한국농림기상학회지, 제14권 제4호(2012) (ISSN 1229-5671)
Korean Journal of Agricultural and Forest Meteorology, Vol. 14, No. 4, (2012), pp. 196~206
DOI: 10.5532/KJAFM.2012.14.4.196

Seasonal Change in C_3/C_4 Mixed Vegetation Populations over Paddy Levees in South Korea

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(Received September 28, 2012; Revised November 16, 2012; Accepted November 26, 2012)

남한의 논둑에 발달한 C_3/C_4 혼생식생의 계절변화

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(2012년 9월 28일 접수; 2012년 11월 16일 수정; 2012년 11월 26일 수락)

ABSTRACT

Studies of seasonal changes in C_3/C_4 mixed communities are rare, particularly in Asian summer monsoon climate zones. In our present study, seasonal changes in the profile and coverage of C_3 and C_4 plants were investigated in 2009 in Haenam, Yeongdong and Cheorwon regions of South Korea (all at different latitudes). The aim was to estimate the impacts of temperature and sunshine duration on species composition and transition timing of the C_3 and C_4 plants. From our results, the number of C_3 plants was found to increase from early spring to mid-May, and then decrease again until September in the Haenam and Yeongdong regions, but continuously increase from early spring to September in the Cheorwon region under relatively low summer temperatures. On the other hand, the number of C_4 plants increased from June or July to September in all three regions. These seasonal changes in species number and ratio have a direct impact upon species diversity which is highest when there are no dominant species. The relative coverage and relative summed dominance ratio (SDR') of the C_3 plants decreased from spring to autumn, but increased for the C_4 plants during this time in an exponential fashion with increasing accumulated temperature and sunshine duration. The transition timing from C_3 to C_4 plants occurred when the sum of sunshine duration for the days with daily mean temperature above 5°C was 1017 hrs for the SDR'.

***Key words*: C_4 plant, Paddy levee, Seasonal change, SDR', Temperature response**

I. INTRODUCTION

Most terrestrial plants can be classified as C_3 or C_4 plants in terms of photosynthetic metabolism (Kortschak *et al.*, 1965; Hatch and Slack, 1966; Black, 1971; Takeda and Fukuyama, 1971). Plants in these two categories have different responses to light intensity (Moss *et al.*, 1961; Hesketh and Moss, 1963), temperature (Long, 1999; Larcher, 2003), soil moisture (Takeda *et al.*, 1977; Takeda *et al.*, 1980; Long, 1999) and CO_2 concentration (Goudriaan, 1989; Tubiello et al., 1999; Kang *et al.*, 2002). Hence, the distribution and growth patterns of C_3 and C_4 plants will be affected by climatic changes including alterations in the ambient CO_2 concentration, temperature and precipitation pattern (IPCC, 2007). Since the discovery of the C_4 photosynthetic pathway (Kortschak *et al.*, 1965; Hatch and Slack, 1966), many studies have reported on the structural

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analysis of C_3 and C_4 plants (Oshugi, 1989; Ueno, 2001; Bang *et al.*, 2009; Voznesenskaya *et al.*, 2010). There have also been numerous reports on the classification of plant species using these photosynthetic pathways (Takeda and Fukuyama, 1971; Noda and Eguchi, 1973; Downtown, 1975; Kyoda, 1992; Liu *et al.*, 2004), and on the geographic distributions of these plant types and their relationship to climatic patterns (Teeri and Stowe, 1976; Teeri *et al.*, 1980; Takeda and Hakoyama, 1985; Ueno and Takeda, 1992; Ehleringer *et al.*, 1997; Collatz *et al.*, 1998; Pyankov *et al.*, 2000).

The temporal and spatial variations of ecophysiological characteristics including biomass, species composition, photosynthesis, coverage, dominance and diversity in C_3/C_4 plant mixed regions have been evaluated in grasslands, desserts and prairies (Ode *et al.*, 1980; Kemp, 1983; Ishikawa *et al.*, 1990; Wang, 2004a, 2004b; Niu *et al.*, 2008). However, only a few studies about temporal and spatial variations in regions of the Asian monsoon climate zone (Okuda, 1987; Mo et al., 2004; Shimoda *et al.,* 2009). In South Korea, C_4 plants are commonly found in areas surrounding crop lands such as paddy levees, upland levees and off-road sides (Chang and Lee, 1983). Interestingly, C_4 plants such as *Digitaria ciliaris*, *Eragrostis ferruginea*, *Eleusine indica* and *Pennisetum alopecuroides* are dominant species that grow in paddy levees (Chang and Lee, 1983). This indicates that C_3 plants (*Oryza sativa* L.) would be replaced by these C_4 plants if the cultivation of rice in paddy fields was discontinued for any reason. In a tropical region of south-western China, C_4 plants have been found to be more prevalent in disturbed and cultivated lands than in other habitat types such as river valleys, rangelands, wet lands, hillsides and the regions susceptible to frost (Wang, 2006). Although C_4 plants represent a large proportion of the vegetation around cultivated lands that could influence crop productivity directly, no research has yet been conducted on this issue.

