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Effect of temperature on rice growth in nutrient solution and in acid sulphate soils from Vietnam

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Abstract

Climatic and soil factors are limiting rice growth in many countries. In Vietnam, a steep gradient of temperature is observed from the North to the South, and acid sulphate soils are frequently devoted to rice production. We have therefore attempted to understand how temperature affects rice growth in these problem soils, by comparison with rice grown in nutrient solution. Two varieties of rice, IR64 and X2, were cultivated in phytotrons at 19/21°C and 28/32°C (day/night) for 56 days, after 3 weeks preculture in optimal conditions. Two soils from the Mekong Delta were tested. Parallel with the growing experiments, these two soils were incubated in order to monitor redox potential (E_h), pH, soluble Al and Fe, soluble, and available P. Tillering retardation at 20°C compared to 30°C was similar in nutrient solutions and in soils. The effect of temperature on increasing plant biomass was more marked in solutions than in soils. The P concentrations in roots and shoots were higher at 20°C than at 30°C, to such an extent that detrimental effect was suspected in plants grown in solution at the lowest temperature. The translocation of Fe from roots to shoots was stimulated upon rising temperature, both in solutions and in soils.This led to plant death on the most acid soil at 30°C. Indeed, the accumulation of Fe in plants grown on soils was enhanced by the release of Fe^{2+} due to reduction of Fe(III)-oxihydroxides. Severe reducing conditions were created at 30°C: redox potential (E_h) dropped rapidly down to about 0 V. At 20°C, E_h did not drop below about 0.2 V, which is a value well in the range of Fe(III)/Fe(II) buffering. Parallel to E_h drop, pH increased up to about 6-6.5 at 30°C, which prevented plants from Al toxicity, even in the most acid soil. Phosphate behavior was obviously related to Fe-dynamics: more reducing conditions at 30°C have resulted in enhancement of available P, especially in the most acid soil.

Introduction

As compared to other cereal crops, rice is particularly sensitive to low temperature, and this climatic factor is limiting production in many countries, at least during the winter season (Nishiyama, 1976). Fundamentally, temperature characteristics of living organisms are controlled by genetic factors (Chang and Oka, 1976; Kaspar and Bland, 1992; Vergara, 1976), so that plant breeding has long been concerned with selecting varieties or cultivars well adapted to temperature stress.

Temperature is influencing nutrient dynamics in soils so that this climatic factor can also limit plant growth indirectly. For example, the release of nitrogen and phosphorus from the mineralization of organic matter is closely dependent on soil temperature (Koerselman et al., 1993; Ponnamperuma, 1976). All thermodynamic and kinetic characteristics governing adsorption, ion exchange, mineral solubilization, and precipitation are functions of temperature. This is true for all types of soil management, but it is still more effective in flooded soils where redox-dependent phenomena are strongly affected by temperature (Ponnamperuma, 1972, 1976; Tsutsuki and Ponnamperuma, 1987). Indeed the rates of reduction reactions are controlled to a great extent by microorganisms, whose metabolic activity has quite high activation energy (Patrick, 1992; Willett, 1991). While under aerobic conditions the oxidation of organic matter has limited

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effects on soil minerals because oxygen serves as electron acceptor, the oxidation of organic matter under anaerobic conditions induces drastic changes in soil constituents such as Mn- and Fe-oxihydroxides, and sulfide can even form at low redox potential. Temperature effects on rice growth is well documented in the literature (Baker et al., 1992; Cho and Ponnamperuma, 1971; Goto et al., 1994; Hung et al., 1992; Munakata, 1976; Resurreccion et al., 1977; Yoshida, 1973). However, to our knowledge, no one has made direct comparison of rice growth in soil and nutrient solution under different temperatures to determine differential effects of the two media on growth and ion uptake. Also, limited information exists in the international literature concerning rice growth on Vietnamese soils.Therefore, this work was conducted in the context of rice production in Vietnam, where a steep positive gradient of temperature is observed from the North to the South of the country.

Three types of experiments were carried out together, at two temperatures (20 and 30°C): 1- rice growing in nutrient solution, 2- rice growing on flooded soils, 3- flooded soils without plants. This experimental scheme was repeated with two rice varieties and with soils from two different sites. Acid sulphate soils were chosen because they are common both in North and South Vietnam, and besides intensive efforts are devoted to developing rice production in these marginal soils.

