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Salinity Effects on Tiller and Leaf Appearance and on Development Rate of Individual Leaf Positions in Irrigated Rice

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Bonn, den 19. März 2004

Keshav Prasad Dahal

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Abstract

Salinity is a major constraint to irrigated rice production in river deltas and former floodplains, particularly in semi-arid and arid climates. Salinity affects one-fifth of the irrigated land worldwide. Two rice cultivars differing in their response to salinity stress were studied for dry matter accumulation, tiller number, leaf number, leaf area, leaf development rate, total leaf duration, relative duration of leaf developmental phases, photosynthesis and sodium and potassium concentrations and distribution in different organs of rice. Plants were hydroponically grown in Yoshida solution in the greenhouse of the Institute of Plant Nutrition in Bonn, Germany from February to May 2003. Plants were subjected to salinity 3 weeks after transplanting. Treatments consisted combination of two salinity (0 and 60 mmol NaCl) and three potassium concentrations (20, 40 and 80 ppm). The total tiller number and their distribution into primary, secondary and tertiary tillers were recorded every three days. Individual leaves from all tillers were evaluated every three days for appearance, extension, senescence and death. Four samplings were conducted in approximately 10 day intervals starting 31 days after transplanting. At each sampling day photosynthesis was measured separately on all physiologically active leaf positions of the main culm. The total number of live leaves and their position on the respective tiller were recorded. The plants were destructively sampled and separated into roots, dead leaves and live leaves and the leaf blade area (position wise) was measured. All samples were oven dried at 70 ^{0}C and weighed for dry matter followed determination of sodium and potassium concentrations by flame photometrically. Salinity reduced dry matter accumulation, tiller number, leaf number and leaf area in all salinity treatments in both varieties. Higher potassium concentrations in the culture solution generally resulted in larger leaf blade areas and higher tiller numbers as compared to lower potassium concentrations and had a mitigating effect on salt induced reductions. The leaf initiation rate was faster under salinity in both genotypes. Salinity increased the senescence rate of individual leaves and significantly shortened the physiologically active period. The sodium and potassium concentrations were generally higher in leaf sheaths. In leaf blades, the sodium concentration generally increased with descending leaf positions, whereas, potassium concentration decreased. The leaf blade to leaf sheath ratio of sodium and potassium concentrations and dry matter accumulation increased over time. No difference was observed in root cation concentrations between rice genotypes, the sodium concentration being generally much higher than the potassium concentration

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3 Introduction

1.1 Background

Rice is the most important food crop for more than half the world's population living in the tropics and sub-tropics. Irrigated and rainfed lowland rice are the most important production systems. Salinity affects one-fifth of the irrigated land worldwide (Koyama et al., 2001). Reducing sodium and chloride uptake into rice while maintaining potassium uptake are characteristics that would aid growth under saline conditions. Salinity is a major constraint to irrigated rice production in river deltas and former floodplains, particularly in semi-arid and arid climates. Irrigated rice is well suited to controlling and even decreasing soil salinity (Wopereis et al., 1998), but rice is a salt susceptible crop and yield losses due to salinity can be substantial (Asch et al., 1997a).

1.2 Tillering pattern and tiller number in rice

Tillers are the branches that develop from the leaf axils at each unelongated node of the main shoot or from other tillers during vegetative growth. When the fifth leaf on the main culm emerges, the first leaf of the tiller comes from the axil of the second leaf on the main culm. Similarly, when the sixth leaf on the main culm emerges, the first leaf of the tiller comes from the axil of the third leaf on that culm. Thus, the n^{th} leaf on the main culm and the first leaf of the tiller that emerges from the axil of the $(n-3)^{th}$ leaf grow synchronously. This rule applies not only to the main culm but to all the tillers (Yoshida, 1981).

On the main culm, the coleoptile and the first leaf normally do not produce tillers; tillering usually starts from the second leaf. On each tiller the prophyll develops before the first leaf emerges. The prophyll, corresponding to the coleoptile on the main culm, lacks a blade and is similar to the sheath in structure. The prophyll, which is white, is enclosed within the leaf sheath on the main culm and is not visible. It is the first leaf that can be seen when a new tiller comes out. Tillers may or may not emerge from the prophyll node (Yoshida, 1981). When the 13^{th} leaf on the main culm emerges, and if tillers come from all except the prophyll nodes, there should be a total of 40 tillers: 9 primary tillers, 21 secondary tillers and 10 tertiary tillers .

The number of tillers determines the number of panicles and therefore the rice grain yield.

According to Grattan, (2002) salt stressed rice plants are smaller, have fewer tillers, less root mass and shorter, thinner, chlorotic leaves compared to non-salinized plants. Consequently salinity has a profound influence on plant and tiller density (number per area). At an EC of 3dS m^{-1}, the rice yield and tiller densities are reduced by one-third and 40 % respectively compared to non-salinized controls (EC = 0.4 dS/m). Increasing salinity linearly reduces the number of tillers per plant (Grattan et al., 2002).

1.3 Leaf development in rice

The age of a rice plant can be expressed as calendar days after germination or seeding. This is only convenient for a particular variety in a particular environment. In order to compare different varieties in different environments, it is better to assess the physiological age by following the leaf appearance and numbering the leaves on the main culm of a rice plant. A typical rice leaf consists of sheath, blade, ligula and auricles. Most early-to medium-maturing varieties develop about 10-18 leaves up to maturity on the main culm (Yoshida, 1981). In photoperiod-insensitive varieties the number of leaves is constant under most conditions. Leaf length increases as the leaf number advances. In most varieties, the second or third leaf from the last is the largest. The last leaf is called the flag leaf. Leaves elongate quickly after emergence, start functioning and complete their elongation (Yoshida, 1981).
The life span of individual leaves after elongation differs widely among leaves and varieties. Upper leaves have longer life spans than lower ones with the flag leaf having the longest life span. At any given growth stage, the rice plant is composed of leaves of physiologically different stages and this suggests that these leaves differ in their contribution to the growth and water use of the whole plant. From panicle initiation to around heading, the rice plant usually has five leaves on the main culm that are physiologically active. The topmost leaf, which is still elongating, is low in photosynthetic activity and depends on the lower leaves for assimilates. The second, third and fourth fully developed leaves from the top have the highest photosynthetic activity among the leaves and supply assimilates to the upper leaves, the stems and the roots. Those photosynthetically active leaves are considered most important for the growth of the whole plant and are called physiologically active centers (Tanaka, 1961). Any leaf serves as a physiologically active center in some point in the plant's life cycle. Since new leaves develop upward as lower leaves die, the physiologically active centers move upward as growth advances. Thus the physiologically active centers may

be the seventh leaf during the tillering stage, move to the 9^{th} and 10^{th} leaves after panicle primordia initiation, and to the 10^{th} and 11^{th} leaves during milky stages of grain filling.

1.4 Salinity, potassium and rice

Salinity is defined as the presence of excessive concentrations of soluble salts in the soil solution. The salts are chlorides and/or sulphates of calcium, magnesium, sodium and potassium. Among those chloride is usually predominant (Brady, 2000). The sources of these salts are the weathering of rocks and minerals, rainfall, ground water and irrigation (Brady, 2000). Salinity occurs in two distinctly different regions: (1) Costal regions where salinity is induced by inundation with seawater containing high amounts of soluble salts and (2) arid and semi-arid regions where evaporation is considerably higher than total precipitation and as a consequence, water movement is upward (capillary movement of water) resulting in the accumulation of salts in the root zone. Salinity is expressed in terms of electrical conductivity (EC), which is measured in decisiemens per meter (dSm^{-1}) or millisiemens per centimeter ($mScm^{-1}$).

It has been shown that salinity has a detrimental effect on rice yield at or above 3.0 dSm^{-1} (Grattan, 2002). Salinity has a negative impact on a number of yield components including stand establishment, tillers, panicles, spikelets per plant, floret sterility, individual grain size, and even delayed heading (Grattan, 2002). The emergence and early seedling growth stages as well as the three-leaf to panicle initiation stages are most sensitive to salinity.

Gas exchange and water use efficiency are key factors for proper growth of rice. These factors vary with the variety, leaf development stages, salinity and relative air humidity (Asch et al., 1998). The effects of salinity on photosynthesis vary among rice cultivars (Asch et al., 2000). For example, salt stress drastically reduced CO_2 exchange rates (CER) in cotton (Plaut and Federmann, 1991) and barley leaves (Rawson, 1986), but had little effect on the leaf CER in wheat (Rawson, 1986), and *Diplachne fusca* (Gorham, 1987; Myers et al., 1990). According to Asch et al. (2000) the CER was generally higher for the first (topmost) than for the second leaf in rice.

Salinity resistance in rice has been a focus in plant breeding for a long time but so far very few salt resistant cultivars have been released (Flowers & Yeo, 1995). This is partly due to the complexity of the phenomenon: rice susceptibility to salinity changes with developmental

stage. Furthermore, the severity of salinity effects is influenced by climatic conditions, such as air humidity (Asch et al., 1995, 1997a, 1997b).

Potassium is an essential element for all living organisms. Not only is the average plant tissue content of K higher than that of other cations, but it is also the most important cation in many physiological and biochemical processes. Adequate potassium (K) nutrition is critical for maximizing rice grain yields. Since K is very mobile within the rice plant, older leaves are depleted of the K needed by younger leaves (David et al., 2002).

The K/Na ratio of the three youngest leaves of a rice plant under salinity measured 60 days after sowing provides a tool to estimate the grain yield loss caused by salinity (Asch et al., 2000). The relative amount of sodium in a young leaf is a better parameter to assess salt stress than the absolute amount of sodium present in that leaf (Asch et al., 2000). Different cultivars may absorb the same high amount of sodium into the leaves, but can differ strongly in the potassium status of the leaves and the yield loss (Asch et al., 1997a). There is a significant correlation between the K/Na ratio of leaves under salinity at different vegetative stages and grain yield relative to fresh water controls (Asch et al., 2000). Reducing sodium and chloride uptake into rice while maintaining potassium uptake would aid growth under saline conditions (Koyama et al., 2001).

Generally the highest sodium and potassium concentrations in rice are found in the stems, which consist mainly of leaf sheaths (Asch et al., 1997b). The leaf sodium concentration depends on the retention capacity for sodium in the leaf sheaths. In leaf blades, generally the sodium concentration increased with descending leaf positions whereas, potassium concentration decreased. In roots, the sodium concentration is generally much higher than the potassium concentration. Varietal differences in cation concentrations were most pronounced in the leaf blades where the rice genotype IR4630 had the lowest sodium and the highest potassium concentrations whereas, the reverse was true for IR31785 (Asch et al., 1997b). No difference was observed in root cation concentrations between rice genotypes.

1.5 Research Questions

Many researches have been carried out so far regarding the effects of salinity on rice plants as mentioned above. The following research questions, which are still unsolved, have been explored in the present study:

I. What is the tillering pattern in salinity stressed rice cultivars? Does salinity affect the total tiller number and the distribution into primary, secondary and tertiary tillers?
II. What are the effects of salinity on leaf appearance pattern, total leaf duration, relative duration of leaf developmental phases and total leaf number in rice cultivars?
III. How long are the leaves physiologically active? Does salinity enhance the senescence rate of different leaf numbers and positions?
IV. Does the physiological potential of individual leaves differ according to their position?
V. What are the effects of different potassium concentrations on salinity induced changes (as mentioned above)?

1.6 Hypothesis and Objectives

Based on the above research questions the following hypotheses are the basis for the objectives and experiments:

I. Salinity reduces the tiller number and leaf number as compared to non-stressed plants.
II. The leaf appearance rate of rice plants subjected to salt stress is likely to be faster than in non-stressed plants.
III. Salinity increases the senescence rate and significantly shortens the physiologically active period of individual leaves.
IV. The physiological potential of individual leaves differs with change in their positions.
V. Higher potassium concentration in the culture solution increases the leaf area and tiller number and has a mitigating effect on salt-induced changes during the entire life span of individual leaves.

Based on these hypotheses the following objectives have been formulated for research for the Master of Science thesis:

II. To assess the effects of salinity on total tiller number, leaf number and total leaf area.
III. To evaluate the effects of salinity on leaf appearance rate and total leaf duration.
IV. To develop a rating system for leaf senescence and leaf rolling scores to describe the developmental stages of any individual leaf independent of the treatment
V. To describe the photosynthetic activities of individual leaves during their different stages of development on the main culm of a rice plant.
VI. To evaluate the effects of different potassium concentrations on salinity induced changes.

In order to achieve these objectives a series of experiments were carried out in the green house and laboratory in Bonn.

2 Materials and Methods

2.1 Experimental site, plant materials and initial growth conditions

2.1.1 Experimental site time frame and climatic conditions

The experiment was carried out in the greenhouse of the Institute of Plant Nutrition, University of Bonn, Germany from February to May, 2003. The daily temperature and relative air humidity from March to end of the experiment, in the greenhouse, were recorded every 30 minutes with a tiny tag. The weekly maximum and minimum temperature and minimum and mean relative air humidity in the greenhouse are shown in **Table 1**.

Table 1. Weekly maximum and minimum temperature and minimum and mean relative air humidity in the greenhouse during the experimental period (19th March 2003 to 11th May 2003).

Weeks	Temperature ^{0}C		Relative Humidity %	
	Maximum	Minimum	Minimum	Mean
March 19-March 25	28	20	16	23
March 26- March 31	34	20	18	32
April 1- April 6	34	20	15	24
April 7- April 13	35	20	8	19
April 13- April 19	35	21	14	25
April 20-April 26	32	21	24	38
April 27- May 3	30	21	29	40
May 4- May 11	31	21	27	41

2.1.2 Plant materials

The rice seeds used in the study were obtained from the West African Rice Development Association (WARDA) 01 B.P. 4029, Abidjan 01, Côte d'lvoire. Two varieties differing in their response to salinity stress, were used in the experiment:

a) IR4630-22-2, medium duration, salt tolerant, selected by WARDA specifically for the Senegal River delta, origin Philippines.

b) IR31785-58-1-2-3-3, short duration, well adapted to Sahelian climatic conditions, WARDA's salt sensitivity check, origin Philippines.

2.1.3 Seed germination

Seeds were soaked, pre-germinated in Petri dishes for 48 hours using tap water and sown in plastic tray (seedbed) containing sand and tap water (**Figure 1**). The seeds were sown in mid February. The seedlings were kept 21 days in the seedbed and then transplanted in culture pots and grown hydroponically.

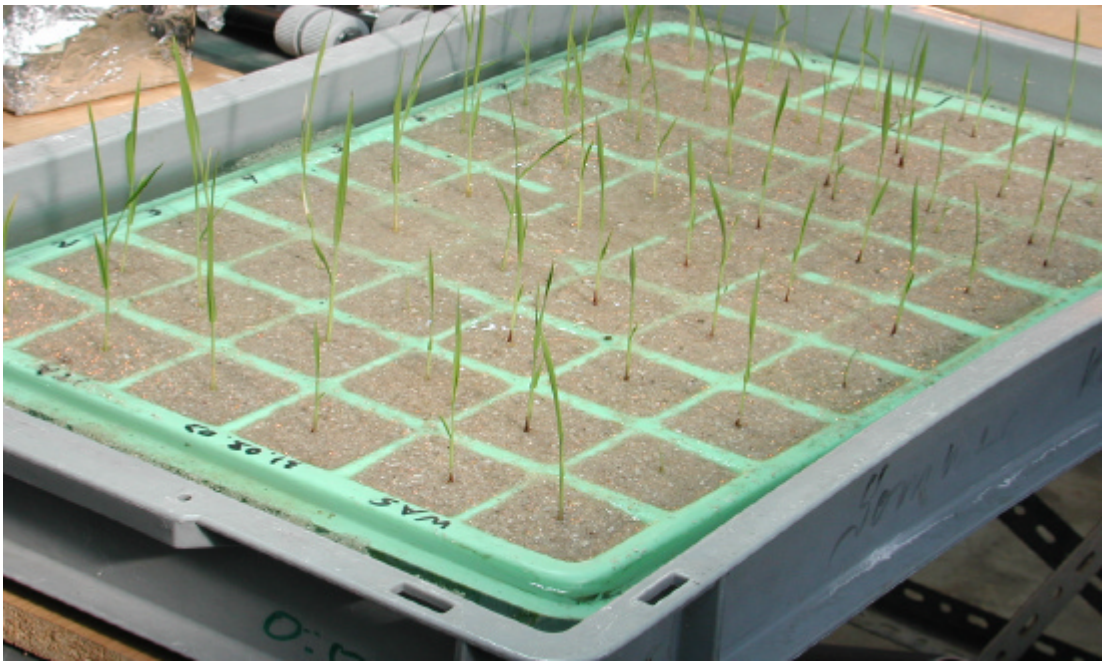

Figure 1. Rice seedlings in tray with sands.

