Eur. J. Agron., 1995, 4(3), 299-308

Growth and yield formation of irrigated, direct seeded rice as affected by nitrogen fertilizer

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Accepted 23 June 1995.

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Abstract

In two experiments performed in 1989 and 1990 in the South of France, the growth and yield formation of direct seeded rice as affected by fertilizer nitrogen (N) management were studied to gain insight in the possibilities of improving fertilizer N efficiency. Initial plant density markedly influenced the time course of N uptake rate. An early decrease in N uptake rates resulted in low shoot N concentrations during the tillering and reproductive growth phases and consequently, in a decrease of the length of the active tillering period. However, appearance rates of leaves and tillers were not clearly affected by N management. The relative mortality rate of tillers during the reproductive phase was linearly related to the decrease in shoot N concentration during that period. Low grain numbers per panicle were related to a low crop N status. The leaf area of the crops was determined by : the size of leaf laminae, the duration of the active tillering phase, the relative death rate of stems and the total number of leaves produced on main stems. Despite these different processes, pooled data from both experiments could be used to establish simple linear relationships between leaf biomass and cumulative shoot N until flowering, and between leaf area index and cumulative shoot N. This implied that until flowering the N use efficiency for leaf production and specific leaf weight were constant. Hence, crop N status and shoot growth rate were directly related to the formation of crop components. However, N uptake rate *per se* was not a reliable variable to relate to production. Despite the latter conclusion, we argued that the risk of a sink-limited yield might be minimized by proper N management. To subsequently reduce the risk of source-limited grain production, a moderate leaf area with high N content during the post-flowering period is recommended.

Key-words : rice, nitrogen, competition, fertilizer-management

INTRODUCTION

It is well known that fertilizer nitrogen (N) use in rice cultivation is generally inefficient (De Datta, 1981 ; Vlek and Byrnes, 1986). For Europe, a maximum N recovery (kg fertilizer N uptake per kg N applied) of 0.32 was found for irrigated rice (Stutterheim *et al.*, 1994) This means that the risk of emission of N from flooded rice fields to the environment is high.

To reduce the risk of environmental pollution by fertilizer N, farmers need to increase the N application efficiency (kg yield per kg N applied). This can be achieved in two ways : 1) increasing grain yield at constant N application level, or 2) reducing fertilizer N input at a constant yield level. In both cases the marginal yield production (MP) is increased. However, to be able to propose a N management that results in a larger MP, more insight is needed in the effects N has on yield formation.

Yield formation in rice may be considered a process in which available carbohydrates accumulate in grain during the grain filling period. Yield formation is considered to be sink-limited when carbohydrate production exceeds the rate of accumulation, while the reverse situation is called source-limited. To obtain

ISSN 1161-0301/95/03/$ 4.00/

insight in the yield formation of a crop, it is necessary to quantify the production of those crop components that determine the sink and source capacity of the crop.

Many studies on the formation of main stems, tillers, leaves, panicles, spikelets and grains have been carried out on transplanted tropical rice (Murata, 1969 ; Matsushima, 1979 ; Akita, 1989), but only few studies exist on the growth and yield formation of temperate direct seeded rice (*spp. japonica*).

Direct seeded, compared to transplanted rice, is characterized by an early canopy closure, a rapid leaf area production and thus a rapid vegetative growth rate. Excessive vegetative growth, however, often leads to tissue-N dilution, and subsequently to carbohydrate shortage and growth reduction in later growth phases (Lemaire and Salette, 1984 ; Dingkuhn *et al.*, 1990 ; Schnier *et al.*, 1990a).

In this paper, we present a study on the effect of N-management on crop growth and yield formation of direct seeded temperate rice. We analyze : 1) how plant density and N-management affected N-uptake, 2) how N-uptake rate and growth were related to each other, and 3) how growth affected yield formation.

MATERIAL AND METHODS

Experimental layout and sampling

Two experiments on irrigated direct seeded rice were laid out in a randomized complete block design with four treatments and three replicates in the Camargue region in the South of France (43° 18'-43° 24' N), in 1989 (EXP89) and 1990 (EXP90). The textural class of the soil in the experimental areas was silt loam in 1989 and loamy sand in in 1990. Plots were 80 m × 12 m.

In both years a combined fertilizer at 34.9 kg P ha^{-1} and 124.5 kg K ha^{-1} was broadcast two days before sowing either with or without a basal N dressing, depending on treatment. A disc harrow was used to incorporate the fertilizer and prepare the seedbed. Seed of the *japonica* cultivar 'Lido' with an average growth duration of 140 days was broadcast at 230 kg ha^{-1} The field was flooded one day after sowing (DAS).

