soil organic matter with increasing altitude. The $\delta^{13}\text{C}$ C value of soil organic carbon at the 1660-m site was -18.2‰ , while the present vegetation $\delta^{13}\text{C}$ value was -18.6‰ , suggesting a similar C₃/C₄ ratio in the past (recorded in soil $\delta^{13}\text{C}$ value) as at the present at this site. However, at the 1715-m and 1830-m sites, the soil $\delta^{13}\text{C}$ values were -19.5‰ and -21.2‰ , whereas the present vegetation $\delta^{13}\text{C}$ values were -22.3‰ and -26.1‰ , respectively. These results strongly suggest that a greater proportion of C₄ plants occupied the communities at the higher altitudes in the past.

Key words : Altitudinal pattern, C₃ and C₄ plants, Carbon isotope ratio, Kirigamine grassland, Past vegetation, Temperature.

Introduction

Temperature is not only known to influence plant growth in numerous ways, but is also an important determinant in the natural distribution of plants. The role of temperature in determining species distribution is currently receiving renewed attention, because it is important in prediction of vegetation response to global climate change (Epstein *et al.* 1997). Since the 1970s numerous studies have been conducted on species distribution along temperature gradients at the latitudinal scale (Teeri and Stowe 1976, Hattersley 1983; Takeda *et al.* 1985; Okuda 1987) and at the altitudinal scale (Tieszen *et al.* 1979; Boutton *et al.* 1980; Rundel 1980; Cavagnaro 1988; Earnshaw *et al.* 1990). These studies have demonstrated the existence of a transition from C₄ to C₃ species along an increasing altitudinal or latitudinal gradient. The analyses often concentrate on the Poaceae, which contains nearly half of all known C₄ species. These studies all indicated that temperature is of primary importance in determining the distribution of C₃ and C₄ species regionally, although water

availability was also important in a few studies (Tieszen *et al.* 1979; Hattersley 1983; Cavagnaro 1988). There were some common findings for the relationship between temperature and the proportion of C₃ and C₄ grasses regionally: (1) Mean minimum temperature for the warmest month often strongly correlated with the relative abundance of C₄ grasses locally, which is suggested to reflect the warmer the nights and the greater success of C₄ taxa (Teeri and Stowe 1976); (2) The C₃-C₄ balance point where C₃ and C₄ grasses each constitutes 50% of the total number, has a mean minimum temperature for the warmest month of 13–15°C in temperate regions (Teeri and Stowe 1976; Ehleringer 1978; Hattersley 1983; Cavagnaro 1988), and of 8°C in tropical regions (Tieszen *et al.* 1979; Rundel 1980); and (3) the absolute limit of C₄ species distributions has a mean minimum of 8–10°C during the warmest month of the year either in temperate or in tropical regions (Teeri and Stowe 1976; Ehleringer 1978; Rundel 1980; Hattersley 1983; Cavagnaro 1988). However, most of these studies were conducted in tropical or temperate semi-arid to arid regions where a temperature (altitudinal or latitudinal) gradient is usually correlated with a soil moisture gradient. This makes it difficult to distinguish the effects of temperature and other environmental factors (*e.g.* soil moisture) on the transition of C₃ and C₄ species (Hattersley 1983; Paruelo and Lauenroth 1996). A few studies in Japan have reported that the distribution of C₃ and C₄ grasses is primarily dependent on temperature-related factors in grasslands at the latitudinal scale (Takeda *et al.* 1985; Okuda 1987; Okuda and Furukawa 1990). However, information still lacks on the distribution of C₃ and C₄ grasses along an altitudinal gradient in Japan.

It is widely accepted that carbon isotope ratios ($\delta^{13}\text{C}$) in soil or plant material can be an essential indicator of the proportion of C₃ and C₄ species at a given altitude (Tieszen *et al.* 1979; Bird *et al.* 1994). Tieszen *et al.* (1979) found that an increase in negative $\delta^{13}\text{C}$ value paralleled the proportion of C₄ species along an increasing altitudinal gradient. The overall processes of decomposition of plant organic materials cause only less than 2‰ changes in the $\delta^{13}\text{C}$ values of the organic carbon remaining in soils, which are due to isotopic fractionation during mineralization and slower decomposition of lignins (Benner *et al.* 1987). The $\delta^{13}\text{C}$ values of vegetation are largely determining soil $\delta^{13}\text{C}$ values (Balesdent *et al.* 1987). Therefore, carbon-isotope analysis of soil organic matter is useful for detecting past vegetation changes (Dzurec *et al.* 1985; Wedin *et al.* 1995).

We previously demonstrated that in the Kirigamine grassland of central Japan, there exists a

sharp transition from *Miscanthus sinensis* Anderss. (C₄ grass) dominance to *Calamagrostis longiseta* Hack. (C₃ grass) dominance as the altitude increases from 1,650 to 1,850 m a.s.l. (Nishimura *et al.* 1997). Because of this sharp transition under a high annual precipitation (>1,665 mm), it suggests that temperature-related factors would principally underline the transition of C₃ and C₄ grasses rather than soil moisture in Kirigamine grassland. However, even under a high annual precipitation, C₃ and C₄ grasses may be distributed differently depending on slope exposure, due to soil moisture condition expecting to be different with slope exposure according to main wind direction. We investigated the altitudinal pattern of the distribution of C₃ and C₄ grasses in the Kirigamine grassland (1,500 to 1,900 m) from 1992 to 1995, and analyzed its relationship to temperature and topographical factors such as slope inclination, slope aspect and soil nitrogen content. The main aim of this study was to clarify how temperature underlines the proportion of C₃ and C₄ grasses along an altitudinal gradient in the Kirigamine grassland, and comparing with the distribution pattern of C₃ and C₄ grasses in other regions. The aim was also to clarify past vegetation based on the changes in carbon isotope ratios of present vegetation and soil organic matter with increasing altitude.

Materials and Methods

1. Site description

The Kirigamine grassland is situated in Nagano Prefecture, central Japan (36°07'N, 138°10'E; see Nishimura *et al.* 1997 for details); the highest peak is Mt. Kurumayama (1,925 m). The semi-natural grassland ranges from 1,500 to 1,920 m a.s.l. and extends over 3,000 ha (Midorikawa *et al.* 1964). The grassland had been mown for animal husbandry since the early seventeenth century (about 370 years ago), but such utilization was stopped in the 1960s (Nishimura *et al.* 1997). Suzuki *et al.* (1981) supposed that the original forest vegetation of this area was dominated by *Abies homolepis* Sieb. et Zucc. and *Abies veitchii* Lindl., which are regarded as indicators of climax coniferous forest in the subalpine climatic zone of Japan (Maekawa 1974). Some *A. homolepis* forest is still present in some places. The annual mean air temperature is 2.5°C at the peak of Mt. Kurumayama and 4.7°C at 1,675 m a.s.l. (Midorikawa *et al.* 1964; Nishimura *et al.* 1997). The warmth index is 47.5 (°C month) at 1,675 m and 35.1 at 1,925 m, and the annual precipitation ranges between 1,665 and 1,855 mm (Nishimura *et al.* 1997). Wind blows from the south mainly throughout the whole year, and during the winter wind direction from S-SSW results in a great amount of snowfall accumulated at north slope (max.