Among nutrients, we have focussed on phosphorus, because the behavior of this element is particularly sensitive to temperature and flooding duration (Koerselman et al., 1993; Patrick, 1992, Ponnamperuma, 1972; Sanyal and De Datta, 1991; Willett, 1982, 1986, 1989, 1991). In addition, phosphorus is often limiting plant growth in acid soils. Iron in plants and soils was monitored along with phosphorus, because Fe-toxicity has often been observed in these soils in the days or weeks following flooding (Ottow et al., 1993; Prade et al., 1988).

Materials and methods

Soil characteristics

The two soils used in this study were collected from the Ap horizon of acid sulphate soils in the Mekong Delta, in the localities of O Mon (soil 1) and Cu Chi (soil 2), at the South-West of Ho Chi Minh-City. Both soils key out as Thionic Fluvisols according to the FAO classification, and as Sulfic Fluvaquent (soil 1) and Sulfic Tropaquept (soil 2) according to the soil taxonomy. After air drying, the soils were crushed and sieved at 2 mm. Important characteristics are given in Table 1.

Preculture at 30°C

Two rice varieties were used: X2 and IR64. These cultivars are widely cultivated in Vietnam, and X2 is known to be more resistant to cold than IR64. Seeds were germinated in distilled water. After 7 days, the young plants were transferred to a nutrient solution with the following composition: N (as NH_4NO_3) 20 mg L^{-1}, P (as KH_2PO_4) 0.05 mg L^{-1}, K (as KCl) 10 mg L^{-1}, Ca (as $CaCl_2$) 10 mg L^{-1}, Mg (as $MgSO_4$) 1 mg L^{-1}, Fe (as FeNaEDTA) 1 mg L^{-1}, trace elements according to Hoagland 1 mL L^{-1} (Tang Van Hai et al., 1989). Two series of 60 plants per variety tightened with cotton on plastic disks were grown on 20 L tanks, and the solutions were renewed every 2 d for 2 weeks. Temperature was 30°C during the day (12 h) and 25°C during the night (12 h). Light intensity was about 250 μmol m^{-2} s^{-1}. This precultivation period produced in 3 weeks healthy plants ready for further treatments.

Hydroponic cultures at 20°C and 30°C

Eight series of 5 plants per variety were transferred on 450-mL vessels to which nutrient solution was continuously supplied by peristaltic pumps at a rate of about 100 mL h^{-1} (Tang Van Hai and Laudelout, 1966). The composition of the solution was the same as above, except that P concentration was increased up to 2 mg L^{-1} to be sure that this element was not limiting plant growth. The plants were grown in two phytotrons (4 series of 5 plants per variety) with different day/night temperature regimes: 21°C/19°C in the one, and 32/28°C in the other. Plants were harvested after 56 d of treatment. Roots and shoots were separated. They were dried at 85°C, weighed, crushed and mineralized at 450°C. After dissolving the dry residue in concentrated HF, H_2SO_4 and $HClO_4$ (details of the method in Jackson, 1982), the P content was measured by colorimetry according to the molybdenum blue method (Watanabe and Olsen, 1965), and Fe was measured by atomic absorption spectrophotometry.

During the growing period, the daily rate of P uptake was evaluated at different times by determining P concentrations and volumes of input and output flowing solutions. Tillering of rice plants also was

Table 1. Selected characteristics of the dry soils before the experiments

Properties	Soil 1	Soil 2	Method
pH			
pH_{H_2O}	4.40	4.05	1:5 soil:water
PH_{KCl}	4.05	3.65	1:5 soil:1 *M* KCl
Carbon (g kg^{-1})	20.7	48.7	Walkley and Black (1934)
Phosphorus (g kg^{-1})			
total P	0.245	0.358	Jackson (1982)
available P	0.032	0.011	Onioani (1973)
Iron (g kg^{-1})			
total Fe	27.1	62.5	Jackson (1982)
dithionite-Fe	4.24	31.3	Merha and Jackson (1960)
oxalate-Fe	3.92	10.3	Blakemore (1983)
Aluminium (g kg^{-1})			
total Al	96.7	65.2	Jackson (1982)
dithionite-Al	0.57	31.3	Merha and Jackson (1960)
oxalate-Al	0.83	2.00	Blakemore (1933)
Size fractions (g kg^{-1})			
(carbon free soils)			
clay (0-2 μm)	490	420	
silt (2-50 μm)	216	176	
sand (50-2000 μm)	284	404	

followed to estimate the retardation effect of cold on growth stages.