Treatments in 1989 were : 1) a control without fertilizer-N application (N0) ; 2) basal application of 160 kg N ha^{-1} as coated controlled-release urea (N1) ; 3) application of uncoated prilled urea (PU) in two splits of 80 kg N ha^{-1} each (N2), at tillering and neck-node differentiation (NND) ; and 4) application of uncoated PU in three splits, a basal dressing of 80 kg N ha^{-1} and two splits of 40 kg N ha^{-1} each, at tillering and NND (N3).

In 1990, a four-level single factor design was used with coated controlled-release urea applied as basal dressing at 0 (N0), 50 (N50), 100 (N100) and 150 kg N ha^{-1} (N150).

In EXP89, plants were sampled at 20, 26, 31, 33, 34, 49, 53, 64, 90, 96, 102, 138, 143, and 144 DAS. In EXP90, sampling was at 26, 31, 34, 59, 62, 68, 82, 87, 90, 129, 130, and 132 DAS. In both years, sampling was carried out by harvesting all plants from four 0.25 m^2 quadrats per plot. Samples were analyzed for the biomass of shoot, root, stem and leaf, tiller and plant number, and shoot-N by a Kjeldahl method (Williams, 1984). Tillers were distinguished from main stems. Leaf area was measured on 10 randomly selected plants per quadrat. The green leaf laminae of each plant were separated from the leaf sheaths and measured with a Delta-T leaf area meter. Leaf area index (LAI), calculated from the four samples per plot, was used for data analysis. At maturity, all leaf material was senescent. In EXP89, leaf appearance on main stems was monitored weekly by marking eight stems per plot and labelling emerged leaves with a small dot of dye. Labelling was postponed until the onset of tillering to avoid possible adverse effects of the dye on young plants. Phenological development in both experiments was monitored by recording the onset of tillering, NND and flowering.

Grain dry mass at harvest was determined from four 0.25 m^2 quadrats per plot. Information on panicle morphology was obtained by analysing 20 panicles, randomly selected from each plot. In EXP90, panicles were sampled weekly after flowering to follow the growth of individual grains. Grains were weighed fresh and oven-dry.

Daily weather data were obtained from a nearby weather station.

Data analysis

Data analysis was mainly carried out on plot means calculated from the data of the four quadrats sampled in each plot. To analyze treatment effects on shoot growth rate and N uptake rate, logistic curves were fitted (procedure NLIN, SAS, 1989) to plot means of shoot dry mass (M_{sh}) and cumulative shoot-N uptake (N_{sh}), both in kg ha^{-1} using the following equation (Table 1) :

$$Y = a_y / (1 + b_y \cdot \exp(-c_y \cdot t)) \qquad (1)$$

with :

a_y = curve parameter related to the asymptote of the curve (kg ha^{-1})

b_y = curve parameter related to the symmetry of the curve

Table 1. *Statistics of logistic functions fitted to time series of plot means per treatment (see text). Data was collected in the Camargue experiments of 1989 and 1990. The level of significance is for all treatments better than* $p = 0.005$, *and for 13 out of the 16 treatments better than* $p = 0.0001$.

EXPERIMENT 1989, SHOOT DRY MASS

Function $M_{sh} = a/(1 + b.\exp(-c.DAS))$

TRT	*n*	*r*
N0	14	0.92
N1	14	0.98
N2	14	0.95
N3	14	0.93

EXPERIMENT 1989, SHOOT NITROGEN CONTENT

Function $N_{sh} = a/(1 + b.exp(-c.DAS))$

TRT	*n*	*r*
N0	12	0.83
N1	12	0.91
N2	12	0.89
N3	12	0.87

EXPERIMENT 1989, SHOOT DRY MASS

Function $M_{sh} = a/(1 + b.exp(-c.DAS))$

TRT	*n*	*r*
N0	12	0.92
N50	12	0.86
N100	12	0.92
N150	12	0.91

EXPERIMENT 1989, SHOOT NITROGEN CONTENT

Function $N_{sh} = a/(1 + b.exp(-c.DAS))$

TRT	*n*	*r*
N0	12	0.90
N50	12	0.84
N100	12	0.87
N150	12	0.88

a, *b*, *c* and *d* are function parameters, DAS = days after sowing, TRT = treatment, *n* = number of replicate means used to fit the functions, *r* = correlation coefficient.

c_y = curve parameter related to the steepness of the curve (d^{-1})

Y = shoot dry mass or shoot-N content (kg ha^{-1})

t = time after sowing (d)

The rates of shoot growth and N uptake were determined as the derivative in time of Equation 1 and subsequently plotted (Figure 1) according to :

$$dY/dt = a_y \cdot b_y \cdot c_y \cdot \exp(-c_y \cdot t) / (1 + b_y \cdot \exp(-c_y \cdot t))^2 \quad (2)$$

Statistical analyses of measured numbers, biomass or area of organs were performed by assigning an average sampling date to three successively sampled blocks. In this way three replicate means per treatment were obtained. Average sampling dates were, 33, 55, 96 and 142 DAS in EXP89, and 30, 63, 86 and 130 in EXP90. To correct for variance heterogeneity, data were transformed to their natural logarithms (Hunt, 1982 ; Gomez and Gomez, 1984). An analysis of variance (procedure GLM, SAS, 1989) and the DMRT-method of Duncan (SAS, 1989) were applied. No curves were fitted to these data.

