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Panicle emergence of tiller types and grain yield of tiller order for direct-seeded rice cultivars

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Abstract

Grain yield of rice (*Oryza sativa*, L.) tillers is critical to rice crop yield and quality but relatively little is known about variations that occur among panicles and grains for tiller types and emergence orders of direct-seeded rice cultivars. The objective of research was to examine how tillering may affect yield and quality at low plant population densities with profuse tillering. Single rice plants were grown in pots in a greenhouse in 1990 and in 1992 and in the field in 1991. The aim was to maximize tillering and thus better see effects of tiller emergence order and type on yield and panicle emergence. Culm and panicle emergence dates were successively later for primary, secondary, and tertiary tillers but with a smaller delay among panicle emergence dates than was observed for tiller emergence. Grain yield of tillers was related more to emergence order than to tiller type. Secondary and tertiary tillers in sufficient numbers could cause delays in crop grain maturity. Specifically, the beginning of grain-filling (closely following top anthesis) was 1 to 5 d later for primary tillers and 3 to 9 d later for secondary tillers, compared to main stems. These data indicate direct-seeded rice cultivars have partial but not complete synchrony of panicle emergence. Consequently, production strategies that increase preflood N to increase tillering in thin (sparsely populated) rice stands, could potentially delay maturity of the crop as well as increase yields.

Keywords: *Oryza sativa*; Tiller development; Rice yield

1. Introduction

In many cereals, grain production by tillers is inconsequential to crop yield except at low plant populations (Simmons et al., 1982; Gerik and Neely, 1987). In rice, however, tillers normally produce a large portion of crop yield even at adequate plant populations (Counce et al., 1992). The physiological age of a grass culm can be expressed by the plastochron index, (Langer, 1972), which is related to the Japanese term *yourei* which means leaf age of a culm (Yosuke Goto, personal communication). Tillers have one less leaf less than the culms from which they emerge but subsequent leaf emergences are synchronized (Katayma, 1951, cited in Goto and Hoshikawa, 1988). *Tiller type* denotes the type of culm from which a tiller emerges. Consequently, a

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primary tiller emerges from a main stem, a secondary tiller emerges from a primary tiller, a tertiary tiller from a secondary tiller, and a quaternary tiller from a tertiary tiller. Goto and Hoshikawa (1988), however, found tiller type was determinative of yourei with primary, secondary, tertiary and quaternary tillers having progressively later yourei compared to the main stem. *Tiller order* refers to the ranking of tiller emergence from first to last to emerge from a plant. Synchrony in panicle emergence means panicles emerge from culms at the same time. The panicle age differences among tillers are believed to be minimal. But, panicle emergence dates, grain, and harvest indices for different classes of rice culms (main stems and primary, secondary, and tertiary tillers) have not been determined for direct-seeded rice cultivars.

Tillers are produced generously by transplanted cultivars of rice and considerable numbers of these tillers produce grain (Yoshida, 1981). Normally 10–30 tillers per plant are produced for transplanted rice and only 2–5 for direct seeded rice (Yoshida, 1981). Counce et al. (1989) reported 87 to 100 of 100 culms of direct-seeded rice produced panicles, depending upon spacing, cultivar, and year. The plants in that study averaged 0.5 to 2.5 tillers/plants depending on treatment while Counce and Wells (1990) and Counce et al. (1992) reported ratios of panicles to initial plant population of 0.8 to 10, depending upon N rate, population and year. Counce and Wells (1990) and Counce et al. (1992) found that rice grain yields at below-optimum and near-optimum populations were increased by additional preflood N primarily through increases in tillering. Resulting delays in total crop maturity by additional preflood N were not assessed in these studies. Because increased preflood N increased yield of sparse stands via increases tillering, one practical application of this research would be to predict whether additional preflood N would potentially delay overall grain maturity as well as increasing grain yields.

For modern direct-seeded rice cultivars, the maturities of tillers and main stems are believed to be synchronized and to differ little although the dates of culm emergence may differ greatly. When profuse tillering occurs in a rice crop, considerable age differences among culms exist, and differences in maturity of culms within plants are observed. Although considerable research has been directed to determining rice yield components (culms m^{-2}, panicles/culm, grains/panicle, filled-grain percentage, and individual grain weight) in response to various treatments, much less has been done to quantify age differences and panicle characteristics among different classes of rice tillers.

The objective of this paper is to learn how tillering may affect yield and quality of rice grain with *low plant population.* To accomplish this, culm and panicle emergence dates, grain yields and harvest index among different types and orders of rice tiller types were measured in environments that allowed considerable tillering.