2.1.4 Plant growth

After 3 weeks in the seedbed, rice seedlings were transplanted into plastic pots (1.2 L each) and grown hydroponically for 60 days (**Figure 2**). At transplanting, the seedlings were supported with foam just above the root to hold transplants in the pots. The pots were covered with aluminium foil to prevent algal growth. All pots, each containing 1 L Yoshida solution (**Table 2** and **Table 3**), were connected and the nutrient solution was circulated daily for about 1.5 hours directly from a buffer tank containing 60L of respective treatment solution. The overflow was prevented by a drainage pipe in the system.The transplanted plants were grown for 3 weeks in 50 % Yoshida solution. Then, they were allowed to grow

for a further 3 weeks in 80 % Yoshida solution followed by 100 % Yoshida solution from 6 weeks onward. The pH was adjusted every 3 days to a value of 5 in the buffer tank using 1 N HCl or 1 M NaOH. The solution was changed every 10 days.

The pH was adjusted. After 3 weeks of transplanting, the plants were subjected to different treatments and replications. The saline treatments were made by applying sodium chloride (NaCl) at a level of 60 mmol corresponding to an EC of 6 dSm^{-1}.

Table 2. Preparation of stock solution.

Element	Reagent	Preparation

		(g/10 litres of distilled water)
N	NH_4NO_3	914
P	$NaH_2PO_4 .2H_2O$	403
K	K_2SO_4	714
Ca	$CaCl_2$	886
Mg	$MgSO_4 .7H_2O$	3240
Mn	$MnCl_2 .4H_2O$	15
Mo	$(NH_4)_6 MO_7O_{24} . 4 H_2O$	0.74
B	H_3BO_3	9.34
Zn	$ZnSO_4 .7H_2O$	0.35
Cu	$CuSO_4 .5H_2O$	0.31
Fe	$FeCl_3 .6H_2O$	77

Table 3. Composition of culture solution.

Element	Milliliters of stock solution per liter of culture solution	Concentration of element nutrient solution (ppm)
N	1.25	40
P	1.25	10
K	1.25	40
Ca	1.25	40
Mg	1.25	40
Mn	Micronutrients 1.25	0.5
Mo		0.05
B		0.2
Zn		0.01
Cu		0.01
Fe		2

For every 30 litres of nutrient solution, the required quantity of each of the above stock solutions (37.5 mL from each) were first added to 5 litres of distilled water and stirred thoroughly to prevent coagulation. The nutrient solution was then made up to final volume.

2.2 Experimental Set-up

Starting 3 weeks after transplanting, the plants were subjected to different treatments and replications. The saline treatments were made by applying sodium chloride (NaCl) at a level of 60 mmol. The treatments were consisted of two levels of salinity (0 and 60 mmol NaCl) in combination with three potassium concentrations (20, 40 and 80 ppm) resulting in the following six treatments.

1. Yoshida Solution with 40 ppm K
2. Yoshida Solution with 40 ppm K and 60 mmol NaCl
3. Yoshida Solution with 20 ppm K
4. Yoshida Solution with 20 ppm K and 60 mmol NaCl.
5. Yoshida Solution with 80 ppm K
6. Yoshida Solution with 80 ppm K and 60 mmol NaCl

Each treatment was replicated three times. Each replication was composed of 1 hill/ variety/treatment and sampling date. The experimental set up is summarized in **Figure 3**.

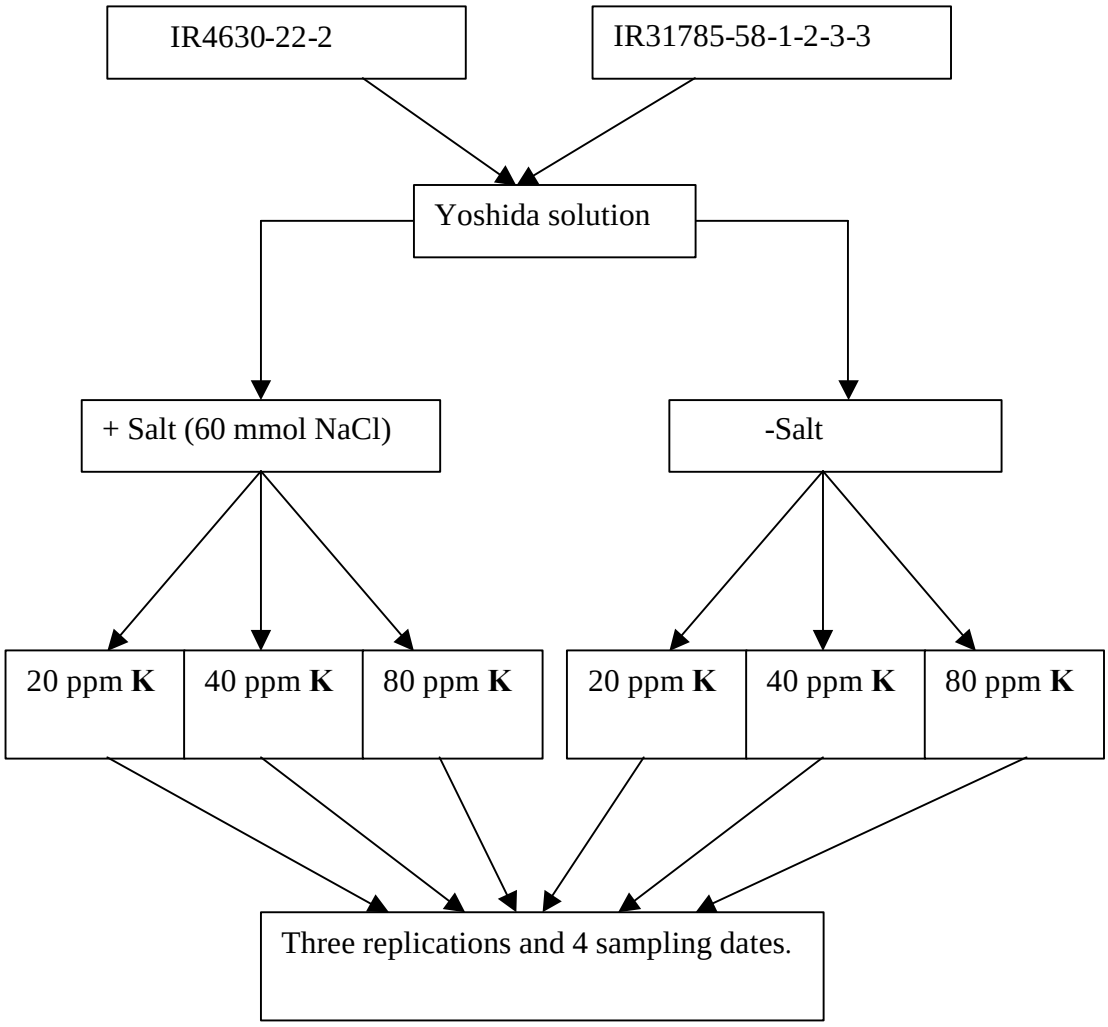

Figure 3. Summary of experimental set up (2 cultivars, 6 treatments, 4 sampling dates and 3 replications = 144 pots).

2.3 Leaf / tiller nomenclature

The leaves on the main culm, primary tillers, secondary tillers and tertiary tillers were marked with threads of different colors representing different leaf numbers (**Figure 4**). The leaves were counted from the buttom to identify their number and from the top to identify their positions on the main culm of a rice plant. The n^{th} leaf number on the main culm was described as MC_n, on the primary tiller as PT_n, on the secondary tiller as ST_n and on the tertiary tiller as TT_n where MC, PT, ST and TT stand for main culm, primary tiller, secondary

tiller and tertiary tiller, respectively. Thus MC_1 refers to the leaf number 1 on the main culm, PT_1; the first leaf number 1 on the primary tiller; ST_1; the leaf number 1 on the secondary tiller and TT_1; the leaf number 1 on the tertiary tiller, respectively.

Figure 4. Tying the leaves using threads of different colours represeting different leaf numbers.

2.4 Sampling and measurements

The tiller types and their origin were identified and recorded. The total tiller number with their distribution into primary, secondary and tertiary tillers was recorded every three days throughout the experimental period.

Individual leaves from all tillers were evaluated every three days for appearance, extension (length, rolling scores) senescence and death. The length of the leaves was measured with a measuring tape to estimate their elongation. Leaf rolling was scored to estimate the leaves developmental stages and was described by percentage of total leaf surface and number as follows:

Percent rolled	**Number given**
0 – 15 %	0
15 – 30 %	1
30-45 %	3
45- 60 %	5
60-80 %	7 and
80-100 %	9

Additionally, leaf rolling was described as upper and lower. Before the full development of leaves or the onset of senescence, the leaf rolling scores were described as upper and vice versa. Leaf senescence was estimated on the basis of necrotic leaf area as percentage of the total leaf surface and grouped as 5% senescence (onset), 25 % senescence, 50 % senescence, 75% senescence and 100% (dead).

Four samplings were conducted in approximately 10 day intervals starting 31 days after transplanting (10 days after treatment application). At each sampling, three replicates from both varieties and treatments were harvested. On each sampling day photosynthesis was measured separately on all physiologically active leaf positions of the main culm (**Figure 5**). The total number of live leaves and their position on the respective tiller were recorded. Afterwards, the plants were destructively sampled and separated into roots, dead and live leaves. The live leaves were then further separated into leaf blade and leaf sheath. Leaf blade area (position wise) was measured with a LiCor 3600 leaf area meter. The samples (roots, dead leaves, leaf blades and leaf sheaths from different leaf positions) were oven dried at 70 ^{0}C. Dry weight was measured using an electronic precision balance and sodium and potassium content of all samples were determined in the laboratory by flame photometer.

Photosynthesis measurement

Photosynthesis was measured with an ADC-LCA4 photosynthesis system (**Figure 5**) using the small leaf chamber on all physiologically active leaves according to their position on the main culm (youngest not yet fully developead leaf, first/second/third and fourth youngest fully developed leaf).

Figure 5. Measuring photosynthesis using an ADC-LCA4 photosynthesis system.

3

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2.5 Sodium and Potassium analysis

All samples (roots, dead leaves, leaf blades and leaf sheaths) were analyzed for sodium and potassium concentrations using a flame photometer.

Samples were cut into small pieces as fine as possible using a knife. About 0.05-0.1 grams of 2- 4 representative sub- samples of each sample were put into centrifuge tubes (10ml volume, 16mm diameter). The tubes were filled with 7 ml of distilled water using a dispensette (0-10ml) and covered with aluminum foil (Figure 6).

The tubes were then autoclaved for 1 hour at 120 ^{0}C followed by 2 hours of cooling. The autoclaved samples were centrifuged at 4000 rpm (g) for 20 minutes at 20^{0}C.
After centrifuging the samples, extracts were filtered into 100ml volumetric flasks. The volumetric flasks were made up to volume with distilled water. The samples were analyzed using a flame photometer.

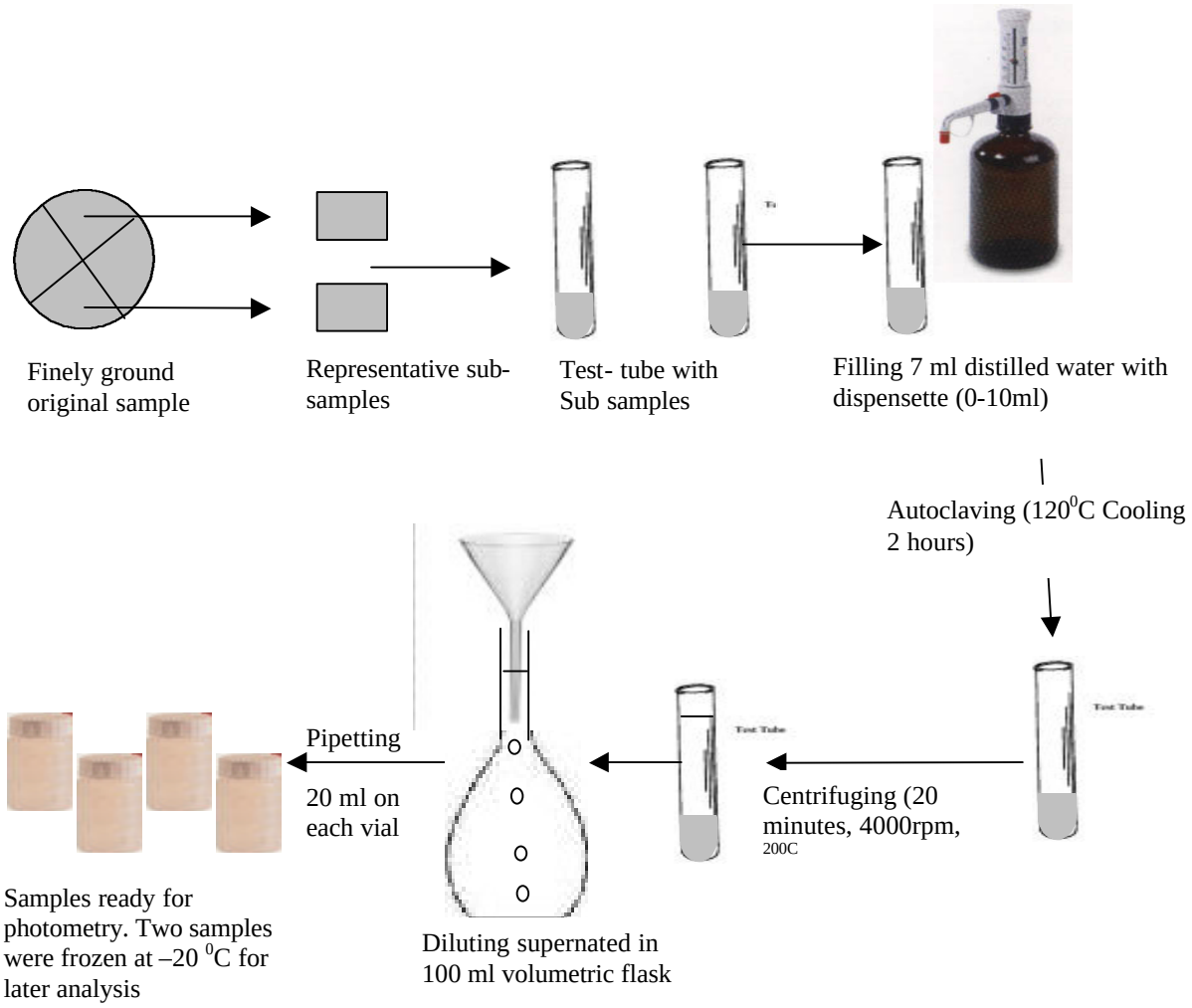

Figure 6. Laboratory procedures to analyse sodium and potassium concentrations.

2.6 Data Analysis.

Results were subjected to analysis of variance (ANOVA). Mean comparisons were analysed by Duncans Multiple Range Test (DMRT) and/or least significance difference (LSD) at 5% level of significance using SPSS 11.0 for Windows. Graphic presentations were done by Microsoft Excel, Sigma Plot 2001 and Origin version 6.1.

3 Results

This chapter illustrates the results of experiments that were conducted under controlled conditions at the University of Bonn, Institute of Plant Nutrition to assess salinity effects on morphological characteristics as well as leaf development and sodium and potassium uptake and distribution in two different rice genotypes.

The results of this study consist of the following sub sections: salinity influence on dry matter accumulation, salinity and potassium influence on tiller number and tillering pattern, salinity and potassium influence on leaf number and leaf area, salinity influence on leaf development and total leaf duration, distribution of sodium and potassium within the plant and distribution of sodium and potassium within the leaves.

3.1 Influence of salinity on dry matter accumulation

The dry matter accumulation in roots, dead leaves and green leaves (separately for each leaf position) was measured at 4 sampling days in ten day intervals starting 31 days after transplanting (see materials and methods 2.2 and 2.4).

The effect of salinity on total dry matter production is illustrated in **Figure 7.** Salinity always reduced total dry matter accumulation ($p < 0.05$). However, the degree of reduction was different in the two genotypes used, with IR31785 being more adversely affected than IR4630.Under saline conditions, root dry matter was more strongly reduced than shoot dry matter. In both varieties, the reduction in dry matter accumulation under salinity as compared to control treatments increased over time.

At 31 days after transplanting (10 days after treatment application), the reductions in shoot dry matter and root dry matter accumulation were 45% and 48% in salt stressed IR31785 as compared to non stressed plants, whereas, at 61 days after transplanting a reduction of 51% and 73% was observed. IR4630 responded less strongly than IR31785 for salinity induced dry matter reduction. The reductions in shoot dry matter and root dry matter accumulation at 31 days after transplanting were 2% and 30% in salt stressed IR4630 as compared to non-stressed plants, culminating in 28% and 58% at 61 days after transplanting, respectively.