The data on yield components per panicle were obtained and analysed differently for each experiment.

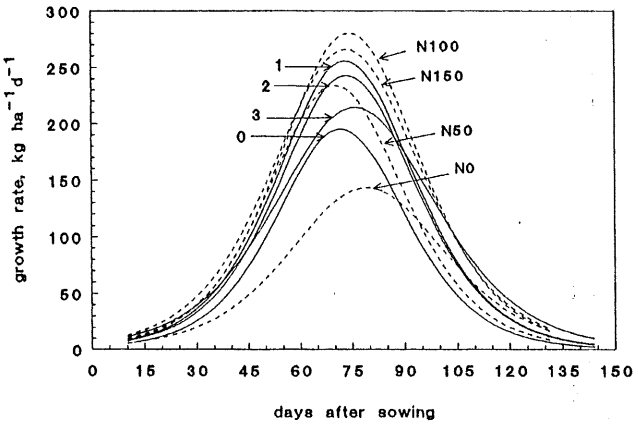

Figure 1. *Calculated shoot growth rate through time in the 1989 (solid lines) and 1990 (broken lines) experiments. 0, 1, 2 and 3 are treatments N0, N1, N2 and N3 in '89, respectively (see text).*

In EXP89, the number and locations of differentiated and degenerated branches and spikelets per panicle were estimated on the 20 panicles per plot. Primary branches per panicle were numbered in the acropetal direction starting from the neck-node. Because abortion of branches and spikelets was restricted to the

lower part of the panicle, only the basal five differentiated primary branches with their secondary branches and spikelets were analysed. Abortion of primary branches, secondary branches or spikelets was recorded by counting the vestiges of these organs on the panicle at harvest (Matsushima, 1979).

In EXP90, plot averages of individual grain dry mass (M_g) and total grain number per panicle were calculated weekly from the 20 panicles per plot. Growth curves of individual grains were derived by fitting logistic functions to the data per plot (*cf.* Equation 1). The mean curve per treatment was calculated by averaging the curve parameters. Statistical analysis of the parameters was performed by an analysis of variance. Subsequently, individual grain growth rate in each treatment was calculated by using the derivative of each average logistic function (*cf.* Equation 2). By definition, maximum growth rate is attained at the point of inflection (t_i), calculated as $\ln b_g/c_g$. A maximum 10-day mean growth rate (M_g') was calculated as the mean of the growth rate at $t_i - 5$ and $t_i + 5$ days.

RESULTS

Rates of growth and N uptake

In EXP89, growth rate in time was lowest at N0 (Figure 1), corresponding to relatively low N-uptake rates (Figure 2). In the other treatments, these rates were not clearly related. Initial average plant densities in that experiment were 338, 377, 389 and 427 m^{-2} at N0, N1, N2 and N3, respectively. Maximum individual plant-N uptake rate was calculated by dividing maximum shoot uptake rate by plant density. This resulted in : 6.87, 9.19, 9.67 and 9.29 mg $plant^{-1}$ d^{-1} for N0, N1, N2 and N3, respectively.

In EXP90, growth and N uptake rates at N0 were relatively low. The other treatments showed no clear relationship between these rates (Figures 1 and 2). Average plant density per treatment was 702, 687, 646 and 664 m^{-2} for N0, N50, N100 and N150, respectively. N uptake rate in time in EXP90 (Figure 2) was relatively low from the onset of tillering (25 DAS) until the later part of the reproductive phase (50-84 DAS). Some N uptake took place during the late reproductive and grain filling phases (84-131 DAS), probably caused by a high crop-N demand (Nielsen, 1983 ; De Willigen and van Noordwijk, 1987). Maximum individual plant N uptake rates were estimated as 1.21, 2.18, 2.29 and 3.11 mg $plant^{-1}$ d^{-1} for N0, N50, N100 and N150, respectively.

Hence, plant density differed markedly between both experiments. The low densities in EXP89 were associated with relatively high maximum plant N uptake rates, while the reverse held in EXP90.