To investigate these questions, we took advantage of one experiment (Study 1 in Materials and methods section) designed to determine the source of the three modes of moisture for the rice crop at harvest. The grain moisture results were reported by Holloway et al. (1995). Two other studies were conducted expressly to see if the findings in Study 1 were confirmed by subsequent results.

2. Materials and methods

Three studies were done to accomplish the objectives. One in the field in 1991, and two in the greenhouse: one in 1991 and one in 1992. All experiments were done at the University of Arkansas, Northeast Research and Extension Center, Keiser, Arkansas (35°40′N, 90°5′W, 75 m asl) with Sharkey silty clay soil (Vertic Haplaquepts by USDA taxonomy, pH 6.7). Weeds were controlled in the field (Study 3) by preflood applications of propanil [*N*-(3,4-dichlorophenyl)propanamide] and thiobencarb [*S*-(4-chlorophenyl)methyl diethylcarbamothioate]. Plots were flooded when rice was at the four- to seven-leaf stage of development. The flood was maintained until near harvest.

2.1. Greenhouse studies

2.1.1. Study 1

A greenhouse experiment was sown with the cultivar Alan in December 1989 and terminated with grain harvest in June 1990. Treatments were 11 dates of harvest, which were 24 and 30 May and 1, 4, 6, 8, 11, 13, 15, 18 and 20 June 1990. Plots were individual plants grown in 0.2-m diameter, 5.8-l, plastic buckets. Plants were arranged in randomized complete blocks with five replications on a single greenhouse bench. Pots were rotated across the length of the bench within each row, containing one replication every 7 d. Replications were rotated across the width of the bench every 14 d. Prior to flooding, plants were arranged within replicates by size, the largest plants being applied to the first replication progressively down to the smallest plants, which were assigned to the fifth replication. This arrangement segregated variation by plant size into replication.

Conditions of the experiment were arranged so as to favor maximum tillering and differences in tiller ages within plants. Pots were fertilized with a dilute solutions of urea at flooding (730 mg N per pot), at panicle differentiation (365 mg N per pot), and 7 d after panicle differentiation (365 mg N per plot). Temperatures in the greenhouse were maintained between 14 and 20°C between sowing and flooding. From the date of flooding onward, temperatures were maintained between 20 and 30°C until the final 11 d (the final five harvest dates) of the experimental period when temperatures ranged between 30 and 44°C. The flood depth was maintained between 2 and 4 cm during tillering.

Supplemental radiation was supplied to the plants by metal halide lamps (MGS Batwing Maxi-Gro HID Plant Grower; GTE/Sylvania, Fall River, MA 02734). The lamps provided a photon flux density of 150–200 μmol m^{-2} s^{-1} at the top of the canopy from 500 to 1900 h daily. The bench was lowered progressively to maintain the height of the lamp above the bench at 1.5 m. On clear days, lamps were turned off from 900 to 1500 h. The air in the greenhouse was maintained at 450 to 500 μl CO_2 l^{-1} during the photoperiod by addition of CO_2. The CO_2 concentration was enriched to correct a deficiency common to greenhouses — low CO_2 levels within the canopy due to poor vertical air movement. Fans were employed to move air vertically and horizontally in the greenhouse. Beginning at flooding, individual tillers arising from each plant were tagged, mapped, and recorded for order of emergence and tiller type. Orientation of the pots was maintained during the experiment to facilitate identification of tillers. Emergence dates of each tiller and panicle were recorded. At harvest, the stubble and panicle were separated for each culm that produced a panicle. Grains were separated from the panicle by the same person during each harvest to standardize the discarding of unfilled grains. The number of grains, weight of grain, and weight of stubble were recorded for each main stem and for each tiller bearing a panicle. The stubble was dried in a forced air oven at 70°C until weights stabilized. Grain moisture was determined for each grain using a single grain moisture meter Model CTR-800; (Shizuoka Seiki Co., 4-1 Yamana, Fukuroi, Shizuoka, Japan 437). From these data, grain yield, harvest index (ratio of grain to the sum of grain and stubble), individual grain weight, and grains/panicle were calculated for each culm bearing a panicle. Beginning on the sixth harvest, unfilled grains were counted prior to discarding them and the filled grain percentage was calculated for each culm.

Analysis of variance was done for the responses with replication, harvest date, tiller type, tiller order of emergence, and interactions being analyzed as sources of variation. Tiller type was treated as a subplot of harvest date treatments for purposes of the analysis.