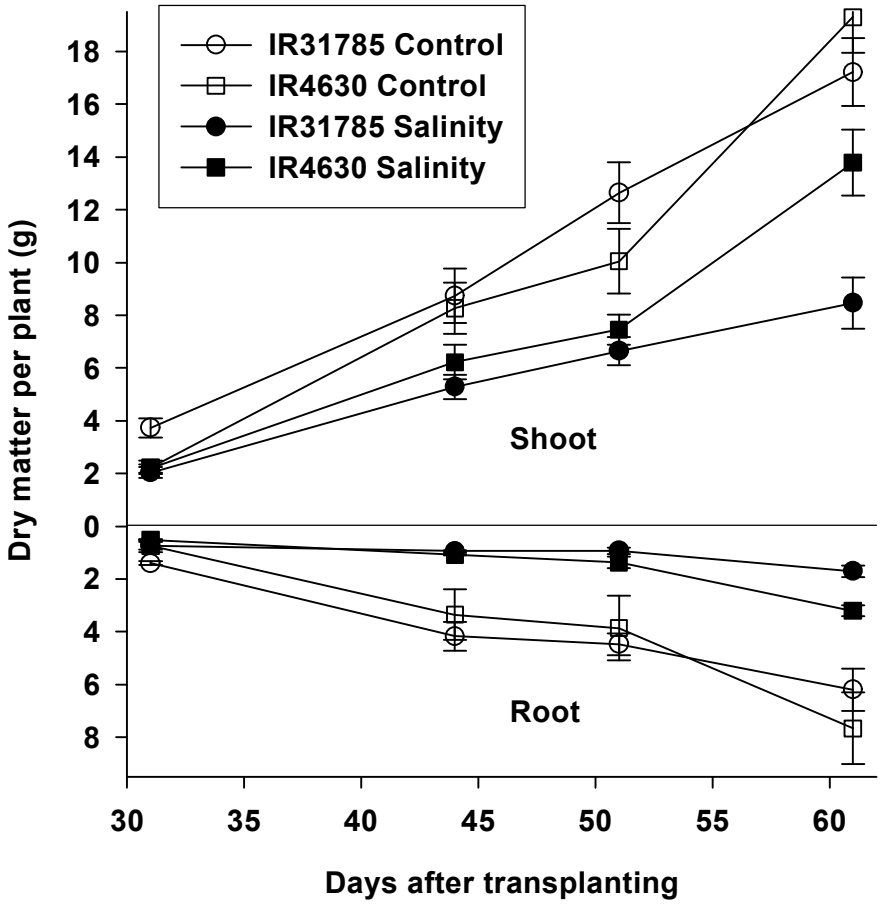

Figure 7. Salinity effect on total dry matter accumulation in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = Standard error of means (n=3).

The salinity influence on dry matter accumulation was further differentited by plant organs

Under saline conditions, significant ($p < 0.05$) reduction in dry matter accumulation was observed in leaf sheaths, leaf blades and roots in both varieties (**Figure 8** and **Figure 9**). The opposite was found in dead leaves, where the total dry matter increased in salt stressed as compared to non-stressed plants over time in both genotypes (**Figure 8**). Salinity increased the dry matter accumulation of dead leaves by 143% and 59% in IR31785 and IR4630 respectively at 61 days after transplanting. The degree of salinity induced dry matter reduction in leaf position zero (youngest not yet fully developed leaf) vary over time.

Dry matter accumulation was significantly higher ($p < 0.05$) in leaf sheaths as compared to leaf blades in both varieties under non-stressed conditions whereas under stressed conditions the share of leaf blades was higher than that of leaf sheaths (**Figure 9**). Under salinity, dry matter accumulation in leaf blades and leaf sheaths decreased over time in both genotypes (**Figure 9**). Reduction was significantly ($p < 0.05$) higher in leaf sheaths as compared to leaf blades in both genotypes at all stages. As compared to IR4630, IR31785 showed a stronger salt-induced reduction in dry matter accumulation in both leaf blades and leaf sheaths. The dry matter reduction of leaf sheaths was generally higher in younger leaves whereas leaf blades were more strongly affected in older leaves. In IR31785, the reduction in dry matter accumulation of leaf blades ranged from 36% to 48%, and of leaf sheaths from 62% to 83% at 61 days after transplanting. At the same time, dry matter of leaf blades was reduced from 18% to 32%, and of leaf sheaths from 42% to 59%.

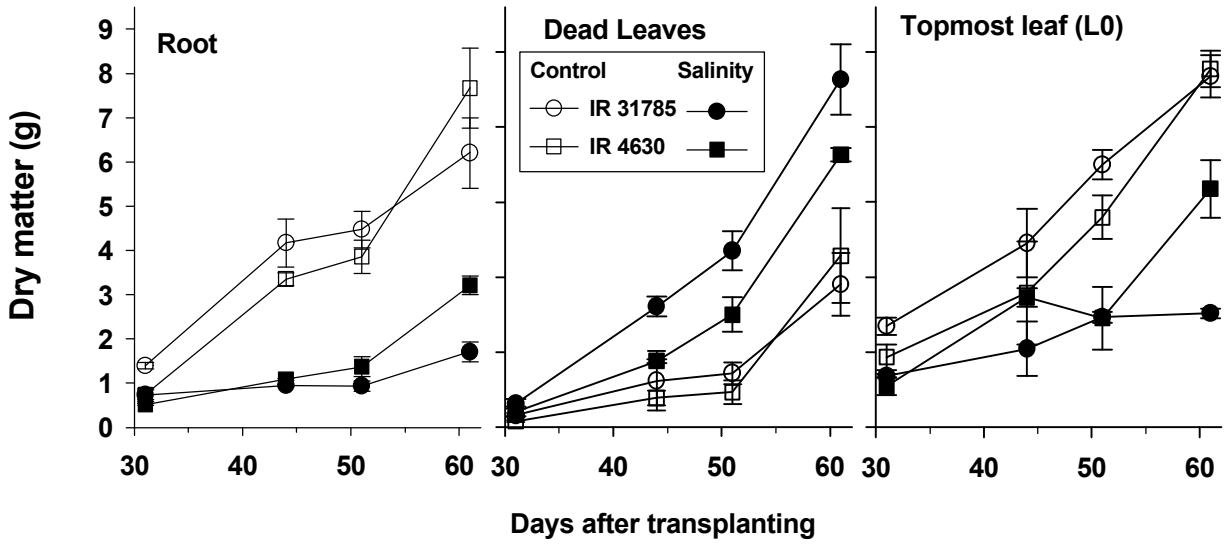

Figure 8. Salinity effect on dry matter accumulation in three different plant organs in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3).

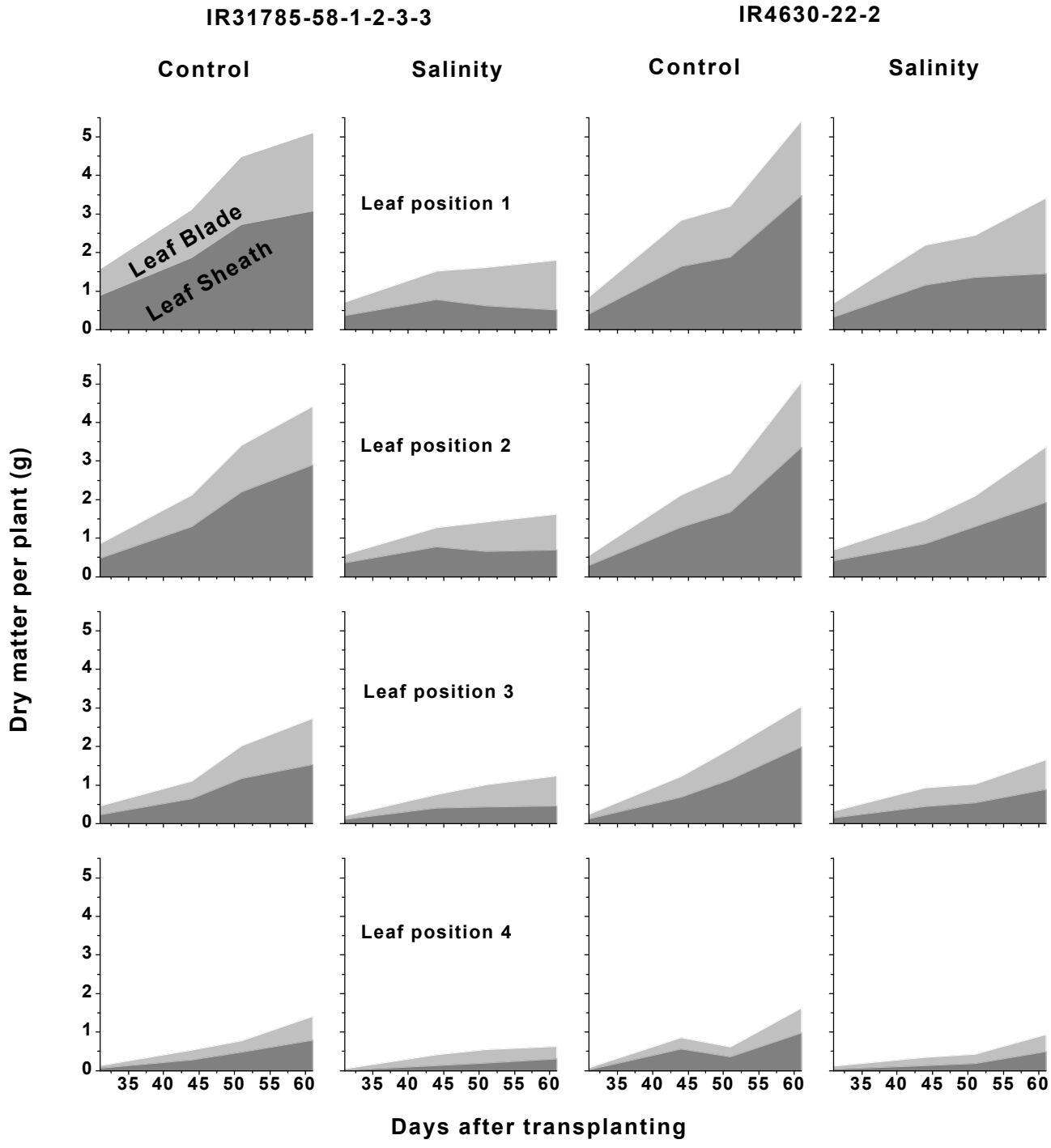

Figure 9. Dry matter accumulation in leaf blades and leaf sheaths over time in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Leaf positions were counted from the top, leaf position 1= youngest fully developed leaf, leaf position 2 = 2nd youngest fully developed leaf, leaf position 3 = 3rd youngest fully developed leaf, leaf position 4 = 4th youngest fully developed leaf.

3.2 Salinity and potassium influence on tiller number and tillering pattern

The primary, secondary and tertiary tillers were observed throughout the experiment in three day intervals for their origin and number and dates were recorded (see materials & methods 2.2 and 2.4).

Salinity reduced the total tiller number in all treatments at all stages (**Figure 10)**. Reduction was observed mostly in tertiary tillers, whereas primary and secondary tillers were less affected (**Figure 11**) IR31785 exhibited stronger reductions than IR4630. Higher potassium concentrations slightly increased the total tiller number in both genotypes under saline and non-saline conditions. The effect of potassium on the total tiller number was higher under saline as compared to non- saline conditions in IR31785, whereas little variation was found in IR4630.

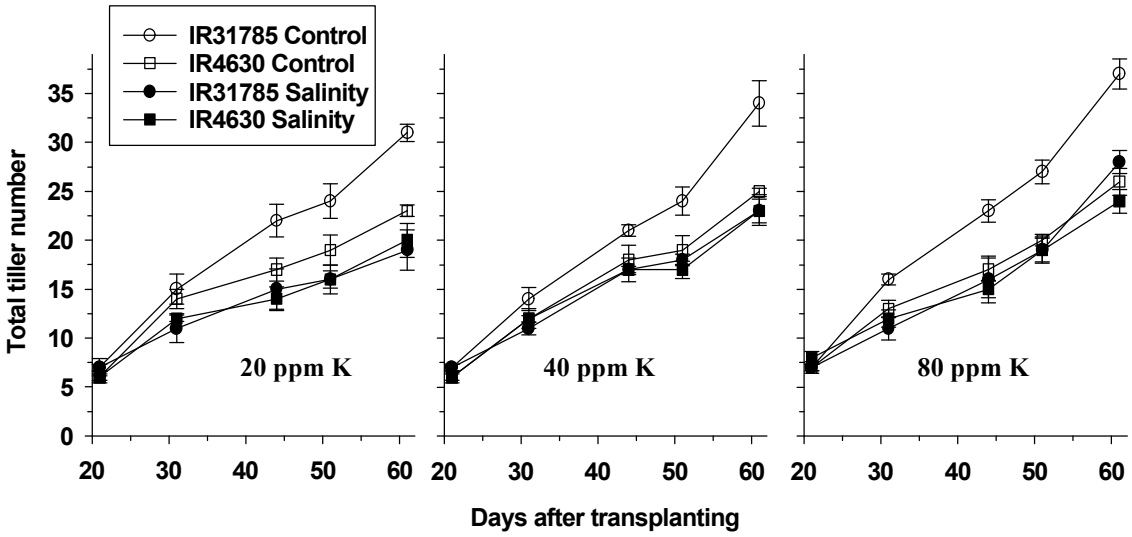

Figure 10. Total tiller numbers at different growth stages of two rice genotypes grown under control and saline conditions combined with three different potassium concentrations. Control = 0 mmol Nacl, saline = 60 mmol Nacl. Stress was applied 21 days after transplanting. Error bars = Standard error of means (n = 3).

Additional potassium mitigated the effects of salinity on the tiller number in both genotypes (**Figure 12**). When plants were grown for 61 days with 20 ppm potassium, salinity reduced the total tiller number by 40% and 14% in IR31785 and IR4630 respectively (**Figure 12**) whereas, at 40 ppm potassium, total tiller numbers were reduced by 33% and 8%, and at 80 ppm potassium by 25% and 8%, respectively. Under non-saline conditions, the total tiller

number was increased by 10% and 9% in IR31785 and IR4630, respectively, when the potassium concentration was doubled from 20 ppm to 40 ppm. The increase was 21% and 14%, respectively, when the potassium concentration was increased 4-fold to 80 ppm.

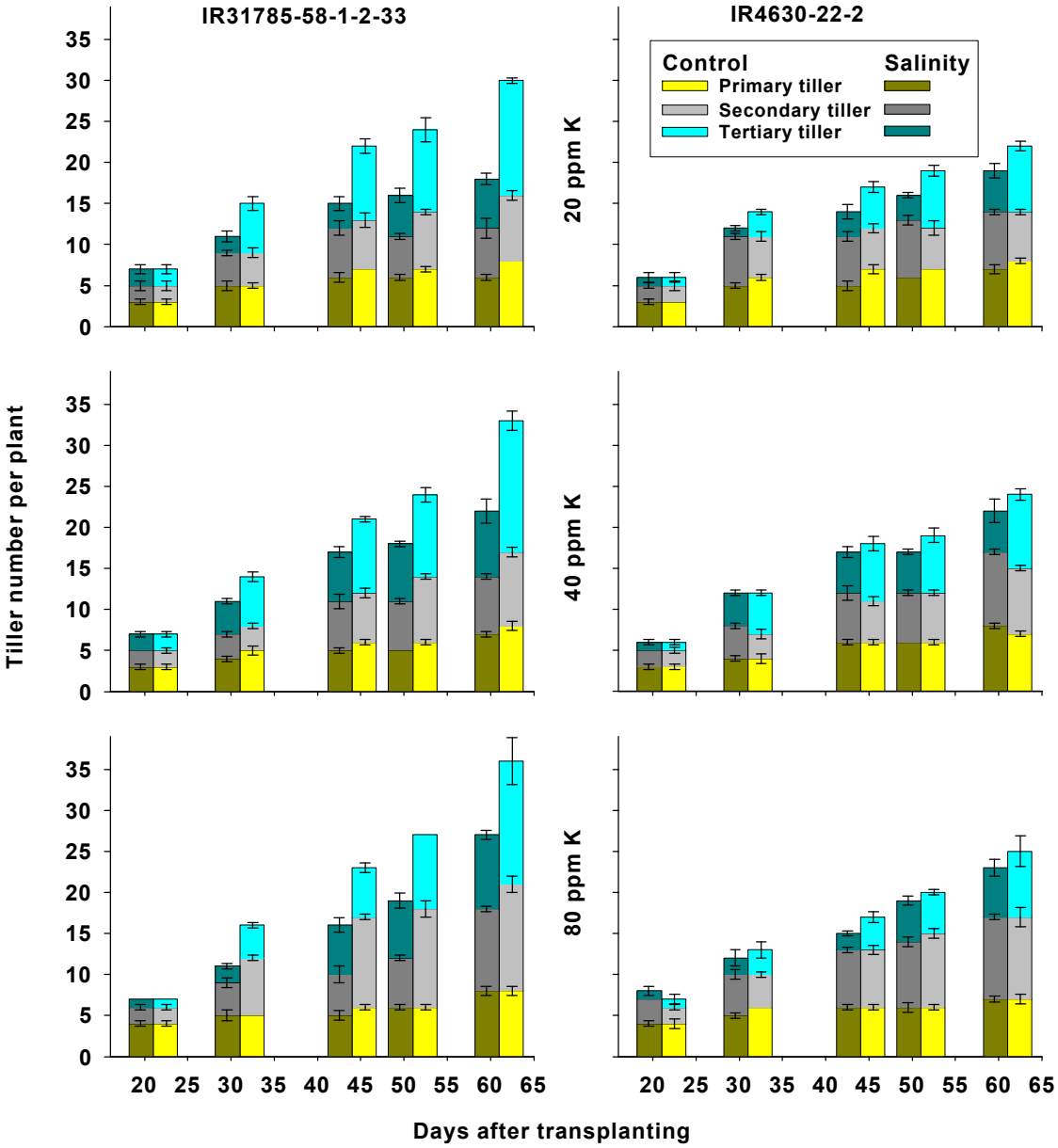

Figure 11. Share of primary, secondary and tertiary tillers in two rice varieties grown under saline and non-saline conditions combined with three different potassium concentrations. Control = 0mmol NaCl, saline = 60 mmol NaCl. Error bars = Standard error of means (n = 3).