Shoot N concentration (NP_{sh}) was calculated using the ratio of cumulative shoot N content to shoot dry mass (N_{sh}/ M_{sh}). In all treatments of EXP89, the N concentration in the crop increased until about mid-tillering, while in EXP90 it decreased monotonically (Figure 3). During the grain filling phase, NP_{sh} in both experiments was quite similar. This was confirmed by measured shoot N contents at flowering : in EXP89 1.2 ± 0.1 per cent averaged over all treatments, and in EXP90 0.9 ± 0.1 per cent.

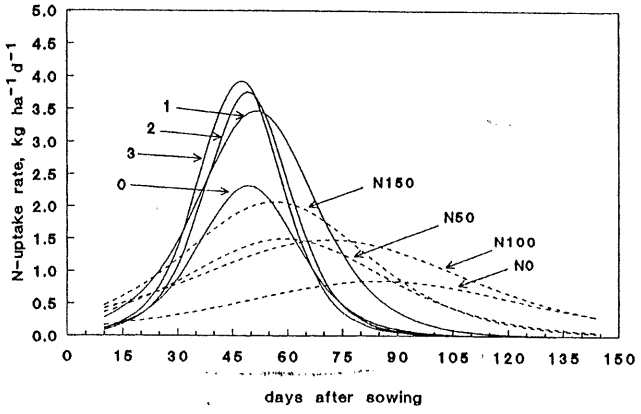

Figure 2. *Calculated shoot nitrogen uptake rate through time in the 1989 (solid lines) and 1990 (broken lines) experiments. Symbols as in Figure 1.*

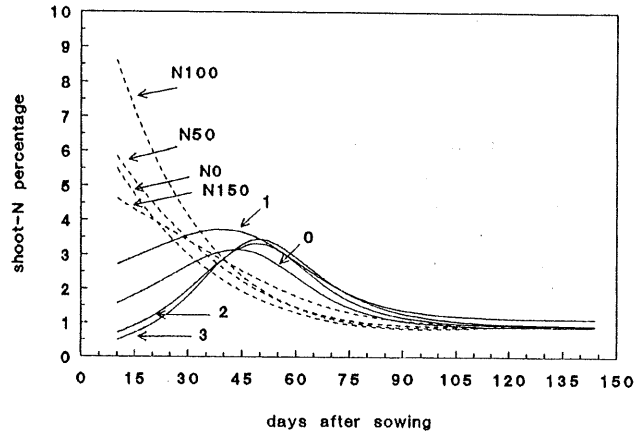

Figure 3. *Calculated shoot nitrogen content through time in the experiments of 1989 (solid lines) and 1990 (broken lines). Symbols as in Figure 1.*

Leaf appearance, tillering and tiller mortality

In EXP89, maximum tillering was observed at 56 DAS, with the lowest and highest average number of tillers per plant at 2.6 in N0, and 3.2 in N1. Leaf appearance rate did not vary significantly among treatments (Figure 4). This suggests that also tiller formation rate was independent of N treatment, considering existing evidence that appearance of leaves and tillers proceeds at similar rates (Masle-Meynard, 1980 ; Yoshida, 1981 ; Hanada, 1982 ; Durr, 1984).

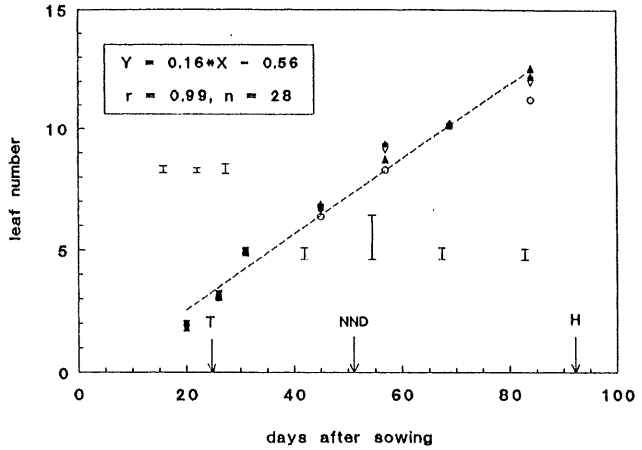

Figure 4. *Leaf number of main stems vs. time in the experiment of 1989. Leaves were numbered in order of appearance. Bars indicate the least significant difference at p = 0.05 (Duncan) between plot means.* ○ = N0, ◆ = N1, ▽ = N2 *and* ▲ = N3. *T = onset of tillering, NND = neck-node differentiation and H = heading.*

In EXP90, maximum tillering was observed at 30 DAS. The lowest average number of tillers per plant was 1.1 at N0 and the highest, 1.4, at N150. Hence, in both experiments, maximum tiller number per plant did not vary greatly among treatments. But the differences between the two experimental years were important. The period of active tillering was much longer in EXP89 than in EXP90.