All the experiments in nutrient solutions were carried out in 4 replicates

Cultures on soils at 20°C and 30°C

Three series of 5 plants per variety, soil type, and temperature were transplanted in plastic pots containing 0.7 kg dry soil mixed with 1.05 L water. Just before planting, the soils were amended with 70 mg N (urea) per pot, 60 mg P (KH_2PO_4) per pot, and 140 mg K (KCl) per pot. Another 70 mg N rate was supplied 20 days later. The water level was regularly adjusted 2 cm above the soil surface to compensate for evapotranspiration. As in nutrient solutions, plants grown on soils were also harvested after 56 d of treatment; the soil material was washed out; and shoots and roots were analysed for dry weight, P, and Fe content as described above. The experiments with plants in soils were carried out in 3 replicates.

Incubation of soils at 20°C and 30°C

In parallel with the growth experiments, and in the same rooms with controlled temperature, samples of the two soils were incubated as follows. Suspensions of 75 g dry soil with 112.5 mL deionized water were stored in well capped cups. After different periods of time (i.e. 8, 16, 26, 36, and 56 days), successive cups were used for analysis.

At each time, pH and redox potential (E_h) were measured in the soil suspensions by potentiometry under N_2 atmosphere, and two drops toluene were added to inhibit further microbial proliferation. After rapid filtration, P, Fe, and Al were measured in the solution phase by colorimetry (P) or by atomic absorption (Fe and Al); these concentrations are referred as soluble ions in the Results and discussion section. The so-called plant-available P was measured in the soil pastes collected on the filters by extraction with 0.1 *N* H_2SO_4, according to the Onioani method (Nguyen Vy and Tran Khai, 1978; Onioani, 1973). The dry

weight of the soil pastes was determined after drying at 105°C.

All measurements were carried out on 2 cups at each time of incubation.

Results and discussion

Plant growth in solution and in soils

A general view of the plant behavior under different treatments is provided by examining the tillering evolution with time (Fig. 1); tillering is indeed an important yield factor especially under stressed conditions (Tang Van Hai et al., 1993). Both rice varieties did not survive for more than 20 days on soil 2 at 30°C. This point will be elucidated later by looking at soil incubation data and mineral concentrations in plants. The greater cold tolerance of the X2 variety is confirmed, in this sense that the tillering retardation at 20°C as compared to 30°C is lower for X2 than for IR64; as obvious from the tillering curves in Figure 1 the ratio of the number of tillers at 30°C as compared to 20°C is always smaller for X2 than for IR64, at least on soil 1 and in solution where comparison is possible. However, after 56 d, only small differences in tiller number are subsisting. It is also worth noticing that the tillering rate is similar in nutrient solution and in soils, which is favourable for reliable comparisons between nutrition characteristics in the two systems.

The vegetative yield at 56 d, as expressed by dry weight of roots and shoots, is presented in Table 2 for all treatments. Little difference is observed between the two rice varieties, so that we can make further discussion without considering this aspect. One can only notice that the dry matter of shoots at 30°C is lower for X2 than for IR64 in nutrient solution. This difference, however, is almost completely rubbed out in soils. At 20°C, both varieties give similar yield. Therefore rather than cold resistance, the behavior of X2 might be described as lower, or slower, response to rising temperature. It is just a matter of reference.

As far as roots are concerned, two features are seen in Table 2. First, root development is always lower in nutrient solution than in soils. This has often been interpreted as a morphological adaptation of roots to nutrient accessibility (Callot et al., 1982; Cope and Hunter, 1967; Markay and Barber, 1984; Rajkai Végh, 1991). In soils, the rate of uptake of most elements is limited by diffusion from bulk soil to root surfaces, whereas the uptake efficiency of root systems in solution is more dependent on nutrient concentrations than on root morphology. The second feature is that the effect of temperature on root weight is small in soils, while it is important in solution. This will be discussed just below.

