Quantitative expression of developmental processes as a function of water temperature in rice (*Oryza sativa* L.) under a cool climate

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Introduction

Sensitivity of rice (*Oryza sativa* L) to various environmental stresses often varies with the developmental stage at the time of expose to stress, and a slight difference in the developmental stage can result in a severe loss in grain yield[29]. Cool injury of spikelet fertility is a typical example. The sensitivity to cool temperature is extremely high at the young microspore stage[16], at which low temperatures can damage the development of pollen cells, leading to poor fertilization of florets and low grain set[6]. After the microspore stage, plants are less sensitive to low temperatures[6]. The rate of grain filling is also reduced by low temperatures due to slower rate of assimilate translocation to grains[1]. Under a cool climate, therefore, the delay of crop development can lead to poor grain filling and therefore lower yield.

A number of studies have been conducted to quantify the progress of developmental stages in rice based on climatic conditions. Temperature is the essential factor determining the developmental progress to be taken into account, and in most models[3,5,7,28] air temperature (Ta) is used basically because the data are widely available. However, in paddy rice grown under flooding conditions, water temperature (Tw) is the major determinant for the development of rice plants particularly in the early growth stages. Matsushima et al.[11] subjected the plants growing in pots to various combinations of Ta and Tw (16-36 °C) at various growth stages, and found that the heading day (HD) was delayed more greatly by low Tw than low Ta in the first half of the growth stages. A significant effect of Tw on HD was also reported by Shibata et al.[18] and Collinson et al.[2]. In the field, Tw is generally different from Ta and the difference is larger in a cool climate[17,23,24,25]. For instance, Tanaka[23] reported that Tw was sometimes as much as 10 °C higher than Ta at the early growth stage in the paddy field of Aomori Prefecture. In fact, deep irrigation with water at a higher temperature than Ta has the advantage of protecting the developing panicles from cool injury at the susceptible stage[15,17]. However, considering the large difference between Ta and Tw and the large impact of Tw on growth, we need to understand the response of the plant development to Tw.

An important advance in crop growth modeling was made in the 1970's, where crop development was dynamically expressed by a continuous variable[26]. In rice, Horie and Nakagawa[7] introduced the developmental index (DVI) to predict the developmental progress based on Ta and daylength. Because many physiological responses are largely dependent on the developmental stage of the crop[29], DVI can be used to reasonably express the age-dependent process quantitatively. Low Tw often decreases the rates of leaf emergence, panicle and culm elongation. The rate of leaf emergence affects leaf expansion, which is the major factor limiting crop growth[19]. Culm length determines the vertical position of the panicle which is an important factor in rice production in a cool climate because Ta and Tw are largely different. Because all of these processes are age-dependent, the effect of Tw on crop growth may also be expressed as a function of DVI.

The objectives of this study are firstly to quantify the dependence of crop development on Tw during the vegetative and reproductive periods from 3-year field experiments. Secondly, we attempted to express the leaf number, floral stage, panicle and culm length by DVI as a function of Tw.

Materials and Methods

Field experiments were conducted at the experimental paddy field of Hokkaido University (43°04'N) in 1997, 1998 and 1999. Germinated seeds of cv. Kirara 397, widely cultivated in Hokkaido, Japan were sown late in April (three seeds per pot, Minoru Industrial co., Japan). Seedlings were raised in a vinyl house and transplanted late in May on the paddy field (Table 1). Each plot received equal amounts of basal fertilizer (9.6, 9.6 and 7.2 g m^{-2} of N, P_2O_5 and K_2O, respectively). The plants were subjected to a low water temperature (Tw) condition either during the vegetative (from 16-21 days after transplanting (DAP) to panicle initiation (PI)) or reproductive period (from PI to full heading) by irrigating cool water (ca 15 °C) from 6:00 to 18:00 at the rate of ca. 300 L min^{-1} in the field. The temperature gradient from the water inlet to the outlet was used to provide three levels of Tw. The water depth was maintained at about 10 cm above the soil surface during the treatment. The size of each plot was 64-100 m^2, enclosed with a plastic board (30 cm in height). The treatments are denoted with the two letters; the first stands for the period (V for vegetative and R for reproductive) and the second for water temperature (L for low Tw and M for moderate Tw). The plot with the highest Tw during both growth periods was designated as Control. In 1997, one plot was irrigated continuously with the water at a moderate temperature during the two periods, this is denoted as CM. No replication was designed, because it was difficult to arrange randomly the plots in the field. Tw below 5 cm from the water surface was measured at the center of each plot with a thermocouple (Copper-Constantan, 0.6 mm in diameter) and recorded on the data logger (IDL-3200, North Hightech Inc., Japan) at a 10-minute interval.

