

Plant Population Effects on Growth and Yield in Water-Seeded Rice

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ABSTRACT

Initial management strategies, such as established plant stand, significantly affect rice (*Oryza sativa* L.) crop development, grain yield, and final profits. Critical rice plant population for optimum yield differs greatly among various cultural systems. The objectives of this study were to: (i) characterize effects of increasing plant population on tillering, yield components, yield, and phytomass development in continuously flooded, direct water-seeded rice culture; and (ii) identify which crop development parameters are associated with optimum grain yield in this cultural system. Two cultivars, S-201 and M-201, were seeded at rates ranging from 120 to 840 seeds m^{-2} on Stockton clays (fine, montmorillonite, thermic, Typic Pelloxererts) in Butte and Colusa counties, California, in 1984 and 1985. Plant populations ranged from 122 to 458 plants m^{-2} . Initial rapid tillering resulted in a maximum tiller density within 37 to 63 d after seeding (DAS). Total above-ground phytomass (TAGPM) was not significantly different among the plant populations, either during or at the end of the growing season. Although final vegetative above-ground phytomass (VAGPM) increased as a function of tiller density, VAGPM above 850 $g\ m^{-2}$ did not result in further yield increases. Grain yields were dependent on final tiller density (FTD) rather than plant population, with yields increasing as FTD increased to 700 tillers m^{-2} . Panicles m^{-2} , a direct result of FTD, was the most important component of yield accounting for 89% of the variation in yield. Final tiller density or the tillering capacity of the rice crop is determined by the environmental limitations and favorability of the growing conditions. Under continuously flooded, direct water-seeded culture, the rice crop functioned more as a population of tillers than a population of plants.

RICE CROP growth follows a predictable pattern leading to grain production. This includes stand establishment, leaf and tiller production, associated dry matter accumulation, and finally the development of the remaining yield components, seeds panicle⁻¹ and filled grain weight. By characterizing these key developmental parameters that lead to yield, future crop management research can be focused on enhancing their contribution to yield.

Numerous researchers have reported that establishing a critical rice plant population was necessary to obtain maximum grain yields. Under transplanted culture, grain yield plateaus were reached with 25 to 200 plants m^{-2} (Akita, 1982; Nguu and De Datta, 1979). Huey (1984) reported an optimum plant population for direct-seeded rice of 161 to 215 plants m^{-2} , which could be achieved by drilling 430 to 645 seeds m^{-2} . Counce (1987) found that populations ranging from 159 to 304 plants m^{-2} produced maximum yields under a dry-seeded, flooded, rice production system. Others have reported seeding rates from 50 to 168 $kg\ ha^{-1}$ were necessary for maximum yields under direct-

seeded culture, depending on planting date (Jones and Snyder, 1987), direct-seeding method and cultivar (Huey, 1984), irrigation method (Akkari et al., 1986), and nitrogen rates (Wells and Faw, 1978).

Potential yield for a given cultural system has also been associated with optimizing yield components: panicles m^{-2} (Vlek et al., 1979), spikelets m^{-2} (Yoshida and Parao, 1976; Yoshida et al., 1972), and grain number m^{-2} (Agasimani et al., 1980). Imposing different plant population treatments induces compensation among yield components in a rice crop.

Previous research to identify the critical plant populations and key yield components responsible for optimizing yield were mostly based on transplanted and drill-seeded culture. Data are limited on rice crop development under continuously flooded, direct water-seeded cultural systems practiced in California. The objectives of this study were to: (i) characterize effects of increasing plant population on tillering, yield components, yield, and phytomass development in continuously flooded, direct water-seeded rice culture; and (ii) identify which crop development parameters are associated with optimum grain yield in this cultural system.

MATERIALS AND METHODS

Plant population trials were conducted at the Rice Experiment Station, Butte County, and in Colusa County, California on a Stockton clay during the 1984 and 1985 growing seasons. Two early maturing cultivars, S-201 and M-201, were seeded at six rates, 120, 240, 360, 480, 600, and 840 seeds m^{-2} , in a randomized complete block factorial, with four replications. Seed was soaked for 24 h before hand broadcasting into 37.2 m^2 continuously-flooded plots.

