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Effects of Temperature on the Development of Rice Panicles

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Abstract The relationship between temperature and spikelet number per panicle in rice was examined. Two experiments were conducted: Experiment 1) a treatment of air temperature (AT) and Experiment 2) a treatment of water temperature (WT). In experiment 1, three regimes of AT were applied: High temperature, 32/24°C (day/night); Medium temperature, 29/21°C; Low temperature, 26/18°C. In Experiment 2, three levels of WT (26, 29, 32°C) were applied in day. WT at night was not controlled independently from the AT. Dry weights were measured at the stage of spikelet differentiation. At heading, dry weights and the number of differentiated spikelets and primary and secondary rachis-branches per panicle were measured. High AT during the early reproductive stage reduced the number of differentiated spikelets. High AT did not decrease dry matter accumulation, but changed the allocation of dry matter among organs. High AT promoted dry matter accumulation to leaves, but decreased dry matter accumulation to tillers. Low WT increased the number of differentiated spikelets, but decreased the number of surviving spikelets through increasing of spikelet degeneration. The WT treatment little affected dry matter accumulation and partitioning among organs. ^{13}C atom percents in leaf blades and leaf sheaths at heading were higher than those in panicles, which result suggested that carbohydrates assimilated at the stage of spikelet differentiation were translocated into actively growing organs such as leaves prior to young panicles. The role of temperature in spikelet differentiation was discussed.
Keywords: ^{13}C, panicle, rice, spikelet, temperature.

Introduction

Spikelet number (SN) is a strong determinant of rice yield. It is thought that SN is determined by the supply of nitrogen (N) and carbohydrates during the reproductive stage (Kobayasi 2000). However, the possibility of the relationship between temperature and SN per unit area was reported (IRRI 1977). Kobayasi and Kito (2003) also revealed low temperature (26/18°C: day/night) in the early reproductive stage increased SN per panicle whereas the temperature treatment did not change N contents in the rice plants. They speculated that low temperature directly promoted spikelet differentiation without changing the supply of carbohydrates and N to panicle primordia.

Rice plants are grown under flooded conditions. Not only air temperature (AT) but also water temperature (WT) and soil temperature affect rice development because shoot apical meristems are in water and soil. WT and AT affect independently rice morphological development such as tillers and leaves (Matsushima et al. 1964).

Temperature in the meristem affects cell division rate and will change the demand of assimilates among leaf blades, leaf sheaths, and young panicles. It is possible that low temperature increase carbohydrate supply in the early reproductive stage and increase the number of differentiated spikelets. The author would like to detect ^{13}C balance among leaf blades, leaf sheaths, and young panicles to determine effects of the supply of carbohydrates on spikelet differentiation.

The objectives of the experiments are two. One is to determine whether both AT and WT affect spikelet number per panicle. The other is to clarify effects of temperature on SN through carbohydrate supply. Using ^{13}C, the relationship between carbohydrates and spikelet number under different temperature regimes were examined.

Materials and Methods

1. Experiment 1 (Air temperature treatment)

(1) Plant culture

A pot experiment was conducted in growth chambers at Shimane University, Matsue, Japan. Rice cultivar 'Koshihikari' was used. Surface-sterilized seeds were germinated at 32°C for 24h. Selected seeds were sown for uniformity on May 1, 2003. Twenty germinated seeds were planted in each Wagner pot (1/5000 a) containing 3.6kg equivalent of oven-dry soil (air-dried Andosol and a granitic saprolite Cambisol mixture, 1:1 volume) using the circular dense-culture method (Satake 1972). The pots were watered at field capacity level for nine days after sowing, and later kept flooded with 2 to 3 cm of water. Tillers were removed when they emerged until the start of the temperature treatments. Liquid fertilizer, containing 0.15g N as ammonium sulfate, 0.15g P_2O_5 as superphosphate, and 0.15g K_2O as potassium chloride, was applied weekly. Five pots were used for each treatment (five replicates).