2.1.2. *Study 2*

Rice plants were sown in the greenhouse on 21 January 1992. The rice was from a numbered line (M15-123) derived from a single F_2 plant from a Bond × Lemont cross made by Karen Moldenhauer. Main stem emergence occurred on 29 January 1992. Plant growth conditions were the same as for Study 1 except for (1) the use of smaller (4.5-l) buckets and (2) temperatures were maintained between 20 and 30°C throughout the study. Plants were harvested at grain maturity on 27 May 1992. The harvesting procedure was the same as in Study 1. Eight plants (one plant per pot) in this study were censured daily.

2.2. *Field study (Study 3)*

'Texmont' rice seedlings transplanted in 18-cm row spacings on 23 May 1991 were thinned to a spacing of approximately 25 (±3) cm between plants on 17 June 1991. Tillers were tagged and tiller type and emergence data noted as the tillers emerged.

Panicle emergence and anthesis dates were recorded for individual culms. At grain maturity, individual panicles were collected, hand threshed, counted, weighed for each culm and moisture determined as in Studies 1 and 2.

3. Results and discussion

3.1. Greenhouse studies

3.1.1. Study 1

For primary and secondary tillers, the effect of tiller order emergence on grain yield was clearly negative (Fig. 1). Culm grain yield was related order of tiller emergence rather than tiller type.

Tillering continued over a period of 25 to 30 d but panicle emergence was confined to a period of 15 to 20 d, and the period was much less for most of the panicles (Fig. 2). While tiller order and culm emergence date were closely related through Tiller 10, there was little or no relationship between order of tiller emergence and panicle emergence for any range of tiller emergence order. There were small, significant differences in panicle emergence among tiller types with primary, secondary, and tertiary tillers exerting panicles progressively later. Consequently, the production of panicles in this experiment demonstrated incomplete synchrony of panicle emergence dates among different tiller types consistent with the findings of Goto and Hoshikawa (1988) for Japanese rice cultivars.

Panicle emergence is followed closely by the commencement of grain-filling. Therefore, these data indicate that grains fill hierarchically. The main stems produce more culms with panicles, and more grains per panicle. Main stems commence grain filling earlier than tillers. Primary, secondary, and tertiary tillers produce progressively fewer panicles per culm, fewer seed per culm, and commence grain filling progressively later than main stems.

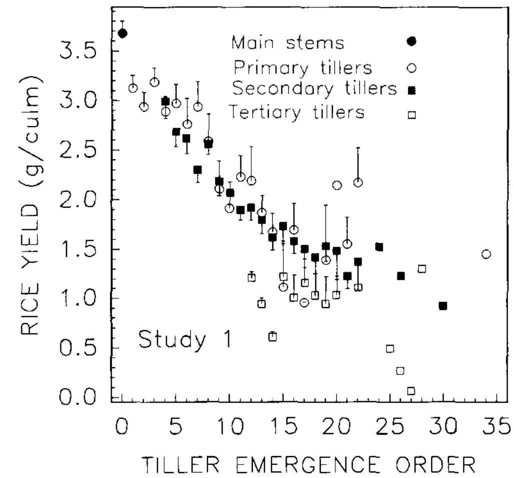

Fig. 1. Alan rice grain yield responses to tiller emergence order for main stems, primary, secondary, and tertiary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, greenhouse-grown, rice plants. The equation $Y = 2.91^{***} - 0.079X^{***}$ ($R^2 = 0.62$) describes the relationship between rice yield and culm emergence order for these data. Half-bars are standard errors of the mean.

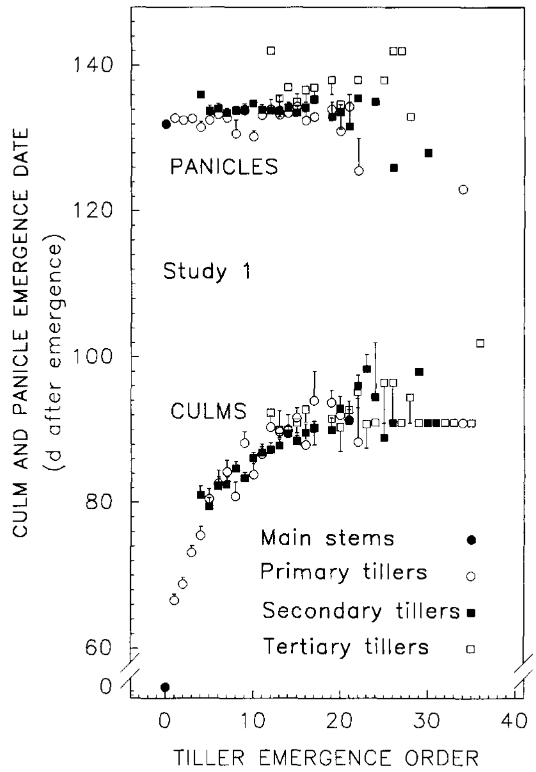

Fig. 2. Alan rice culm and panicle emergence date responses to tiller emergence order for main stems, primary, secondary, and tertiary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, greenhouse-grown, rice plants. Half-bars are standards errors of the mean.