The Butte trials were seeded 10 May 1984 and 16 May 1985. Nitrogen was incorporated pre-plant at 145 $kg\ N\ ha^{-1}$ both years. In 1985, an additional 34 $kg\ N\ ha^{-1}$ was applied aerially 51 DAS.¹ Herbicide applications included: 10 $kg\ a.i.\ ha^{-1}$ molinate (S-ethyl hexahydro-1H-azepine-1-carbothioate) in split applications, 5 $kg\ a.i.\ ha^{-1}$ incorporated pre-plant and 5 $kg\ a.i.\ ha^{-1}$ broadcast post-plant onto flooded soil; and 1.1 $kg\ a.i.\ ha^{-1}$ bentazon (3-[1-methylethyl]-1H-2,1,3-benzothiadiazin-4[3H]-one 2,2-dioxide) at 35 and 52 DAS in 1984 and 1985, respectively. Water depth was held at 10 cm from seeding until 65 DAS, when it was raised to 20 cm until the fields were drained approximately 30 d before harvest.

The Colusa trials were seeded 3 May 1984 and 30 Apr. 1985. Nitrogen was incorporated pre-plant at 168 $kg\ N\ ha^{-1}$ both years, and 34 $kg\ N\ ha^{-1}$ was applied aerially at 71 and 45 DAS in 1984 and 1985, respectively. Herbicide applications included: 5 and 7 $kg\ a.i.\ ha^{-1}$ molinate 10 DAS in 1984 and 1985, respectively; 1.1 $kg\ a.i.\ ha^{-1}$ bentazon at 36 and 59 DAS in 1984; and 1.3 and 0.6 $kg\ a.i.\ ha^{-1}$ MCPA ([4-chloro-2-methylphenoxy] acetic acid) at 36 and 69 DAS in 1985. Water depth was maintained at 15 cm from seeding until 65 DAS, then raised to 20 cm until the fields were

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¹ Abbreviations: DAS, days after seeding; TAGPM, total above-ground phytomass; VAGPM, vegetative above-ground phytomass; FTD, final tiller density; YLD, grain yield; PMS, panicles per square meter; SP, spikelets per panicle; PFS, percent filled spikelets; GW, grain weight; and MTD, maximum tiller density.

Table 1. Main effects summary for stand establishment, yield and yield components in water-seeded rice.

Location	Treatment	Established plant stand m ⁻²	Yield kg ha ⁻¹	Yield components			
				Panicle density m ⁻²	Grain weight mg	Spikelets panicle ⁻¹ no.	Filled spikelet %
Butte	Year						
	1984	306	10 985	696	25.3	70.7	86.2
	1985	306	9 849	694	25.9	70.5	86.2
	Cultivar						
	S201	284	10 600	716	26.4	71.8	85.7
	M201	328	10 233	674	24.9	69.4	86.7
	Seeding rate (seeds m ⁻²)						
	120	122	9 759	571	25.2	90.8	86.6
	240	222	10 404	700	25.6	74.8	85.8
	360	291	10 596	655	25.8	71.6	86.2
	480	371	10 546	709	25.5	64.3	85.6
	600	369	10 580	728	25.9	63.1	86.2
	840	458	10 617	807	25.9	58.9	86.8
	Colusa	Year					
1984		276	9 603	538	26.3	77.2	80.3
1985		285	9 982	599	25.7	84.0	88.5
Cultivar							
S201		270	9 851	600	26.7	78.2	84.3
M201		290	9 644	536	25.2	83.2	84.5
Seeding rate (seeds m ⁻²)							
120		129	8 683	450	25.7	101.3	80.7
240		188	9 504	499	25.9	92.8	83.2
360		225	9 573	548	26.1	81.4	85.5
480		324	9 989	583	25.9	78.0	85.5
600		362	10 152	648	25.9	68.1	85.4
840		451	10 585	683	26.2	62.0	86.2

drained 33 and 25 d before harvest in 1984 and 1985, respectively.

Sampling to evaluate established plant stand, tiller and above-ground phytomass production began on 21 to 23 DAS, corresponding to the fifth mainstem leaf stage and appearance of the first primary tiller. The 1984 Colusa location was first sampled at 49 DAS. Sampling continued at 14 to 21 d intervals through the completion of flowering, with a final sample at harvest. Plants from a representative 0.07 m² area were removed, rinsed free of soil, and placed in cold storage. Within several days plants were thoroughly washed, roots discarded, and the number of plants, actively growing tillers, and panicles were counted. Mainstems were not distinguished from tillers, consequently both mainstems and tillers were collectively counted and referred to as tillers. The established stand reported was the average of plant counts from the sampling dates through heading. Yield components were determined at harvest. Grain yield was taken from the unsampled center 13.0 m² area with a small plot combine and corrected to 14% moisture.