In our present study, we have investigated the effects of seasonal change on C_3/C_4 mixed plant communities in paddy levees in terms of species number, species diversity, coverage, and dominance. Especially, we focused on the transition timing from C_3 to C_4 dominance.

II. METHODS AND MATERIALS

2.1. Study sites

Three survey sites at different latitudes in South Korea, Haenam (N34° 31' E126°33', 5 m a.s.l.), Yeongdong (N36° 08' E127°45', 169 m a.s.l.) and Cheorwon (N38° 12' E127° 15', 189 m a.s.l.), were selected in 2009 to monitor seasonal variations in the C_3 and C_4 plant profiles over paddy levees. Weather data including precipitation and sunshine duration were collected from weather stations nearest to each survey site, which were managed by the Korea Meteorological Administration. Air temperatures at 1.3 m above ground were measured at each study site using Hobo Data Loggers (TidbiT v2 Temp Logger, Onset®, Massachusetts). Mean annual temperature of Haenam (13.8°C) was highest, and Cheorwon (10.1°C) was lowest among the survey sites (Table 1). Annual precipitation was highest at the Cheorwon site (2044.5 mm) and lowest at the Yeongdong (900.0 mm) site. Annual sunshine duration was similar among the three survey sites (2055 hrs for Haenam, 2047 hrs for Yeongdong, 2075 hrs for Cheorwon).

2.2. Vegetation survey

In each survey site, five linear plots (2×1 m^2) were set along the paddy levees. To evaluate the dominance of different plants and the species diversity in each plot, the height and coverage of all plant species were recorded through the growing season (from February to September in 2009). The surveys were conducted six

Table 1. Localities and climatic factors of the study sites

	Study sites		
	Haenam	Yeongdong	Cheorwon
Latitude	N34°31'29.5"	N 36°08'30.2"	N38°12'00.3"
Longitude	E126°33'42.4"	E127°45'28.7"	E127°15'08.3"
Elevation (m)	5	169	189
Mean annual temperature (°C)	13.8	11.8	10.1
Annual precipitation (mm)	1276.5	900.0	2044.5
Sunshine duration (hrs)	2054.6	2046.7	2075.4

Table 2. The date of vegetation survey in Haenam, Yeongdong and Cheorwon regions

Survey series	Survey date		
	Haenam	Yeongdong	Cheorwon
1	-	24 February (55)	20 February (51)
2	26 March (85)*	24 March (83)	25 March (84)
3	17 May (127)	7 May (127)	13 May (133)
4	16 June (167)	17 June (168)	19 June (170)
5	14 July (195)	16 July (197)	27 July (208)
6	19 August (231)	4 September (247)	3 September (246)

*The values are days of year

times in the Yeongdong and Cheorwon regions and five times in the Haenam region. The detailed survey data obtained for each site are listed in Table 2. Plant growth in paddy levees in Korea is generally managed using herbicides or a grass cutter, but the experimental plots in this study were not disturbed during the study period.

2.3. Data analysis

The summed dominance ratio (SDR) for the plant species in each plot was calculated as follows (Numata, 1966):

SDR=(H'+C')/2 where H' (%) and C' (%) are the ratios of the recorded values for each species at their greatest height (H, cm) and coverage (C, %) in each plot, respectively. The SDR' was then calculated as the percentage SDR for each species compared with the total SDR value for all species within a plot as follows:

$$SDR' = SDR_i / \Sigma DR$$

where SDR*i* is the SDR for species *i*.

The diversity index was calculated by the Shannon-Wiener equation (Shannon and Wiener, 1949) using the SDR' of each species within a plot as follows:

$$\text{Diversity Index} = -\Sigma P_i \cdot \text{LN}(P_i)$$

where P*i* is the SDR' for species *i*.

Accumulated temperature (AT_5 or AT_{10}) was calculated as:

$$AT_5 = \Sigma\ (\text{daily mean temperature} - 5^{\circ}C)$$
$$AT_{10} = \Sigma\ (\text{daily mean temperature} - 10^{\circ}C)$$

Accumulated sunshine duration (ASD) was calculated as the sum of the daily sunshine duration for the period in which the daily mean temperature was above 5°C (ASD_5) or 10°C (ASD_{10})

Regressions of the proportion of C_4 species against accumulated temperature and sunshine duration and the generation of all graphs were performed using SigmaPlot® 11 (Systat Software, Inc., 2008).

III. RESULTS

3.1. Species composition and diversity

We obtained seasonal variation data on the number of C_3 and C_4 plant species at the three study sites. C_3 plants were found to be more abundant at all sites throughout the seasons (Fig. 1), increasing in number from early spring to mid-May, and then decreasing from mid-May to September, in the Haenam and Yeongdong regions. In the Cheorwon region, however, the number of C_3 plants steadily increased from early spring to September. The increase in the number of C_4 plants began from mid-June in the Haenam and Yeongdong regions, and in late-July in the Cheorwon region, until September.