Table 1
Yield components, harvest index and duration of period between culm emergence and panicle emergence by culm type from Study 1 in a greenhouse at Keiser, Arkansas, in 1990

Culm type	Culms per plant	Panicles per plant	Grains per plant No.	Percent filled grain [a]	Harvest index [b]	Duration to period from culm to panicle emergence days
Main stem	1.0	1.0	194	76	0.39	133
Primary tillers	6.0	5.9	875	76	0.41	56
Secondary tillers	9.1	7.8	916	81	0.42	49
Tertiary tillers	2.6	1.1	89	74	0.33	47
$LSD_{0.01}$	1.0	1.0	119	5	0.03	2

[a] Percent filled grain = (filled grain/(filled grain + blanks)) × 100.
[b] Harvest index is the ratio of grain to the sum of grain + stubble.

The number of culms per plant from greatest to least were secondary, primary, tertiary, and main stems (Table 1). There were negligible numbers of quaternary tillers. The data also reveal that main stems, primary, secondary and tertiary tillers produced progressively fewer panicles per culm. Primary and secondary tillers each produced more grains per plant than either main stems and tertiary tillers. Percent filled grain was greater for secondary tillers than for other types of culms but did not differ among the other types of culms. Harvest index for secondary tillers was greater than that of main stems, and harvest index for tertiary tillers was less than for any of the other three types of culms. Days between culm and panicle emergence were greatest for main stems and progressively less for primary, secondary and tertiary tillers.

3.1.2. Study 2

Culm and panicle emergence dates and anthesis dates were progressively later (compared to main stems) for primary, and secondary tillers (Table 2). Grains per culm were greater for main stems and progressively less for primary and secondary tillers. Grain weights did not differ among culm types. Percent filled grains was greatest for main stems, and did not differ between primary and secondary tillers.

Grain yield per culm declined with tiller emergence order and the differences among tiller types presented on Table 2 were likely the result of later tiller emergence for secondary tillers rather than tiller type (Fig. 3).

Emergence of primary tillers was linear with time until Tiller 5 emerged, thereafter culm emergence was much more rapid as primary tillers began to generate secondary tillers (Fig. 4). A great degree of synchrony of panicle emergence is evident with no clear relationship between tiller emergence order and panicle emergence date. Secondary tillers had later panicle emergence dates than primary tillers even when compared within the same emergence orders. As in the Study 1, grain yield per culm followed

Table 2
Culm characteristics of M15-123 (an F_2 derived line from a Lemont by Bond cross) rice plants in Study 2

	Days after main stem emergence				Grains per culm No.	Harvest index No.	Individual grain weight (mg/grain)	Percent filled grain (%)
	Emergence date		Anthesis date					
	Culm	Panicle	Top [b]	Bottom				
Main stems	0 (0) [a]	79 (1)	81 (1)	86 (1)	166 (8)	0.510 (0.066)	25.6 (0.3)	91.2 (0.1)
Primary tillers	27 (1)	84 (3)	86 (3)	91 (1)	127 (5)	0.507 (0.008)	25.5 (0.2)	84.0 (1.3)
Secondary tillers	35 (1)	88 (2)	90 (4)	95 (4)	94 (4)	0.517 (0.013)	25.1 (0.3)	86.1 (1.9)

The plants were grown in the greenhouse at Keiser, Arkansas from January through May 1992.
[a] Means (standard errors of the mean).
[b] Anthesis date recorded for top and bottom halves of panicles.