In the saline treatment, the total tiller number was increased by 22% and 15% in IR31785 and IR4630, respectively, when the potassium concentration was doubled from 20 ppm to 40 ppm. The increase was 50% and 21% when the potassium concentration was increased 4-fold to 80 ppm (**Figure 12**).

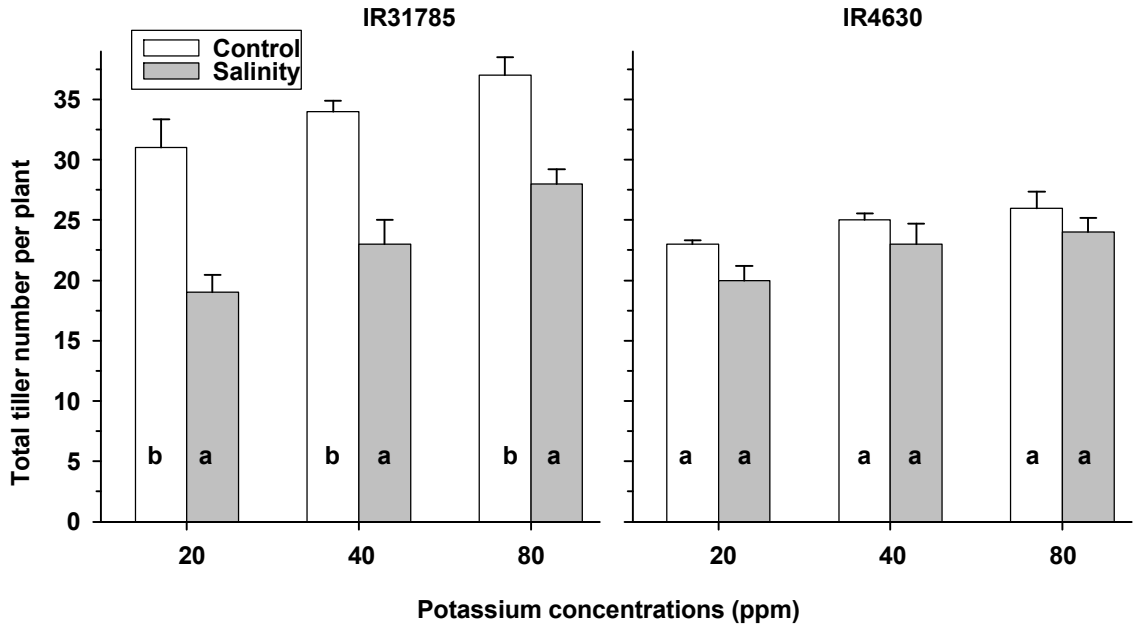

Figure 12. Total tiller numbers at 61 days after transplanting in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and salinity = 60 mmol NaCl. Error bars = Standard error of means (n = 3). a and b are homogenous groups according to Duncan Multiple Range Test (DMRT, $p < 0.05$).

In summary, the total tiller number was more severely reduced by salt stress in IR31785 as compared to IR4630. Additional potassium had a positive influence on the tiller number in both genotypes under saline and non-saline conditions, the effect being greater in IR31785. The mitigating effect of potassium was more pronounced under non-saline conditions in IR31785.

3.3 Salinity and potassium influence on leaf number and leaf area

Total leaf numbers and total leaf area by position were determined in ten-day intervals starting 31 days after transplanting (see materials and methods 2.2 and 2.4).

The effect of salinity and influence of potassium on salinity-induced changes in leaf number and leaf area are illustrated in **Figure 13** and **Figure 15** respectively. Salinity always reduced the total leaf number and total leaf area in all treatments. The reduction was generally more in IR31785 ($p < 0.05$) as compared to IR4630. Higher potassium concentration increased the total leaf number and total leaf area in both varieties under saline and non-saline conditions. However, the positive effect of potassium on total leaf number and leaf area was relatively higher in saline conditions as compared to non-saline conditions. Furthermore, salinity induced reductions were lowest in plants grown with 80 ppm, intermediate with 40 ppm and highest with 20 ppm potassium in both varieties. Higher potassium concentrations mitigated the effect of saline conditions on leaf number and leaf area in both varieties. The reduction in total leaf area **(Figure 15)** was mostly associated with a reduction in total leaf number (**Figure 13),** which was further associated with the reduction in total tiller number (**Figure 10**) and premature death of leaves (**Figure 18** and **Figure 19**).

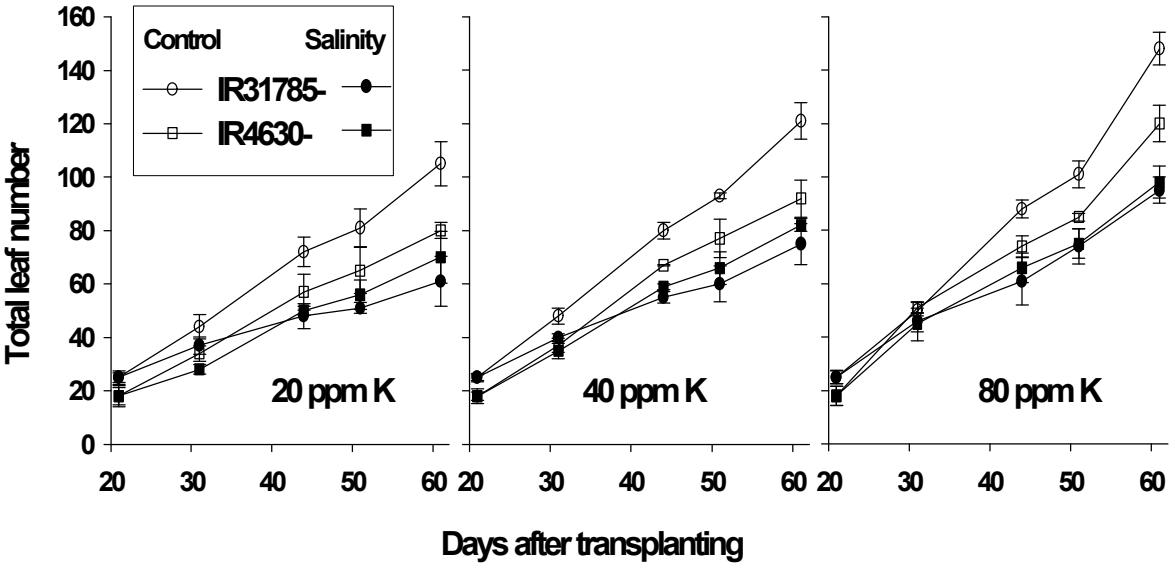

Figure 13. Total leaf number at different growth stages of two rice genotypes grown under control and saline conditions combined with three different potassium concentrations. Treatments were started 21 days after transplanting. Control = 0 mmol NaCl and salinity = 60 m mol NaCl. Error bars = standard error of means (n = 3).

Figure 13 shows the total leaf number reduction due to salinity stress at different potassium concentrations. At 61 days after transplanting, salinity reduced the total leaf number) by 42% and 14% in IR31785 and IR 4630, respectively, at 20 ppm potassium concentration, whereas

at 40 ppm potassium the total leaf number was reduced by 38% and 12%, and at 80 ppm potassium concentration by 36% and 10%, respectively (**Figure 14**).

In the saline treatments the total leaf number was increased by 24% and 17% in IR31785 and IR4630 respectively, when the potassium concentration was doubled from 20 ppm to 40 ppm. The increase was 57% and 38% respectively, when the potassium concentration aws 4-fold to 80 ppm (**Figure 14**). Under control conditions, the total leaf number was increased by 15% and 14% in IR31785 and IR4630, respectively, at 40 ppm compared to 20 ppm potassium concentration and by 41% and 36% at 80 ppm potassium concentration compared to 20 ppm potassium (**Figure 14**).

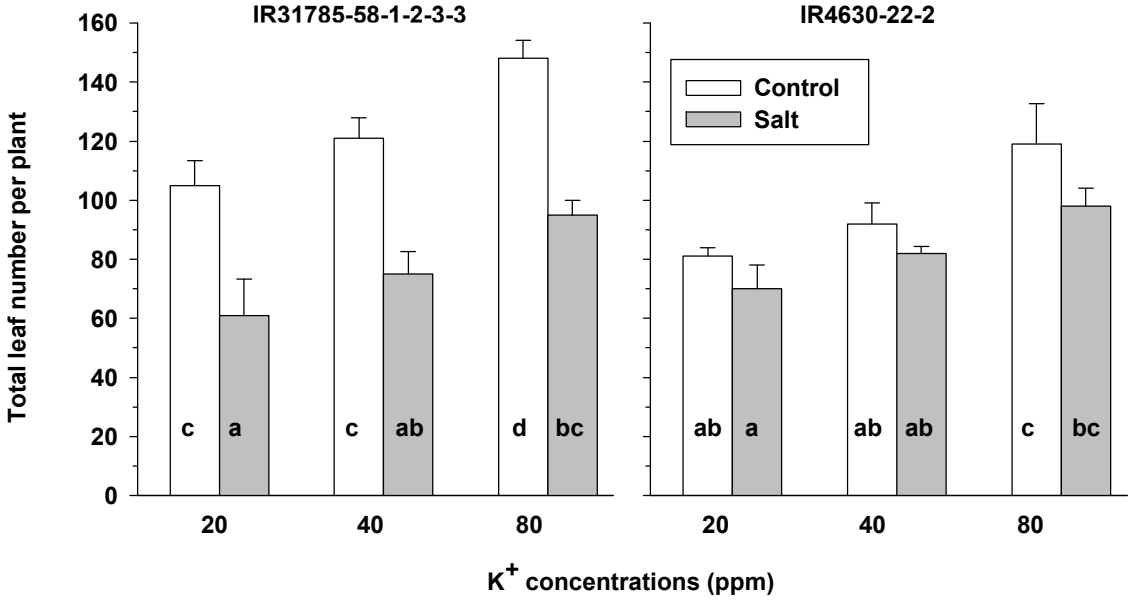

Figure 14. Total leaf number at 61 days after transplanting in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3). a, b, c and d are homogenous groups according to Duncan Multiple Range Test (DMRT, $p < 0.05$).

Salinity always reduced the total leaf area over time in both genotypes (**Figure 15**). The reduction in leaf area occurred in all leaf positions. Varietal differences in salinity induced changes in leaf area were most prominent at 20 ppm potassium concentration in which the total leaf area was reduced by 49% and 18% in IR31785 and IR4630, whereas at 40 ppm potassium concentration, the reduction was 44% and 16 %, and at 80 ppm 39% and 11% respectively, at 61 days after transplanting (**Figure 16**). Potassium influence was highly

positive under saline treatments; the total leaf area at 61 days after transplanting was increased by 20% and 8% in IR31785 and IR4630 when the concentration was doubled from 20 ppm to 40 ppm. The increase was 42% and 27 % when the potassium concentration was 4-fold to 80 ppm (**Figure 16**). Under control conditions, the increase in total leaf area due to additional potassium was 9% and 5% for IR31785 and IR4630 at 40 ppm and 19% and 17% at 80 ppm compared to 20 ppm potassium concentration (**Figure 16**).

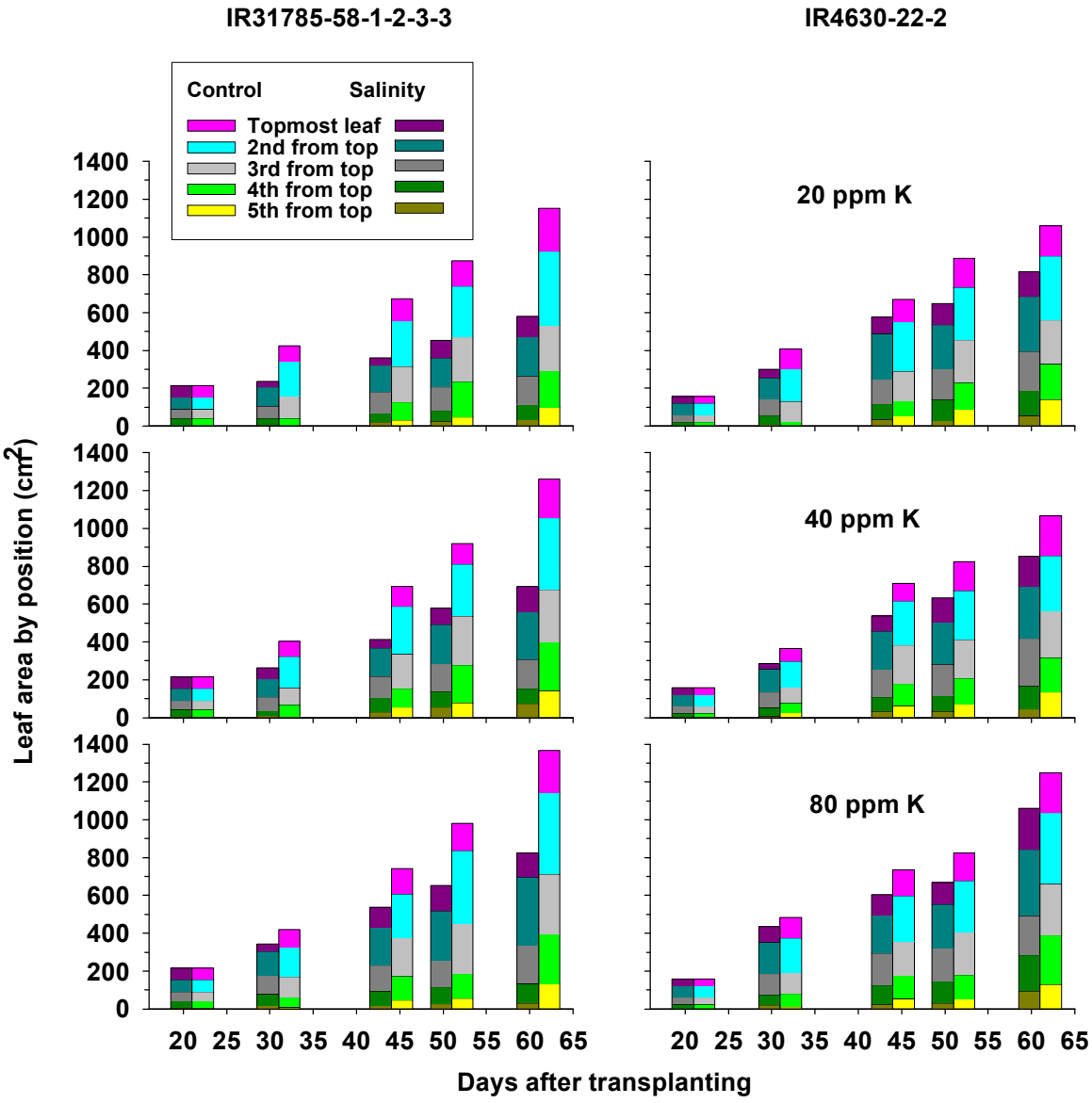

Figure 15. Leaf area of five different leaf positions at different growth stages in two rice genotypes grown under control and saline conditions combined with three different potassium concentrations. Topmost leaf = youngest leaf, not yet fully developed. Control = 0 mmol NaCl and saline = 60 mmol NaCl.