In both years, a considerable loss in stem number was observed, especially during the reproductive phase. The relative stem mortality (RSTM), estimated by expressing plot means per treatment of stem numbers as percentage of the numbers present at NND stage, was proportional to the decline in shoot N content (ΔNP_{sh}) during the reproductive phase :

$$RSTM = 0.32 \cdot NP_{sh} - 0.05 \quad (r = 0.89; p = 0.0001 ; n = 24) \quad (3)$$

Leaf area expansion and phenological development

In EXP89, some significant differences between treatments in maximum leaf size were observed for leaves at identical positions on the main stem. At N0, leaves were smaller at position 10 and 11, while in N1 leaves were larger at position 9. At other positions, differences were not significant (data not presented). Total leaf number per main stem was lowest at N0 (Figure 4).

The dates of the onset of tillering, NND and flowering were similar among treatments in both experiments (data not presented). This indicates an absence of a significant N effect on phenological development rate. The same conclusion may be arrived at on the basis of the leaf appearance rate in EXP89 (Figure 4), considering that in rice (as in wheat) leaf appearance rate is related to phenological development rate (Matsushima, 1979 ; Kirby, 1990 ; Miglietta, 1992).

Up to flowering, the following linear relations were found between pooled plot means of leaf dry mass (M_l in kg ha^{-1}), N_{sh} and LAI over both experimental years :

$$M_l = 19.8 \cdot N_{sh} - 9.1 \quad (r = 0.94 ; p = 0.0001 ; n = 72) \quad (4)$$

$$M_l = 418.7 \cdot LAI - 46.8 \quad (r = 0.98 ; p = 0.0001 ; n = 63) \quad (5)$$

$$LAI = 0.05 \cdot N_{sh} - 0.1 \quad (r = 0.95 ; p = 0.0001 ; n = 72) \quad (6)$$

Hence, N-use efficiency for leaf production, and specific leaf weight, were about constant until flowering, 19.8 kg leaf dry weight per kg N absorbed and 418.7 kg leaf dry weight per ha leaf, respectively. A similar linear relation between LAI and N_{sh} was found for wheat (Groot, 1987).

Leaf dynamics were thus strongly related to cumulative shoot N, while no apparent relationship existed between the rates of growth and N uptake. Maximum growth rate at each treatment, plotted against the total shoot N content at the time of maximum growth (Figure 5), demonstrates that the N-use efficiency for growth rate (kg dry mass ha^{-1} d^{-1} per kg N) was higher in EXP90 than in EXP89, at least at maximum growth. This implies that in both years similar growth rates could have been realized at different levels of cumulative shoot N

Yield formation and yield components

Yield at N0 in EXP89 was limited by low panicle density, despite some compensation through higher

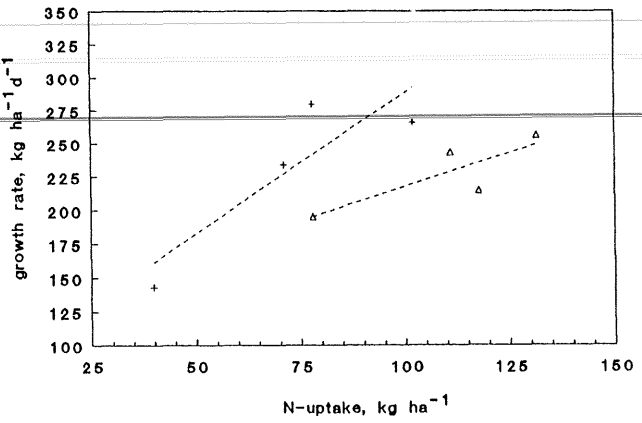

Figure 5. *Maximum growth rates attained in each treatment, against cumulative shoot nitrogen uptake at maximum growth. +, treatment means experiment 1990, △, treatment means experiment 1989.*

grain weights (Table 2). Final grain yields at N1, N2 and N3 were not significantly different, which indicates that total carbohydrate supply to grains must have been similar under these three treatments, despite differences in LAI at flowering (Table 2).

Grain numbers at N0 and N2 were reduced mainly because fewer primary branches were differentiated (Table 3). The relatively limited abortion of secondary branches and the better grain filling in N0 compensated somewhat for the lower grain number. In N2, significantly more secondary branches aborted than in the other treatments.

In contrast to EXP89, grain number per panicle limited grain yields in EXP90 (Table 2). Grain number per panicle increased with higher N application levels. The high growth rate observed during the reproductive phase at N100 seems at first sight inconsistent with reduced grain numbers, but when growth rate was expressed on a plant basis, a reduced number of spikelets per panicle was consistent with a carbohydrate shortage on the individual plant level (Matsushima, 1979).