500 cm) than at south slope (around 50–100 cm) (Midorikawa *et al.* 1964 ; Nishiwaki 1982). The soil type in this area is classified as Andosol, which originates mainly from volcanic ash and is very rich in organic matter (Midorikawa *et al.* 1964). The present grassland vegetation consists of perennial tall-grass communities dominated by *M. sinensis* (C₄) at lower altitudes and by *C. longisetata* (C₃) or partly by *C. langsdorffii* (Link) Trin. (C₃) at higher altitudes. A very slow succession of this grassland toward forest is occurring (Nishimura *et al.* 1997 ; Shimoda 2001). The 8-year (1994–2000) vegetation data from 1,600-m site showed that current *Miscanthus sinensis* grassland in Kirigamine is in a stable situation (Shimoda 2001). It suggested that the *Miscanthus sinensis* grassland in Japan could maintain for several tens years or more than hundreds years after abandoned (Sakanoue 2001). We therefore have enough reasons to consider that current vegetation may be determined by environmental factors in a greater degree in the Kirigamine grassland after abandoned for more than 30 years.

2. Field surveys and data analysis

A general vegetation survey (floristic composition of 31 stands at different altitudes) was carried out in early July of 1992, 1993, and 1994 (see Nishimura *et al.* 1997 ; detailed data are also available from the first author of present paper). Eight plots (stands), which we regarded to have typical floristic composition at different altitudes of the grassland, were selected for biomass sampling and carbon isotope analysis : plots 1 (1,630 m), 24 (1,660 m), 18 (1,710 m), 25 (1,715 m), 20 (1,790 m), 15 (1,830 m), 5 (1,850 m), and 31 (1,920 m). The air temperature (at 1.0 m high) was measured at 1,672 m (site-a) and 1,805 m (site-b) from June 1995 to October 1997, by using two KADEC recorders (Kona System Co., Ltd., Tokyo, Japan). Each recorder was put in a hand-made woody box with four legs, and the temperature sensor was shaded by the box and set at a wind-draw well place for each site. The air temperature (annual mean, annual minimum, and minimum temperature for the warmest month (August)) of each plot was calculated from the local rate of change of temperature with altitude, around 0.60°C per 100 m of altitude, which was determined from the air temperature data for 1995–1997 at site-a and site-b. StatView version 5.0J (Version 1998, SAS Institute Japan Ltd., Tokyo, Japan) was used for all statistical analyses.

We surveyed each stand in six 1-m² quadrats, since total surveyed area of 6-m² was large enough for the minimal area of the grassland (Numata 1976). At each stand, slope inclination was recorded using a ranking scale of 0–4, where 0 was no inclination, 1 was very slight (<5°), 2 slight (5–10°), 3 moderate (10

–15°), and 4 steep (>15°). Slope aspect was numbered as the following designations : 0=north facing, 90= east or west facing, and 180=south facing. Since the main wind direction blows from the south, the south slope is expected to have limited soil moisture comparing to the north slope. Therefore, the greater number of slope aspect indicated the relatively limited soil moisture of the site (we excluded the 4 sites with flat topography for the statistical analysis in order to make the relationship of vegetation and slope aspect more clearly, i.e. n=22). The % coverage of each species within each quadrat was estimated, and the mean of the six quadrats was calculated. Changes in the biomass of C₃ and C₄ grasses with altitude were measured from 1630 m to 1920 m in late August 1994, when the Kirigamine grassland maximized its standing biomass (Midorikawa *et al.* 1964). In plots 1, 24, 25, 20, 15, and 31, six 1-m² quadrats were laid out randomly, and the aboveground parts were cut and separated to grasses (each species), the dwarf bamboo *Sasa chartacea* Makino var. *nana* (Makino) S. Suzuki and others (non-grass species), and dried at 80°C for 48 hours.

Seasonal changes in standing biomass at different altitudes were measured from June to September in 1993 (plots 1, 18, 5) and 1994 (24, 25, 15). We sampled one 1-m² quadrat in each plot to measure the aboveground biomass of each grass species, *Sasa chartacea*, and other non-grass species, which were dried at 80°C for 48 hours. Plant samples collected in July 1993 were used for carbon isotope analysis.

3. Soil sampling

Soil samples (removed of roots) were collected from different altitudes (plots 24, 25, 15) on 19 June 1995. The soil was sampled every 5 cm from soil surface to 15 or 20 cm depth by soil core samplers (100 cm³), and two points (5-m distance with each other) were sampled for each plot. Soil samples were dried at 105°C for 48 hours and weighed. Soil carbon (C) and nitrogen (N) contents were measured with a NC-analyzer (Sumigraph Model NC-800, Shimadzu Co. Ltd., Tokyo, Japan). The left soil samples were used for carbon isotope analysis.

4. Carbon isotope analysis

Dried samples (soil or plant materials) were ground into fine powder in a vibration mill (Heiko Co. Ltd., Tokyo, Japan). The carbon isotope ratios ($\delta^{13}\text{C}$) of the samples (each containing 300 to 800 μg C) were determined with an isotope ratio mass spectrometer (ANCA-SL, Europe Scientific Ltd., Crewe, UK). L-Alanine was used as the working standard with a $\delta^{13}\text{C}$ value of -21.9‰ in reference to the PDB (belemnite from the Pee Dee Formation in South Carolina) standard. The $\delta^{13}\text{C}$ of organic matter is expressed as per mil deviation, calculated with Eq. 1

$$\delta^{13}\text{C}(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where R is $^{13}\text{C}/^{12}\text{C}$ (O'Leary 1981; Yoneyama *et al.* 2001). For each sample, the analytical error was within $\pm 0.15\text{‰}$ (detailed description for carbon isotope analysis has given in Yoneyama *et al.* 2001).

Plant samples collected in July 1993 from different altitudes (plots 1, 18, 5; each one 1-m^2 quadrat), which divided into each grass species, *Sasa chartacea* and other non-grass species, were used for the carbon isotopic analysis. For each plot, the grass $\delta^{13}\text{C}$ value ($\delta^{13}\text{C}$ value of total grass biomass) can be calculated by a mass-balance equation (Bird *et al.* 1994) (Eq. 2):

$$\text{grass-}\delta^{13}\text{C} = \sum_{i=1}^n (\delta^{13}\text{C}_{\text{grass}(i)} \times \alpha_{\text{grass}(i)}) \quad (2)$$

where $\delta^{13}\text{C}_{\text{grass}(i)}$ is the carbon isotope ratio of grass species (i), and $\alpha_{\text{grass}(i)}$ is the % biomass of grass species (i) to total grass biomass, i is the number of grasses for the plot ($i=1, \dots, n$). Similarly, plant $\delta^{13}\text{C}$ value ($\delta^{13}\text{C}$ value of total plant biomass) of the plot can be calculated as the sum of $\delta^{13}\text{C}$ value of each species multiplied by its % of biomass (% of total biomass). The calculated grass- or plant- $\delta^{13}\text{C}$ value was theoretically equal to the value measured with the well-mixed sample of total grass biomass or total biomass, respectively (Earnshaw *et al.* 1990).