The effect of temperature on shoots is well marked, both in soils and in solution. But the most striking feature is that the dry matter of shoots at 20°C is lower in nutrient solution than in soils, whereas the opposite is true at 30°C. There is no reason to believe that nutrient availability is lower in solution than in soil, more especially as solution was continuously renewed. We checked that no major element was exhausted in output solutions. However, extremely high P-concentrations are found in shoots and roots at 20°C for plants grown in nutrient solution (Table 3). These P-concentrations are about 5 times greater than the ones observed in plants grown on soils at 20°C, and they are well above the range normally observed in rice plants; values of 1000 to 2500 mg P kg^{-1} in leaves at maximum tillering are reported as "normal" by Uexkull (1976) and Benton Jones et al. (1991). The P-concentration in our flowing solutions (i.e. 2 mg P L^{-1}) obviously exceeded the requirements of rice plants at 20°C, to such an extent that direct or indirect detrimental effects were likely to occur. There is much debate in the literature whether or not there is "phosphorus toxicity"; phosphate-induced micronutrient deficiency can be the reason for apparent P-toxicity (Kirkham, 1982). At 30°C, although the rate of P uptake from solutions is higher than at 20°C (Fig. 2), the P content in shoots remains at the upper limit of the range considered as normal. In roots at 30°C, the P concentrations are much lower than at 20°C, but they are still higher in solution than in soils. This could be attributed as well to translocation limitations in solution as to P limitations in soils. As a matter of fact, the P concentration that we have fixed in the flowing solutions can no longer be considered as really detrimental at 30°C, whereas it obviously was at 20°C. The activation of plant metabolism from 20 to 30°C involves increased production of plant tissues and dilution of absorbed P.

Flooding acid soils always involves a risk of releasing Fe^{2+} ions in solution that can be toxic for rice plants. Therefore, examining the Fe-content in plants can generally give good indication of possible excess of this element in the root environment. Fe-concentrations in roots and shoots for all treatments are presented in Table 4. The Fe-concentrations are much greater in plants grown on soils than in plants grown in nutrient solution. In this case, Fe-uptake

Table 2. Biomass of roots and shoots after 56 days treatment (g DM for 5 plants)

Growth substrate	Variety	20°C		30°C	
		Roots	Shoots	Roots	Shoots
Soil 1	IR64	6.35 (0.36)[a]	5.25 (0.36)	7.35 (0.40)	25.32 (0.93)
	X2	6.22(0.29)	6.01 (0.43)	7.96 (0.44)	22.19 (1.21)
Soil 2	IR64	5.76 (0.57)	5.06 (0.83)	4.05 (0.50)	10.40 (0.60)
	X2	6.59 (0.99)	5.18 (0.52)	2.95 (0.36)	9.38 (0.55)
Nutrient solution	IR64	1.65 (0.02)	3.07 (0.20)	6.31 (1.27)	43.27 (4.02)
	X2	1.36 (0.06)	3.59 (0.15)	5.01 (0.22)	31.30 (1.88)

[a] In parenthesis - standard deviation.

Table 3. Phosphorus concentration in roots and shoots after 56 days treatment (g P kg^{-1})

Growth substrate	Variety	20°C		30°C	
		Roots	Shoots	Roots	Shoots
Soil 1	IR64	1.53 (0.20)[a]	2.40 (0.29)	0.96 (0.11)	1.59 (0.09)
	X2	1.19 (0.01)	2.50 (0.11)	0.69 (0.08)	1.83 (0.15)
Soil 2	IR64	1.25 (0.06)	2.04 (0.42)	1.07 (0.16)	1.77 (0.07)
	X2	1.07 (0.15)	2.11 (0.09)	0.93 (0.11)	2.30 (0.11)
Nutrient solution	IR64	5.46 (0.57)	11.01 (0.97)	1.86 (0.17)	2.26 (0.16)
	X2	6.21 (0.34)	10.79 (0.10)	2.28 (0.18)	3.49 (0.22)

[a] In parenthesis - standard deviation.

Table 4. Iron concentration in roots and shoots after 56 days treatment (g Fe kg^{-1})

Growth substrate	Variety	20°C		30°C	
		Roots	Shoots	Roots	Shoots
Soil 1	IR64	15.35 (0.77)[a]	0.44 (0.09)	3.37 (0.27)	0.55 (0.04)
	X2	16.26 (0.92)	0.36 (0.03)	3.12 (0.17)	0.43 (0.05)
Soil 2	IR64	43.31 (4.73)	1.11 (0.17)	75.52 (2.31)	2.52 (0.18)
	X2	38.86 (1.57)	1.96 (0.07)	88.99 (11.36)	2.91 (0.35)
Nutrient solution	IR64	0.38 (0.07)	0.08 (0.02)	0.23 (0.03)	0.22 (0.01)
	X2	0.34 (0.09)	0.09 (0.02)	0.16 (0.01)	0.25 (0.01)

[a] In parenthesis - standard deviation.