(2) Air temperature treatment

Three regimes of AT were applied: High temperature, 32/24°C (day/night); Medium temperature, 29/21°C ; Low temperature, 26/18°C. The temperature treatments began on June 27 and ended on July 8. After the treatments, pots were transferred to a sun-lit growth chamber (29/21°C).

(3) Measurements

Three plants per pot were sampled on the day finishing the treatments (the stage of spikelet differentiation) and at heading. Dry weights were measured after drying samples under 80°C for more than 48h.

At heading, more than five panicles were sampled from each pot to measure the number of differentiated and degenerated primary rachis-branches (PBs), secondary rachis-branches (SBs), and spikelets. The number of surviving and degenerated spikelets, PBs, and SBs were counted according to Kobayasi et al. (2001a). The number of degenerated organs was measured by counting the vestiges of degenerated organs on the panicles. The number of differentiated spikelets was defined as the sum of the numbers of the surviving spikelets and the degenerated spikelets. Similarly, the numbers of differentiated PBs and SBs were obtained.

2. Experiment 2 (Water temperature treatment)

(1) Plant culture

Rice cultivar 'Akenohoshi' was used because it has a large number of spikelets per panicle and moderate photoperiodic sensitivity. The culture method was similar to Experiment 1. Sowing date was August 19, 2003. All plants were grown under a natural day length for nine days, and then exposed to a long-day condition (14h photoperiod) to prevent panicle differentiation until the start of the WT treatment. For the long-day treatment natural daylight was supplemented with artificial light of four metal halide lamps from 5 a.m. to 7 a.m. and from 5 p.m. and 7 p.m.

On October 6, pots were transferred into a growth chamber (artificial light with 3 metal halide lamps and 3 sodium-vapor lamps, 10h photoperiod). AT was 29°C at day and 21°C at night. Three levels of WT (26, 29, 32°C) were applied in the day. WT at night was not controlled independently from the AT. The WT treatments were kept for ten days.

(2) $^{13}CO_2$ feeding and analysis of ^{13}C

$^{13}CO_2$ gas was generated from 99atom% sodium bicarbonate by adding 1.5M sulfuric acid and mixed with the air in the growth chamber. $^{13}CO_2$ was assimilated for about 7h (from 08:00 to 15:00, October 11). At the end of the assimilation, three plants per pot were immediately collected and ^{13}C and ^{12}C contents in the plants were analyzed, using differential infrared absorption spectrometry (EX-130S infrared $^{13}CO_2$ analyzer, Japan Spectroscopic Co. Ltd, Tokyo, Japan).

(3) Measurements

Other measurements were similar to Experiment 1.

Results

1. Experiment 1 (Air temperature)

(1) Number of spikelets

High AT during the early reproductive stage reduced the number of differentiated spikelets through reducing the number of both PBs and SBs differentiated (Table 1). Temperature affected little the degeneration of spikelets and rachis-branches so that the numbers of surviving PBs, SBs, and spikelets were mainly determined by the number of differentiated PBs, SBs, and spikelets.

Table 1. The effect of air temperature (℃) on spikelet number components (Experiment 1)

Temperature (day/night)	Number of differentiated spikelets	Number of differentiated primary rachis-branches	Number of differentiated secondary rachis-branches	Number of degenerated spikelets	Number of degenerated primary rachis-branches	Number of degenerated secondary rachis-branches	Number of surviving spikelets	Number of surviving primary rachis-branches	Number of surviving secondary rachis-branches
32/24	71.8±1.5	8.41±0.13	9.44±0.41	31.0±1.2	1.22±0.14	7.38±0.34	40.8±1.1	7.19±0.15	2.06±0.25
29/21	73.3±2.1	8.44±0.16	10.25±0.49	30.9±1.6	1.03±0.13	7.81±0.42	42.4±1.3	7.41±0.17	2.44±0.24
26/18	83.2±4.0	9.11±0.26	11.78±1.04	34.8±2.4	1.78±0.22	7.89±0.72	48.4±2.8	7.33±0.37	3.89±0.72

Table 2. Dry weight (mg per plant) at the stage of spikelet differentiation and at heading (Experiment 1)