We can calculate the proportion of C_3 plant-derived C (X) or C_4 plant-derived C ($1-X$) for soil carbon using Eq. 3 as suggested by Yoneyama *et al.* (2001).

$$\delta^{13}\text{C}_{\text{soil}} = \delta^{13}\text{C}_{\text{C}_3} \times X + \delta^{13}\text{C}_{\text{C}_4} \times (1-X) \quad (3)$$

where $\delta^{13}\text{C}_{\text{soil}}$ is the $\delta^{13}\text{C}$ value of soil carbon, $\delta^{13}\text{C}_{\text{C}_3}$ is the $\delta^{13}\text{C}$ value of C_3 plant-derived carbon ($= -26.2 \sim -26.7\text{‰}$, calculated from Table 2) and $\delta^{13}\text{C}_{\text{C}_4}$ is the $\delta^{13}\text{C}$ value of C_4 plant-derived carbon ($= -10.2 \sim -12.5\text{‰}$, calculated from Table 2) in the soil.

Results

1. Altitudinal pattern of the distribution of C_3 and C_4 grasses in the Kirigamine grassland

Out of 151 species found, eight C_3 and three C_4 grasses (excluding the C_3 dwarf bamboo *Sasa chartacea*) were found in this grassland (also see Nishimura *et al.* 1997, which gives detailed results of the general vegetation surveys). Briefly, in the Kirigamine grassland the C_4 grass *M. sinensis* dominates sites lower than 1,650 m, whereas the C_3 grass *C. longisetata* dominates sites higher than 1,750 m. *C. langsdorffii* communities usually occur at snowy sites above 1,800 m, and *C. hakonensis* Franch et Savat communities appear mainly at windswept sites near mountaintops (around 1,900 m). The other C_3 and C_4 grasses exist as accompanying species in the plant communities. The studied area covered two main slopes: western and eastern. The transition from *M. sinensis* to *C. longisetata* communities on the western main slope (plots 1 to 25, 31) is about 100 m higher than the transition on the eastern main slope (plots 26 to 30). Such a difference between the two main slopes is more likely due to effects of a large-scale topography, such as varying in wind-swept and accumulation of snow during winter (Nishimura *et al.* 1997). Therefore we used data from the western main slope (plots 1 to 25, 31) to analyze the effects of slope inclination and aspect on vegetation in a microclimate scale. Results and discussion below are referred to data from the western main slope only.

Figure 1 shows that the % coverage of C_4 grasses declined and that of C_3 grasses increased with increasing altitude in the Kirigamine grassland. The C_4 -grass percentage (% of total grasses in coverage)

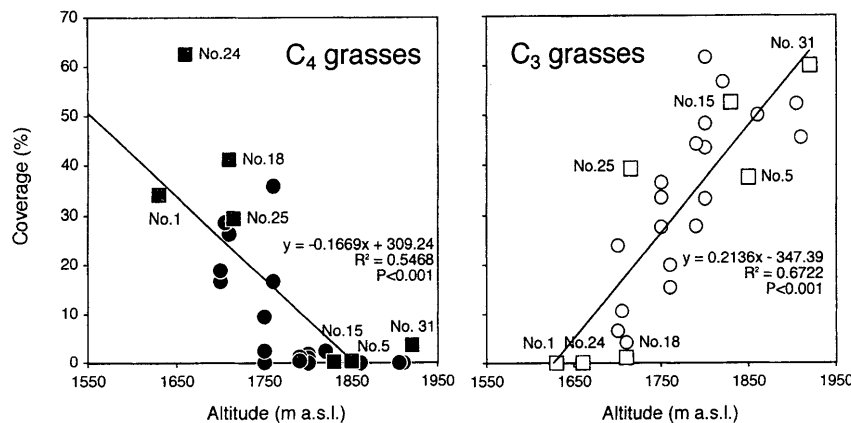


Fig. 1. Changes in coverage (%) of C_4 and C_3 grasses in total plants along the altitudinal gradient in the Kirigamine grassland (July, 1992 to 1994). Square (■ or □) shows the plots selected for biomass sampling and carbon-isotope analysis.

decreased sharply above 1,700 m, whereas the C₃-grass percentage increased with increasing altitude, to totally replace C₄ grasses above 1,800 m (Fig. 2a). This transition from C₄ to C₃ grasses occurred in a narrow altitude range between 1,670 and 1,770 m, with only 1°C difference in mean air temperature (1995–1997 KADEC data): i.e. annual mean temperature of 3.8 to 4.8°C or mean minimum air temperature of 12 to 13°C in the warmest month (August). In other words, the C₃-C₄ balance point (C₄ and C₃ grasses each constituting 50% coverage) in this grassland had a mean August minimum temperature of 13°C. Furthermore, in the Kirigamine grassland the C₄-C₃ transition mainly occurred between the C₄ grass *M. sinensis* and the C₃ grass *C. longiseta*, as measured with relative coverage of total grasses (Fig. 2b).

The August standing biomass (Fig. 3) of this grassland declined with increasing altitude from 695.8 ±