Fig. 2 shows the seasonal changes in species diversity at each survey region. The diversity of plant species was increased prior to the appearance of C_4 plants, and then dramatically decreased in the Haenam region. In contrast, the level of species diversity continuously increased until September in the Cheorwon region. In the Yeongdong region, the species diversity level reached its highest value when the C_3 and C_4 plants co-existed for the first time and decreased thereafter. Significant differences were not evident among the dominant species in the surveyed regions with an SDR' > 10% (Table 3). Most of the C_3 plants with high SDR' values (including *Alopecurus aequalis*, *Stellaria alsine* var. *undulata*, *Capsella bursapastoris*, *Cerastium glomeratum* and *Cardamine flexuosa*) appeared in spring. However, some C_3 plants such as *Bidens frondosa*, *Mosla punctulata* and *Ludwigia prostarata* exhibited high SDR' values

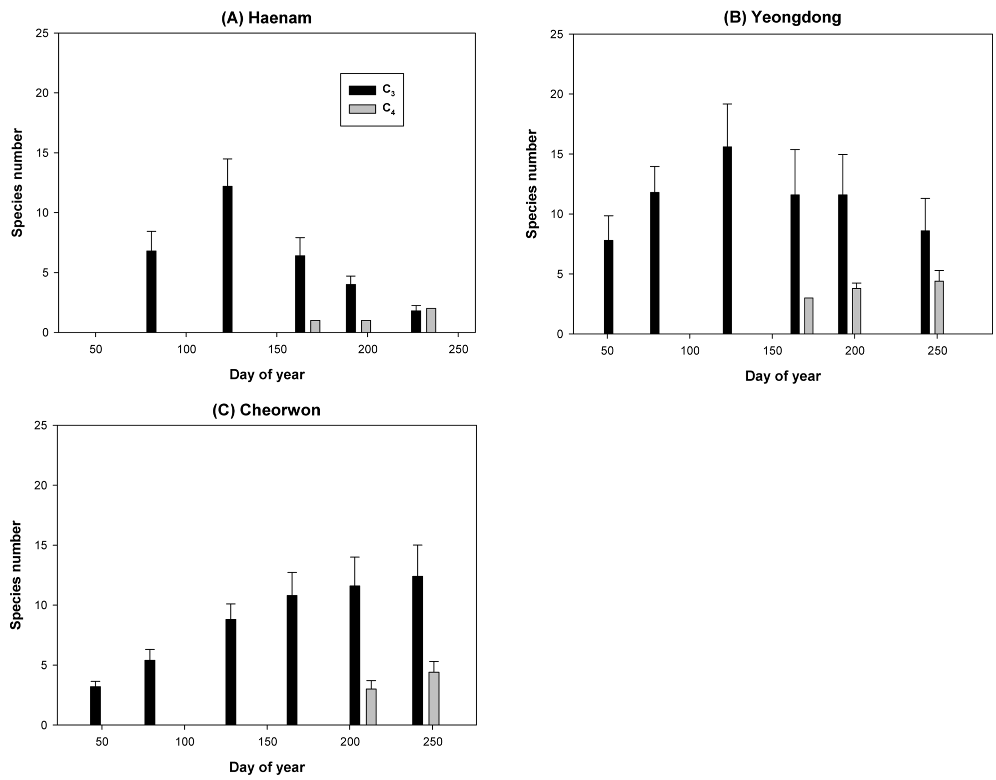

Fig. 1. Seasonal changes in the number of C_3 and C_4 plants in Haenam (A), Yeongdong (B) and Cheorwon (C) regions. Error bars represent the standard deviation (n=5).

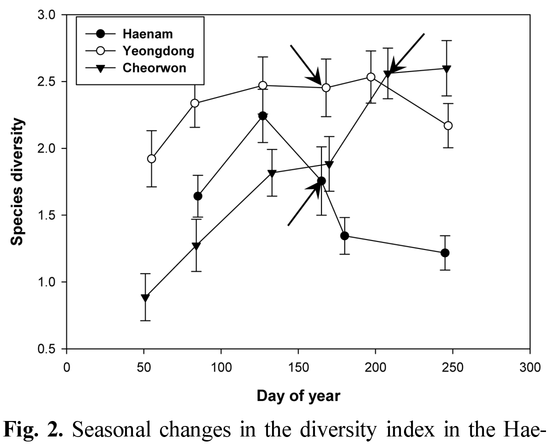

Fig. 2. Seasonal changes in the diversity index in the Haenam, Yeongdong and Cheorwon regions. Arrows indicate the survey date on which C_4 plants appeared for the first time. Error bars represent the standard deviation (n=5).

after summer. C_4 plants with high SDR' values (including *Digitaria ciliaris*, *Echinochloa crusgalli* var. *oryzicola*, *Setaria glauca* and *S. viridis*) appeared after mid-June.