Temperature (day/night)	Spikelet differentiation			Heading				
	Leaf blade	Leaf sheath	Tiller	Leaf blade	Leaf sheath	Dead leaf	Tiller	Panicle
32/24	405±45	342±65	14±8	556±89	775±165	222±71	40±15	104±23
29/21	385±34	478±70	76±31	579±81	782±148	151±29	77±29	93±26
26/18	268±35	368±56	138±67	742±199	856±216	168±26	93±44	78±17

Table 3. The effect of water temperature (℃) on spikelet number components (Experiment 2)

Water temperature	Number of differentiated spikelets	Number of differentiated primary rachis-branches	Number of differentiated secondary rachis-branches	Number of degenerated spikelets	Number of degenerated primary rachis-branches	Number of degenerated secondary rachis-branches	Number of surviving spikelets	Number of surviving primary rachis-branches	Number of surviving secondary rachis-branches
32	149.8±4.3	10.4±0.2	29.8±1.4	84.8±5.8	2.63±0.32	20.3±1.5	65.0±7.8	7.75±0.37	9.50±1.68
29	143.8±7.2	9.6±0.3	30.0±1.7	87.8±6.0	2.67±0.37	21.4±1.4	56.0±5.8	6.89±0.51	8.56±1.30
26	167.0±9.0	11.1±0.4	32.6±1.9	111.8±6.8	2.88±0.48	25.6±1.5	55.3±4.4	8.25±0.62	7.00±0.76

Table 4. Dry weight (mg per plant) at the stage of spikelet differentiation and at heading (Experiment 2)

Water temperature	Spikelet differentiation			Heading				
	Leaf blade	Leaf sheath	Tiller	Leaf blade	Leaf sheath	Dead leaf	Tiller	Panicle
32	547±140	454±109	88±156	898±38	1024±73	74±5	318±210	103±27
29	566±34	470±35	346±346	865±44	1063±59	66±32	772±317	158±3
26	540±45	508±67	79±142	938±103	1117±156	89±20	357±272	127±54

(2) Dry weight and distribution

High AT did not decrease dry matter accumulation from panicle initiation to the stage of spikelet differentiation (Table 2). However, dry matter distribution among organs was changed by the AT treatment. High AT promoted dry matter accumulation to leaves, but decreased that to tillers. Lower AT promoted tillering, in particular, at the late vegetative stage (Hanada 1993).

Although the AT treatment did not affect dry matter production during the treatment, high AT reduced total dry weight at heading.

2. Experiment 2 (Water temperature)

(1) Number of spikelets

Low WT increased the number of differentiated spikelets, but decreased the number of surviving spikelets through increase of spikelet degeneration (Table 3). The degeneration of both PBs and SBs was promoted by low WT.

(2) Dry weight and distribution

The WT treatment little affected dry matter accumulation and partitioning among organs during the treatment (Table 4). At heading, plants at the low WT treatment gained slightly more assimilates. But the differences between the WT treat-

Table 5. Distribution of ^{13}C among organs (mg per plant) at heading (Experiment 2)

Water temperature	Leaf blade	Leaf sheath	Dead leaf	Tiller	Panicle
32	2.12±0.04	2.24±0.15	0.12±0.01	0.73±0.49	0.26±0.06
29	2.01±0.06	2.38±0.13	0.11±0.06	1.77±0.72	0.39±0.01
26	2.18±0.30	2.42±0.36	0.15±0.03	0.81±0.62	0.31±0.13

Table 6. ^{13}C Atom % among organs at heading (Experiment 2)

Water temperature	Leaf blade	Leaf sheath	Dead leaf	Tiller	Panicle
32	1.120±0.003	1.112±0.002	1.112±0.006	1.109±0.001	1.095±0.001
29	1.129±0.002	1.122±0.001	1.121±0.008	1.116±0.002	1.101±0.002
26	1.125±0.001	1.120±0.002	1.120±0.004	1.111±0.002	1.102±0.001

ments were small.