The daily mean Tw was expressed as the average of maximum and minimum temperatures. Air temperature (Ta) at 1.5 m from the soil surface was also recorded at the Experimental Farm, Faculty of Agriculture, Hokkaido University. The date of PI was determined as the time when the average length of the young panicles on 5 main stems reached 1 mm, based on the periodical observations of panicle primordia. The number of protruded panicles was counted for all the tillers of 20 hills in each plot. The heading day (HD) was determined as the date when 50% of the tillers (excluding late tillers) had emerged ears. In 1997, the development of the panicles as well as culm length was measured for the main stems of five hills at 3-d interval under a stereoscopic microscope. Floral stage was also determined according to Hoshikawa[8]. The leaf number on the main culm was measured weekly for ten hills in each experimental plot in all years. The process of rice development was expressed quantitatively by the DVI according to Horie and Nakagawa[7]. Here, we define DVI as 0 at seedling emergence, 1 at PI and 2 at HD. The average rate of development (DVR) was given by the reciprocal of the growth duration (DVR=1/(days of growth period)). In our study, DVI at transplanting was given by dividing leaf number at transplanting (Tp) by leaf number at PI, assuming that the leaf number is linearly related to the developmental stage before PI[4]. Parameters for the quantitative relationship between DVR and Tw were determined for randomly selected data sets (six for the vegetative period and 12 for the reproductive period), and the remaining data sets were used for independent testing (Table 1 and 2). Mean square error (MSE) for the estimate was calculated as the root of the squares of differences between observed and predicted values divided by (n minus number of parameters). To describe the relationship between DVI and leaf appearance or panicle length, we tested three functions (Gompertz function: $f(x) = a \times exp(b \times exp(cx))$, Logistic function: $f(x) = a/(1 + exp(b - cx))$, Richards' function: $f(x) = a(1 + exp(b(x - c)))^d$) by the simplex method (CoPlot, version 3.00, CoHort Software, Minneapolis, USA). These are all sigmoid functions but with different inflexion points. For the relationship between culm length and DVI, three nonlinear functions (Exponential function: $f(x) = a \times exp(bx)$, Hoerl's function: $f(x) = a \times xb \times exp(cx)$, Power function: $f(x) = a \times x^b$) were tested by the ordinary least square method by linearizing the functions. These functions can give different degree of curvature.

Table 1. Crop management.

Year	Sowing Date	Date	Transplanting (Tp) Density	Leaf age	DVItp
1997	23 Apr.	27 May	16×33cm	5.2	0.50
1998	22 Apr.	26 May	13×33cm	5.2	0.51
1999	21 Apr.	26 May	13×33cm	5.1	0.51

DVItp: DVI at transplanting, estimated from laef age.

Results

Air and water temperatures

Air temperature (Ta) (average of 5 successive days) increased gradually from Tp (0 DAP) to HD (61–80 DAP), ranging from 11.0 to 26.8 °C (Fig. 1). Ta during the early vegetative period in 1999 was higher than that in 1997 and 1998. During the reproductive period, Ta in 1997 and 1999 was higher by ca. 1 °C than in 1998.