3.2. Transition timing

Based on the observed seasonal changes in relative coverage of C_3 and C_4 plants, the transition timing (from the point at which C_3 and C_4 plants showed a 1:1 coverage or equal SDR') from the dominance of C_3 to C_4 plants was about 162 and 169 days of the year in the Haenam and Yeongdong regions, respectively (Figs. 3A and 3B). Following the transition from C_3 to C_4 plants in terms of relative coverage, the difference between the relative coverage values of the C_3 and C_4 plants was greater in the Haenam than in the Yeongdong region. However, this transition was not exhibited in the Cheorwon region which had a relatively lower temperature (Table 1, Fig. 3C).

The variation in the SDR' for C_3 and C_4 plants showed a similar pattern in terms of the season and location as it did with respect to relative coverage (Fig. 4). However, the transition timing from C_3 to C_4 plants in the case of season and location was about 199 days of the year in the Haenam region indicating that this was delayed by 37 days in comparison with the result obtained for the relative coverage (Fig. 4A). A seasonal

Table 3. Dominant C_3 and C_4 plants occurring in the Haenam, Yeongdong and Cheorwon regions and their average SDR' (%). Dominant species show an SDR' of above 10%

Study site species name	Survey series						C_3/C_4
	1	2	3	4	5	6	
Haenam							
Alopecurus aequalis	-	18.0	15.2	16.4	0	0	C_3
Stellaria alsine var. *undulata*	-	2.5	9.0	15.7	0	0	C_3
Capsella bursapastoris	-	18.7	0	0	0	0	C_3
Cerastium glomeratum	-	23.8	6.2	0	0	0	C_3
Bidens frondosa	-	0	0	0	13.1	17.8	C_3
Digitaria ciliaris	-	0	0	24.2	49.0	44.6	C_4
Echinochloa crusgalli var. *oryzicola*	-	0	0	0	0	27.9	C_4
Yeongdong							
Alopecurus aequalis	18.4	12.2	6.5	2.2	0	0	C_3
Stellaria alsine var. *undulata*	21.3	16.5	12.6	5.2	2.4	0	C_3
Capsella bursapastoris	7.7	6.2	14.3	0	0	0	C_3
Cardamine flexuosa	12.0	8.9	7.5	0	0	0	C_3
Bidens frondosa	0	0	0	0	8.4	19.3	C_3
Digitaria ciliaris	0	0	0	8.7	12.8	9.6	C_4
Setaria glauca	0	0	0	13.2	12.2	21.4	C_4
Setaria viridis	0	0	0	9.3	10.4	7.8	C_4
Cheorwon							
Alopecurus aequalis	66.9	55.4	35.2	35.4	4.2	1.2	C_3
Stellaria alsine var. *undulata*	14.7	9.8	5.9	6.5	7.1	2.8	C_3
Capsella bursapastoris	0	6.7	12.7	0	0	0	C_3
Mosla punctulata	0	0	0	4.0	13.2	11.3	C_3
Ludwigia prostrata	0	0	0	2.1	8.8	10.0	C_3
Digitaria ciliaris	0	0	0	0	8.3	10	C_4
Echinochloa crusgalli var. *oryzicola*	0	0	0	0	0	12.7	C_4

adjustment from C_3 to C_4 plant dominance in the SDR' was not observed in the paddy levees of the Yeongdong and Cheorwon regions (Fig. 4B and 4C).

IV. DISCUSSION

Previous studies on the seasonal change characteristics of C_3 and C_4 plants have indicated that C_3 plants flourish in the cool spring and autumn seasons whereas C_4 plants are active during the hot summer (Tieszen *et al.*, 1979; Ode *et al.*, 1980; Okuda, 1987; Niu *et al.*, 2005, 2006, 2008; Shimoda *et al.*, 2009). It has been reported also that two groups of C_3 and C_4 plants have differences in phenology and photosynthetic activity, mainly in terms of temperature (Williams, 1974; Ode *et al.,* 1980; Monson and Williams, 1982; Ishikawa *et al.*, 1990; Mishio and Kawakubo, 2000). In our present study, we found a cause by which SDR' of C_3 and C_4 plants changed with seasonal and regional differences.

