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Within-Panicle Variability of Grain Filling in Rice Cultivars with Different Maturities

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With one figure and 3 tables

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Abstract

Rice (*Oryza sativa* L.) milling quality is a complex trait and influenced by many factors including the uniformity of grain filling and other grain characteristics. Although much is known concerning genotypic differences in rate and duration of grain filling, quantitative information on uniformity or non-uniformity of grain filling and kernel characteristics on the panicle is lacking. This study investigated and compared the degree of non-uniformity of grain filling among 6 rice cultivars of different grain types, maturities, and the plant characteristics that may influence the uniformity of grain filling. Models of grain growth and rate of growth were developed for grains on the upper, middle and lower parts of the panicle. Non-uniformity of grain filling parameters (duration and rate of grain filling, maximum grain weight) were estimated and compared among cultivars of different grain types and maturities. Results showed that, in general, grain size and rate of filling decrease from upper part to the lower part of the panicle. The ranges among grain growth curves from the upper, middle and lower parts of the panicle of the very early, and early maturing cultivars were greater than those of intermediate and late maturing cultivars. However, non-uniformity of grain filling is not necessarily a function of maturity. Plant and grain characteristics such as even distribution of grain size, high grain filling rate between 10—15 days after heading, and optimum weight ratio of panicle to above-ground leaf and stem matter may be selected for by breeders to improve the uniformity of grain filling, independent of maturity.

Introduction

Rice (*Oryza sativa* L.) is an annual plant which develops a determinate panicle on each tiller. Anthesis starts from the top and moves toward the lower part of the panicle (NAGATO and CHAUDHRY 1969, XU and VERGARA 1986). Normally, about 7 to 10 days are required for a panicle to complete anthesis (VERGARA 1980, YOSHIDA 1981). In California, 100 % heading occurs at about 90 days after planting for very early maturing cultivars, 90—97 days for early maturing cultivars, 98—105 days for intermediate maturing cultivars, and longer than 105 days for late maturing cultivars.

Grain filling after anthesis follows the order of flowering (XU and VERGARA 1986). Hence, grains at the upper part of the panicle usually become mature while grains at the lower portion of the panicle are still filling. Therefore, an early harvest will result in both yield and quality losses due to greenish or immature grains. Late harvesting can lead to losses in grain yield because of problems associated with shattering, birds, insects and diseases. Late harvesting

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may also reduce the milling quality of rice since grains which are too dry are subjected to diurnal fluctuations in humidity and temperature which induce fissuring (KUNZE 1985). Fissured grains normally break during the milling process and thus reduce head rice yield. Therefore, reducing the variation in maturity within a panicle could greatly increase grain yield and reduce potential loss in milling quality.

The maturity of grain is usually defined as the stage at which the grain has attained maximum weight. Grain weight is dependent on the amount of photosynthate translocated to the grain. The amount of translocated photosynthate depends on the rate and duration of the translocation processes, which are commonly known as the rate and duration of grain filling.

Although much is known concerning genetic variation among genotypes in both rate and duration of grain filling (NAGATO and CHAUDHRY 1969, YOSHIDA and HARA 1977, JONES et al. 1979, FUJITA et al. 1984), knowledge is lacking about the variation in rate and duration of grain filling among grains within a panicle, or the degree of uniformity of grain filling. The objectives of this study were to investigate (i) the differences in uniformity of grain filling among rince cultivars of different maturity; and (ii) the factors influencing uniformity of grain filling.

Materials and Methods

Field experiments were conducted at the Rice Experiment Station, Butte County (39° 26′ N, 121° 49′ W), and in Colusa County (39° 9′ N, 122° 9′ W) in California during the 1984 and 1985 growing seasons. Six rice cultivars representing four maturity groups and three grain types (Table 1) were selected for the study. The experiment was conducted by using a randomized complete block design with 4 replications. Presoaked seeds were sown in preflooded plots (6.1 m × 7.62 m) on 30 April and 16 May in 1984 and 3 May and 10 May in 1985 for the Colusa and Butte trials, respectively.