Individual grain growth was only slightly affected by N management (Table 4). Parameters a, b_g and c_g (*cf.* Equation 1) did not significantly differ among N application levels. M_g' was lowest at N150. Although differences in M_g' were not significant, maximum

Table 2. *Yield components and production obtained in the experiments of 1989 and 1990. Treatment averages of each variable followed by the same letter are not significantly different at* $p = 0.05$.

EXPERIMENT 1989	N0	N1	N2	N3
Panicles m^{-2}	542^{a}	709^{b}	684^{b}	678^{b}
Tot. no. of grains per panicle	69.1^{ab}	72.0^{b}	63.9^{a}	70.2^{b}
— completely filled	62.4^{a}	58.9^{a}	56.3^{a}	61.2^{a}
— partly filled or empty	6.7^{a}	13.0^{b}	7.6^{a}	9.0^{a}
Individual grain dry mass (mg)	21.9^{a}	20.3^{c}	21.2^{b}	20.8^{bc}
Total dry grain yield (g m^{-2})	530.8^{a}	649.5^{b}	648.6^{b}	654.5^{b}
LAI at flowering	3.98^{a}	6.97^{c}	5.36^{bc}	5.19^{ab}

EXPERIMENT 1990	N0	N50	N100	N150
Panicles m^{-2}	620^{a}	615^{a}	676^{a}	691^{a}
Tot. no. of grains per panicle	32.4^{a}	46.2^{b}	47.8^{b}	57.5^{b}
— completely filled	30.6^{a}	43.4^{b}	43.8^{b}	51.7^{b}
— partly filled or empty	1.8^{a}	2.8^{a}	4.0^{b}	5.8^{b}
Individual grain dry mass (mg)	24.7^{a}	24.5^{ab}	23.9^{b}	24.5^{ab}
Total dry grain yield (g m^{-2})	411.3^{a}	580.4^{b}	728.5^{c}	732.7^{c}
LAI at flowering	1.74^{a}	3.27^{b}	4.71^{c}	5.34^{c}

N0 = no N-application, N1 = 160 kg urea-N basally applied as controlled-release fertilizer, N2 = two split applications of 80 kg urea-N each as prilled urea, N3 = three split application in fractions of 80, 40 and 40 kg urea-N as prilled urea. N50, N100 and N150 indicate the basal application of, respectively, 50, 100 and 150 kg urea-N as controlled-release fertilizer. LAI = leaf area index.

Table 3. *Panicle morphology at different nitrogen treatments in the 1989 experiment. Numbering of branches started at the base of the panicle. Different letters between values in a row indicate a significant difference at* $p = 0.05$.

Experiment 1989	N0	N1	N2	N3	CV (%)
no. of differentiated PB	7.9[a]	8.5[b]	8[a]	8.5[b]	8.3
no. of spikelets on first 5 PB	39.8[a]	36.4[bc]	35.8[c]	37.8[b]	14.3
% aborted of PB 1	5.12[a]	6.13[ab]	7.40[b]	5.90[a]	33.6
% aborted of PB 2	1.39[a]	1.59[a]	2.13[a]	1.65[a]	92.3
% aborted of PB 3	0.06[a]	0.00[a]	0.10[a]	0.11[a]	254.6
% aborted SB	14.34[a]	18.77[b]	18.89[b]	18.09[b]	20.9

N0 = no N application. N1 = 160 kg urea N, basally applied as controlled-release fertilizer. N2 = two split applications of 80 kg urea N, each as prilled urea. N3 = three split application in fractions of 80, 40 and 40 kg urea N as prilled urea. PB = primary rachis branches of the panicle, SB = secondary rachis branches. CV = coefficient of variation.

Table 4. *a) Treatment averages of individual grain dry mass (mg) through time as obtained in the 1990 experiment. b) Characteristics of average logistic curves obtained for each N-application level in that experiment. Grain dry mass data per treatment and curve parameters per N application level are not significantly different at* $p = 0.05$ *if they have identical letters.*

a)

DAYS AFTER HEADING	N0	N50	N100	N150
2	3.6[a]	3.5[a]	3.4[b]	3.3[b]
9	4.3[ab]	5.4[a]	3.4[b]	3.7[b]
16	9.2[a]	9.0[a]	8.6[a]	7.2[a]
23	17.2[a]	17.3[a]	15.5a	11.0[b]
27	20.5[a]	19.8[a]	18.2[ab]	15.3[b]
38	23.5[a]	22.7[ab]	22.1[ab]	21.2[b]
48	23.2[a]	22.7[a]	22.3[ab]	21.2[b]