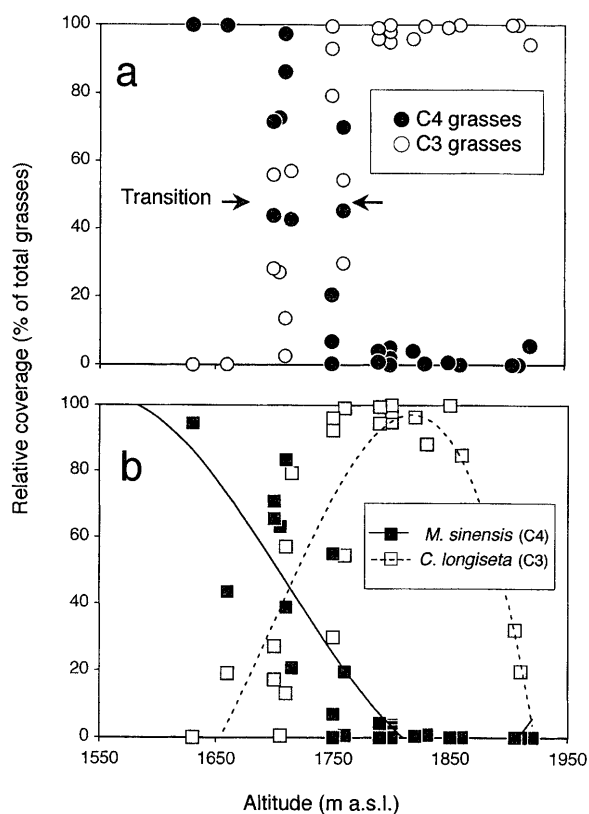


Fig. 2. Changes in relative coverage (% of total grasses) of (a) C₄ and C₃ grasses, and (b) dominant species with altitude in the Kirigamine grassland (July, 1992 to 1994). Arrows in (a) indicate the transition of C₄ to C₃ grasses from 1670 m to 1770 m. (b) indicates the transition of C₄ and C₃ grasses mainly occurred between *Miscanthus sinensis* (C₄) and *Calamagrostis longiseta* (C₃) in the grassland. Regression equation for *M. sinensis* is $y = 1.048E - 5x^3 - 0.054x^2 + 92.007x - 51849.61$ ($R^2 = 0.865$, $P < 0.001$), and for *C. longiseta* is $y = -1.884E - 5x^3 + 0.097x^2 - 164.327x + 92722.55$ ($R^2 = 0.801$, $P < 0.001$).

78.7 g DM m⁻² at low altitude (1,630 m) to 297.9 ± 39.9 g DM m⁻² at high altitude (1,920 m). The percentage of total grass biomass declined from 75% of the total plant biomass to 40% as the altitude increased from 1,630 m to 1,920 m (Fig. 3). However, the C₄-grass biomass decreased and the C₃-grass biomass increased with increasing altitude (Figs. 3, 4). Among all species, *M. sinensis* (C₄) and *C. longiseta* (C₃) were the most important contributors to the total standing biomass (Fig. 4). Similarly, there was a decrease in the *M. sinensis* biomass (% of total biomass) but an

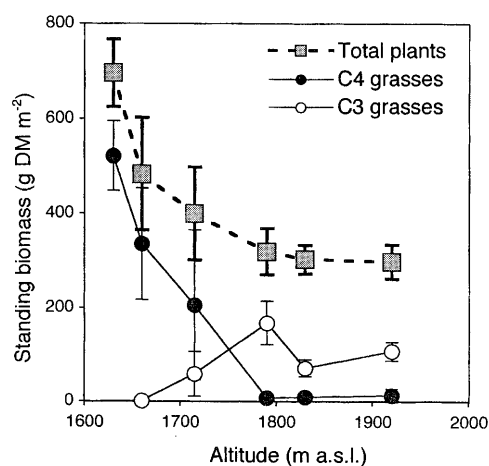


Fig. 3. Changes in standing biomass (total plants, C₄ and C₃ grasses) along the altitudinal gradient in the Kirigamine grassland (August 25 to September 6, 1994). Error bar for total plants represents the standard deviation ($n = 6$).

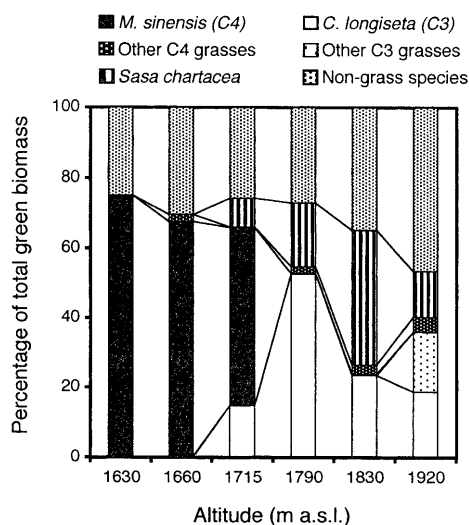


Fig. 4. Changes in percentage of dominant species, other C₄ and C₃ grasses, and non-grass species with increasing altitude in the Kirigamine grassland, as measured with biomass data collected from August 25 to September 6, 1994.

increase in the *C. longisetata* biomass with increasing altitude. Other C_4 grasses, such as *Arundinella hirta* (Thunb.) C. Tabaka and *Eccoilopus cotulifer* (Thunb.) A. Camus, were also found at higher altitudes (e.g. 1,830 m). At higher altitudes, *Sasa chartacea*, forbs, and woody plants occupied a relatively large proportion of the total standing biomass. Two other *Calamagrostis* species-*C. hakonensis* and *C. langsdorffii*-became dominant above 1,900 m (Fig. 4; also see Nishimura *et al.* 1997).

Table 1 shows the coefficients of correlation of the distribution of C_4 and C_3 grasses with climatic and topographical factors in the Kirigamine grassland. The C_4 -grass percentage (measured as % of total grasses in coverage or biomass) showed a significantly negative correlation with altitude, and a positive correlation with temperature-related factors. Conversely, the C_3 -grass percentage showed a significantly positive correlation with altitude, and

a negative correlation with all temperature-related factors. Although calculation of temperature, i.e. from the local rate of temperature changing with altitude, would cause redundancy in the parameters between altitude and temperature, it will not change the fact that distribution of C_3 and C_4 grasses was significantly correlated to altitude which often strongly correlated with temperature-related factors. The proportions of C_4 and C_3 grasses, however, showed no significant correlation with slope inclination and aspect within the western main slope. Interestingly, the proportion of C_4 grasses showed a weak positive correlation with slope aspect ($r=0.329$, $P>0.05$, $n=22$), although the correlation was not statistical significant. It suggested that the proportion of C_4 grasses might be greater in the south, east and west slope than in the north slope.

Because there was a similar trend in the seasonal changes in biomass between 1993 and 1994, the

Table 1. Correlation coefficients of the distribution of C_3 and C_4 grasses with climate and topography in the Kirigamine grassland (***) $P<0.001$. ** $P<0.01$. * $P<0.05$).

	Coverage (% of total plants)		Coverage (% of total grasses)		Biomass (% of total plants)		Biomass (% of total grasses)	
	C_4 grasses	C_3 grasses	% C_4 grasses	% C_3 grasses	% C_4 grasses	% C_3 grasses	% C_4 grasses	% C_3 grasses
Number of samples (plots)	26	26	26	26	6	6	6	6
Sampling area (m ² per sample)	6×1 m ²	6×1 m ²	6×1 m ²	6×1 m ²	6×1 m ²	6×1 m ²	6×1 m ²	6×1 m ²
Climate								
Annual mean air temp. (°C)	0.746***	-0.825***	0.801***	-0.801***	0.915**	-0.760	0.902*	-0.902*
Annual minimum air temp. (°C)	0.736***	-0.824***	0.798***	-0.798***	0.914**	-0.756	0.900*	-0.900*
August minimum air temp. (°C)	0.742***	-0.824***	0.799***	-0.799***	0.916**	-0.760	0.902*	-0.902*
Topography								
Altitude (m a.s.l.)	-0.739***	0.820***	-0.795***	0.795***	-0.914**	0.758	-0.901*	0.901*
Slope inclination	-0.336	0.248	-0.348	0.348	-0.332	0.330	-0.297	0.297
Slope aspect	0.329	-0.055	0.280	-0.280	0.122	-0.038	0.078	-0.078