Prior to flooding, experimental plots in Butte County were incorporated with 138 kg N ha^{-1} and 52 kg P ha^{-1} in 1984, and 159 kg N ha^{-1} and 77 kg P ha^{-1} in 1985. An additional 34 kg N ha^{-1} was applied 51 days after sowing (DAS) in 1985. Water depth was maintained at 10 cm from sowing to 65 days after sowing. After 65 DAS, water depth was raised to 20 cm and maintained at this level throughout the growing period. Plots were drained at approximately 30 d before harvest. The experimental plots at Colusa were incorporated prior to flooding with 168 kg N ha^{-1} and 73 kg P ha^{-1} for both years. Water depth was maintained at 15 cm from sowing until 65 DAS, then raised to 20 cm and maintained at this level throughout the growing season. Fields were drained at 33 d in 1984 and 25 d in 1985 before harvest. These trials were conducted in the same field with the same management practices as reported by MILLER et al. (1991). Additional crop management details can be found in that article.

Sampling procedures were similar for both years and locations. Ten panicles from each plot were randomly collected every 3—4 days from the time of 100 % heading until maximum panicle weight was observed. The panicle samples were oven-dried at 75 °C for 36 hours, after which panicle dry weight was obtained. Each panicle was separated into 3 parts — upper, middle and lower. One hundred grains form each part were randomly taken from the panicle samples and the dry weight recorded.

A second order logistic equation,

$$GW = a_0 / (1.0 + a_1 (EXP(-(a_2T + a_3T^2)))), \quad [1]$$

was used to fit the data of grain growth over time, where GW represents the 100-grain weight, T represents time, and a_i's are model coefficients. A nonlinear algorithmic procedure (SAS Institute, 1982) was used to estimate these coefficients. These model coefficients were used to estimate grain filling parameters. The maximum grain weight (MGW) and the duration of grain filling (DGF) were obtained by the numerical approximation method when the weight gain between consecutive days was less than 1 % per day.

Grain filling rate was calculated using the derivative of Equation 1:

$$dGW/dT = (a_0a_1\beta\alpha)/(1 + (a_1\alpha))^2, \quad [2]$$

where $\beta = (a_2 + 2a_3T)$ and $\alpha = EXP(-(a_2T + a_3T^2))$. The second derivative of Equation 1,

$$d(GW)^2/dT^2 = (2a_3 - \beta^2 + \gamma)\delta, \quad [3]$$

where $\delta = (2a_1\beta^2\alpha)/(1 + a_1\alpha)$ and $\delta = (a_0a_1\alpha)/(1 + a_1\alpha)^2$, was used to estimate the time required to reach maximum rate of grain filling (MRGF). The time to reach MRGF was obtained when $d(GW)^2/dT^2$ was less than 0.001. Consequently, the MRGF was obtained from values of the rate equation (Eq. 2) that corresponded to the time needed to reach maximum grain filling rate. Mean filling rate (MFR) was obtained by dividing the MGW by DGF.

Results

A simple description of the six cultivars (*M101, M301, S201, L202, M302, M7*) used in this study and the observed average number of days to reach 100 % heading for each cultivar are presented in Table 1. As expected the

Table 1. Cultivar characteristics and days to 100 % heading

Cultivar	Maturity Type	Grain Type	Days to 100 % heading Butte	Colusa
M101	Very early	Medium	90	92
M201	Early	Medium	94	104
S201	Early	Short	94	104
L202	Early	Long	94	104
M302	Intermediate	Medium	104	111
M7	Late	Medium	115	121