The Haenam and Yeongdong regions of South Korea, which have a high annual mean temperature and many hot days in summer, showed a decrease in the number of C_3 plants and an increase in the number of C_4 plants after May (Table 3 and Fig. 1). The number of day for which the temperatures were above 25°C (high temperature) was 31 and 20 days in Haenam and Yeongdong regions, respectively, but only one day in Cheorwon. Okuda (1987) reported similar results, but found that C_4 plants had an earlier occurrence date than that found in our three study sites. The reason is most likely to be that perennial C_4 plants (e.g., *Miscanthus sinensis*, *Zoysia japonica*, *Imperata cylindrical* and *Arundinella hirta*) represented the majority of the C_4 plants at the study sites of the Okuda report, which were semi-natural grasslands. In contrast, the predominant C_4 plants observed in our study (e.g., *Digitaria ciliaris*, *Setaria glauca*, *S. viridis* and *Echinochloa crusgalli* var. *oryzicola*) were annual plants. In addition, the proportion of

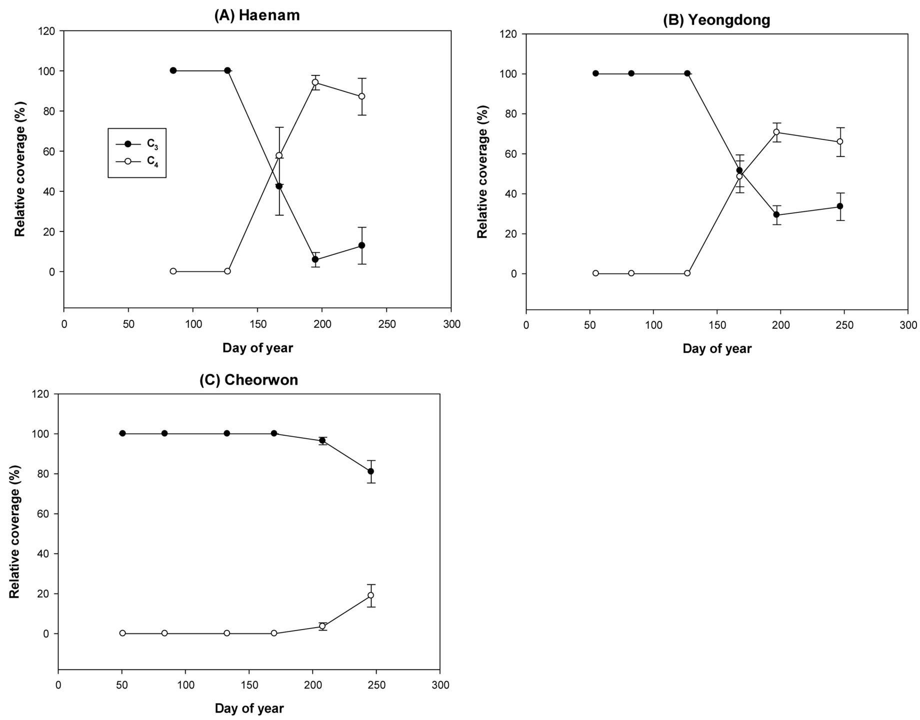

Fig. 3. Seasonal changes in the relative coverage of C_3 and C_4 plants in the Haenam (A), Yeongdong (B) and Cheorwon (C) regions. Error bars represent the standard deviation (n=5).

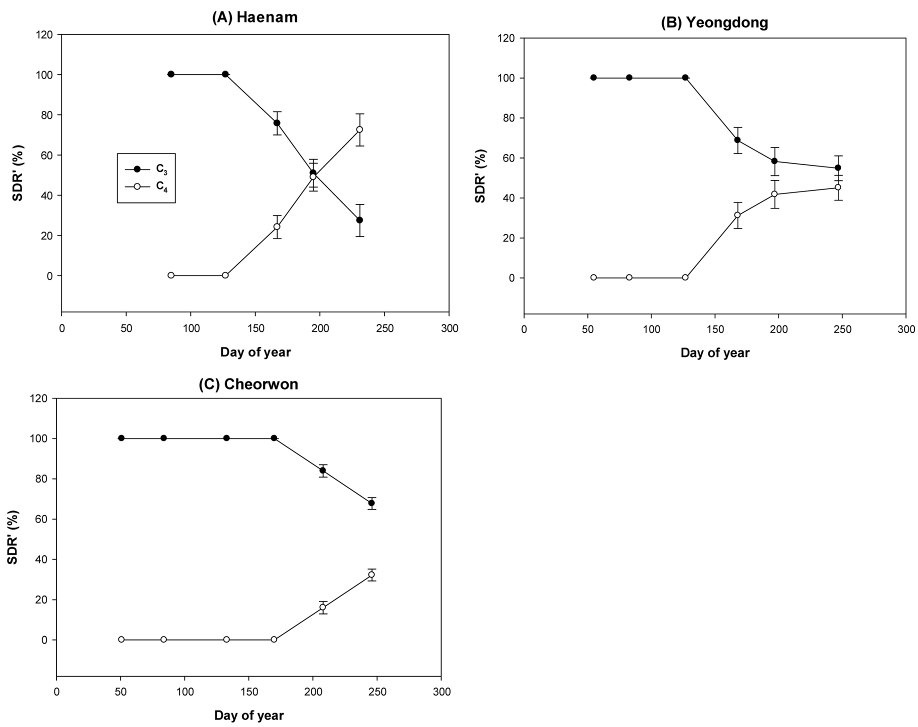

Fig. 4. Seasonal changes in the SDR' values of C_3 and C_4 plants in the Haenam (A), Yeongdong (B) and Cheorwon (C) regions. Error bars represent the standard deviation (n=5).