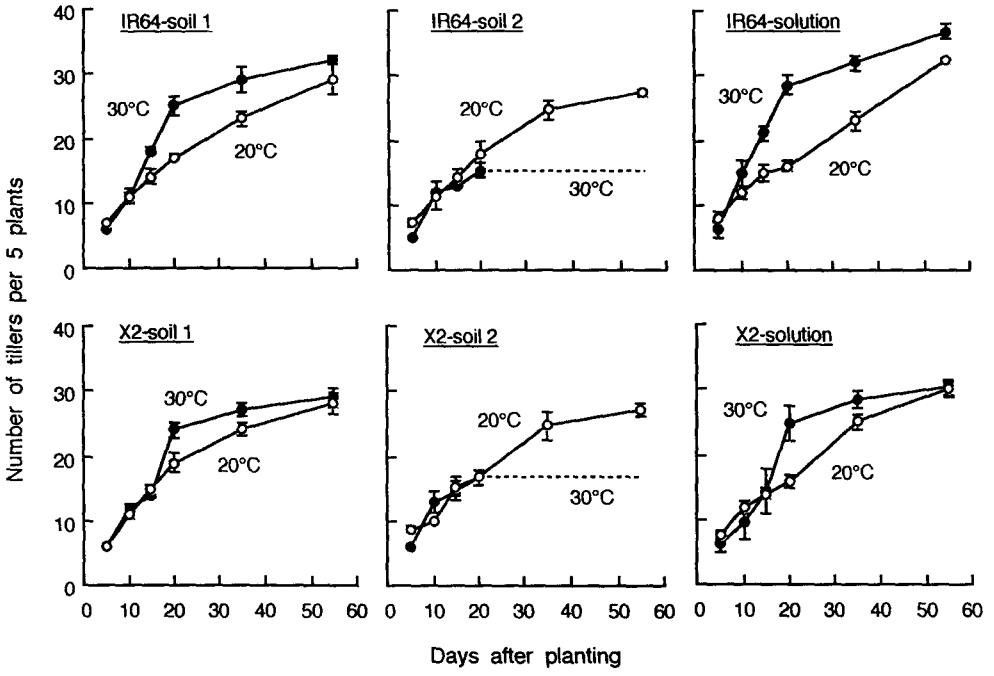

Fig. 1. Number of tillers as a function of time, for 2 rice varieties (IR64 and X2) grown in soil 1, soil 2, and nutrient solution, at 2 temperatures. Bars indicate standard deviations. Dashed lines for soil 2 indicate that the plants died after 20 days at 30° C.

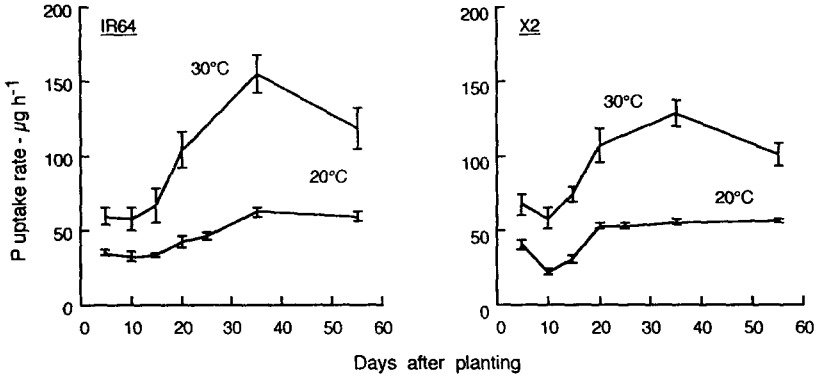

Fig. 2. Rate of P uptake for 2 rice varieties (IR64 and X2) grown in nutrient solution at 2 temperatures. Bars indicate standard deviations.