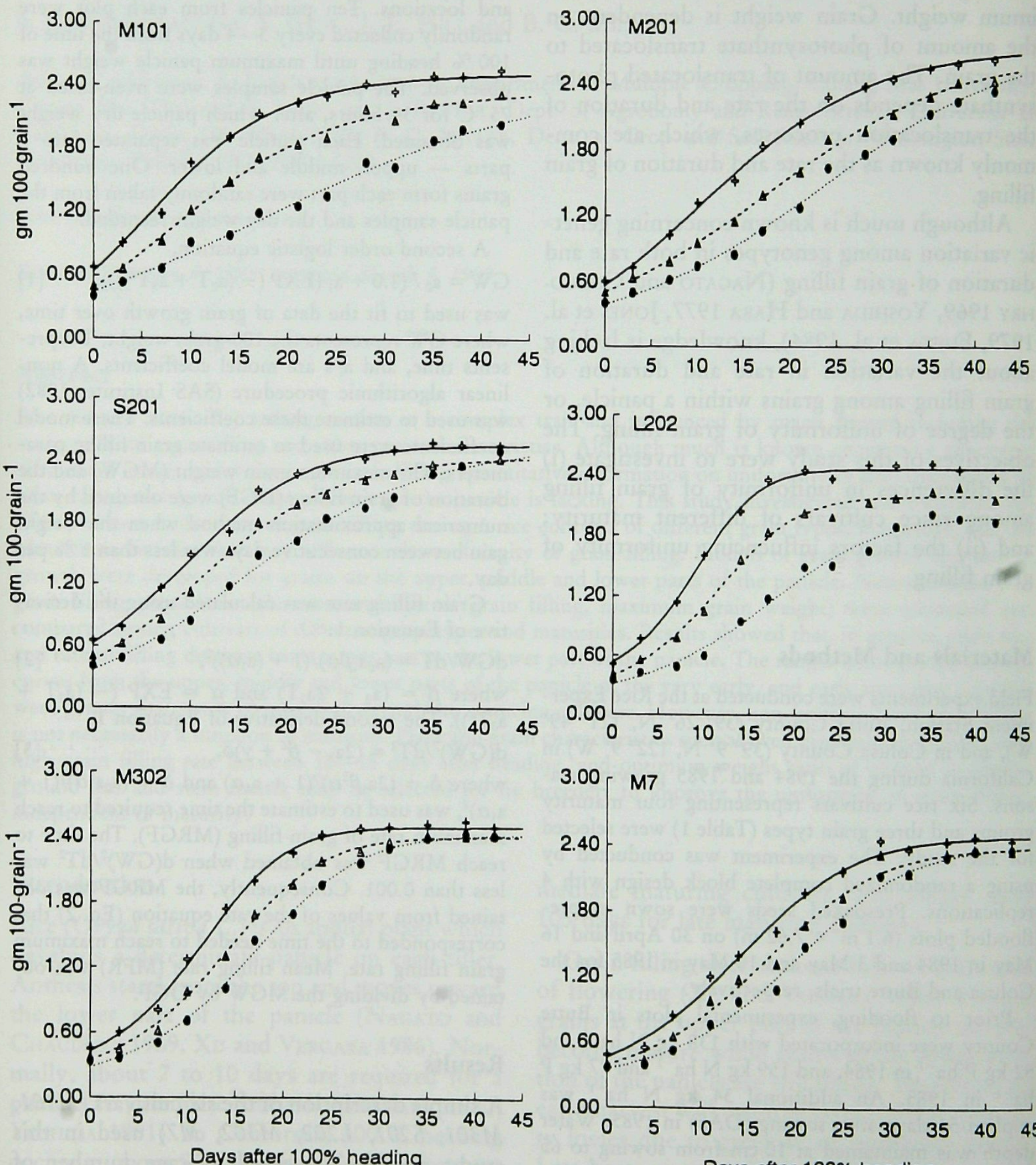

Fig. 1. Grain growth curves: (——) represents grains of upper part, and (- - - - - - - -) represents grains of the middle part and (· · · · · · · ·) represents grains of lower part of the panicle

Table 2. Summary of grain filling parameters: the duration of grain filling (DGF), maximum rate of grain filling (MRGF), mean filling rate (MFR) and maximum grain weight (MGW) of grain from the upper, middle, and lower part of the panicle