C_3 plants drastically decreased after the appearance of C_4 plants in the Haenam region levees due to the limited number of plants that occupied the sites (e.g., *Digitaria ciliaris* and *Echinochloa crusgalli* var. *oryzicola*) (Table 3). On the other hand, the number of C_3 plants continually increased in the Cheorwon region, and C_4 plants occurred later in this region than in other study sites.

These seasonal changes in species number and dominance ratios of C_3 and C_4 plants directly affected the levels of plant species diversity. Species diversity was found to peak at the point at which no specific plant species dominated the population (Table 3, and Fig. 2). This diversity change trend is similar to that reported previously in instances of succession, the process whereby one plant community changes and becomes another (Mattews, 1992; Peet, 1992; Jones and Moral, 2005). Hence, diversity of both primary and secondary succession increases early and decreases later in this process with a peak at an intermediate stage. The continuous increase in species diversity in the Cheorwon region was therefore the result of the C_4 populations such as *A. aequalis* and *S. alsine* var. *undulate* (which had disappeared during late summer in the Haenam and Yeongdong regions and remained until autumn in the Cheorwon region) and C_3 plants such as *Mosla punctulata* and *Ludwigia prostrate* (which newly appeared).

With respect to the observed seasonal changes in the relative coverage and SDR' of C_3 and C_4 plants (Figs. 3 and 4), the values of the C_3 plants decreased from spring to autumn whereas those of the C_4 plants increased. These patterns were similar to those reported in previous studies (Tieszen *et al.*, 1979; Ode *et al.*, 1980; Okuda, 1987; Shimoda *et al.*, 2009).

We considered soil moisture (Takeda *et al.*, 1977; Takeda *et al.*, 1980; Long, 1999), temperature (Long, 1999) and sunshine duration as environmental conditions affecting the development of C_4 plants. According to the comparison among the soil moisture contents of three regions, there was no statistically significant difference (Fig. 5). Therefore, it is not likely that soil moisture caused the seasonal and regional differences in the growth of C_4 plants.

The annually accumulated temperature of Haenam region was the highest (3478.6° day for AT_5, 2227.2 °C day for AT_{10}), Cheorwon region was the lowest (2755.3°C day for AT_5 and 1651.3°C day for AT_{10}) among the survey regions (Fig. 6). We evaluated the relationship between the accumulated temperature (AT_5 or AT_{10}) and SDR' of C_4 plants in the Haenam and Yeongdong regions where the dominant plant species changed from C_3 to C_4 when passing the high temperature

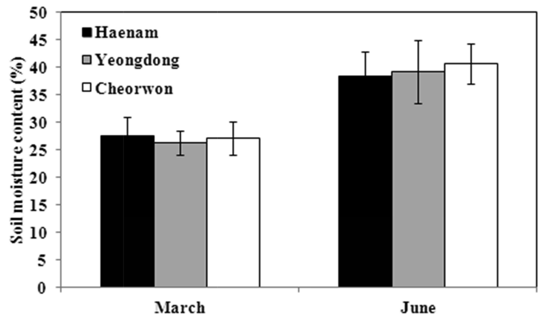

Fig. 5. Soil water content of three survey regions. Error bars represent the standard deviation (n=5).

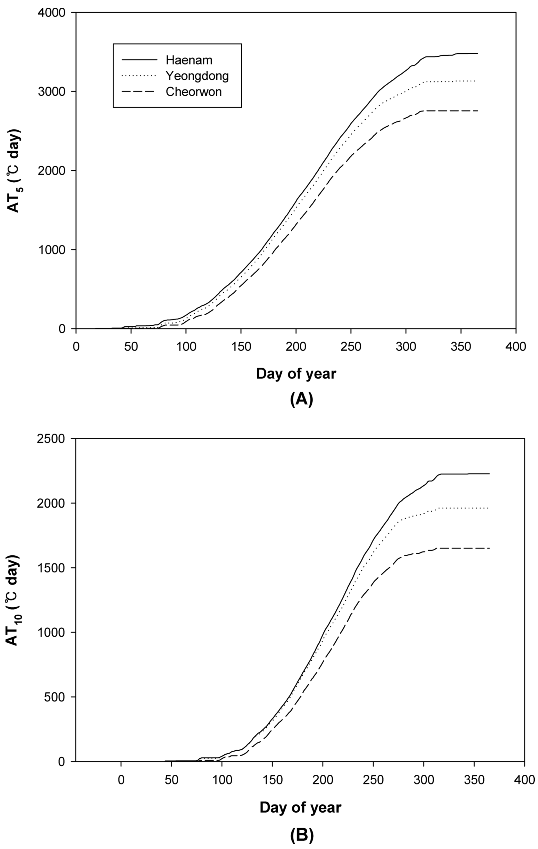

Fig. 6. Seasonal changes of AT_5 (A) and AT_{10} (B) of three survey regions. AT_5 and AT_{10} is the sum of daily temperature for the period of daily mean temperature above 5 or 10, respectively.