Repeated plant sampling data were analyzed across years as a split split-plot for each location similar to the repeated observations analysis of Little and Hills (1978). Years were main effects with replications nested within years, and factorial cultivar × seeding rate treatments were subplots. Repeated samplings were sub-subplots, with years nested within sampling dates. Yield component and yield data were analyzed across years as a split-plot, with years as main effects, replications nested within years, and factorial cultivar × seeding rate treatments as subplots.

The relative importance of yield components were summarized using an approach similar to Yoshida and Parao (1976). Grain yield (YLD) was a function of panicles m⁻² (PMS), spikelets panicle⁻¹ (SP), percent filled spikelets (PFS), and grain weight (GW):

$$YLD = PMS \times SP \times PFS \times GW$$

This yield component equation is transformed with the log function to create an additive model:

$$\ln(YLD) = \ln(PMS) + \ln(SP) + \ln(PFS) + \ln(GW)$$

Multiple, forward stepwise regression was performed with this additive model, using the maximum R² method of variable selection (SAS Institute, 1985). Yield components for each seeding rate and location were averaged across years and cultivars for this analysis.

RESULTS

Stand Establishment

Broadcasting 120 to 840 seeds m⁻² resulted in an established stand of 122 to 458 plants m⁻² at Butte and 129 to 451 plants m⁻² at Colusa averaged across years (Table 1). The actual plant stand established with 120 seeds m⁻² ranged from 122 to 129 plants m⁻² due to slightly uneven broadcasting of the seed. Seedling survival was an inverse, linear function of seeding rate, declining to 54% at 840 seeds m⁻². Early season growing conditions were less favorable at Colusa than Butte, resulting in an average of 25 fewer plants m⁻² at Colusa. At Colusa, deeper water levels (15 to 20 cm) during vegetative development and greater weed pressure from smallflower umbrellaplant (*Cyperus difformis* L. CPYOI) may have contributed to lower seedling survival.

Tiller Development

Tiller density increased significantly with increasing seeding rate and established plant stand throughout the growing season (Table 2, 3, Fig. 1). In three of the

Table 2. Analysis of variance summary, across years, for repeated phytomass sampling dates in the Butte and Colusa rice trials.

Source	Butte			Colusa		
	df	Tillers m ⁻²	Total above-ground phytomass	df	Tillers m ⁻²	Total above-ground phytomass
Significance of <i>F</i> values						
Year (Y)	1	NS	NS	1	**	*
Error a	6			6		
Cultivar (C)	1	NS	*	1	**	NS
Seeding rate (SR)	5	**	NS	5	**	NS
C × SR	5	NS	NS	5	NS	NS
Y × C	1	*	NS	1	NS	NS
Y × SR	5	NS	NS	5	NS	NS
Y × C × SR	5	NS	NS	5	NS	NS
Error b	66			66		
Sampling date (D{Y})	11	**	**	9	**	**
C × D(Y)	11	NS	**	9	NS	NS
SR × D(Y)	55	**	NS	45	**	NS
C × SR × D(Y)	55	NS	NS	45	NS	NS
Residual error	396			324		
Coefficient of variation (%)						
		28.2	26.4		27.5	25.4

*,** Significant at the 0.05 and 0.01 probability levels, respectively. NS, not significant at the 0.05 probability level.

Table 3. Analysis of variance summary, across years, for final phytomass sampling date in the Butte rice seeding rate trials.

Source	df	Tillers m ⁻²	Above-Ground phytomass		Yield	Panicles m ⁻²	Grain weight	Spikelets panicle ⁻¹	Percent filled spikelets
			Total	Vegetative					
Significance <i>F</i> values									
Year (Y)	1	NS	NS	NS	**	NS	*	NS	NS
Error a	6								
Cultivar (C)	1	NS	**	**	*	NS	**	**	NS
Seeding rate (SR)	5	**	NS	NS	*	**	NS	NS	NS
C × S	5	NS	NS	NS	NS	NS	NS	NS	NS
Y × C	1	NS	NS	NS	*	NS	NS	NS	NS
Y × SR	5	NS	NS	NS	NS	NS	NS	NS	NS
Y × C × SR	5	NS	NS	NS	NS	NS	NS	NS	NS
Error b	66								
Coefficient of variation (%)									
		16.4	15.7	16.7	7.3	16.3	3.1	10.6	5.6