Cultivar	DGF (days)				MRGF (mg 100-grain^{-1} day^{-1})				MFR (mg 100-grain^{-1} day^{-1})				MGW (gm 100-grain^{-1})			
	Upper	Middle	Lower	Mean	Upper	Middle	Lower	Mean	Upper	Middle	Lower	Mean	Upper	Middle	Lower	Mean
M101	27.5	35.2	43.4	35.4	100.1	80.2	59.1	79.8	87.4	65.7	48.9	67.3	2.52	2.43	2.15	2.37
M201	31.7	37.3	41.9	37.0	111.9	91.6	87.8	97.1	90.4	65.6	58.9	71.6	2.63	2.44	2.33	2.47
S201	29.9	32.6	41.9	34.8	122.9	111.8	97.7	110.8	95.2	86.6	67.0	82.9	2.65	2.52	2.54	2.57
L202	21.4	31.6	38.6	30.6	174.4	120.8	89.9	128.4	117.1	83.3	59.9	86.8	2.61	2.40	2.18	2.40
M302	28.6	31.4	35.8	31.9	122.0	114.8	107.6	114.8	87.3	76.2	68.1	77.2	2.57	2.45	2.45	2.49
M7	33.4	35.1	36.6	35.0	101.4	103.2	100.5	101.7	75.4	69.0	63.8	69.4	2.52	2.37	2.36	2.42
LSD (0.05)	3.7	4.2	4.1	3.5	16.4	17.4	14.7	12.7	14.7	7.5	5.7	7.8	0.067	0.076	0.098	0.070

number of days to complete heading increased when the cultivar maturity became later. In addition, the number of days to 100 % heading was greater for all cultivars at Colusa than at Butte.

The grain filling parameters (DGF, MRGF and MFR) and MGW for the 3 panicle parts are summarized in Table 2. The second order logistic model used to generate the grain filling parameters fit the grain growth data extremely well as indicated by R^2 values no smaller than 0.99. These high R^2 values suggest that reliable estimates of grain filling parameters can be derived from the fitted curves. Growth curves for 100-grain weight of each of the three parts of the panicle are shown in Figure 1 for each cultivar.

Significant differences in the DGF were found among cultivars. The DGF ranged from 21.4 days for *L202* to 33.4 days for *M7* for grain from the upper part of panicle, from 31.4 days for *M302* to 37.3 days for *M201* for the middle part of the panicle and 35.8 days for *M302* to 43.4 days for *M101* for grain at the lower part of panicle. Among the cultivars studied, *L202* required the fewest number of days (21.4 days) for grains on the upper part of the panicle to reach maximum weight, but the DGF increased significantly for the lower part of the panicle. In contrast, the number of days required to reach maximum grain weight for the upper part of the panicle of *M7* was the highest among genotypes studied (33.4 days), but the DGF for the lower part of the panicle was not significantly higher. Overall, grains on the upper part mature faster than grains on the middle and lower parts of the panicle. Differences in DGF among panicle parts reflect the degree of uniformity of grain filling.

L202 had the greatest MRGF (174.4 mg 100-grain^{-1} day^{-1}) for grains on the upper part of the panicle but a significantly lower MRGF for the lower part (89.9 mg 100-grain^{-1} day^{-1}). The MRGF of *M7* (average 101.7 mg 100-grain^{-1} day^{-1}) was much more uniform throughout the panicle than in the other cultivars. Overall, the MRGF decreased from the upper toward the lower part of the panicle for all cultivars. Similar results were observed for the MFR.

For all cultivars, grains on the upper part of the panicle were heavier than grains on the middle and lower parts. *S201* had the greatest average grain weight (2.57 mg per 100 grains) while *M101* and *L202* had the smallest grain weights.

Discussion

Data obtained in this study clearly demonstrated that growth characteristics differ among grains according to their location on the panicle. In general, grain weight and rate of filling decreased from the upper to the lower part of the panicle. The ranges between grain growth curves from the upper, middle and lower parts of the panicle of the very early and early maturing cultivars were greater than those of intermediate and late maturing cultivars. The within-cultivar similarity in grain growth curves of the intermediate and late cultivars indicates a greater uniformity of grain development in these cultivars in contrast to the very early and early cultivars.