In the vegetative period, average water temperature (Tw) during the treatment period (20–25 d) differed by 4.6–5.5 °C (data not shown), but from Tp to PI the difference in Tw among the experimental plots was 2.0–2.7 °C (Table 2). During the reproductive period (from PI to HD), Tw differed by 5.4–6.6 °C among the plots (Table 3). There was a yearly variation in Tw associated with Ta. Tw was relatively high during the vegetative period in 1999 and during the reproductive period in 1997. Although cool water was supplied only during the daytime, Tw was consistently lower than normal in the plots irrigated with cool water (data not shown).
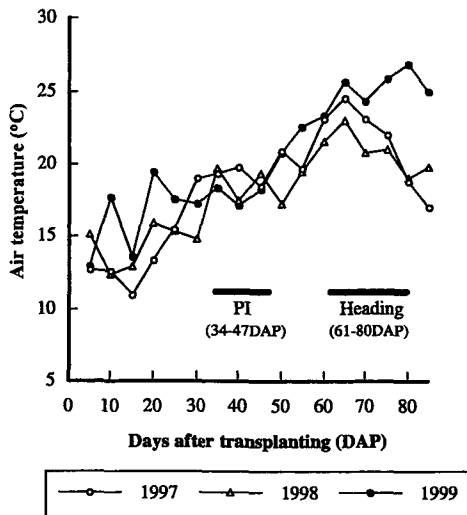
Table 2. Water temperature (Tw) and the duration from transplanting (Tp) to panicle initation (PI).

Year	Treatment	Tw ±s.d. (°C)	Tp-PI (d)
1997	Control	20.9 ± 2.8	39
	VL	18.2 ± 1.4	46
	CM	19.7 ± 1.6	43
1998	Control*	20.8 ± 2.4	39
	VL*	18.8 ± 2.6	47
	VM	19.6 ± 1.9	42
1999	Control	21.6 ± 2.3	34
	VL	19.3 ± 2.0	40
	VM*	20.5 ± 1.8	36

* indicaters date used in Fig. 3.
VL-VM : Treatment during vegetative period.
CM   : Treatment during vegetative and reproducitve periods.

Table 3. Water temperature (Tw) and the duration from panicle initation (PI) to heading stage (HD).

Year	Treatment	Tw ±s.d. (°C)	PI-HD (d)
1997	Control	25.1 ± 2.4	25
	VL	26.0 ± 1.7	25
	RL	18.5 ± 2.2	34
	CM	19.3 ± 1.6	32
1998	Control*	22.9 ± 2.1	27
	VL	24.5 ± 1.4	26
	VM	23.7 ± 1.4	28
	RM*	19.5 ± 1.5	37
1999	Control*	23.3 ± 1.6	27
	VL	25.4 ± 1.3	26
	VM	24.2 ± 1.8	27
	RL	17.9 ± 1.9	38
	RLM	19.4 ± 1.4	36
	RM	20.0 ± 1.3	34

* indicaters date used in Fig. 3.
RL-RM : Treatment during reproductive period.

Fig. 1. Air temperature (average of 5 days) during the season.

Growth periods and developmental rates (DVR)

Both vegetative and reproductive periods were prolonged as much as 14 d by decreasing Tw (Table 2 and 3). The delay in PI (6-8 d) in VL and VM plots did not affect the duration from PI to HD. The DVR during both periods was positively and tightly correlated with Tw (Fig. 2). In both periods, the relationship was linear in the range of 18.2-21.6 °C during the vegetative period and in the range of 17.0-26.0 °C during the reproductive period, and was conserved in all three years. The correlation coefficients were high in both periods, indicating the strong influence of Tw before heading on DVR, although it is well known that the effect of Tw on the development becomes smaller as the growth stage proceeds[11]. The model based on the linear response to Tw was tested with three independent data sets for each period, which were not used for the parameterization (Fig. 3). The estimated values agreed well with the observed values with MSE < 2.37 d (n=6).
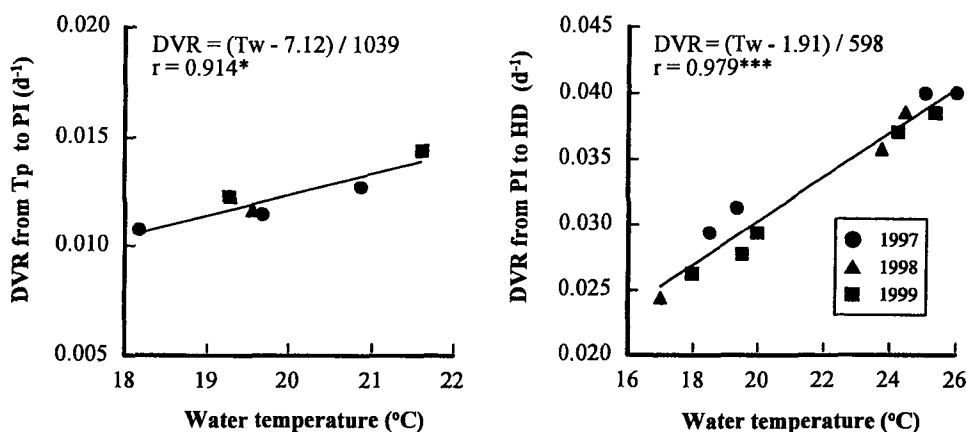