*,** Significant at the 0.05 and 0.01 probability levels, respectively. NS, not significant at the 0.05 probability level.

four trials, rapid initial tiller production resulted in a maximum tiller density within 37 to 63 DAS. This was followed by a period of tiller attrition, in which the number of actively growing tillers declined until reaching a constant tiller density by heading. Early, excessive tillering, not observed at Colusa, 1985, and generally lower tiller densities at Colusa could have resulted from smallflower umbrellaplant competition and higher water levels.

A comparison of the Butte and Colusa trials suggests that tiller density was affected more by the environment than plant population (Fig. 2). Although the stand established at both sites was nearly identical, maximum and final tiller densities at Butte were an average of 354 and 151 tillers m⁻² higher, respectively, than at Colusa. Clearly, plant population was an inadequate predictor of final tiller density, the first yield component developed, among environments. Final tiller density (FTD) for both locations was a linear function of the maximum tiller density (MTD):

$$\text{FTD} = 233 + 0.41 \text{ MTD} (r^2 = 0.96).$$

Although higher MTD led to greater FTD, stands with higher MTD had higher tiller attrition and therefore lower tiller survival percentages. An increase in the MTD from 600 to 1400 tillers m⁻² reduced final tiller survival from 80 to 58% of MTD.

Phytomass Development

Total above-ground phytomass (TAGPM) was not significantly different among plant populations, either during or at the end of the growing season (Table 2, 3, 4, Fig. 3, 4a). Although the growing season pattern of dry matter accumulation (Fig. 3) differed significantly among the trial sites, the final productivity in three trials deviated only 23 g m⁻² from the 1966 g m⁻² TAGPM average. Throughout the growing season S-201 produced significantly greater TAGPM than M-201 as a result of more rapid stand establishment and generally higher tiller densities.

Final vegetative above-ground phytomass (VAGPM) increased with increasing plant population, and was higher at Butte than at Colusa (Fig. 4c). Interestingly,

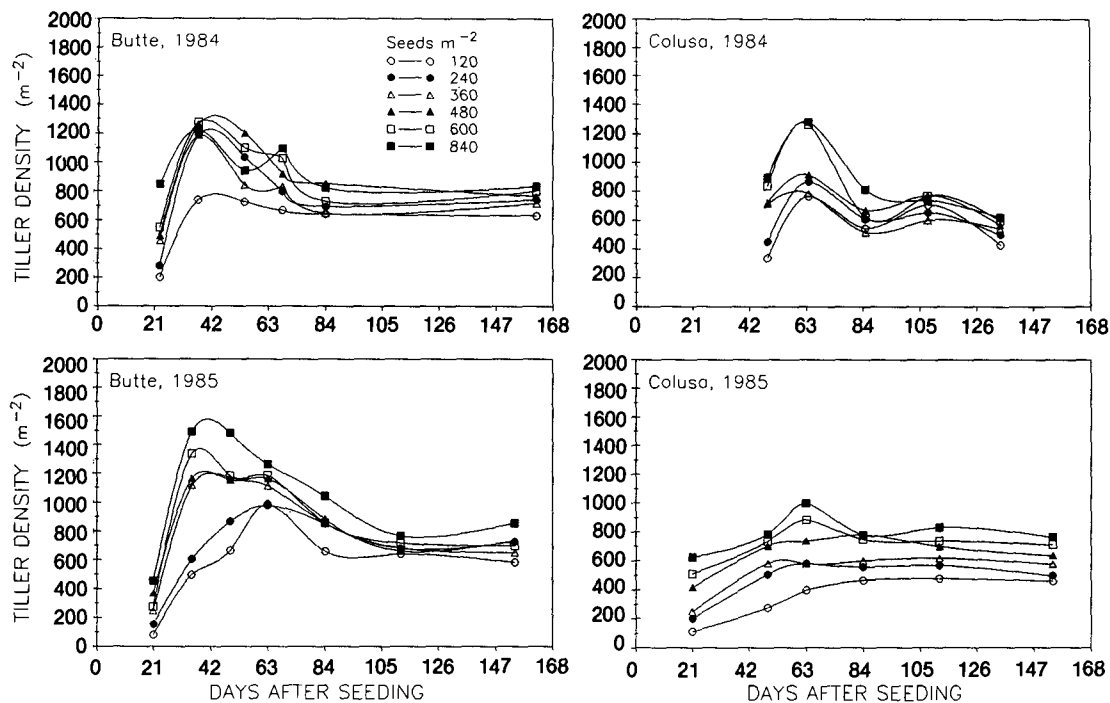


Fig. 1. Temporal pattern of rice tiller development, averaged across cultivars.