In summary, the total leaf number and leaf area was more severely reduced by salt stress in IR31785 as compared to IR4630. IR31785 responded better to potassium nutrition under non- saline conditions. Additional potassium had a positive influence in both genotypes under salt stress, the effect being greater in IR31785.

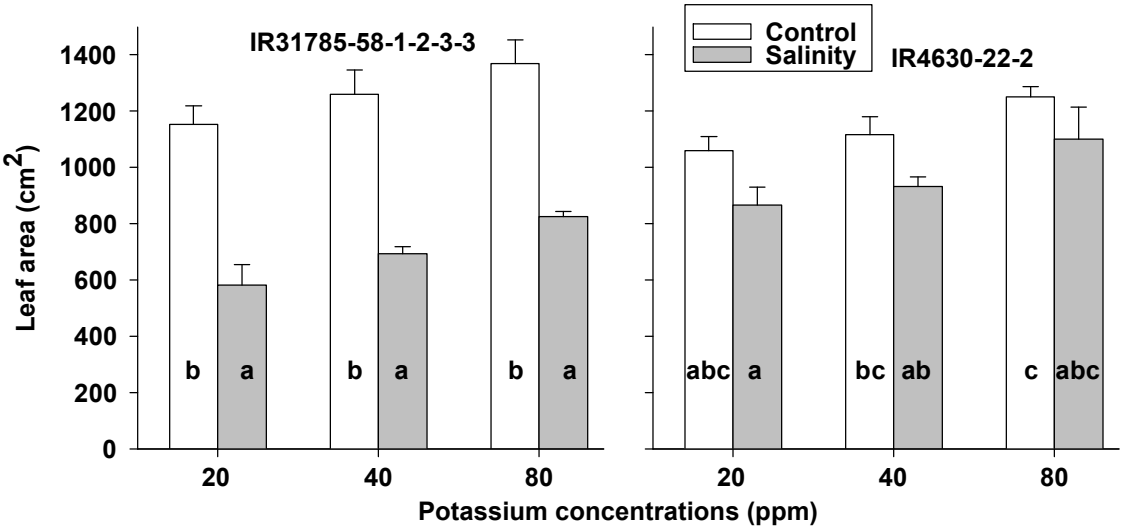

Figure 16. Total leaf area at 61 days after transplanting in two rice genotypes grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3). a, b and c are homogenous groups according to DMRT ($p > 0.05$).

3.4 Salinity influence on leaf development

All leaves from the main culm and all tillers were evaluated throughout the experiment for their life cycle in three day intervals (see materials and methods 2.2 and 2.4). Leaf appearance, leaf elongation, leaf rolling scores, leaf senescence and finally leaf death dates were recorded.

5 Leaf duration and relative duration of leaf development phases

The leaf development phases were generalized to fit in a subjective scale ranging from -1 to 1 (**Figure 17**). In this system, –1 stands for leaf initiation, -0.5 for leaf appearance, -0.2 for

60% leaf elongation, which was considered the start of a leaf's physiologically active period, 0 for full leaf extension, 0.5 for onset of senescence, 0.7 for 50% senescence which was considered the end of leaf's physiologically active period and finally 1 for 100% senescence (death). Here, all the developmental stages were directly observed in plants except the leaf initiation, which was simulated on the basis of other developmental stages. From -1 to -0.2 the leaf was described as a positive sink, -0.2 to 0.7 as a source (physiologically active) period and from 0.7 to 1 as a negative sink. **Figure 17** represents the total leaf duration and the relative duration of developmental phases of leaf number 1 on the main culm of IR4630 under non-saline conditions. The same system was applied for all succeeding leaves of IR4630 and IR31785 under both saline and non-saline conditions.

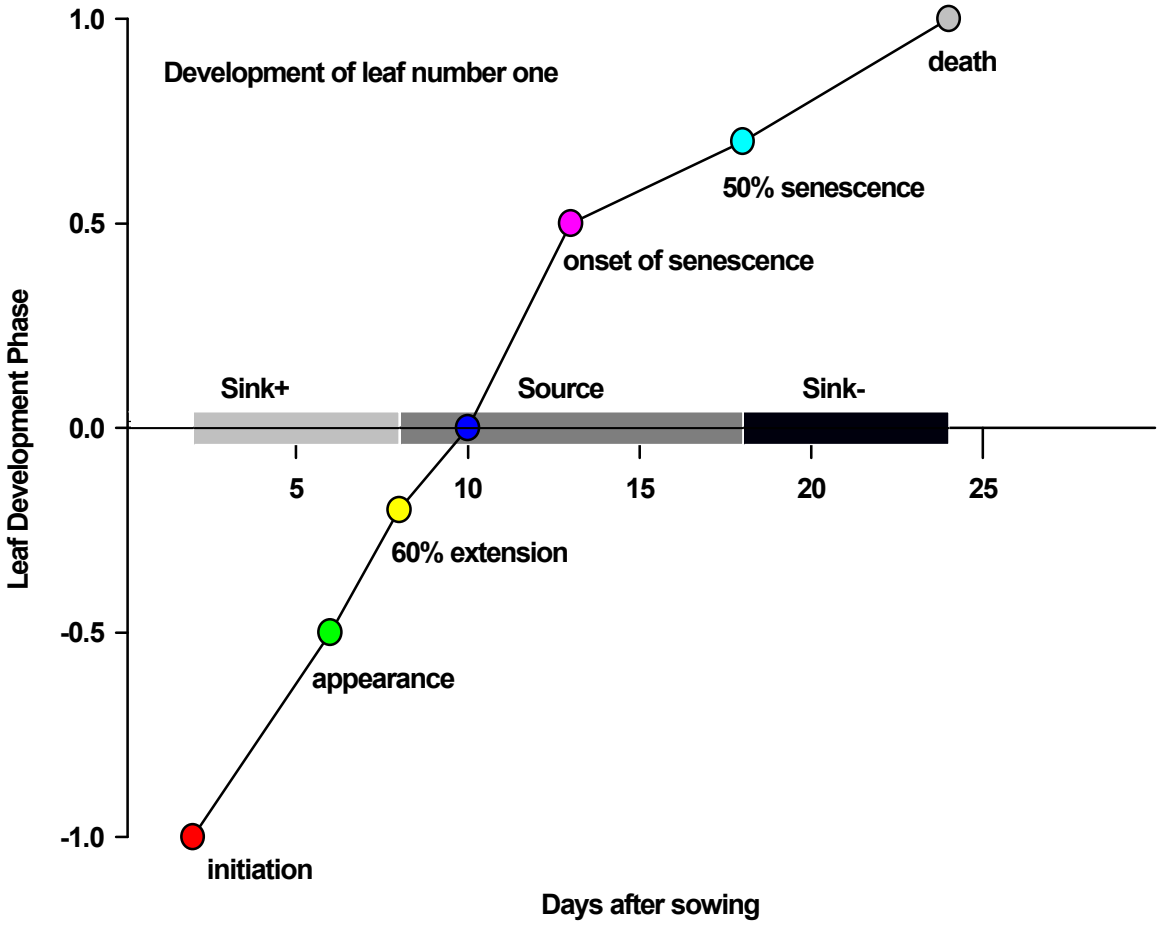

Figure 17. Development of leaf number 1 (by appearance) on the main culm of IR4630 grown under non-saline conditions.

Salinity reduced the total leaf duration in both genotypes. This reduction was more pronounced in IR31785 ($p > 0.05$) as compared to IR4630 (**Figure 18** and **Figure 19)**.

The reduction in total leaf duration was found to be a consequence of the reduction in the leaf's physiologically active period, early senescence and premature death. The reduction in the leaf's physiologically active period varied from 4 to 12 days in salt stressed IR31785 whereas in IR4630, the difference ranged from 1 to 4 days. In **Figure 20,** the different leaf phases (positive sink, source, negative sink) are shown as percentage of the total leaf duration. The percentage of the physiologically active period increased slightly in early and late leaves of salt stressed IR31785, whereas in IR4630 this percentage varied with leaf number (**Figure 20**). Under control conditions, the percentage of the physiologically active period of the leaves ranged from 45% to 55% in both genotypes. Under saline conditions, this ratio ranged from 41% to 55% in IR4630, and from 45% to 61% in IR31785.

6 Salinity and leaf initiation rate

Salinity increased the leaf initiation rate in both genotypes (**Figure 21**). However, genotypes differed in their response to salinity induced changes in leaf initiation. In IR4630, salinity did not affect leaf initiation up to leaf number 3. Starting with leaf number 4, leaf initiation was accelerated: leaf number 4 appeared 2 days earlier and leaf number 13 appeared 9 days earlier under saline than under control conditions. In contrast to this, leaf initiation in IR31785 was affected earlier, starting with leaf number 2, which appeared 1 day earlier, to leaf number 13, which appeared 14 days earlier in IR31785 in saline conditions as compared to non-saline conditions. Leaf initiation was generally earlier in IR4630 as compared to IR31785 under control conditions and the opposite was true under salinity (**Figure 21**). The difference in leaf initiation rate between saline and non-saline treatments increased with each Succeeding leaf in both varieties.

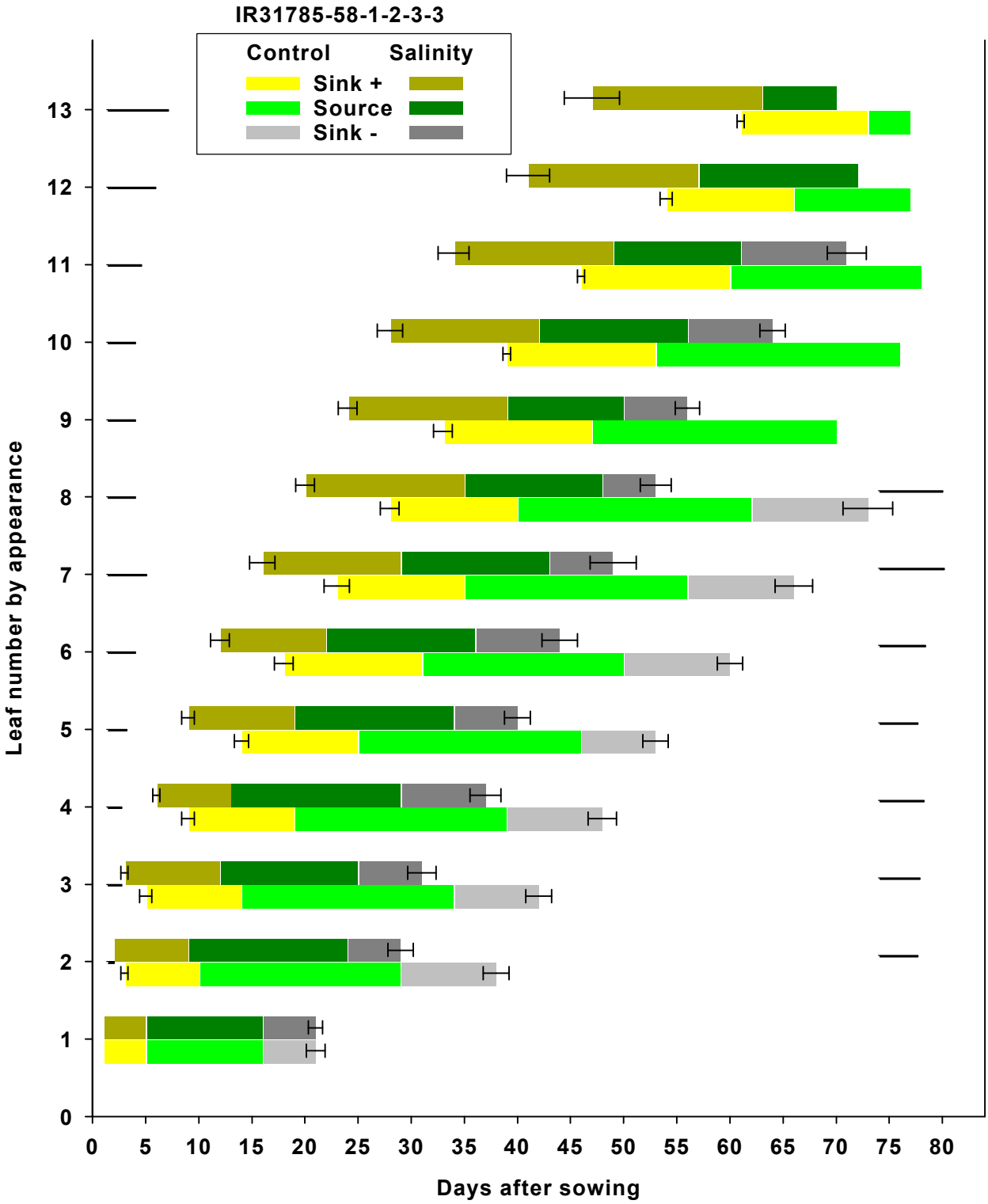

Figure 18. Total leaf duration and relative duration of developmental phases of different leaves on the main culm of the susceptible rice variety IR31785 grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3). Bold lines = least significant difference between treatments (left for leaf initiation and right for leaf death) with $p < 0.05$.

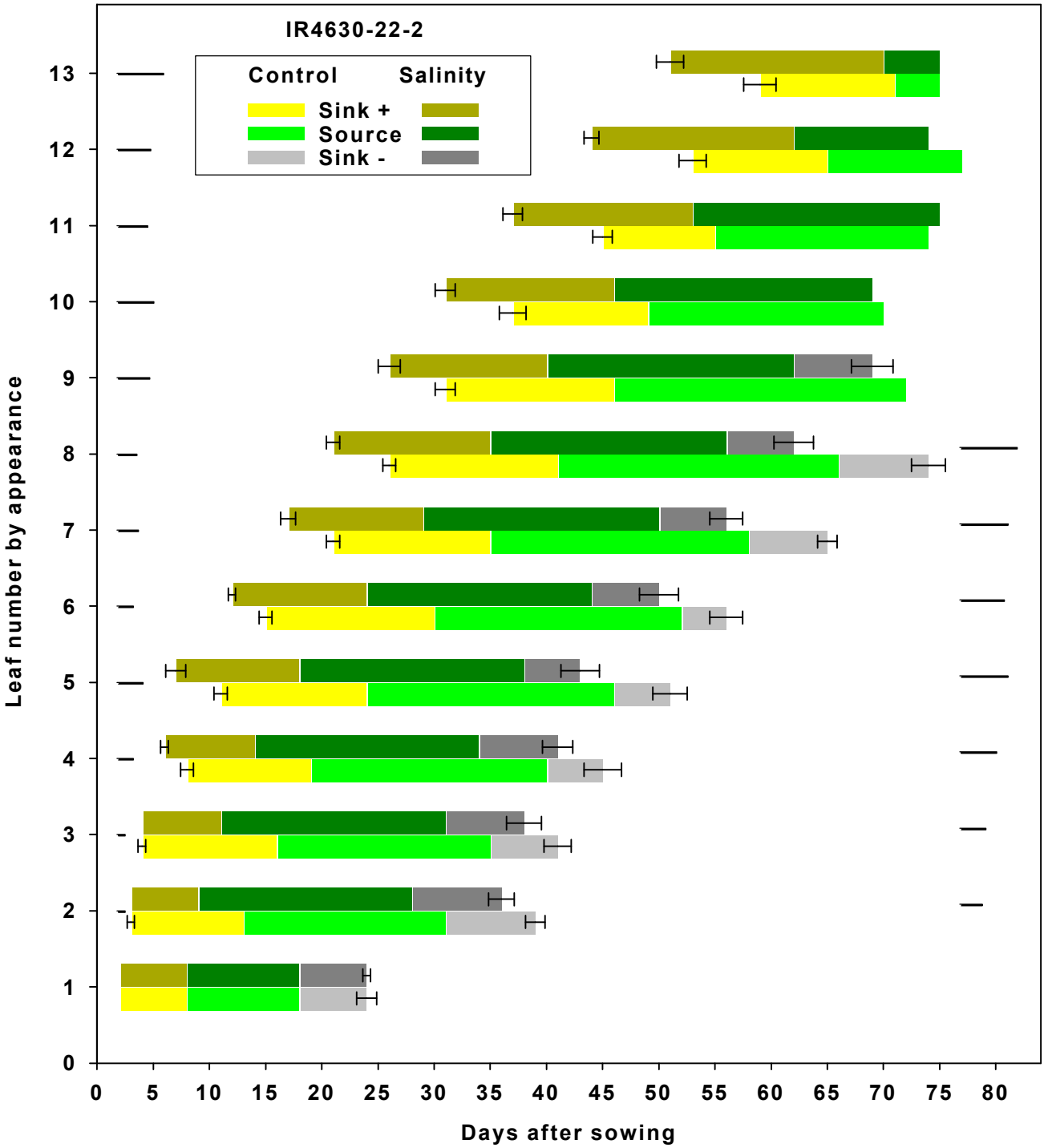

Figure 19. Total leaf duration and relative duration of developmental phases of different leaves on the main culm of the tolerant rice variety IR4630 grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n =3). Bold lines = least significant difference between treatments (left for leaf initiation and right for leaf death) with $p < 0.05$.