Fig. 2. Correlation of water temperature with the developmental rate (DVR) from transplanting (Tp) to panicle initiation (PI) and from PI to heading stage (HD) in 1997, 1998 and 1999.
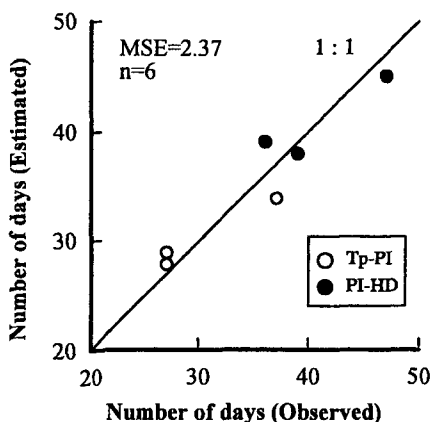

Fig. 3. Relationship between estimated and observed number of days from transplanting (Tp) to panicle initiation (PI) and from PI to heading stage (HD) of the data, which is not used for parameterization in Fig. 2.

Leaf appearance

The leaf number at the same day greatly varied with the Tw during the vegetative and reproductive periods (Fig. 4, left). The rate of leaf appearance was lowered by the VL treatment given from 16-21 to 34-47 DAP, but the final leaf number was similar in all plots. The RL treatment, given from 34-42 to 69 -74 DAP, also lowered the rate of leaf appearance. However, the rate of leaf appearance at the same DVI was scarcely influenced by Tw (Fig. 4, right), suggesting that the effects of Tw on the rate of leaf emergence can be well expressed as a function of DVI. Three different non-linear functions were tested to find an appropriate mathematical expression for the relationship. There was no large difference in goodness of fit among three functions (R^2=0.975-0.980), but Gompertz and Richards' functions with the smallest inflexion point showed no distinct pattern of variation in the residual plot, while Logistic function tended to overestimate the leaf number at early growth stages. In both good fit functions of Gompertz and Richards', we selected the former to express the relationship because of the smaller number of parameters.
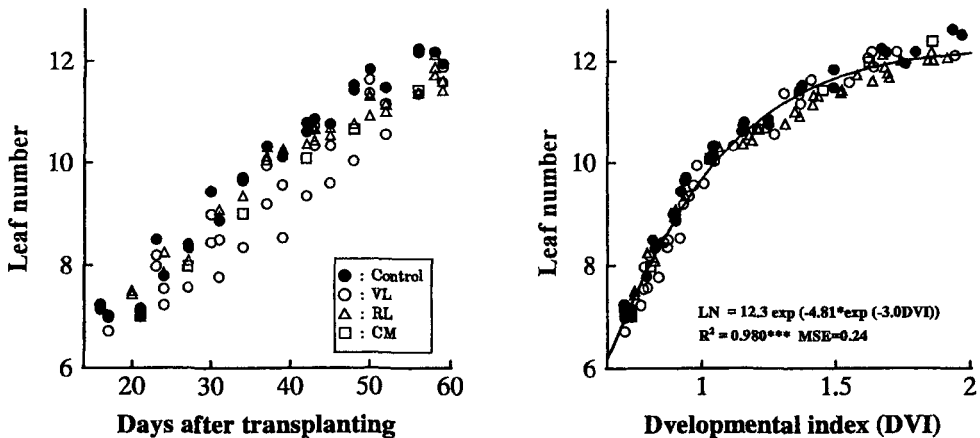

Fig. 4. Leaf number on the main stem in 1997, 1998 and 1999.
       LN: Leaf number

Panicle development and culm elongation

The delay of HD due to low Tw was accompanied with a substantial delay in the developmental stage in young panicles (Table 4). Low Tw during the reproductive period (RL) delayed the progress of panicle development at all stages after spikelet initiation. Even the duration after the stage at which the auricle distance was 0 (around the meiosis stage) to heading was prolonged by 3 d despite the fact that the panicle had already emerged above the water surface at this stage. A similar delay was also observed in CM plot, where the treatment was imposed for both vegetative and reproductive periods. On the other hand,

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Table 4. Date at each floral stage in 1997.