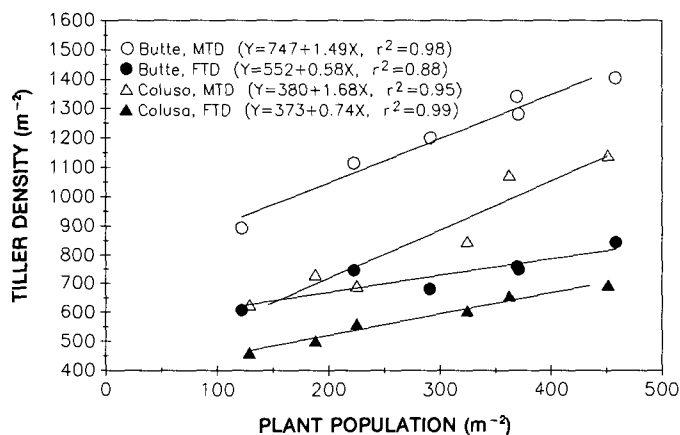


Fig. 2. Plant population affect on maximum tiller density (MTD), and final tiller density (FTD) of rice at Butte and Colusa, averaged across years and cultivars.

the site dependency of final VAGPM on plant population was not observed when the final VAGPM was associated with the FTD (Fig. 4d). Final VAGPM increased with increasing FTD, but VAGPM above 850 g m⁻² did not contribute to further yield increases.

Grain Yield

Plant population influenced grain yield within each trial site (Fig. 4e). At Butte, yield plateaued in populations greater than 200 plants m⁻², yet at Colusa a similar yield plateau was not observed. Yield and tillering responses to plant population were both site dependent. However, grain yields were more clearly dependent on FTD than on plant population, independent of location (Fig. 4f). Grain yields increased with increasing tiller density up to about 700 tillers

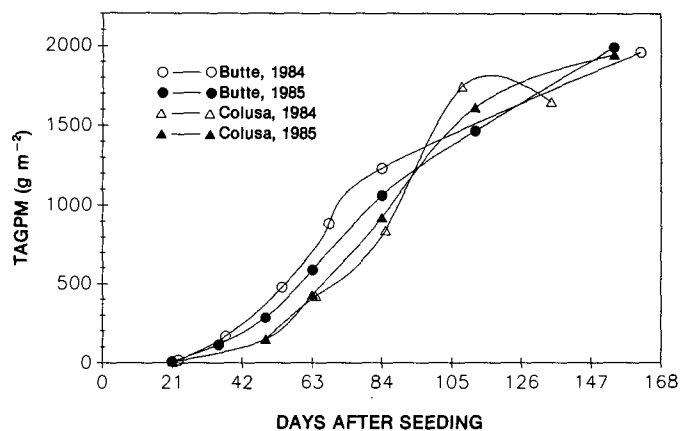


Fig. 3. Development of total above-ground phytomass (TAGPM), averaged across cultivars and seeding rates.

m⁻². Significant year \times cultivar interaction for yield at both locations resulted from significantly lower yields of M-201 than S-201 in 1985 as compared with 1984 (Table 3, 4).

Yield Components

The response of panicles m⁻² (PMS) to plant population was similar to the response of tillers m⁻² (Table 1, 3, 4). Panicles m⁻² averaged 95 and 98% of FTD at Butte and Colusa, and was not influenced by plant population. Significant cultivar \times year and cultivar \times seeding rate interaction for grain weight (GW) at Colusa resulted from very small differences in seed weight among years and plant populations. The GW range among plant densities was 1.0 mg seed⁻¹ for S-201 versus 0.5 mg seed⁻¹ for M-201, within each year at Colusa. Percent filled spikelets were significantly

Table 4. Analysis of variance summary, across years, for final phytomass sampling date and yield of rice in the Colusa trials.