The differences among cultivars can also be characterized by the grain filling rate curves. The upper part of the panicle of the very early maturing cultivar (*M101*) reached MRGF at about 5 days after 100 % heading (DAH); for the early maturing cultivars (*M201, S201,* and *L202*) at about 10 DAH; for the intermediate maturing cultivar (*M302*) at about 12 DAH; and for the late maturing cultivar (*M7*) at about 15 DAH. Clearly the time required to reach maximum rate of grain filling on the upper part of the panicle was directly related to cultivar maturity. In contrast, there was no apparent relationship between maturity and the time required for completing the process of grain filling. Thus, early maturing cultivars do not necessarily exhibit shorter reproductive growth (a phenomenon which is also indicated by the differences among the maturity groups in DGF as shown in Table 2). The rate of grain filling is considerably more variable for grains on the lower part of the panicle. The time required to reach the peak rate and the time to complete the process of grain filling increased progressively from the upper to the lower part of the panicle. As the rate of grain filling on the upper part of the panicle decreased, the rate of grain filling on the lower part increased until the peak rate was reached. The rates of grain filling for grains on different parts of the panicle converged about the same rate between 15 to 20 DAH. Generally speaking, cultivars with higher rates of grain filling at the convergence point tend to be more uniform in grain filling between panicle parts. This grain filling characteristic is worth further investigation for breeding purposes.

Nagato and Chaudhry (1969) found that the first flowering spikelets on the upper branches of the panicle reached maximum weight more rapidly than those on lower branches. Ahn et al. (1988) reported that the rate of grain filling depended upon the position and type (primary or secondary) of the branch on a panicle. They observed that spikelets on the top primary branch had a progressively higher grain filling rate than that of the middle and lower primary branches. They also indicated that grain filling rate of primary branches was faster than that of secondary branches. Sasahara et al. (1982) suggested that the rapid grain filling rate of grains on the upper part of the panicle may be due to the apical dominance or position effect.

Grain filling processes are also a function of source and sink relationships. The rate of assimilate flow in the phloem can be affected by the rate of acceptance by sinks (Gardner et al. 1985). Jones et al. (1979) showed that grain filling rate of rice was positively correlated with grain size. Hence, a larger sink size associated with a greater rate of translocating assimilates into that sink.

Field observations showed that *L202* had a different distribution of rachis-branches on the panicle than did the other cultivars. The greatest abundance of spikelets on rachis-branches of *L202* were on the upper part of the panicle with less on the middle and only a few on the lower part of the panicle. As a result, there was a greater number of grains clustered at the upper part of the panicle which, in turn, generated a stronger pulling force for assimilate, and enhanced the grain filling rate. Therefore, the large variation in grain filling rate among the panicle parts of *L202* may partially be attributed to the uneven distribution of grain on the panicle. Similar results were reported by Sasahara et al. (1982) that the rapid grain filling rate in indica rice was possibly due to more abundant distribution of spikeltes on the secondary rachis-branches at the upper part of the panicle as compared to japonica rice.

In rice plants, the accumulation of starch and other components in grain depends almost entirely on the assimilates produced by the foliage leaves and leaf sheaths (TSUNODA and TAKAHASHI 1984). Few assimilates produced before heading contribute to grain yield (TSUNODA and TAKAHASHI 1984). Consequently, most assimilates produced after heading are directly translocated to grains on the panicle. The amount of above-ground vegetation after heading is directly related to the potential amount of assimilate that can be produced by the plant during the grain filling period. It is likely that a greater amount of assimilate produced after heading would result in a more uniform grain filling within the panicle. An evaluation was made to determine if the weight ratio of panicle to above-ground leaf and stem matter would influence the rate and evenness of assimilate translocation to grains.

Table 3. Means of above-ground leaf and stem weight, panicle weight and the ratio of panicle weight and above-ground leaf and stem weight

Cultivar	AGV (gm m^{-2})	Panicle weight (gm m^{-2})	Ratio
M101	817	1005	1.23
M201	858	1006	1.18
S201	920	1122	1.22
L202	910	903	0.99
M302	1065	992	0.93
M7	1170	764	0.67
LSD (0.05)	98	95	0.07

In this study, the intermediate and late maturing cultivars had a larger above-ground vegetation and smaller panicle weight than those of the very early and early maturing cultivars (Table 3). These results offer an explanation for the uniformity in grain filling rate and size of the intermediate and late maturing cultivars as compared to the very early and early maturing cultivars.