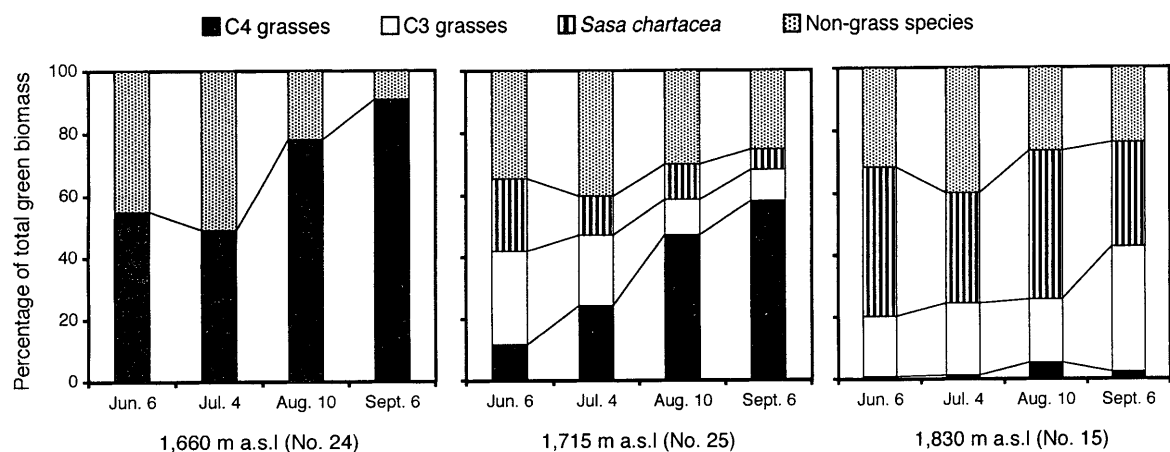


Fig. 5. Seasonal changes in percentage of C_4 and C_3 grasses and other species at three altitudes in the Kirigamine grassland (June to September, 1994).

results of 1994 are illustrated in Figure 5 for explanation. At the low altitude of 1,660 m, C₄ grasses (mainly *M. sinensis*) were dominant throughout the growing period from June to September. The C₄-grass biomass was maximized in early September at 1,660 and 1,715 m. However, at 1,715 m (C₃-C₄ transition), the C₃ grasses (mainly *C. longisetata*) dominated the early growing season till early summer. The percentage of C₄ grasses (mainly *M. sinensis*), as a measure of % of total biomass, increased greatly in

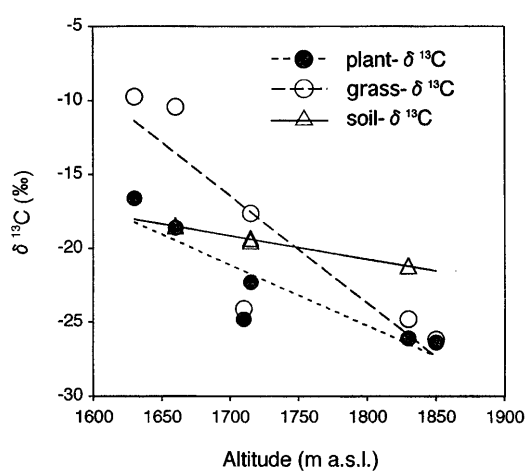


Fig. 6. Changes in carbon isotope ratios ($\delta^{13}\text{C}$) of plants and soils with altitude in the Kirigamine grassland (plant- $\delta^{13}\text{C}$ is the carbon isotope ratio of total, and grass- $\delta^{13}\text{C}$ is carbon isotope ratio of total grass biomass; Biomass data were from July of 1993 and 1994). Regression equations are :
for plant- $\delta^{13}\text{C}$: $y = -0.0413x + 49.135$
($R^2 = 0.816$, $P < 0.05$)
for grass- $\delta^{13}\text{C}$: $y = -0.0727x + 107.07$
($R^2 = 0.770$, $P < 0.05$)
for soil- $\delta^{13}\text{C}$: $y = -0.0162x + 8.3289$
($R^2 = 0.994$, $P < 0.001$).

August and reached the maximum in early September. At the high altitude of 1,830 m, the C₃ grass *C. longisetata* dominated, and *Sasa chartacea*, forbs, and other species occupied a relatively large proportion of the stand. However, the proportion of C₄ grasses (*A. hirta* and *E. cotulifer*) was extremely low at this site (1,830 m).

2. Carbon isotope ratios of present vegetation at different altitudes

Table 2 shows the $\delta^{13}\text{C}$ values of plant materials from different altitudes. In the Kirigamine grassland, the C₄ grasses had less-negative carbon isotope ratios (-9.7‰ to -15.3‰), whereas the C₃ species had more-negative values (-25.0‰ to -28.4‰). On the other hand, both grass and plant $\delta^{13}\text{C}$ values showed a decreasing tendency as altitude increased from 1,630 m to 1,850 m (Fig. 6). The grass $\delta^{13}\text{C}$ values changed from -9.7‰ to -26.2‰ and showed a negative correlation with altitude ($r = -0.877$, $P < 0.05$, $n = 6$), and the plant $\delta^{13}\text{C}$ changed from -16.6‰ to -26.4‰ and also showed a negative correlation with altitude ($r = -0.903$, $P < 0.01$, $n = 6$).

3. Soil C and N contents and soil $\delta^{13}\text{C}$ values at different altitudes

Table 3 shows soil C and N contents at different altitudes. There was no difference in total N content (g N/100 cm³ soil volume) with either altitude or soil depth ($P > 0.05$), although there was an increasing trend in the percentage of soil N with increasing altitude (from 1.45% to 1.71% as the altitude increased from 1,660 to 1,830 m). The percentage of soil C was slightly higher at high altitude (1,830 m), but total C content (g C/100 cm³ soil volume) also showed no statistical difference with either altitude or soil depth ($P > 0.05$, Table 3). Yoneyama *et al.* (2001) analyzed carbon and nitrogen content of soils from all over Japan and found that if pH of the soils was

Table 2. $\delta^{13}\text{C}$ values of the plant species collected from different altitudes in the Kirigamine grassland in July 2-3, 1993.