Source	df	Above-Ground phytomass			Yield	Panicles m ⁻²	Grain weight	Spikelets panicle ⁻¹	Percent filled spikelets
		Tillers m ⁻²	Total	Vegetative					
Significance <i>F</i> values									
Year (Y)	1	NS	*	NS	NS	NS	**	*	*
Error a	6								
Cultivar (C)	1	**	*	NS	NS	*	**	NS	NS
Seeding rate (SR)	5	**	NS	NS	**	**	NS	**	*
C × S	5	NS	NS	NS	NS	NS	*	NS	NS
Y × C	1	NS	**	*	**	NS	**	*	NS
Y × SR	5	NS	NS	NS	*	NS	NS	*	NS
Y × C × SR	5	NS	NS	NS	NS	NS	NS	NS	NS
Error b	66								
Coefficient of variation (%)									
		20.7	18.0	19.6	7.9	20.9	1.9	15.0	5.5

*,** Significant at the 0.05 and 0.01 probability levels, respectively. NS, not significant at the 0.05 probability level.

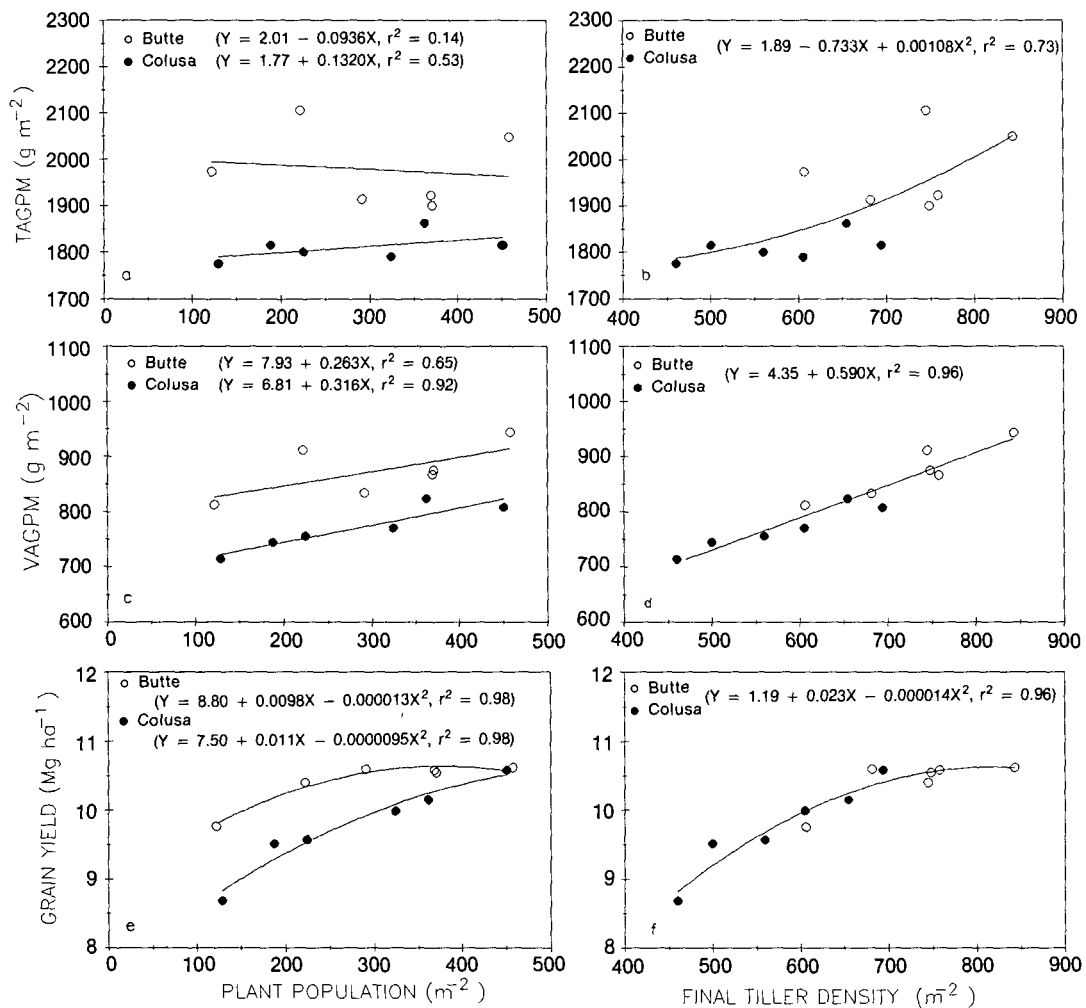


Fig. 4. Plant population and tiller density affect on final total above-ground phytomass (TAGPM), final vegetative above-ground phytomass (VAGPM), and grain yield of rice at Butte and Colusa, averaged across years and cultivars.

lower than normal at Colusa in 1984, with PFS below 80% at 120 and 240 seeds m⁻².