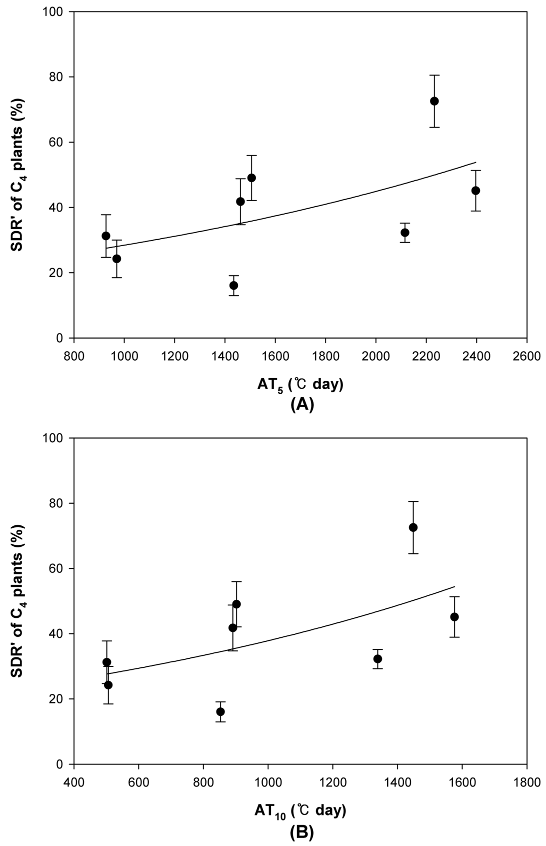

Fig. 7. Relationships between AT_5 (A) or AT_{10} (B) and SDR' values of C_4 plants. The data sets analyzed were those that showed changes in tandem with the accumulated temperature. The accumulated temperature is the sum of the daily temperatures for the period in which the daily mean temperature was above 5 (AT_5) or 10°C (AT_{10}). Error bars represent the standard deviation (n=8). The regression equations were y=18.0046 exp(0.0005x) (R^2=0.34, P=0.1321, n=8) for AT_5 and y=20.1553 exp(0.0006x) (R^2=0.35, P=0.1245, n=8) for AT_{10}.

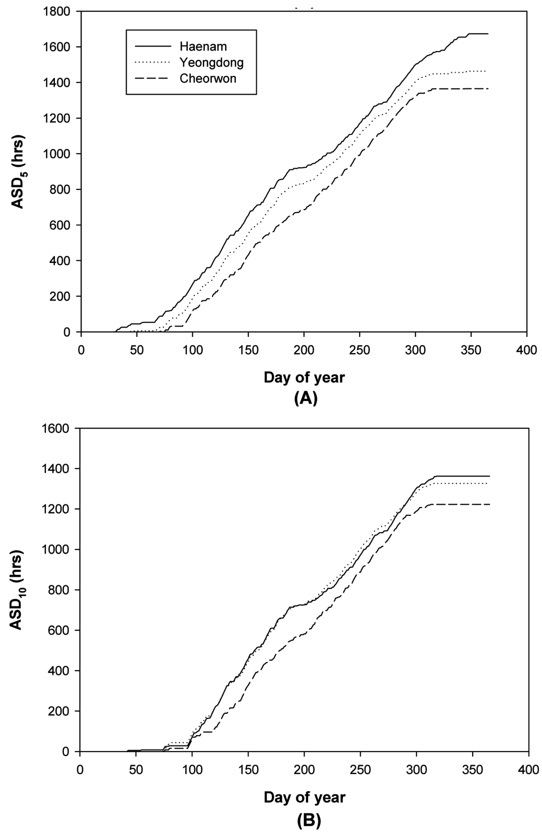

Fig. 8. Seasonal changes of ASD_5 (A) and ASD_{10} (B) of three survey regions. ASD_5 and ASD_{10} is the sum of daily sunshine duration for the period of daily mean temperature above 5°C or 10°C, respectively.

period in summer. The SDR' of C_4 plants exponentially increased with increasing accumulated temperature (Fig. 7), but the difference was not statistically significant (P=0.1321 for AT_5 and P=0.1245 for AT_{10}). Accumulated temperature did not explain the change of C_4 plants.

We contrived accumulated sunshine duration (ASD) to consider the effects of both temperature and light (sunshine duration) to the development of C_4 plants (Fig. 8). In the ASD_5, there was statistically significant difference among the survey regions ($P<0.05$). In the ASD_{10}, the difference between Haenam and Yeongdong region was not statistically significant ($P>0.05$). The SDR' of C_4 plants exponentially increased with increasing ASD (Fig. 9). The results were statistically significant for ASD_5 (n=8, $P<0.05$), but not for ASD_{10}. According to the regression equations of ASD_5 vs. SDR' of C_4 plants, the transition timing from C_3 to C_4 plants occurred when the ASD_5 was 1017 hrs. The ASD_5 in the Haenam and Yeongdong regions reached 1017 hrs on August 15 (227 days) and August 25 (237 days) in 2009, respectively. Our results may thus be an effective index for predicting the transition timing of dominant plants in C_3/C_4 mixed communities.