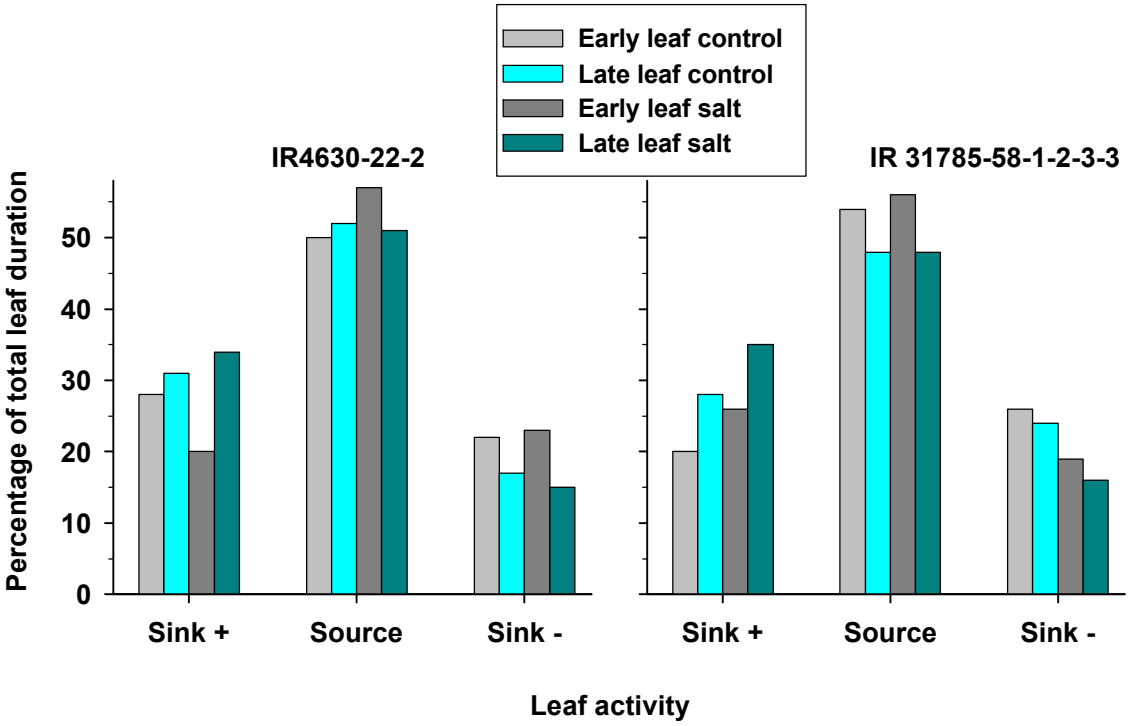

Figure 20. Percentage of different leaf periods relative to the total leaf duration in two rice varieties grown under control and saline conditions. Control = 0 mmol NaCl and salinity = 60 mmol NaCl. early leaf = leaf number 2, and late leaf = leaf number 8.

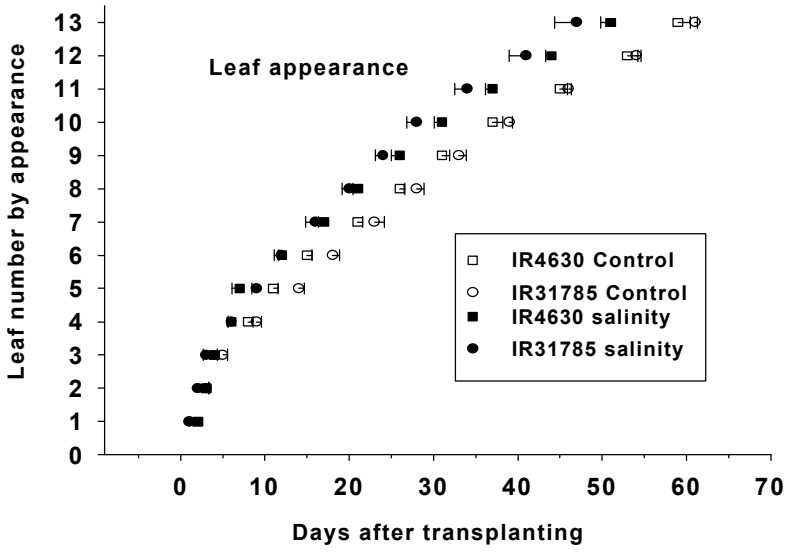

Figure 21. Leaf appearance in two rice varieties grown under saline and non-saline conditions. Non saline = 0 mmol Nacl and saline = 60 mmol NaCl. Eroor bars = standard error of means (n = 3).

7 Salinity influence on leaf development rate and total leaf duration

Leaf development rate was decreased in later leaves in both genotypes under both saline and non-saline conditions (**Figure 22**). Leaf development was faster under salinity for both genotypes. The increase in the leaf development rate was more pronounced in the susceptible genotype than tolerant one.

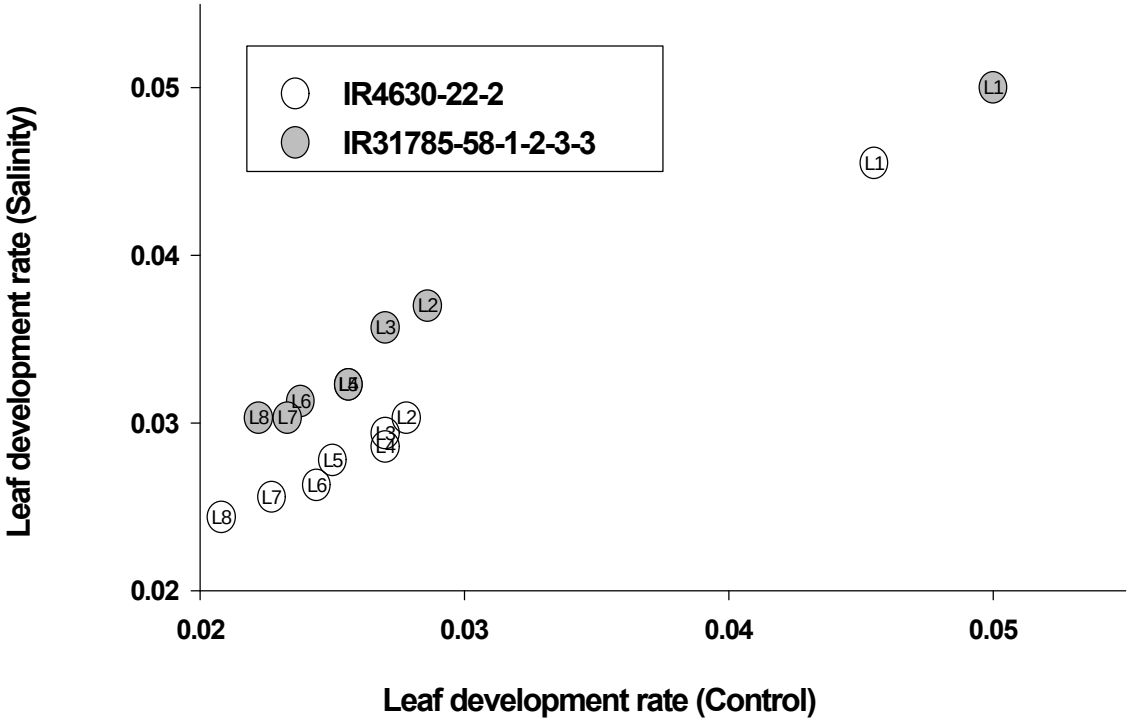

Figure 22. Leaf development rate of two rice varieties grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. The leaves were numbered by appearance. Leaf development rate was calculated by dividing 1 with total duration of respective leaf.

Total leaf duration was strongly reduced in IR31785 subjected to salt stress ($p < 0.05$) as compared to IR4630 (**Figure 23**). Reduction in total leaf duration between salt stressed and non-stressed plants ranged from 20% to 27% in IR31785 and from 5% to 15% in IR4630. Leaf duration was reduced least in leaf number four and highest in leaf number eight in both genotypes.

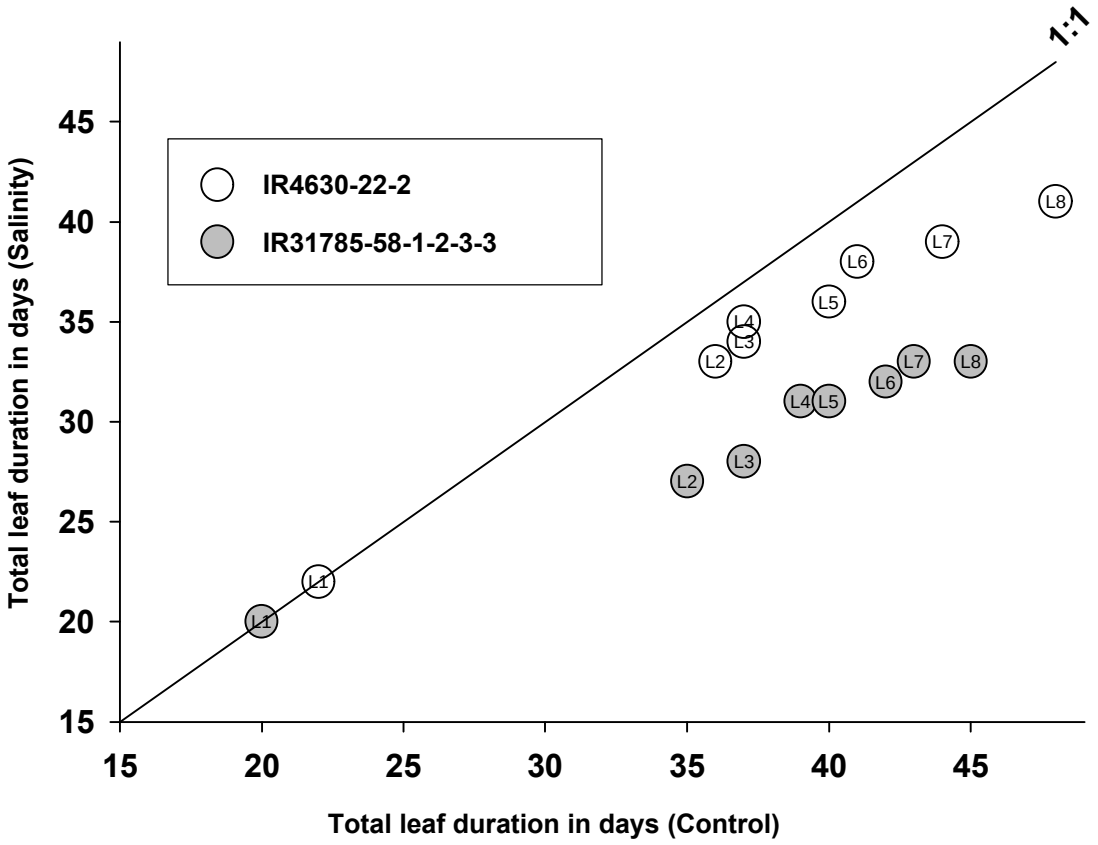

Figure 23. Total leaf duration of different leaf numbers (by appearance) of the main culm of two rice varieties grown under saline and non-saline conditions. Saline = 60 mmol NaCl and non saline = 0 mmol NaCl

3.4.4 Salinity and leaf senescence rate

Salinity accelerated the leaf senescence rate in both genotypes (**Figure 24**). In IR31785, the difference in the onset of senescence in salt stressed as compared to non-stressed conditions was smallest in leaf number 2, as the onset of senescence occured 4 days earlier and largest in leaf number 11 where the onset of senescence occured 14 days earlier. In salt stressed IR4630, this difference ranged from 4 days earlier in leaf number 2 to 7 days earlier in leaf number 11 as compared to non-stressed conditions. In general, after completing their

physiologically active periods (50% senescence), leaves died-off faster in salt stressed plants (**Figure 18** and **Figure 19)**. This acceleration ranged from 2 to 6 days in IR31785 and from 1 to 2 days in IR4630.

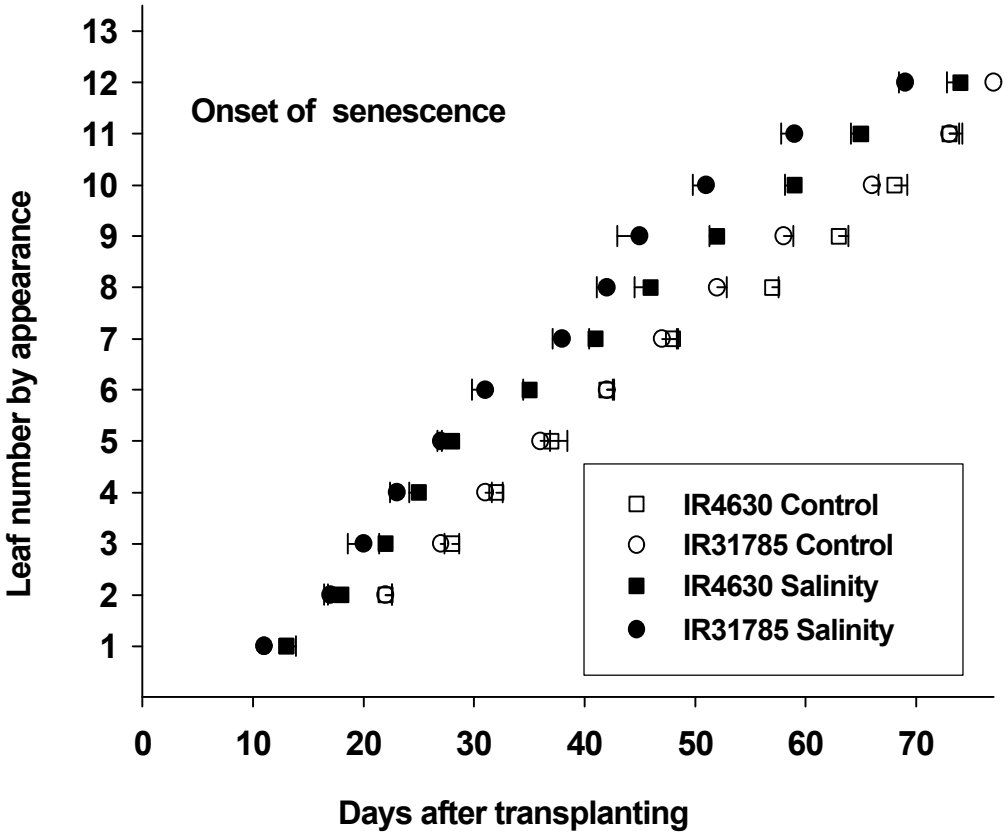

Figure 24. Onset of senescence in different leaf numbers on the main culm of two rice varieties grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3).

3.4 Sodium and potassium distribution within the plant

The plants were destructively sampled at four sampling dates in 10 day intervals starting with 31 days after transplanting and root, dead leaves and live leaves position wise were separated and sodium and potassium concentrations of the samples were flame photometrically determined (see materials and methods 2.4 and 2.5).

Figure 25 and **Figure 26** illustrates the sodium and potassium distribution within the plant at four different stages: 21, 44, 51 and 61 days after transplanting for two rice genotypes.