Stage	Control	VL	RL	CM	DVI
1. Primary Rachis Branch	29 Jun.	**5 Jul.**	29 Jun.	**3 Jul.**	0.92-0.94
Initiation	(4)	(5)	(4)	(5)	
2. Secondry Rachis Branch	3 Jul.	**10 Jul.**	3 Jul.	**8 Jul.**	0.97-1.03
Initiation	(2)	(2)	(2)	**(1)**	
3. Panicle Formation (PL=1mm)	5 Jul.	12 Jul.	**5 Jul.**	**9 Jul.**	0.99-1.06
	(2)	(2)	**(2)**	(2)	
4. Spikelet Initiation	7 Jul.	14 Jul.	**7 Jul.**	**11 Jul.**	1.05-1.12
	(4)	(3)	**(6)**	(5)	
5. End of Spikelet Differentiation	11 Jul.	17 Jul.	**13 Jul.**	**16 Jul.**	1.17-1.28
	(9)	(9)	**(13)**	(12)	
6. Auricle distance = 0	20 Jul.	26 Jul.	**26 Jul.**	**28 Jul.**	1.53-1.63
	(10)	(11)	**(13)**	(13)	
7. Heading	30 Jul.	6 Aug.	**8 Aug.**	**10 Aug.**	1.98-2.01
Days from 1-7		(31)	(32)	(40)	(38)
Days from 3-7		(25)	(25)	(34)	(32)

( ) : Number of days between stages. PL : Panicle length, Bold letters indicte the date under low temperature.