is limited by the Fe-concentration supplied with the nutrient solution, whereas in soils, the reduction of Fe(III)-oxihydroxides can provide plants with huge amounts of soluble Fe(II). However part of the Fe^{2+} ions can reoxidize in the rhizosphere, so that the coating of roots with Fe(III)-oxihydroxides results in spectacular Fe-concentrations as shown in Table 4. The highest Fe-content in roots is observed for soil 2 at 30°C: 7.6 (IR64) and 8.9 (X2) percent of root weight is due to Fe, which represents about 15 percent of Fe-oxihydroxides, if calculated as $Fe(OH)_3$. It is not surprising that rice plants did not survive for more than 3 weeks under these conditions. At 20°C, the Fe-content in roots from soil 2 amounts to about 4 percent, which is still high although plants obviously tolerate this level. Accumulation of Fe in roots is lower in soil 1 than in soil 2. This is related to the lower Fe-content in soil 1 as shown in Table 1. More puzzling is the fact that the roots from soil 1 accumulate 5 times less Fe at 30°C than at 20°C. The stimulation of plant metabolism upon a 10 degree increase may result in enhanced Fe-translocation from roots to shoots. Indeed considering Fe-concentration and dry matter of shoots, one can estimate that the Fe-quantity accumulated in

shoots is about 5 times greater at 30°C than at 20°C (more exactly 6 times for IR64 and 4.4 times for X2). The hypothesis of enhanced Fe-translocation is supported by the results from nutrient solution. The Fe-concentration in leaves is about 3 times higher at 30°C than at 20°C for solution cultures despite huge increase in dry matter production at 30°C.

Different values for critical Fe-levels in leaves have been reported in the literature and toxicity thresholds range from 250 to 800 mg kg^{-1} (Fageria et al., 1981; Genon et al., 1994; Ottow et al., 1993; Tanaka et al., 1966; Uexkull, 1976; Wells et al., 1993). These limits are obviously exceeded in soil 2, whereas the values observed in plants from soil 1 lie in the critical range. The Fe-concentrations in shoots from nutrient solution are also not far from critical values at 30°C. Consequently, our results obtained from soil and solution experiments suggest that excessive Fe-concentrations in rice leaves may result both from positive effect of rising temperature on Fe-uptake and from Fe-solubilization by reduction reactions in flooded soils.

Changes in soil conditions at 20 and 30° C

The data obtained from soil incubation can help to identify mechanisms independent of plant growth although plants themselves induce processes in soils that cannot be inferred in their absence. Therefore, results obtained, on soils with no plants only give partial information on the true environment of roots. Nevertheless, incubating soils can give a qualitative indication of the chemical changes that plants have to face when soil temperature is raised from 20 to 30°C.

The effect of temperature on reducing conditions in the two soils is illustrated in Figure 3a. At 20°C, the redox potential, E_h, decreases down to about 200 mV, while E_h values at 30°C are close to, or even lower than, 0 mV. As recalled in the introduction, reduction processes are promoted by soil microflora, which explains the great effect of temperature on E_h. At 20°C, the Fe(III)/Fe(II) system limits the drop in redox potential and the acceptance of electrons by Fe(III)-constituents can afford the needs of anaerobic bacteria for oxidizing organic matter. At 30°C, bacterial activity is stimulated and causes an increased rate of electron release, which creates conditions for sulphate reduction (Lefroy et al., 1993). In parallel to the E_h drop, pH increases rapidly after flooding because reduction reactions consume protons (Fig. 3b). This rise in pH reduces Al-toxicity hazard in acid soils. Indeed soluble Al drops to a negligible value at 30°C (Fig. 3c). The main difference between soil 1 and soil 2 with respect to E_h, pH, and soluble Al is that these properties rapidly reach stable values in soil 1, whereas progressive changes are observed in soil 2. As a plausible, although likely partial, hypothesis for explaining this difference, we can mention that soil 2 had a lower initial pH than soil 1, which could have delayed the development of bacteria after soil wetting. As pH increases, new bacterial populations progressively can appear. Soil 1 was less acidic, so that intense microbial activily could have been initiated only after a few days of flooding.

The reduction of soils normally involves the release of Fe^{2+} ions. However, Fe^{2+} solubility is lowered upon rising pH (Lindsay, 1988). Consequently, the Fe-concentration in soil solution is difficult to predict because, as E_h decreases, pH increases. The net result of these opposite influences on soluble Fe is shown in Figure 3d. At 20°C, the Fe-concentration in solution increases regularly for the entire flooded period, whereas at 30°C, soluble Fe tends to decrease with time after the first week in soil 1 and after 2-3 weeks in soil 2. This means that at 30°C the effect of raising pH rapidly dominates the effect of dropping E_h. The intense peak of soluble Fe noticed in soil 2 at 30°C certainly explains the death of rice plants in this soil after about 3 weeks. The higher Fe-concentrations in plants grown on soil 2 (Table 4) are also clearly related to the higher capacity of this soil to release soluble Fe.