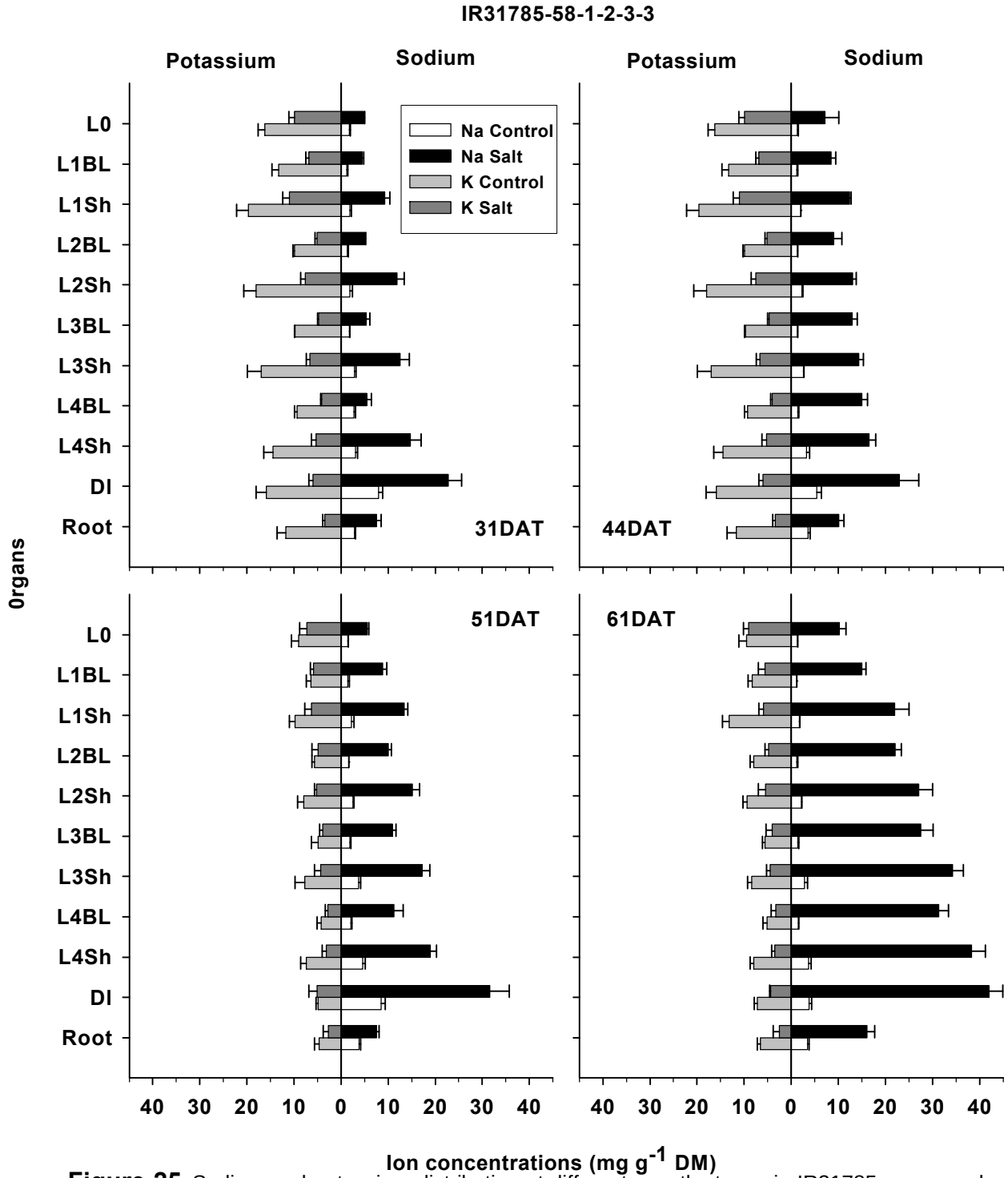

Figure 25. Sodium and potassium distribution at different growth stages in IR31785 grown under control and saline conditions. Control = 0 mmol NaCl and saline = 60 mmol NaCl. Error bars = standard error of means (n = 3). L0 = youngest not yet fully developed leaf, L1 = first youngest fully developed leaf , L2 = second youngest fully developed leaf , L3 = third youngest fully developed leaf, L4 = fourth youngest fully developed leaf. BL = Leaf blade and Sh = Leaf sheath. See appendix for least significant difference between leaf blades and between leaf sheaths.

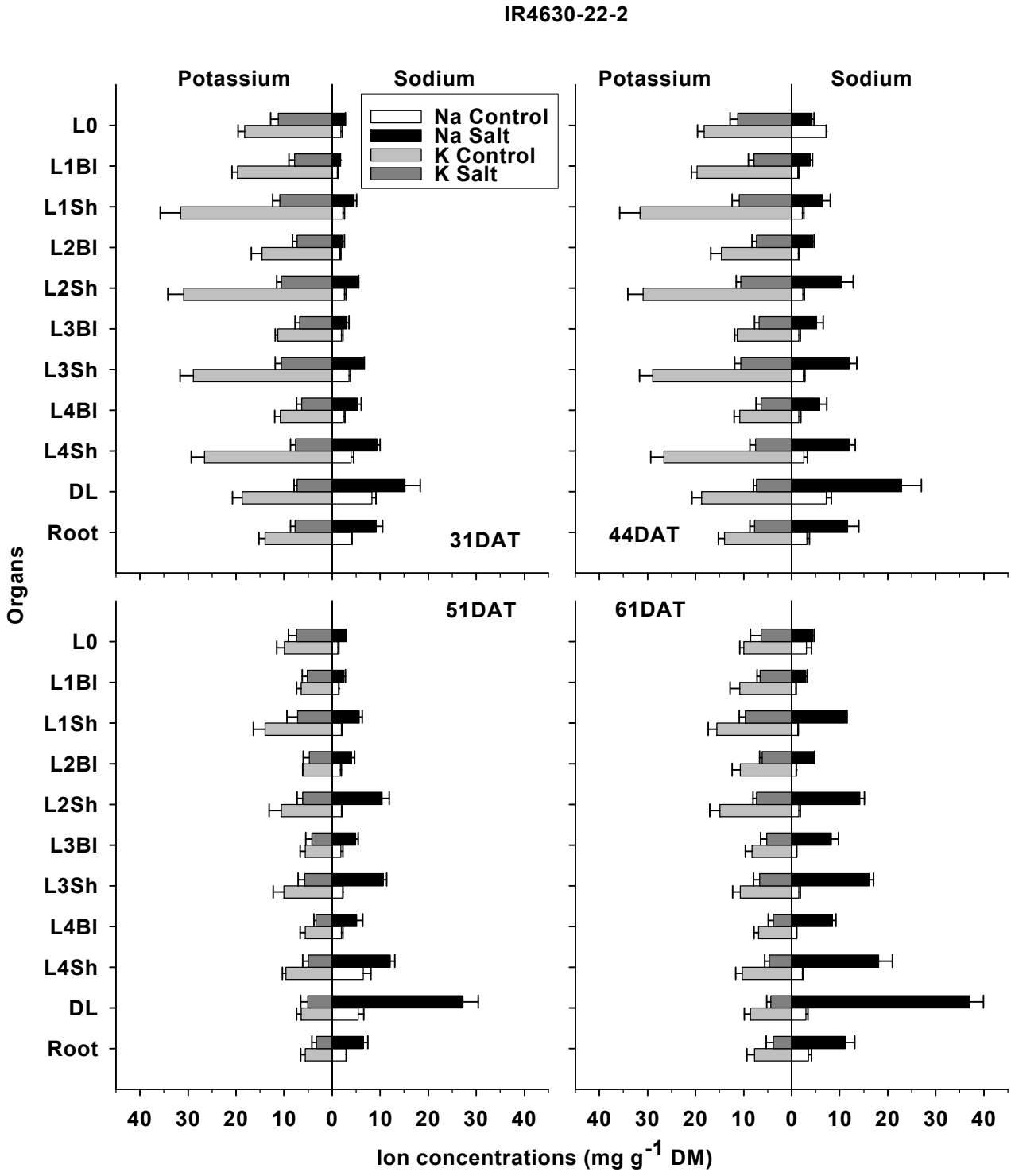

Figure 26. Sodium and potassium distribution at different growth stages in IR4630 grown under control and salinity in the green house Bonn (2003). Control = 0 mmol NaCl and salinity = 60 mmol NaCl. Error bars = Standard error of means (n = 3). L0 = youngest not yet fully developed leaf, L1 =first youngest fully developed leaf , L2 = second youngest fully developed , L3 = third youngest fully developed leaf, L4 = fourth youngest fully developed leaf. BL = Leaf blade and Sh = Leaf sheath. See table ( ) for least significant difference between leaf blades and between leaf sheaths.

The sodium concentrations in all organs increased over time in both varieties under saline and control conditions. However, the increase was more pronounced under saline conditions. In contrast to sodium, potassium concentrations decreased in all organs over time in both varieties under saline and non-saline conditions.

Highest sodium concentrations were found in dead leaves followed by leaf sheaths, roots and leaf blades at all times in both varieties under saline conditions (**Figure 25** and **Figure 26**). However, sodium concentrations of leaf blades and roots fluctuated over time.

Under control conditions sodium concentrations were generally low, with concentrations being higher in leaf sheaths than blades.

Potassium concentrations were highest in leaf sheaths followed by leaf blades and roots in both varieties under both treatments. Root sodium and potassium concentrations did not vary much between varieties but varied strongly between treatments in all stages. The sodium concentration was generally much higher than the potassium concentration under salinity and vice versa under control.

3.5 Sodium and potassium distribution within the leaf

Youngest leaf had lowest sodium concentrations and highest potassium concentrations. Sodium and Potassium concentrations were particularly higher in leaf sheaths as compared to leaf blades. This effect was particularly pronounced under saline condition for sodium and under non-saline conditions for potassium (**Figure 27**). Potassium concentrations were generally higher in IR4630, whereas sodium concentrations were generally higher in IR31785.

3.6 Share of sodium and potassium between leaf blades and leaf sheaths and comparison with dry matter

The leaf blade to leaf sheath ratio of sodium and potassium contents differed among the leaf levels, varieties and treatments over time (**Figure 28)**.

The leaf blade to leaf sheath ratio of sodium contents increased in all leaf positions except for a slight decrease in leaf position 4 over time in salt stressed IR31785. The salt stressed IR4630 did not show any significant changes in leaf blade to leaf sheath ratio of sodium contents in any leaf position except for a slight decrease in leaf position four over time.

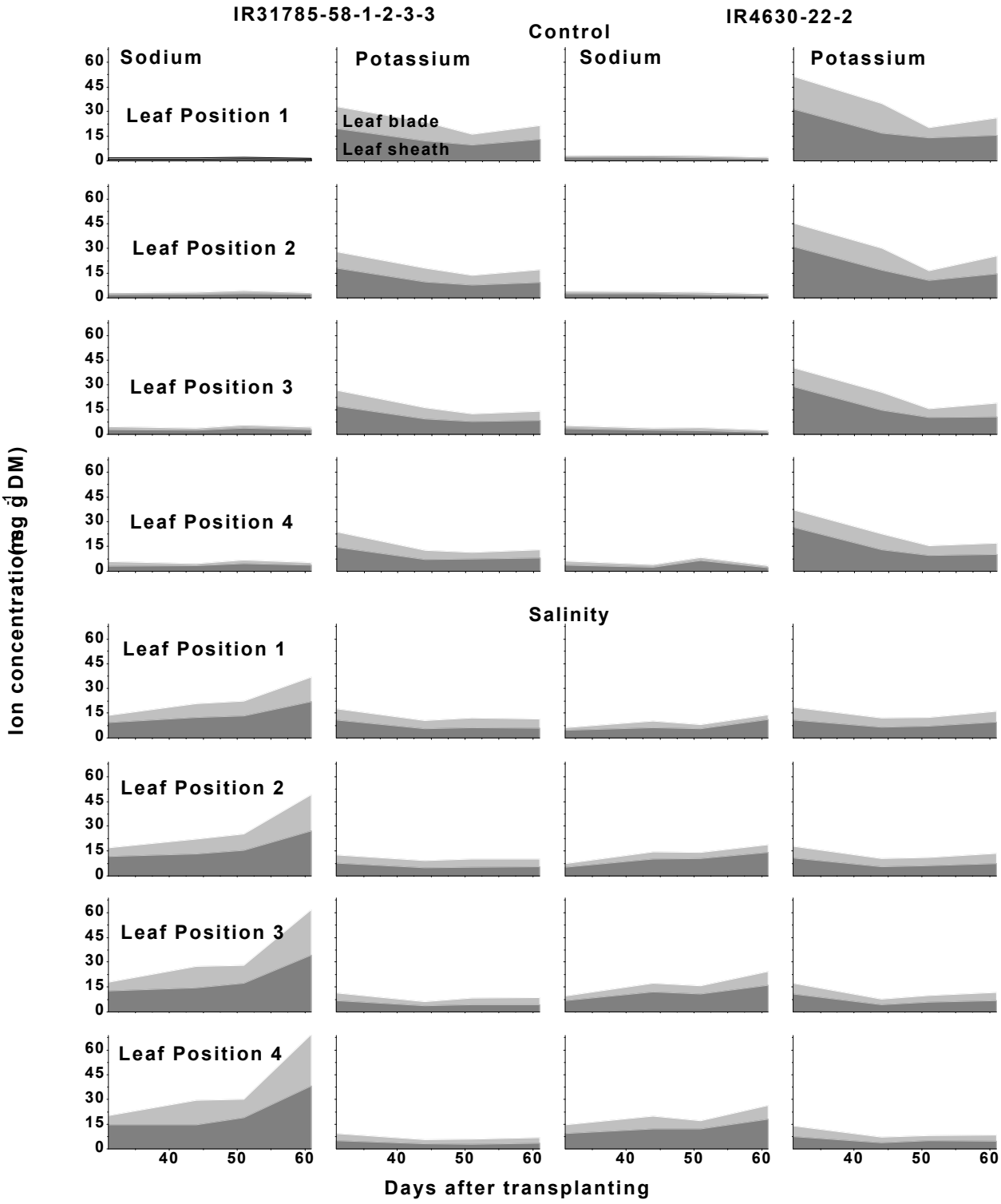

Figure 27. Sodium and potassium distribution in leaf blades and leaf sheaths of two rice varieties at different growth stages under control and saline conditions. Control = 0 mmol NaCl and salinity = 60 mmol NaCl.

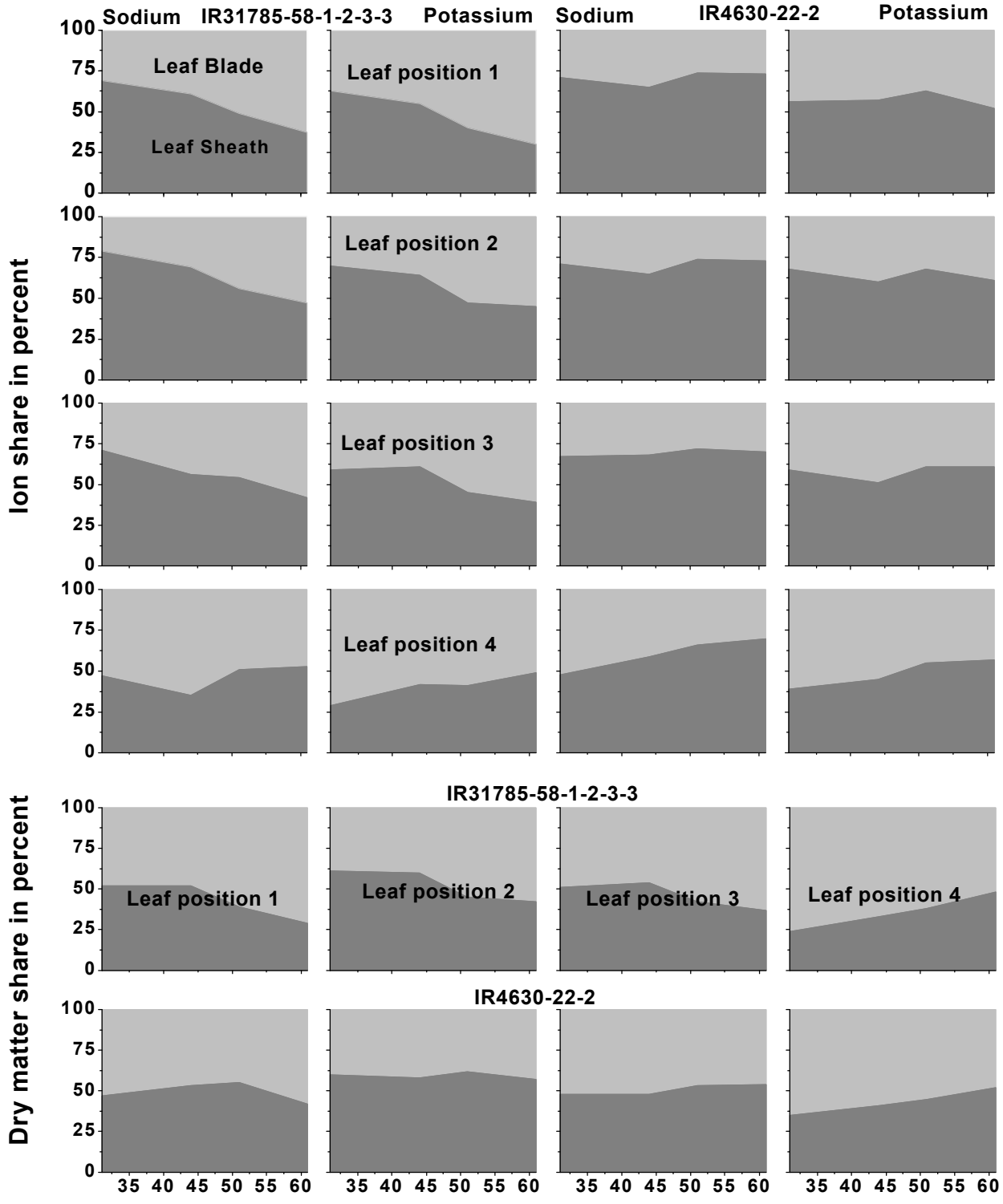

Figure 28. Percent share of sodium and potassium (upper graph) and dry matter (lower graph) between leaf blades and leaf sheaths in two rice genotypes grown under saline conditions (60 mmol NaCl).