(3) ^{13}C assimilation and distribution

Distribution of ^{13}C among organs at heading was not influenced by the WT treatment (Table 5). ^{13}C atom percents in leaves and stems at heading were higher than those in panicles (Table 6). These results suggest that most of carbon and carbohydrate assimilated at the stage of spikelet differentiation were translocated into actively growing organs such as leaves prior to young panicles, which are small and need less assimilates.

Discussion

Both low AT and WT promoted spikelet differentiation. Lower AT increased spikelet number per unit area (IRRI 1977) and per panicle (Kobayasi and Kito 2003). Young panicles are in the water or in the soil when they are differentiated, and after internode elongation, the leaf sheaths covering young panicles go out of the water and into the air. Matsushima et al. (1964) revealed AT and WT affected independently rice morphological growth and development.

Organ morphogenesis such as tillering and leaf elongation is strongly affected by temperature (Hanada 1993, Sato 1993). Cell division and elongation are sensitive to temperature. Shoot and root apical meristems will demand carbohydrates, proportional to cell division activity.

In the experiment 1, AT affected little the degeneration of spikelets and rachis-branches. On the other hand, low WT increased spikelet degeneration. Shoot apical meristems and tiller buds are in the water or in the soil. Tillering is promoted more under lower WT than under lower AT (Matsushima et al. 1966). Increased tillers might comsume more assimilates and increase spikelet degeneration due to the shortage in assimilates.

^{13}C assimilation experiment shows that carbon and carbohydrates assimilated at the stage of spikelet differentiation were translocated to leaves which was actively growing and extending, and not to young panicles which were just differentiated and small. Assimilate partitioning would not be the cause of spikelet differentiation. After determining of panicle size, assimilation partitioning will be determined by the balance of demand in assimilates among organs. In this experiment, roots were not observed. Root growth was also affected by WT (Matsushima et al. 1968). About a quarter of assimilates was translocated into roots (Yamaguchi and Tanaka 1993). Young panicles might compete with roots and other organs for assimilates.

After determination of the number of differentiated spikelets, a lot of carbohydrates were translocated into growing panicles as they grow larger. The demand in carbohydrates for spikelet differentiation might be a little (Kobayasi et al. 2001b). What determine spikelet number during the reproductive stage through temperature? Low temperature will lengthen the period of spikelet differentiation. The length of the period in spikelet differentiation (Rahman and Wilson 1977) would affect spikelet number.

Conclusion

Both low AT and low WT increased the number of dif-

ferentiated spikelets per panicle. The temperature treatments did not change the allocation of assimilates among organs such as leaf blades, leaf sheaths, and young panicles. ^{13}C atom percents in leaves and stems at heading were higher than those in panicles, which result suggested that carbohydrates assimilated at the stage of spikelet differentiation were translocated into actively growing organs such as leaves prior to young panicles.

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* In Japanese with English summary

** In Japanese

幼穂の発育に及ぼす温度の影響

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要旨　温度と１穂穎花数の関係を２つの実験から調査した．実験１では３段階の気温処理を与えた:高温区 32/24℃（昼温/夜温），中温区 29/21℃，低温区 26/18℃．実験２では３段階の水温処理（26, 29, 32℃）を気温（29℃）とは独立に昼間に与えた．夜の水温は気温（21℃）と合わせた．穎花分化始期に器官別乾物重を測定した．出穂期に器官別乾物重，分化穎花数，分化１次枝梗数，分化２次枝梗数などを測定した．生殖成長期初期の高気温によって分化穎花数が減少した．高気温によって乾物生産量は減少しなかったが，各器官への分配が変化した．すなわち高気温によって葉身重がより大きくなり，分げつ重は小さくなった．低水温は分化穎花数を増加させたが，退化穎花数を増加させたために，現存穎花数はむしろ減った．水温処理は乾物生産量にもその各器官への分配へもほとんど影響を与えなかった．出穂期における^{13}C atom%は葉身および葉鞘において高く，穂では低かった．このことから幼穂よりもさかんに成長している葉身などへ穎花分化始期では同化された炭水化物が転流していると考えられた．