As far as phosphorus is concerned, the capacity of soils to provide for plant needs depends not only upon concentrations in solution but also upon the rate at which this solution can be replenished from different P-pools. More than for any other nutrient, numerous soil testing methods have been proposed to account for P-availability (Abrams and Jarrell, 1992; Verma and Tripathi, 1982). The Onioani method based on H_2SO_4 extraction has been successfully used for assessing P-status of rice soils in Vietnam (Nguyen Vy and Tran Khai, 1978).

Figure 4 shows data obtained for the original soil samples without P addition. The soluble and available P-pools are higher in soil 1 than in soil 2, and although the same P rate was added to both soils at planting, the P concentrations in roots and shoots are also higher in soil 1 than in soil 2 at 20°C (Table 3). It means that the base level of soil phosphorus has not been totally rubbed out by fertilization. At 20°C, the water-soluble phosphorus presents variations with time that are close to what is observed for soluble Fe. At this tempera-

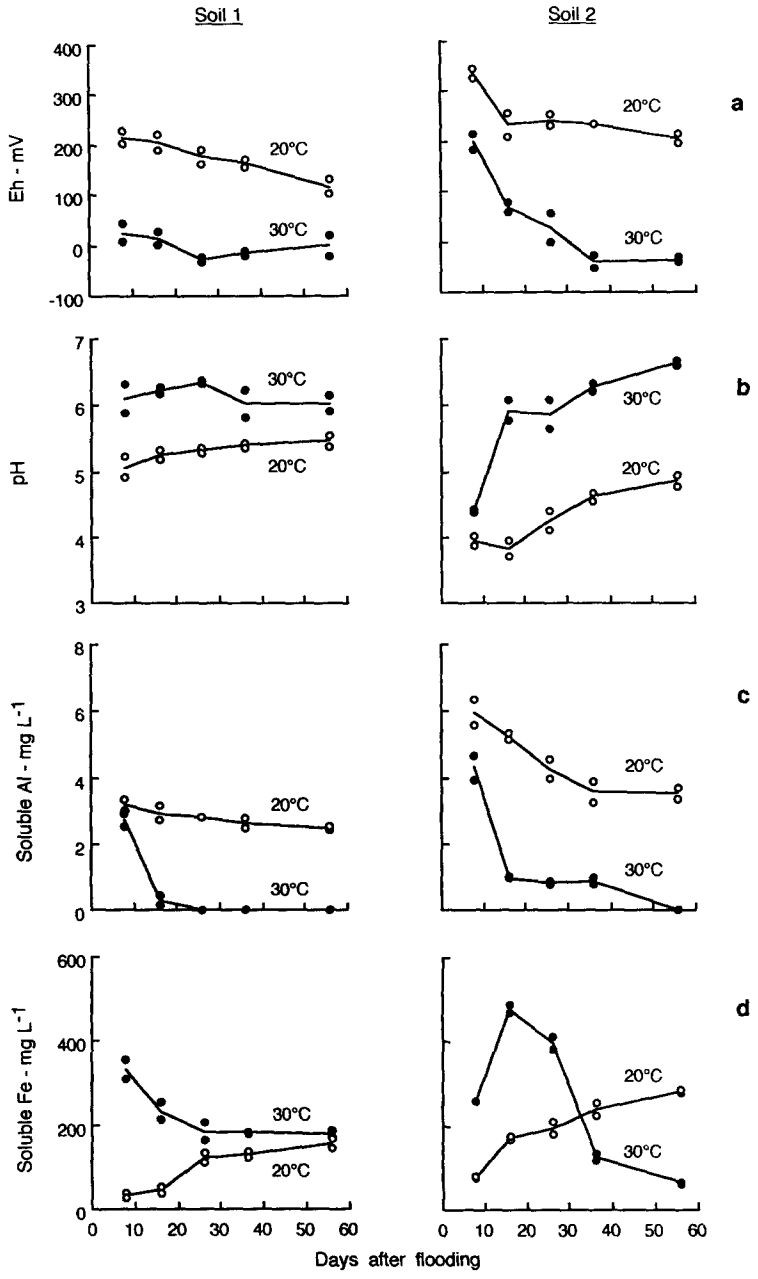

Fig. 3. Redox potential (Eh)(**a**), pH(**b**), water-soluble Al(**c**) and water-soluble Fe(**d**) in soil 1 (left) and soil 2 (right) as a function of flooding duration at 20 and 30°C.