N0, N150, N100 and N150 indicate the basal application of, respectively, 0, 50, 100 and 150 kg urea N as controlled-release fertilizer.

b)

N-APPLICATION (kg ha^{-1})	b_g	c_g (d^{-1})	a_g (mg)	t_i (d)	M_g' (mg d^{-1})
0	20.3[a]	0.167[a]	24.0[a]	17.8[a]	0.96[a]
50	16.7[a]	0.160[a]	23.5[a]	17.3[a]	0.88[a]
100	21.1[a]	0.163[a]	22.9[a]	18.8[a]	0.88[a]
150	17.8[a]	0.127[a]	23.4[a]	22.4[b]	0.71[a]
C.V. (%)	38.7	18.1	2.7	5.6	13.9

a_g, b_g and c_g are curve parameters related to, respectively, the saturation asymptote, the symmetry and the steepness of the growth curve. t_i = day after heading at which the point of inflection of the growth curve is reached. M_g' = average maximum growth rate of individual grains. C.V. = coefficient of variation of parameter estimates.

growth rate tended to decrease when grain number per panicle increased (Figure 6). Only t_i differed significantly among treatments. At N150, t_i was 3.6 to 4.6 days longer than in other treatments (Table 4). As a result, physiological maturity was delayed in N150.

Hence, in EXP90 yield was mainly sink limited, except at N150. In EXP89, the relatively high leaf area at flowering did not contribute to higher yields, which could be interpreted, incorrectly, as a sink-limited yield. The relatively large number of grains and panicles per unit area (Table 2) indicate that other factors than leaf area limited the source capacity of the crop.

Overall, the highest yields per unit area were obtained at N100 and N150 in EXP90. They corresponded to high growth rates during panicle formation stage (Figure 1) resulting in greater grain numbers per panicle. Lower temperatures during the grain filling period in EXP90 may also have played a decisive role in causing yield differences between both years

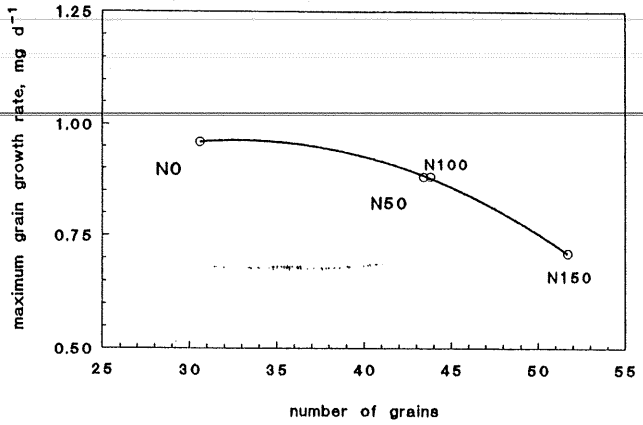

Figure 6. *Maximum growth rate of individual grains as function of the number of filled grains per panicle in the experiment of 1990. Symbols represent treatment means.*

(Spiertz, 1977 ; Vos, 1981). Cumulative average 24 h temperature during the first 20 days after flowering was 497.5 °C *d* in EXP89 and 459.8 °C *d* in EXP90.

DISCUSSION

The formation of yield-determining crop components in our experiments was greatly affected by N. Also, an important feed-back existed between N-dependent processes, *e.g.* total tiller number was increased by N availability through extension of the tiller formation period, but this resulted in a large decrease of shoot N percentage during the panicle formation stage. In turn, the latter process correlated positively with stem mortality (Equation 3). Such feed-back mechanisms complicate the quantification of N-effects on crop growth.

A second important point to note is that the interaction between plant density and soil N-availability at the onset of growth had a major influence on crop behaviour at later growth stages. In highly controlled cultivations, plant density can be adjusted at will. In irrigated rice grown in the Camargue, 50 to 70 per cent of the seed sown is lost (Stutterheim, 1995), and crop establishment may be highly variable, not only between years but also between fields. Hence, as long as plant emergence and establishing is not better controlled, it remains difficult to give quantitative advice in terms of N management. This is well demonstrated by our study, in which the large differences in plant density prevented formulation of precise advice. However, enough evidence was obtained to discuss the issue of N management in relation to crop status in qualitative terms.

The effect of initial plant density was mainly on the dynamics of shoot N uptake rate. It was shown that on a soil low in fertility (EXP90), high plant densities lead to early competition for soil N as indicated by the low maximum plant uptake rates and the early shoot N dilution.