Species	Type	$\delta^{13}\text{C}$ value (‰) ^{a)}		
		1,630 m (No. 1)	1,710 m (No. 18)	1,850 m (No. 5)
<i>Miscanthus sinensis</i>	C ₄	- 9.7	-10.7	
<i>Arundinella hirta</i>	C ₄		-15.3	-14.4
<i>Eccoilopus cotulifer</i>	C ₄		-10.0	-11.4
<i>Calamagrostis longisetata</i>	C ₃		-25.0	-25.7
<i>C. hakonensis</i> + <i>C. langsdorffii</i>	C ₃			-25.0
<i>Agrostis clavata</i>	C ₃			-28.4
<i>Sasa chartacea</i>	C ₃	-27.2	-26.3	-26.4
Non-grass species (mixed sample)	C ₃		-26.0	-26.7

^{a)} Carbon isotope ratio of aboveground green parts (leaf, stem and ear).

lower than 7.0, the form of the soil carbon was mostly organic. Since the pH (H₂O) of our soil samples was between 4.3 and 4.5, it indicated that total soil carbon content was approximately equal to soil organic carbon content.

$\delta^{13}\text{C}$ values of soil organic matter (excluding roots) at different altitudes are shown in Table 3 and Figure 6. The negative soil $\delta^{13}\text{C}$ value decreased with increasing altitude, from $-18.2\text{‰} \pm 0.40\text{‰}$ at 1660 m to $-21.2\text{‰} \pm 0.26\text{‰}$ at 1,850 m. This variation in soil $\delta^{13}\text{C}$ values with altitude was highly significant ($P < 0.001$). However, the soil $\delta^{13}\text{C}$ values showed no significant difference with soil depth ($P > 0.05$ at all sites).

The proportion of C₄ plant-derived C for the soils from different altitudes decreased with increasing altitude, i.e. 51.4, 42.2 and 35.0% for 1660, 1,715 and 1,830 m respectively. In other words, the proportion of C₃ plant-derived C for soil increased with increasing altitude (48.6, 57.8 and 65.0% for 1,660, 1,715 and 1,830 m respectively).

Discussion

1. Transition of C₄ and C₃ grasses in the Kirigamine grassland

Intensive field studies conducted in the Kirigamine subalpine grassland especially between the 1960s and 1980s investigated vegetation types and succession

in the grassland (Iwaki *et al.* 1964 ; Midorikawa *et al.* 1964 ; Tsuchida and Numata 1979 ; Nishiwaki 1982 ; Shimoda 2001). The early studies did not report the existence of *Calamagrostis* communities in this grassland (Iwaki *et al.* 1964 ; Midorikawa *et al.* 1964). Tsuchida and Numata (1979) reported that the *M. sinensis* community occurred below 1750 m and the *Sasa chartacea*-*C. longisetata* community above 1,750 m or on wind-swept sites in the grassland. Later, Tsuchida (1982) described vegetation types of the Kirigamine grassland in details, in reference to the results of Tsuchida and Numata (1979). However, little information addresses the altitudinal pattern of the distribution of C₃ and C₄ grasses in the grassland.

Our results indicate that there is a sharp transition from C₄ grasses (mainly *M. sinensis*) to C₃ grasses (mainly *C. longisetata*) between 1,670 m and 1,770 m (Figs. 1, 2, 4) in the Kirigamine grassland. The C₄-grass percentage (measured as % of total grasses in coverage or biomass) decreased and the C₃-grass percentage increased with increasing altitude (Figs. 2, 4). The significant correlation between the proportion of C₄ and C₃ grasses and temperature-related factors (Table 1) suggests that temperature is an important factor in the proportion of C₃ and C₄ grasses along the altitudinal gradient in the grassland. Estimation of temperature from local rate of temperature changing with altitude would cause redundancy in

Table 3. Carbon and nitrogen contents and $\delta^{13}\text{C}$ of the soils from different altitudes in the Kirigamine grassland. Values are shown as mean \pm mean deviation ($n=2$, but except for 15-20 cm depth). The soil samples were collected in June 19, 1995. Two-way ANOVA was used for the statistical analyses.

Altitude (m a.s.l.)	Soil depth (cm)	Carbon content ^{a)}		Nitrogen content ^{a)}		C/N ratio	$\delta^{13}\text{C}$ ^{a)} (‰)
		(C%)	(g C/100 ml)	(N%)	(g N/100 ml)		
1,660 m (No. 24)	0-5	25.94 \pm 1.29	8.59 \pm 0.26	1.64 \pm 0.11	0.54 \pm 0.01	15.8	-18.7 \pm 0.10
	5-10	22.96 \pm 0.34	8.80 \pm 0.18	1.42 \pm 0.01	0.55 \pm 0.01	16.2	-18.3 \pm 0.30
	10-15	22.35 \pm 0.41	8.73 \pm 0.24	1.36 \pm 0.05	0.52 \pm 0.01	16.4	-17.7 \pm 0.55
	15-20	22.03	9.39	1.38	0.57	16.0	-18.2
	average	23.32 \pm 1.31	8.88 \pm 0.26	1.45 \pm 0.10	0.55 \pm 0.02	16.1	-18.2 \pm 0.28
1,715 m (No. 25)	0-5	25.53 \pm 0.68	9.14 \pm 0.26	1.61 \pm 0.04	0.58 \pm 0.02	15.9	-19.5 \pm 0.10
	5-10	25.36 \pm 0.04	7.63 \pm 0.04	1.64 \pm 0.05	0.49 \pm 0.02	15.5	-19.4 \pm 0.40
	10-15	23.95 \pm 0.62	8.62 \pm 0.30	1.44 \pm 0.09	0.52 \pm 0.04	16.6	-19.5 \pm 0.05
	15-20	22.67	6.68	1.32	0.51	17.1	-19.4
	average	24.38 \pm 1.07	8.02 \pm 0.86	1.50 \pm 0.12	0.53 \pm 0.03	16.3	-19.5 \pm 0.05
1,830 m (No. 15)	0-5	28.68 \pm 0.75	7.77 \pm 0.83	1.78 \pm 0.03	0.48 \pm 0.06	16.1	-21.4 \pm 0.05
	5-10	27.66 \pm 0.35	8.77 \pm 0.62	1.74 \pm 0.03	0.55 \pm 0.03	15.9	-21.2 \pm 0.01
	10-15	26.86 \pm 0.45	9.01 \pm 1.69	1.68 \pm 0.04	0.56 \pm 0.10	16.0	-20.9 \pm 0.02
	15-20	26.05	9.27	1.62	0.58	16.1	-21.1
	average	27.31 \pm 0.86	8.71 \pm 0.47	1.71 \pm 0.06	0.54 \pm 0.03	16.0	-21.2 \pm 0.15

^{a)} Variation in C%, N% and $\delta^{13}\text{C}$ are significant with altitude ($P < 0.01$). Variation in all measurements are not significant with soil depth ($P > 0.05$).