The weight ratio of panicle to above-ground leaf and stem is a measure of plant type which need not be related to maturity. Thus it is possible to improve the uniformity of grain filling within each maturity group through an improvement of the plant type as represented by the suggested weight ratio. For practical and management reasons, rice growers prefer early maturing cultivars. An improvement in the uniformity of grain filling is a key factor in improving the desirable performance of early maturing cultivars. Results of this study suggest that maturity is not necessarily the cause of the non-uniformity of grain filling. It happens in California that some of the early maturing cultivars had less desirable traits (such as non-uniformity in grain size and in grain filling rate on the panicle and large panicle to above-ground leaf and stem weight ratio) related to non-uniformity of grain characteristics on the panicle. An improvement of these traits through breeding could result in improved early maturing cultivars.

The observed differences in grain filling parameters among cultivars, however, could be attributed to either genetic or environmental influences. This is because each cultivar did not reach 100 % heading at the same time. Thus the different periods of grain filling among the cultivars could represent different environments. It is known that ambient temperature during grain filling can influence the rate and duration of grain filling (FUJITA et al. 1984 and YOSHIDA and HARA 1977). In our study, however, the differences in temperature ranges during the grain filling period among cultivars were negligible for both the Butte and Colusa trials. Therefore, the observed differences among cultivars were largely due to genetic rather than environmental factors.

Zusammenfassung

Uniformität der Rispenentwicklung von Reiskultivaren mit unterschiedlichen Reifezeiten

Die Reis (*Oryza sativa* L.)-mahlqualität ist eine komplexe Eigenschaft und wird von zahlreichen Faktoren, einschließlich der Einheitlichkeit der Kornfüllung und anderer Korneigenschaften beeinflußt. Obwohl zahlreiche Informationen bezüglich genotypischer Differenzen hinsichtlich der Rate und der Dauer der Kornfüllung bekannt sind, besteht ein Mangel an Informationen hinsichtlich der Einheitlichkeit oder Uneinheitlichkeit der Kornfüllung und von Korneigenschaften der Rispe. Die vorliegende Untersuchung vergleicht den Grad der Uneinheitlichkeit der Kornfüllung von sechs Reiskultivaren unterschiedlichen Korntyps, unterschiedlicher Reife und unterschied-

licher Pflanzeneigenschaften, die Einfluß auf die Einheitlichkeit der Kornfüllung nehmen können. Modelle für Kornwachstum und Wachstumsrate wurden für Körner des oberen, mittleren und unteren Abschnitts der Rispe entwickelt. Uneinheitlichkeit der Kornfüllung (Dauer und Rate der Füllung sowie maximales Korngewicht) wurden geschätzt und mit den Kultivaren unterschiedlichen Korntyps und unterschiedlicher Reife verglichen. Die Ergebnisse zeigen, daß die Korngröße und Kornfüllungsrate grundsätzlich vom oberen zum unteren Teil der Rispe abnimmt. Die Bereiche der Kornwachstumskurven des oberen, mittleren und unteren Teils der Rispe sehr früher und früher Kultivare waren größer als diejenigen der Kultivare mittlerer und später Reife. Allerdings ist Uneinheitlichkeit der Kornfüllung nicht zwingend eine Funktion der Reife. Pflanzen- und Korneigenschaften, wie z. B. gleichmäßige Verteilung der Korngröße, hoher Kornfüllungsrate zwischen dem 10. bis 15. Tag nach dem Rispenschieben sowie ein optimales Verhältnis des Gewichtes der Rispe zu dem oberirdischen Pflanzenteil an Blatt- und Sproßmasse können für die Selektion vom Züchter verwendet werden, um die Einheitlichkeit der Kornfüllungsphase unabhängig von der Reife zu verbessern.

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