the low Tw during the vegetative period (VL) did not affect the rate of panicle development during the reproductive period. Panicle elongation for about 10 days after initiation of primary rachis branch (DAI) was not influenced by the low Tw, but the rate of the elongation thereafter was largely reduced by low Tw (Fig. 5a). However, there was no significant difference in the final panicle length among the plots, the average being 158 mm with a standard error of 1.1. The panicle length in each plot is well expressed as a function of DVI (Fig. 5b). These non-linear functions were tested to give an appropriate expression of the relationship between the panicle length and DVI. Goodness of fit and the residual analysis indicated that Richards' function best described the relationship ($R^2 = 0.986$). The estimated parameters for Richards' function indicated that the point of inflexion occurs when panicle length reaches 55% of the full length, which is larger than that for the other functions (37% for Gompertz and 50% for Logistic). Because the length of the panicle is known to reflect the floral stage[8], this function can be used to identify the critical stage of cool injury under different Tw. The rate of culm elongation after 15 DAI was also lowered by a low Tw during the reproductive period in RL and CM plots, and the effect became clearer with increasing DAI (Fig. 5c). However, the culm length at each Tw plot was also well expressed as a function of DVI (Fig. 5d). We tested three functions for the relationship between culm elongation and DVI, and found that Hoerl's function with the strongest degree of curvature gave a better fit ($R^2 = 0.958$) than Exponential function ($R^2 = 0.938$) and Power function ($R^2 = 0.902$). This function along with the panicle length allows us to estimate the position of the panicle in relation to flooding water, and thereby gives information on the thermal condi-
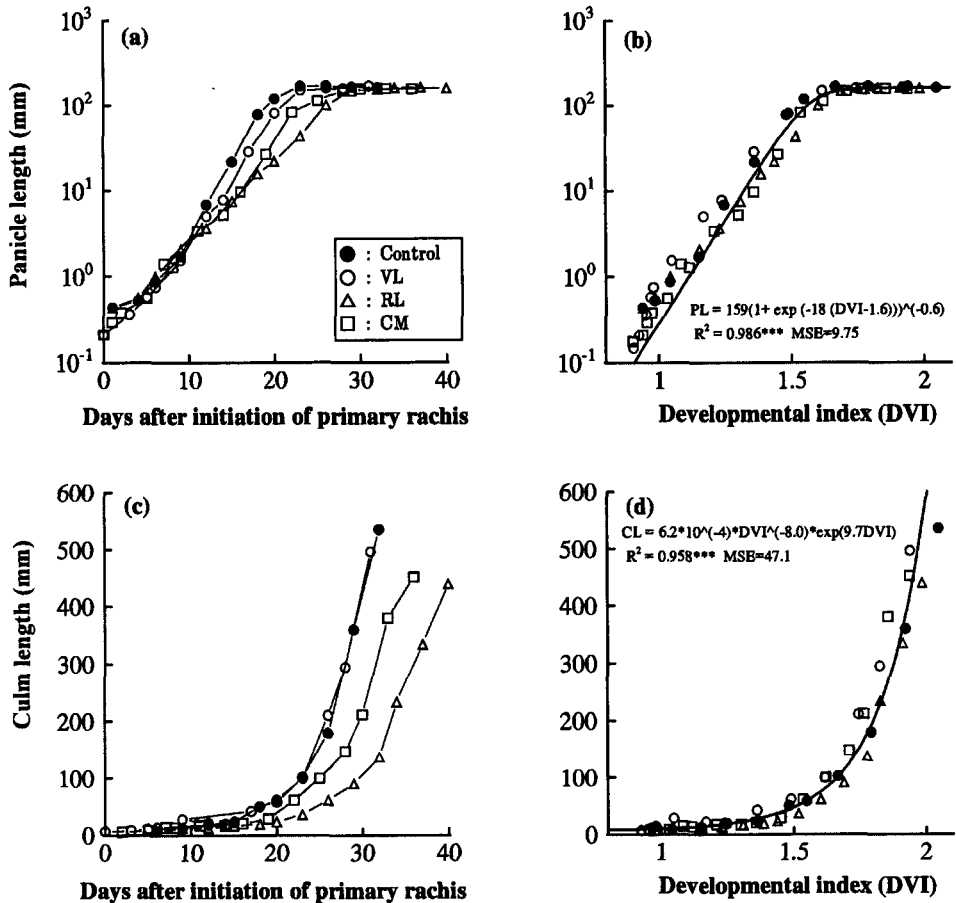
Fig. 5. Panicle length (a, b) and culm length (c, d) on the main stem in 1997.
PL: Panicle length, CL: Culm length

tions of the panicle at any given stages.

Discussion

A number of models for the developmental response to Ta have been developed in rice plants[3,5,7,20,28], which showed a high accuracy in predicting the time of major developmental stages.   However it is well known that Tw plays a major role in the growth of paddy rice.   Matsushima et al.[11] investigated the effects of Ta and Tw at different stages on rice growth, and showed that Tw affected rice development independent of Ta particularly in the early growth stages.   The importance of Tw rather than Ta has also been reported by Shibata et al.[18] and Collinson et al.[2]   In the field, it is well known that Tw is different from Ta[17,23,24,25]   Tanaka[23] reported that Tw is as much as 10 °C higher than Ta in the field condition.   For accurate prediction of crop development, particularly where

Tw and Ta are largely different, the effect of Tw needs to be taken into account.

We found a close and positive relationship between DVR and Tw during the vegetative and the reproductive periods (Fig. 2), as often observed between DVR and Ta[3,20]. DVR has been reported to show an asymptotic response to Ta[2,7]. However, we found a linear relationship between DVR and Tw in the temperature range of 17–26 °C, which can cover most of the temperature variation in Hokkaido. The simple correlation between DVR and Tw agreed quite well with the data that was not used for the parameterization (Fig. 3). Good agreement between observed and measured values over the years with different Ta confirmed the strong dependence of DVR on Tw, even when the panicle emerged above the water surface.

In addition to temperature, daylength is known to affect rice development[29], and have strong interactions with temperature[14]. However, varieties in Hokkaido including "Kirara 397" are not photosensitive so that there was no need to take into account the factor of photoperiod in our model.

The developmental responses to Tw in the vegetative and the reproductive periods indicated that PI is delayed by 3 days and HD by 2 days by a 1 °C drop of Tw around 20 °C. In Hokkaido, a 5-d delay in HD results in a 0.5–1.0 °C decrease of average Ta during the ripening stage[25], which can reduce the grain filling[1] and eating quality[22].