the parameters between altitude and temperature. However, it will not change the fact that temperature is principle control on the distribution of C₃ and C₄ grasses in the grassland, because it is reasonable to consider altitude highly correlated to temperature at a local scale. On the other hand, Table 3 shows that there was no statistical distinction between soil C and N contents (g/100 cm³ soil volume) and altitude, suggesting that N content or other soil nutrients may be less responsible for the transition of C₃ and C₄ grasses in the grassland. In the meanwhile, there was no significant correlation between the percentage of C₄ and C₃ grasses and topographical factors such as slope inclination and aspect in a microclimate scale within the western main slope (Table 1). It must be pointed out that there was a weak positive correlation between C₄-grass percentage and slope aspect ($r = 0.329$, $P > 0.05$), and indicating that the percentage of C₄ grasses might be greater in the south, east and west slopes than in the north slope (Table 1). This suggests that C₄ grasses may be advantage at the habitats with relatively limited soil moisture even under a high annual precipitation. However, this tendency may be also explained partly by the great amount of snowfall during winter and the late snow-melt of spring in the north slope (Nishiwaki 1982). We therefore suggest that soil moisture may be less responsible for determining the proportions of C₃ and C₄ plants in the Kirigamine grassland, according to the two facts that (1) the proportion of C₃ and C₄ grasses was not significantly correlated to slope aspect which reflected soil moisture condition in a certain degree, and (2) the high annual precipitation (1,665 to 1,855 mm) of the grassland. Two studies support this suggestion (Takeda *et al.* 1985; Okuda 1987), demonstrating that temperature is the principle factor in determining the percentage of C₃ and C₄ grasses in Japan in regions with high annual rainfall and small seasonal changes in rainfall.

The transition from C₄ to C₃ grasses occurred in a narrow altitude range (1,670 to 1,770 m) in the Kirigamine grassland (Fig. 2), compared with the C₃-C₄ transition in other altitudinal gradients (Tieszen *et al.* 1979; Boutton *et al.* 1980; Rundel 1980; Cavagnaro 1988; Earnshaw *et al.* 1990). For instance, the transition occurred between 1,405 and 2,420 m in shortgrass prairie in North America (Boutton *et al.* 1980). Varied altitude ranges of the C₃-C₄ transitions may be explained by the dominant C₃ and C₄ species differing with investigated altitudinal gradients. The C₃-C₄ transition in shortgrass prairie (Boutton *et al.* 1980) occurred among short grasses such as *Bouteloua gracilis* (C₄) and *Agropyron smithii* (C₃). However, in the Kirigamine grassland, the transition occurred among

tall grasses, which expected to have a keener competition for light resources than shortgrass communities. Such a sharp C₃-C₄ transition in Kirigamine grassland can be explained by the keener displacement between the two tall grasses, *M. sinensis* (C₄) and *C. longiseta* (C₃), as showed by Figure 2 b. Evidences support this explanation, such as seasonal changes in light intensity and productive structure of communities from different altitudes and net photosynthesis of dominant species, will give and discuss more detailed in the subsequent paper and data are also available from Mo (1997). Although the C₃-C₄ transition was sharper in the Kirigamine grassland, the C₃-C₄ balance point (C₄ and C₃ grasses each constituting 50% coverage) in Kirigamine had a mean August (the warmest month) minimum temperature of 13°C. This was in rough agreement with the balance point in other temperate regions (Ehleringer 1978; Hattersley 1983; Cavagnaro 1988), however, higher than that of tropical and subtropical regions such as Kenya (Tieszen *et al.* 1979) and Hawaii (Rundel 1980). It demonstrates that the altitudinal C₃-C₄ transition of higher latitudes seems to have a higher mean minimum temperature of the warmest month for the C₃-C₄ balance point. Conversely, in the tropical regions with little seasonal changes in temperature, the C₃-C₄ transition tends to have a lower mean minimum temperature of the warmest month for the balance point. That is, C₄ plants require a warmer summer for distribution to higher latitudes.

In the Kirigamine grassland the C₄ *M. sinensis* communities (Fig. 4) were restricted to altitudes lower than 1,800 m with a mean August minimum temperature around 12°C, which seemed to be higher than the absolute limit of C₄ species distributions in other temperate and tropical regions, i.e. a mean minimum temperature of 8-10°C for the warmest month (Teeri and Stowe 1976; Ehleringer 1978; Rundel 1980; Hattersley 1983; Cavagnaro 1988). However, small stands of *M. sinensis* were found even at the top of Mt. Kurumayama in rocky or bare sites, where *M. sinensis* may lack competition from neighbors. Other C₄ grasses, *A. hirta* and *E. cotulifer*, were also found higher than 1,800 m (Fig. 4; see also Nishimura *et al.* 1997). These facts suggest that the physiological limit for C₄ grasses in the grassland would occur above 1,920 m, the top of the grassland with a mean minimum temperature of 11°C for the warmest month.

Seasonal changes in the proportion of C₄ and C₃ grasses (Fig. 5) indicated that there was a decrease in C₃-grass percentage and an increase in C₄-grass percentage from June to September in the C₃-C₄ transition zone (e.g. 1,715 m). This suggests the occurrence of a seasonal shift of productive activities from C₃ to

C₄ grasses with increasing temperature there. Such a seasonal pattern of C₃ and C₄ species was also found in C₃-C₄ mixed prairies in North America (Ode *et al.* 1980; Monson and Williams 1982; Monson *et al.* 1983), where there was a shift from C₃-dominant to C₄-dominant from spring to midsummer, and back to C₃-dominant in the fall. Ode *et al.* (1980) pointed out that this seasonal displacement between C₃ and C₄ species resulted from the differential responses of C₄ and C₃ photosynthetic pathways to temperature. C₄ plants have physiological advantages over C₃ plants, in terms of high potential productivity and efficiencies of water and nitrogen use, especially at high light intensities, at high temperatures, and with limited soil moisture (Black 1973; Berry and Bjorkman 1980). However, low temperatures may minimize these advantages (Long 1983). Mo (1997) produced photosynthetic evidence to show that *M. sinensis* (C₄) differed from *C. longisetata* (C₃) in response to temperature under controlled conditions. Mo (1997) also measured the single-leaf photosynthetic rate with a portable photosynthetic system (Type LCA-4, ADC, UK) in the Kirigamine grassland, and found that in early summer *C. longisetata* had a similar photosynthetic rate as *M. sinensis* ($12.0 \pm 1.63 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $11.3 \pm 1.98 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively; 19 June 1995). However, the photosynthetic rate of *M. sinensis* ($16.9 \pm 0.60 \mu\text{mol m}^{-2} \text{s}^{-1}$) was substantially greater than that of *C. longisetata* ($9.04 \pm 2.20 \mu\text{mol m}^{-2} \text{s}^{-1}$) in late summer (25 July 1995). The differences between C₃ and C₄ plants in photosynthetic temperature responses have often been discussed in relation to altitudinal or latitudinal distribution patterns of C₃ and C₄ grasses (Teeri and Stowe 1976; Ehleringer 1978; Tieszen *et al.* 1979; Earnshaw *et al.* 1990). In the subsequent paper, we will give more information on the differentiation between the C₃-grass *C. longisetata* and the C₄-grass *M. sinensis*, in terms of productive structure and net photosynthesis, and discussing the regulating role of temperature on inter-specific competition among the two species differing in photosynthetic pathways.