An increase in the mean global temperature, as a result of rising atmospheric carbon dioxide and other greenhouse gases, would provide favourable temperature conditions for C_4 plants, which may results in the changes of species diversity and the transition timing from C_3 to C_4 plants in the vegetations surrounding

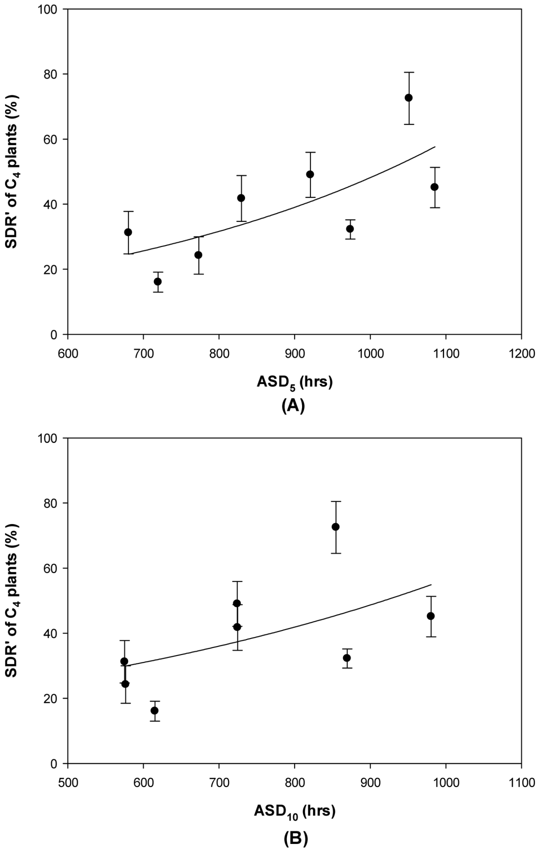

Fig. 9. Relationships between ASD_5 (A) or ASD_{10} (B) and SDR' values of C_4 plants. The accumulated sunshine duration is the sum of the daily sunshine duration for the period in which the daily mean temperature was above 5 (ASD_5) or 10°C (ASD_{10}). Error bars represent the standard deviation (n=8). The regression equations were y=5.9030 exp(0.0021x) (R^2=0.52, $P<0.05$, n=8) for ASD_5 and y=12.5996 exp(0.0015x) (R^2=0.31, P=0.1531, n=8) for ASD_{10}.

crop lands. These changes may induce the changes of agricultural practices such as weeding and disease and insect pest control.

적 요

본 연구에서는 기후변화가 농업생태계 식물군락에 미치는 영향을 해석하기 위하여 기상요건이 다른 해남, 영동, 철원 3지역의 논둑에서 시기별로 식생변화를 조사하였다. 그 결과 출현종수에서 C_3식물은 해남과 영동에서는 이른 봄부터 5월 중순까지 증가하다가 C_4식물이 출현하는 이후부터 계속적으로 감소하였지만, 철원에서는 이른 봄부터 가을까지 계속적으로 증가하는 경향을 나타냈다. C_4식물은 해남과 영동에서는 6월 중순, 철원에서는 7월 하순에 출현하여 가을까지 계속적으로 증가하는 경향을 나타냈다. 종다양성의 계절변화에서 해남은 C_4식물이 출현하기 전에 가장 높은 값을 나타냈으며 이후에는 급격히 감소하였다. 영동은 C_3와 C_4식물이 혼생하는 초기에 가장 높은 값을 나타냈으며 이후에 서서히 감소하였다. 철원은 감소경향이 나타나지 않고 계속적인 증가 패턴을 나타냈다. 이들 논둑에 출현하는 식물을 C_3와 C_4 두 그룹으로 나누어 상대피도 및 상대우점율의 계절변화를 확인한 결과 지역별 차이를 나타내기는 하지만 C_3식물에서 C_4식물로 교대가 나타나는 것을 확인할 수 있었다. 이러한 교대시기를 온도와 일조시간을 고려한 관계식을 이용하여 추정할 수 있었으며, 일평균기온 5 이상인 날에 대한 일조시간의 누적 합이 1017시간에서 논둑식생의 상대우점율이 C_3식물에서 C_4식물로 교대하는 것으로 예측했다. 이러한 연구결과는 기후변화에 따른 국내 식생분포의 예측에도 중요한 기초자료로 활용될 수 있을 것으로 판단된다.

ACKNOWLEDGMENTS

This study was carried out with the support of "Research Program for Agricultural Science & Technology Development (Project No.PJ008954)", National Academy of Agricultural Science, Rural Development Administration, Republic of Korea.

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