The quantitative expression of the progress of the developmental stage such as DVI has a great advantage in explaining the variation in the rates of age-dependent processes. Nakagawa and Horie[13] indicated that the difference in panicle length and floral stages corresponded well with DVI, which is expressed as a non-linear functions of Ta and day length. It is well known that the sensitivity to the mid-season cool damage is largely dependent on the stage of panicle development[6,16] and the DVI approach has been used to quantify the degree of cool injury[27]. The present study showed that the large difference in the rates of panicle development under the conditions with different Tw was closely associated with the difference in DVI and that Richards' function represented well the relationship between the developmental stage and DVI (Fig. 5b). The most sensitive stage to the mid-season cool damage (auricle distance = 0) was identified as around DVI=1.6 (Table 4), which was similar to that found by Yajima et al.[27].

The rate of culm elongation is another important factor in rice production under cool environments because this determines the vertical position of the developing panicle. Until the panicles emerge from the water surface, Tw determines the panicles temperature. In fact, since Tw is generally higher than Ta[17,23,24,25], deep-water management is the most important cultivation practice to protect developing panicles from cool air[15,17]. The rate of culm elongation was reduced with the decreasing Tw (Fig. 5c). A number of factors are involved in the regulation of culm elongation, which include nutrient availability, light and

water status of the plants[9,10], but the present study showed that culm length could be well expressed as a non-linear function of DVI (Fig. 5d). The function together with that for panicle length can be used to determine the position of the panicle under different Tw conditions in relation to water depth. In order to cover panicles fully with the flooding water at DVI=1.6, the minimum depth of the water would be about 20 cm provided that the planting depth is 3 cm below the soil surface.

DVI could also be used to show the variation in the rate of leaf emergence at different Tw (Fig. 4). Although it has been reported that the responses of leaf emergence and crop development to Ta are different[12], the change in leaf number could be expressed by DVI as a function of Tw within the temperature range studied. Recently, Shimono et al.[19] found a close correlation between the leaf area growth and the leaf emergence rate. The function of Tw obtained for leaf number could well be used to give a leaf expansion rate, which is the major determinant for crop growth under sub-optimal Tw[19].

In conclusion, our 3-year field trial confirmed the strong dependence of DVR on Tw during the vegetative and reproductive growth periods. A simple linear function was found to represent well the relationship between DVR and Tw. The model indicated that the error in estimation was within 2.4 days. Another merit of using DVI was that panicle development, culm length and leaf number are well represented as the non-linear functions of DVI, which can be used to identify the positions of the panicles and leaf growth under different thermal conditions. Although the data for Tw are generally less available than those for Ta, methods for estimating Tw based on the energy balance are emerging[21]. Where Ta and Tw are largely different as under the cool climates, the developmental response to Tw obtained in this study will improve the accuracy of estimation of developmental progresses and can be incorporated in the crop growth model.

Summary

Development of rice plants (*Oryza sativa* L.) under flooding conditions is strongly affected by water temperature (Tw). Although a number of models for the developmental progress have been developed based on air temperature, quantitative expression of the effect of Tw is still limited. We therefore conducted a three-year field trial in Sapporo (43°04′N), Japan to determine the effect of Tw during the vegetative and reproductive periods in the development of rice

plants. Cool water of ca. 15 °C was irrigated for 20-34 days during each period and three to four plots with different Tw were provided. The average daily Tw in each plot ranged from 17.0 to 26.0 °C. The process of rice development was expressed by the developmental index (DVI, Horie and Nakagawa[7]). The average developmental rate (DVR, the reciprocal of growth duration) was closely and linearly correlated with Tw during the vegetative (r=0.914*) and reproductive periods (r=0.979***) and the relations was conserved over the years. This simple correlation between DVR and Tw agreed well with the data that were not used for parameterization (The mean square error = 2.4 d). Tw-dependent variation in the developmental stage such as leaf number, panicle length and culm length were well expressed as a function of DVI. The developmental response to Tw in the present study will improve the accuracy of estimation of developmental progresses and can be incorporated in the crop growth model.

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