The relative importance of each yield component was evaluated by the order of inclusion into the multiple forward stepwise regression procedure and the additional contribution each yield component made

to the total variation in yield (Table 5). Panicles m⁻² was used in the regression procedure for simplification because it is a direct function of FTD. Panicles m⁻² was the most important component of yield, accounting for 89% of the variation in yield. The significance of PMS determining yield is further evidence for the

Table 5. Yield components contribution to grain yield of rice in water-seeded rice.

Yield component†	Contribution to total variation in yield (R ²)
GW	2
PFS	72
SP	82
PMS	89
PMS + PFS	91
PMS + PFS + SP	92
PMS + PFS + SP + GW	92

† PMS = Panicles m⁻²; PFS = Percent Filled Spikelets; SP = Spikelets Panicle⁻¹; GW = Grain Weight.

importance of reaching a critical tiller density for optimizing yield within a given environment.

DISCUSSION

Researchers have reported a range of rice plant densities necessary to achieve the yield potential for a given cultural system (Akita, 1982; Huey, 1984; Nguu and De Datta, 1979). In contrast to the relatively narrow plant stand goal of 161 to 215 plant m⁻² reported by Huey (1984) for drill seeded rice, grain yield under continuously flooded, direct water-seeded culture was maximized over a broad range of plant populations (222 to 451 plants m⁻²). The yield response to plant population under continuously flooded, direct water-seeded culture, was clearly dependent on the site and environment.

Donald (1963) and Fischer et al. (1976) suggested that maximum cereal grain yields were achieved at plant populations that resulted in near maximum total dry matter production. Yet in this study maximum rice grain yields were not associated with a critical plant population which resulted in near maximum TAGPM or VAGPM. Instead, a critical FTD of approximately 700 tillers m⁻² was necessary to reach the yield optimum.

Following the temporal pattern of tiller development we found that FTD or final tiller capacity more accurately reflected the limitations imposed within a given environment rather than plant population. Weed pressures at Colusa in 1985 limited the typical, excessive tiller development. Higher water management levels, early in the growing season, also contributed to the lower tillering capacity at the site. Scardaci et al. (1987) found that higher water levels reduced rice phytomass and tillers plant⁻¹, and delayed initial tiller appearance resulting in lower final tiller densities. Peterson et al. (1982) suggested that inhibition of tiller appearance is an indicator of stress in wheat. Under continuously flooded culture the rice plant is stressed until the plant has emerged from the water. Maintaining higher water levels prolongs this period of stress.

These studies suggest that PMS was the primary determinant of yield under continuously flooded, direct water-seeded rice culture. Panicles m⁻² accounted for 89% of the variation in yield. Since PMS is a direct function of FTD, a high tillering capacity is necessary to achieve the high yield potential in continuously flooded, direct water-seeded rice, just as Yoshida et al. (1972) reported for the transplanted cultural system.

Yet, in drill seeded rice the established plant population had the most significant influence on panicle density, with tillering contributing little except when the plant stand was very low (Jones and Snyder, 1987; Faw and Porter, 1981). Kawano and Tanaka (1968) reported tillers m⁻² was both positively and negatively correlated with grain yield depending on the cultivar and crop environment.

In addition to the importance of tiller and panicle density to yield, the tiller density achieved within a given site appeared to reflect the growth limitations imposed by that environment. Effectively the tillering capacity at a given site was a quantification by the rice crop of the favorability of the growing conditions. Ishizuka (1971) similarly reported that panicles m⁻² reflected the environmental and nutritional conditions of the rice crop at the maximum tillering stage. This suggests that under continuously flooded, direct water-seeded culture, the rice crop functions more as a population of tillers rather than a population of plants. Future research efforts must focus on management actions which affect the early season establishment of a critical tiller density.

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