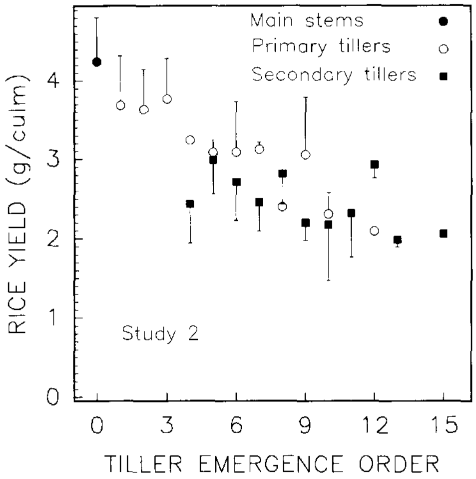

Fig. 3. M15-123 rice grain yield responses to tiller emergence order for main stems, primary, and secondary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, greenhouse-grown, rice plants. Half-bars are standard errors of the mean.

tiller emergence order and panicle emergence dates were determined by tiller type.

3.2. Field study (Study 3)

For Texmont rice growing in the field in 1991, there were 30 d between emergence of main stems and tillers (Table 3). Panicle emergence dates for main stems and primary tillers were about the same and 4 d earlier than secondary tillers. Anthesis at the tops and bottoms of panicles was earliest for main stems, slightly later for primary tillers, and considerably later (3–4 days) for secondary tillers.

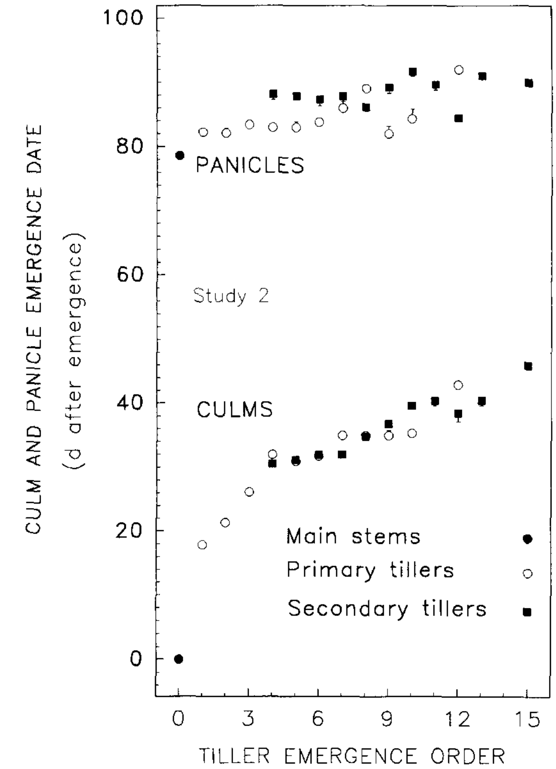

Fig. 4. M15-123 rice culm and panicle emergence date responses to tiller emergence order for main stems, primary, and secondary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, greenhouse-grown, rice plants. Half-bars are standards errors of the mean.

Grain yield per culm tended to be slightly less for later tiller orders (Fig. 5). Culm emergence dates were closely related to tiller emergence order (Fig. 6). As in Studies 1 and 2, panicle emergence was

Table 3
Culm characteristics of Texmont rice plants from Study 3 conducted in the field at Keiser, Arkansas during of 1991

Tiller type	Days after planting		Grain yield (g/plant)	Anthesis days after planting		Percent filled grain (%)	Individual grain weight (mg/grain)	
	Culm emergence date	Panicle emergence		Top half of panicle [b]	Bottom half of panicle		Top half of panicle [b]	Bottom half of panicle
Main stem	10 (0) [a]	101 (1)	2.31 (0.18)	103 (1)	105 (1)	94 (2)	24.1 (0.9)	20.6 (1.2)
Primary	41 (2)	101 (1)	2.26 (0.12)	104 (1)	107 (1)	95 (1)	24.6 (0.6)	24.6 (0.6)
Secondary	40 (2)	105 (1)	1.78 (0.20)	106 (1)	109 (1)	92 (2)	25.9 (1.2)	21.3 (0.7)

[a] Means (standard errors of the mean).
[b] Panicles were divided into top and bottom halves by branch number.

first for main stems, next for primary tiller and last for secondary tillers. Panicle emergence dates were essentially unrelated to tiller order. As illustrated in Table 3, tiller type influenced panicle emergence and anthesis dates while tiller emergence order influenced grain yield per culm.

In this study, tiller type largely determined panicle emergence date and tiller order determined grain yield per culm with yield decreasing with tiller emergence order. Grain filling would commence first for main stems, second for primary tillers, third for secondary tillers, and fourth for tertiary tillers. The incomplete synchrony of grain filling found in this study indicates tiller types can be conceived as a waiting line whose members are allowed to enter based on preference for main stems, primary, secondary, and tertiary tillers. Specifically, the beginning of grain-filling (closely following panicle emergence and anthesis) was 1 to 5 d later for primary tillers and 3 to 9 days later for secondary tillers, compared to main stems. Although the differences in grain maturity by different types of tillers appear small, their effect on realized crop yield and maturity are potentially important to producers.