A simple equation previously defined by Nielsen (1983) can be used to illustrate these findings :

$$dN_c/dt = D \cdot I_N \cdot L \qquad (7)$$

where :

dN_c/dt = N uptake rate of the crop (kg ha^{-1} d^{-1})
D = plant density (ha^{-1})
I_N = net inflow rate of N into roots (kg m^{-1} d^{-1})
L = effective root length per plant (m)

Hence, N uptake rate can increase with D, I_N or L. However, these parameters are not independent. Average individual plant N uptake rate ($I_N \cdot L$) depends on plant properties and on soil N availability. In the exponential growth phase, plants growing at moderate densities (thus without severe competition for N), will increase their N uptake rate ($I_N \cdot L$). As a result, total shoot N uptake also increases. However, if D is too high and/or soil N availability is relatively low, early competition for N may negatively affect $I_N \cdot L$, resulting in lower shoot N uptake rates.

An early decrease in individual plant N uptake rate, and thus in tissue N concentration, negatively affects tillering of such a plant (Durr, 1984 ; Wada *et al.*, 1986). In practice, this means that at a given level of soil fertility, at high plant density fewer tillers will be produced than at low plant density. Application of fertilizer N may then help to increase tiller number by extending the active tillering period.

Shoot N percentage decreased during the reproductive growth phase in both experiments, and relative stem mortality was linearly related to that decrease. Also, grain numbers per panicle were low in most of the treatments in EXP90, due to a combination of high plant density and low shoot N.

Both stem mortality and reduced spikelet production indicated a shortage in carbohydrates during the reproductive growth phase. As it has been shown that the N content and the photosynthetic capacity of leaves are closely related (Kisthitani *et al.*, 1972 ; Shieh and Liao, 1987 ; Sinclair and Horie, 1989), the low carbohydrate production during the reproductive growth phase may be attributed to the low shoot N status.

The high growth rates in EXP90 due to high plant densities, and the high N-use efficiency for growth rate, resulted in high yields at N100 and N150. Also, low temperatures might have favoured grain filling. The relatively high N-use efficiency for growth rate may be related to the late N uptake in EXP90, which

could have led to N enrichment of active leaf material. Fertilizer-N application in the first half of the reproductive growth phase may thus serve for maintaining main stems and tillers and for increasing spikelet production.

Leaf area was affected in several ways : 1) the lamina area of individual leaves decreased when no N was applied (Biscoe and Willington, 1985) ; 2) the duration of tiller formation varied, presumably depending on shoot N content (Ishizuka and Tanaka, 1969 ; Schnier *et al.,* 1990b) ; 3) the relative loss rate of stems with shoot N dynamics (Dingkuhn *et al.,* 1990) ; and 4) the total number of leaves that emerged on the main axis was lower when no N was applied (Durr, 1984). Despite these different mechanisms, the relations between leaf biomass, or leaf area, and cumulative N uptake until flowering were linear. Using N uptake as input, these relations permit the calculation of LAI increase on a daily basis, which can be used for estimation of daily crop production. This, however, was beyond the scope of this paper.

Grain yield is mainly determined by weather and source capacity during the grain filling phase, provided i) the grain sink capacity is assured by N application at the reproductive growth phase, and ii) pests and diseases are controlled. However, it was shown that a high leaf area around flowering was not a guarantee of sufficient source capacity. Moreover, a high leaf area may be counter-productive when respiration increases through high temperatures. Hence, to reduce the risk of source limitation through weather, a moderate leaf area seems advisable. Another aspect that affects source capacity is the remobilization of amino-acids and ageing of leaves (*e.g.* Sinclair and de Wit, 1975), which decreases photosynthetic capacity. Additional N supply at the onset of grain filling may partly reduce these self-destructing processes. In accordance with other findings (Evans and Wardlaw, 1976 ; Yoshida and Parao, 1976), we consider that a moderate leaf area with high N content at the onset of the grain filling phase will reduce the risk of source-limited grain production. This can be achieved by additional N application after panicle initiation.

The lack of relationship between the rates of growth and N uptake may be explained by a different impact of environment on both rates, *e.g.* an increase in temperature may decrease growth rate through higher respiration, but it may increase N uptake rate through higher root activity or soil-N mineralization. Furthermore, the reaction time of N uptake rate to limiting conditions is relatively short compared to that of growth rate. Hence, N uptake rate *per se* is not a reliable variable to relate to crop production.

It is concluded that for a better quantification of interactions between crop and environment in irrigated rice in the Camargue, additional research is needed. To explore feed-back mechanisms, crop growth models may be informative. Using such models, it may be possible adapt fertilizer N management to actual growth conditions in a more precise manner.

ACKNOWLEDGEMENTS

The authors are grateful to B. Nougarèdes and R. Hammond for their technical assistance and to the colleagues of AB-DLO and TPE-WAU for their useful comments. We appreciate the financial assistance that was received from DGXII of the EC through research grant ERB4040PL910066.

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