ture, soluble P increases regularly in both soils after flooding. This is likely due to solubilization of Fe(III)-oxihydroxides upon reduction and concomitant release of adsorbed or occluded P, as well as to reduction of strengite $FePO_4.2H_2O$ to vivianite $Fe_3(PO_4)_2.8H_2$ (Patrick and Mahapatra, 1968; Sanyal and De Datta, 1991; Willett, 1986, 1991). At 30°C, soluble P continuously decreases to negligible values in soil 2, while it reachs a maximum and thereafter decreases in soil 1. As shown above, the reducing conditions are much more severe at 30°C than at 20°C; and the higher pH values observed at 30°C induce reprecipitation of Fe-oxihydroxides, likely as amorphous ferrosoferric hydroxides, which have high P-fixation capacity (Vo

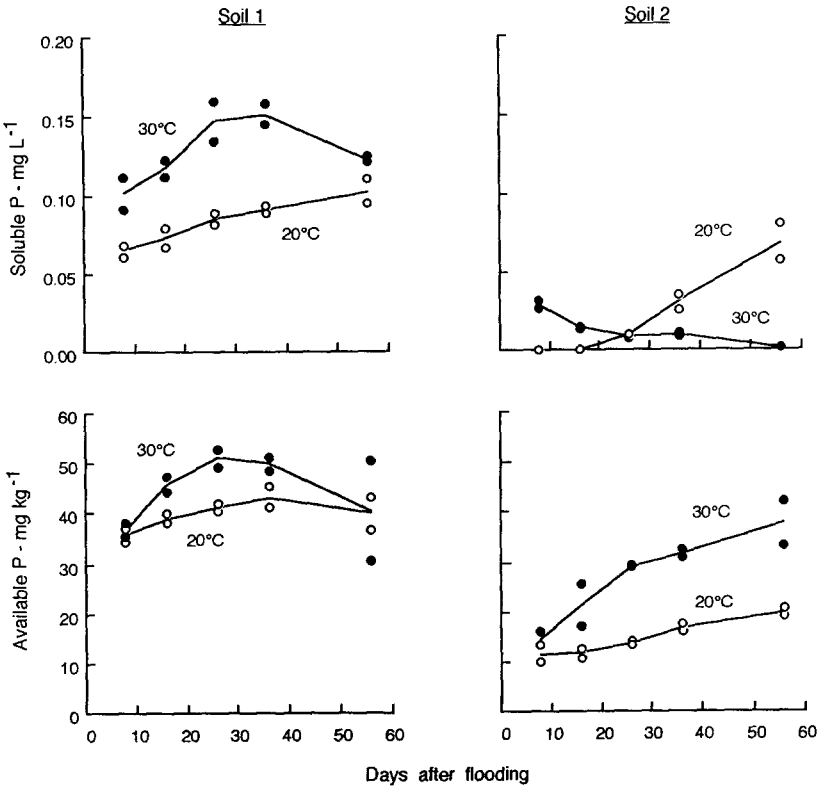

Fig. 4. Water-soluble and "available" P in soil 1 (left) and soil 2 (right) as a function of flooding duration, at 20 and 30° C.

Dinh Quang and Dufey, 1995). This process is more effective in soil 2 than in soil 1, because of difference in Fe-content. For the same reason, the available P-pool clearly increases in soil 2, because it includes phosphate adsorbed on amorphous Fe-oxihydroxides, whereas few variations are observed in soil 1, where new formation of highly reactive Fe-oxihydroxides is clearly less intense.

Conclusions

The net effect of temperature on rice growth in flooded acid soils is a combination of various factors, which according to this study, can be summarized as follows:

1. Tillering retardation at low temperature is similar in nutrient solutions and in soils.

2. The positive effect of temperature on plant biomass is more pronounced in nutrient solution than in soils.

3. Raising temperature in flooded acid soils results in more severe reducing conditions, which can be either beneficial or detrimental to rice growth.

Negative effects include:

a. Redox potential drops to lower values at 30° C than at 20° C, which can result in the release of more detrimental compounds upon rising temperature;

b. The intense release of soluble Fe^{2+} in the days or weeks following flooding can induce severe Fe-toxicity for plants. Also rising temperature stimulates Fe-translocation from roots to shoots, as noticed in nutrient solution.

Positive effects include:

a. High pH values are reached after flooding at 30° C, which eliminates Al-toxicity hazards in acid soils,

b. Available phosphate increases with temperature in the most acid soil.

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