Additional early season nitrogen (compared to N needs for adequate populations) is needed to produce maximum yields for inadequate rice populations (Wells and Faw, 1978; Counce and Wells, 1990; Counce et al., 1992). Increased tillering was the primary reason for the increased yields. Increased tillering is also likely to delay crop maturity period for direct-seeded rice cultivars if more than 5 tillers per plant are produced.

Gravois and Helms (1996) found that plant populations and seeding rates higher than necessary for maximum grain yield, sometimes increased head rice yield. One reason for the finding of Gravois and Helms may be that if population is dense enough, only the earliest plants to emerge will yield grain (Counce and Keisling, 1995). A second reason would be that tillering can be virtually eliminated by a dense enough plant population.

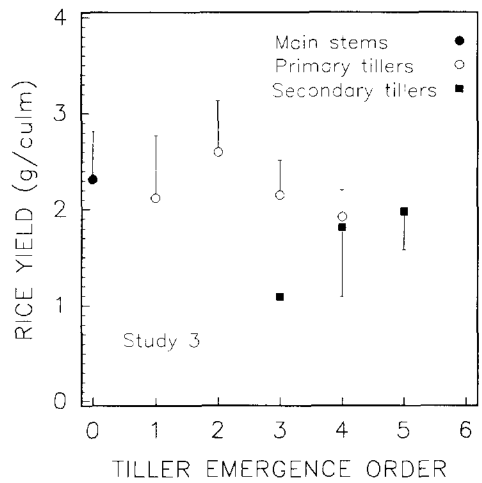

Fig. 5. Texmont rice grain yield responses to tiller emergence order for main stems, primary, and secondary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, field-grown, rice plants. Half-bars are standard errors of the mean.

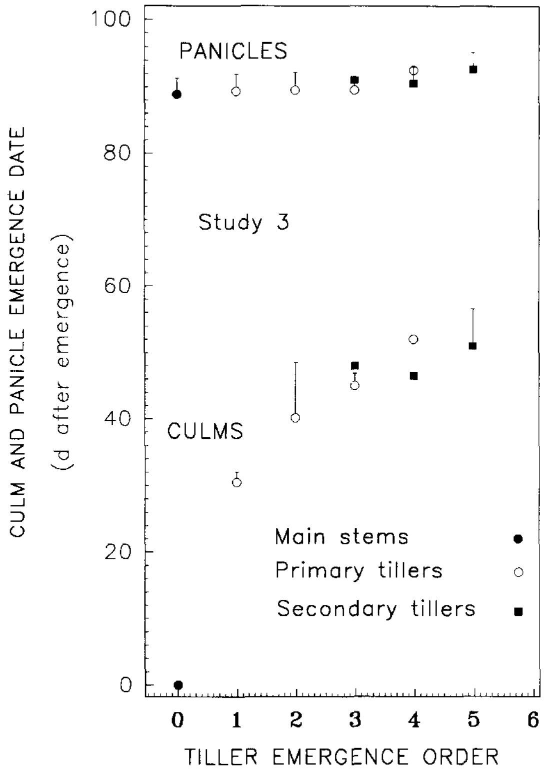

Fig. 6. Texmont rice culm and panicle emergence date responses to tiller emergence order for main stems, primary, and secondary tillers. Points are means for the different types and orders of tillers for a given date after seedling emergence plotted against order of tiller emergence on individual, field-grown, rice plants. Half-bars are standards errors of the mean.

4. Conclusions

(1) Tiller type determined panicle emergence. Main stem panicles emerged first followed successively by primary, secondary and tertiary tillers.

(2) Tiller emergence order determined yield per culm. The first tillers to emerge yielded more and the later ones progressively less.

(3) Based on the results of this set of experiments, increasing nitrogen for inadequate rice plant populations could delay maturity of the crop.

4.1. Future direction

It would be useful to understand more about tillering in dence plant populations. This is difficult, however, because making tiller counts in such populations is extremely disruptive. It would be interesting, for example, to tag panicles emerging from the crop and to work successively down the mature row separating plants tagged at emergence, identifying tillers by type, and then separating plant and culm-within-plant effects. Even in a fairly dense population, tillers could account for a considerable amount of yield if early emerging, dominant plants tillered profusely.

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