Overall, our results indicate that there is a transition of C₄ and C₃ grasses in the Kirigamine grassland, and that temperature is the principle factor determining the proportion of C₄ and C₃ grasses along the altitudinal gradient in the grassland. However, further information is still required to explain how temperature determines the distribution of C₃ and C₄ species locally. Mo *et al.* (1997) suggested that the restriction of *C. longisetata* communities to higher altitudes is not due to a physiological limit to their growth at lower altitudes and warmer temperatures, but because they may fail to compete with *M. sinensis* at lower altitudes. A direct test is needed to

clarify the function of temperature in competition between the C₄ grass *M. sinensis* and the C₃ grass *C. longisetata*.

2. Isotopic evidence for changes in past vegetation in the Kirigamine grassland

Carbon isotope ratios ($\delta^{13}\text{C}$) in soil or plant materials can be used to measure the proportion of C₃ and C₄ species at a given altitude (Tieszen *et al.* 1979; Bird *et al.* 1994). In the Kirigamine grassland, C₃ plants had $\delta^{13}\text{C}$ values ranging from -25.0‰ to -28.4‰ with a mean of -26.0‰ , whereas C₄ plants had values ranging from -9.7‰ to -15.3‰ with a mean of -12.0‰ (Table 2). The large difference in $\delta^{13}\text{C}$ values between C₃ and C₄ plants is mainly due to the larger ^{13}C discrimination of RuBP carboxylase in C₃ plants than of PEP carboxylase in C₄ plants (O'Leary 1981). The increment of negative plant and grass $\delta^{13}\text{C}$ values with increasing altitude (Fig. 6) indicated that C₄-percentage decreased but C₃-percentage increased with increasing altitude in the grassland. A similar change in plant $\delta^{13}\text{C}$ values was observed in the transition from C₄ to C₃ grasses along an increasing altitudinal gradient in Kenya (Tieszen *et al.* 1979).

The average difference in $\delta^{13}\text{C}$ between C₃ and C₄ plants is approximately 14‰ (-26‰ for C₃ plants and -12‰ for C₄ plants), however, biochemical fractions differ from whole plant values by only 1-3‰ in isotopic composition (Dzurec *et al.* 1985). We measured the carbon isotope ratios of cultivated plants and also found that root $\delta^{13}\text{C}$ usually had a value of 1-2‰ greater than that of aboveground biomass, which was 1.0‰ greater in *C. longisetata* and 1.5‰ in *M. sinensis* respectively (data not shown). As plant materials are degraded and transformed into soil organic matter, their carbon isotope ratios are reflected in those of the soil organic matter (Dzurec *et al.* 1985; Balesdent *et al.* 1987; Benner *et al.* 1987). Thus, the $\delta^{13}\text{C}$ values of soil organic matter are a historical record of the vegetation at a site (Wedin *et al.* 1995). In the Kirigamine grassland, the proportion of C₄ plant-derived C for soil decreased (51.4% at 1,660 m to 35.0% at 1,830 m) and that of C₃ plant-derived C increased with increasing altitude (48.6% at 1,660 m to 65.0% at 1,830 m), indicated that historically the transition of C₃ and C₄ existed in the grassland. Moreover, the $\delta^{13}\text{C}$ value of soil organic matter (-18.2‰) at 1,660 m (plot 24) was almost equal to that of the present vegetation (-18.6‰). This finding suggests that there was a similar C₃/C₄ ratio in the past at this site as at present. However, at 1,715 m and 1,830 m, the less-negative soil $\delta^{13}\text{C}$ values (-19.4‰ and -21.1‰ , respectively) and the more-negative plant $\delta^{13}\text{C}$ values (-22.3‰ and -26.1‰), indicate that the proportion of C₄ plants could have been greater in

the past than at present at these sites. This suggestion is supported by the study of Midorikawa *et al.* (1964), in which a vegetation survey in August 1960 showed that the C₄ grasses *M. sinensis* and *A. hirta* dominated most of the Kirigamine grassland. At the same time, *A. hirta* communities were found above 1,800 m, around 1 km northwest of Mt. Kuru mayama (Midorikawa *et al.* 1964). It is highly probable from the soil $\delta^{13}\text{C}$ data that in the past, probably when the grassland was mown for animal husbandry, *A. hirta* and *M. sinensis* dominated more at high altitudes (*e. g.* plot 15, 1,830 m). In other words, the C₃-C₄ transition might occur at higher altitudes in the past than in the present, and the use of mown for animal husbandry may be advantage for the growth of C₄ plants (or disadvantage for the growth of C₃ plants) at the higher altitudes in the past. Analysis of buried phytoliths may give more details of which plant species were dominant in the past (Sase and Kato 1976).

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* : In Japanese with English summary.

** : In Japanese only.

要 旨

莫 文紅*・西村 格**・曾我有紀子*・山田恭子*・米山忠克*** (2004) : 霧ヶ峰草原における C₃ と C₄ 植物の分布および標高に伴う植物と土壌の炭素安定同位体比の変化. 日草誌 50, 243-254. 筑波大学生物科学系 (305-8572 つくば市天王台 1-1-1), * 研究実施時 : 岐阜大学流域環境科学研究センター (501-1193 岐阜市柳戸 1-1), ** 元富山大学理学部 (930-8555 富山市五福), 現在 : 320-0066 宇都宮駒生 1-6-4, *** 東京大学大学院生命科学研究所応用生命化学専攻 (113-8657 東京都文京区弥生 1-1-1)

本研究は C₃ と C₄ イネ科草本の構成割合の標高に伴う分布と温度要因との対応関係を明らかにすることを目的とし、霧ヶ峰草原 (1,500~1,920 m) における C₃ と C₄ 植物の標高分布パターンと温度・地形・土壌炭素および窒素含有量など環境要因との関係解析を行った。その結果、構成割合は標高が高くなるにつれて C₄ 優占から C₃ 優占へと変化することが明らかとなった。さらに、C₃ と C₄ 植物の移行帯では、春から夏にかけて C₃ 優占から C₄ 優占に変化することから、温度上昇にともなって構成割合が変化することも明らかになった。そして標高に伴う構成割合の変化と環境要因との関係解析の結果、温度関連因子と有意な相関関係が得られたが、その他の環境要因については有意な相関が得られなかった。このことから C₃ と C₄ イネ科草本の構成割合の標高に伴う分布の違いは温度が第一の要因であると考えられる。また、標高に伴う現存植生の炭素安定同位体比 ($\delta^{13}\text{C}$) および土壌炭素安定同位体比の変化から霧ヶ峰草原における過去の C₃ と C₄ 植物の標高に伴う構成割合の変化は現在と異なり、C₄ 植物が現在よりも高標高まで分布していたことが示唆された。

キーワード : 温度, 過去植生, 霧ヶ峰草原, C₃ と C₄ 植物, 炭素安定同位体比, 標高分布パターン.