The salt stressed IR31785 showed strong increase in leaf blade to leaf sheath ratio of potassium contents in all leaf positions except relatively decrease in leaf position 4 over time. The salt stressed IR4630 did not show any significant changes in leaf blade to leaf sheath ratio of potassium contents in all leaf position except relatively decrease in leaf position 4 over time.

The leaf blade to leaf sheath ratio of dry matter accumulation generally increase in all leaf positions except slight decrease in leaf position 4 over time in salt stressed IR31785 (**Figure 28)** The salt stressed IR4630 did not show any significant changes in leaf blade to leaf sheath ratio of dry matter accumulation in all leaf position except relatively decrease in leaf position 4 over time.

8 Discussion

4.1 Salinity influence on dry matter accumulation

Salinity influence on dry matter accumulation in rice has been showed before. Salinity induced dry matter reduction was less in tolerant IR4630 than in susceptible IR31785 (Asch, et al., 1997). We found the similar results: IR31785 was more adversely affected in total dry matter accumulation compared to IR4630 under saline conditions (Figure 7). Moreover, salinity induced dry matter reduction was higher in leaf sheaths compared to leaf blades (Figure 9). The reason for higher reduction in leaf sheath dry matter accumulation compared to leaf blades was, probably, due to a higher sodium concentration in leaf sheaths as compared to leaf blades. Similarly, less reduction in dry matter in IR4630 suggests a higher tolerance to salinity than in IR31785.

4.2 Salinity and potassium influence on tiller number and tillering pattern

Very few studies have been conducted on salinity influence on tiller number in rice. According to Grattan et al. (2002) salt stressed rice plants have fewer tillers compared to non-stressed plants. At an EC of 3dS m^{-1}, the rice yield and tiller densities were reduced by one-third and 40 % respectively compared to non-salinized controls (EC = 0.4 dS/m). Salinity linearly reduced the number of tillers per plant with increasing salinity (Grattan et al., 2002). Yoshida (1981) has shown tiller production and distribution into primary secondary and tertiary tillers in rice under normal growth conditions. But the influence of salinity on tiller distribution into primary, secondary and tertiary tillers is still unknown. We recorded the total tiller number and their distribution into primary, secondary and tertiary tillers at 4 different dates in rice grown under saline and non- saline conditions and three different potassium concentrations. Salinity reduced total tiller number at all stages in both genotypes (**Figure 10**). Salinity induced reduction was observed higher in tertiary tillers whereas primary and secondary tillers were less affected (**Figure 11**). Moreover, tiller number was less affected by salinity in IR4630 compared to IR31785. This shows that the genotype IR4630 is more tolerant to salinity induced tiller reduction than IR31785. Additional potassium mitigated the effects of salinity on tiller number in both genotypes. This shows that the application of additional potassium nutrition could be an alternative to reduce the salinity stress on total tiller number in rice plant.

4.3 Salinity and potassium influence on leaf number and leaf area

No literature was found regarding the salinity and potassium influence on leaf number and leaf area in rice and other cereal crops except for some observations on salinity influence on flag leaf area in rice (Ashraf et al.,1998). Our study showed that salinity negatively affected total leaf number and leaf area at different stages of plant growth (Figure 13 and Figure 15). There was no significant reduction in the total leaf number but reduction occured in the total number of live leaves at different plant growth stages. Leaves died earlier in salt stressed plants (Figure 18 and Figure 19) which resulted in lower numbers of live leaves at all stages. The reduction in total live leaf number was because of the reduction in total tiller number in salt stressed plants (Figure 10). Salinity induced reduction in leaf area was found the consequence of reduction in total tiller number and total live leaf number in salt stressed plants. Additional potassium mitigated the effects of salinity on total leaf number and total leaf area. This shows that potassium has some mechanism to decrease the salinity-induced reduction in total leaf area.

IR4630 was less affected by salinity compared to IR31785 in total leaf number and total leaf area. Moreover, salinity significantly reduced total leaf number and total leaf area in IR31785, whereas in IR4630 reductions were not significant. This suggests that IR4630 can tolerate the salinity stress on total leaf number and total leaf area and opposite is true for IR31785.

4.4 Salinity influence on leaf development and total leaf duration

According to Yeo et al. (1991), addition of 50 mM NaCl to greenhouse-grown *rice* cv. Pokkali (tall) and Amber (intermediate) and 2 dwarf lines had little effect upon the time of leaf initiation, but leaf mortality before normal senescence was increased and the onset of senescence was advanced. There was no significant effect on the day-to-day growth pattern, nor on the ultimate length of leaves that were developing at the time of, or shortly after, salinization. Leave*s* that developed after prolonged exposure of the plants to salinity were shorter. Addition of NaCl, KCl or mannitol to the root medium brought about cessation of leaf elongation within 1 min. Similar experiments were conducted by Lee et al. (1991) and Misra et al.(1997). Salinity reduced leaf growth in susceptible rice cultivars grown under 50 mmol NaCl. Our reseach showed that total leaf duration was reduced in both rice genotypes

subjected to salt stress as compared to non-stressed plants (Figure 18 and Figure 19). The reduction in total leaf duration was found a consequence of the reduction in the leaf's physiologically active period, earlier senescence (Figure 24) and premature death of leaf. Leaf initiation was earlier in salt stressed plants (Figure 21). The earliness in leaf initiation was the result of premature death of older leaves, which led plants to initiate leaves earlier so that plant was able to recover the biomass loss. Leaf's physiologically active period was reduced in salinity stressed plants compared to non-stressed plants but leaf's physiologically active period over its total duration was at par between stressed and non-stressed plants (Figure 20). Leaf's physiologically active period was reduced due to early senescence of leaves. Lutts et al (1996) has observed an incresase in leaf senescence rate in salinity stressed plants. The reduction in total leaf duration led plants to develop faster under salinity. Leaf development and total leaf duration were less affcted by salinity in IR4630 as compared to IR31785 (Figure 18 and Figure 19).

4.5 Distribution of sodium and potassium within the plants

Sodium and potassium concentrations were found to be higher in the stems, which consisted mainly of leaf sheaths (Asch et al., 1997). Root sodium and potassium concentrations did not differ between rice varieties, the sodium concentration being generally much higher than the potassium concentration. Varietal differences in cation concentration were most pronounced in the leaf blades, the sodium concentration increasing by leaf position (descending), and potassium decreasing (Asch et al., 1997). IR4630 had the lowest sodium and the highest potassium concentrations, and the reverse was true for IR31785.

According to Mitsuya et al. (2002), sodium content was higher in older leaves and in the basal part of the leaves in salt-treated plants. In the fourth leaf of salt-treated plants, Na content was highest in the middle part of the leaf sheath and decreased towards the tip of the leaf blade.

Similar findings were observed by Yan et al. (1994); leaf sodium concentration decreasing from older to younger leaves in rice plants. Within the same leaf layer, more sodium was distributed into the sheath and less into the blade. Salt-tolerant rice variety had a lower sodium concentration and ratio of blade sodium to sheath sodium contents (Na B:S) in

younger leaves, and higher elongation rate of younger leaf blades. The sodium/potassium ratio was lower in tolerant cultivars and higher in sensitive cultivars (Mandal et al., 1999).
We found increasing sodium concentrations in all organs over time in both varieties under saline and control conditions (**Figure 25** and **Figure 26**). However, the slope was steeper under saline. In contrast to sodium, potassium concentrations decreased in all organs over time in both varieties under saline and non-saline conditions. This explains that salt contents in different organs of rice increases as the plant gets more stressed to salinity. Increase in salinity leads to decrease in potassium concentration. There must be some poor mechanism in plants to reduce potassium uptake as the sodium uptake is increased.
Highest sodium concentrations were found in dead leaves followed by leaf sheaths, roots and leaf blades illustrating that higher sodium concentration in leaf causes leaf to die. Furthermore, leaf sheaths retain large amounts of sodium and, as the leaf sheaths get saturated, extra sodium is driven to leaf blades. Similarly reduction in total dry matter accumulation was stronger in leaf sheaths compared to leaf blades under salinity, which led to increase in leaf blade to leaf sheath ratio of dry matter accumulation over time (**Figure 28**). These resulted to increase in leaf blade to leaf sheath ratio of sodium content over time. The relationship between sodium and potassium concentrations in different leaf positions were found opposite to each other. Sodium concentrations were higher in older leaves where as potassium concentrations were higher in younger leaves.

Overall, higher sodium concentrations were observed in IR31785 than in IR4630. Although comparatively less than IR31785, IR4630 still had high sodium contents in different plant organs. However, salinity induced changes on dry matter accumulation, tiller number, leaf number, leaf area, total leaf duration etc. were less in IR4630. This proves that IR4630 takes-up less sodium and more potassium, therefore growth reductions are not as severe and water use efficiency may be higher.

9 Conclusions

This study was conducted to assess the effects of salinity on dry matter accumulation, tiller number, leaf number, leaf area, leaf development rate, total leaf duration, relative duration of leaf developmental phases, photosynthesis and sodium and potassium concentrations and distribution in different organs of two rice cultivars differing in their response to salinity stress.

Salinity reduced dry matter accumulation in both genotypes. However, genotypes differed in the degree of salinity induced dry matter reductions. Salinity significantly reduced total tiller number in IR31785, whereas in IR4630 reduction was not significant. Moreover, the tertiary tillers were strongly reduced by salinity while primary and secondary tillers were less affected. Leaf number and leaf blade area were always reduced by salinity in both varieties over time. Higher potassium concentrations in the culture solution resulted in larger leaf area and higher tiller number as compared to lower potassium concentrations and had a mitigating effect on salt induced reductions on plant growth parameters. Salinity increased the leaf initiation rate in both genotypes. Salinity increased the senescence rate of individual leaves and significantly shortened the physiologically active period of the leaves. The sodium and potassium concentrations were generally higher in the leaf sheaths than in leaf blades. In leaf blades, the sodium concentration generally increased with descending leaf positions whereas, potassium concentration decreased. The leaf blade to leaf sheath ratio of sodium and potassium concentrations and dry matter accumulation increased over time. No difference was observed in root cation concentrations between rice genotypes, the sodium concentration being generally much higher than the potassium.

In general, higher sodium concentrations were observed in IR31785 than in IR4630. Salinity induced changes on all growth parameters (dry matter accumulation, tiller number, leaf number, leaf area, total leaf duration etc.) were less pronounced in IR4630 compared to IR31785. It is concluded that IR4630 takes-up less sodium and more potassium, therefore growth reductions are not as severe and water use efficiency may be higher.

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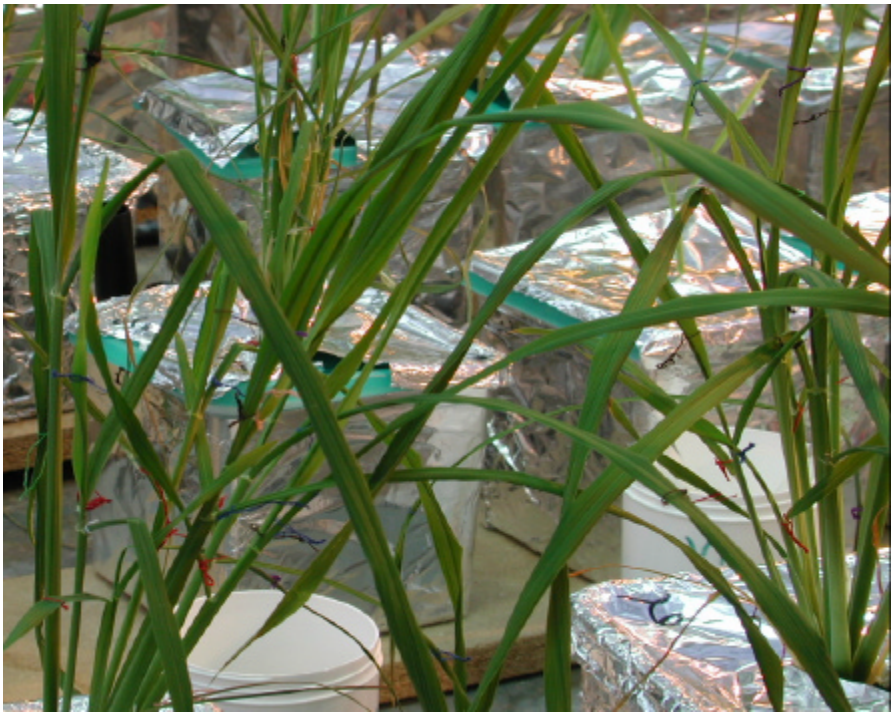
Appendix

IR31785 growing at 80 ppm potassium concentration under control condition.



IR31785 growing at 40 ppm potassium concentration under saline condition

SE (between the replications) and LSD (between leaf blades and leaf sheaths) in IR4630

Organs/DAT		Control Unit = mg^{-1} g DM				Salinity Unit = mg^{-1} g DM			
Replication = 3		Means		SE		Means		SE	
Organs	DAT	Na	K	Na	K	Na	K	Na	K
Root	31	3.9552	13.9326	0.2169	1.2744	9.1902	7.7305	1.3432	0.9751
Dead leaves	31	8.2599	18.7733	0.8316	1.9256	15.1438	7.2816	3.1647	0.6519
Leaf position zero	31	1.8214	18.1702	0.2848	1.3935	2.7071	11.1724	0.0948	1.6139
Leaf blade 1	31	1.0290	19.7111	0.1545	1.1704	1.6817	7.8141	0.0644	1.1400
Leaf blade 2	31	1.6477	14.5442	0.1899	2.2500	2.1349	7.3319	0.4496	0.9214
Leaf blade 3	31	1.9511	11.3575	0.3212	0.4908	3.0385	6.7197	0.5183	1.0390
Leaf blade 4	31	2.3904	10.7325	0.3081	1.2465	5.3494	6.2994	0.6618	1.1296
Leaf sheath 1	31	2.2281	31.5302	0.2983	4.2590	4.5823	10.8634	0.4982	1.4611
Leaf sheath 2	31	2.5704	30.9085	0.3458	3.2177	5.1695	10.5988	0.3458	0.9438
Leaf sheath 3	31	3.4552	28.8384	0.4119	2.8398	6.4990	10.5561	0.2420	1.3043
Leaf sheath 4	31	3.9163	26.5578	0.4913	2.7367	9.2742	7.5586	0.7466	1.1152
LSD leaf blades	31	Na = 0.6846		K = 3.8658		Na = 1.2878		K = 2.8604	
LSD leaf sheath	31	Na = 1.0609		K = 8.9450		Na = 1.3368		Na = 3.2932	
Root	44	3.1499	8.8109	0.5723	1.3432	11.6596	3.0719	2.3682	0.4468
Dead leaves	44	7.1778	11.8960	1.0677	0.9604	22.9173	9.5227	4.1322	1.0007
Leaf position zero	44	1.4359	12.6883	0.0355	0.3676	4.1900	7.4769	0.5097	0.5860
Leaf blade 1	44	1.2636	17.5722	0.2081	2.0801	3.8567	5.4594	0.5019	0.3500
Leaf blade 2	4	1.3804	13.3585	0.1558	1.6399	4.3163	4.9482	0.3370	0.2786
Leaf blade 3	44	1.4904	10.7717	0.2910	0.9434	5.2189	3.6239	1.3467	0.4902
Leaf blade 4	44	1.5219	9.612	0.3517	0.6510	5.8060	3.2549	1.4997	0.3075
Leaf sheath 1	44	2.2117	17.0940	0.3367	2.9943	6.3805	6.4718	1.6430	0.2665
Leaf sheath 2	44	2.3540	16.6941	0.2624	2.7485	10.2554	5.5235	2.5472	0.4404
Leaf sheath 3	44	2.4820	14.6040	0.3251	2.2465	11.9371	4.1147	1.6420	0.2080
Leaf sheath 4	44	2.5408	13.1568	0.7884	1.6353	12.0547	3.9660	1.1732	0.1450
LSD leaf blades	44	Na = 0.7080		K = 3.8899		Na = 2.8361		K = 0.9858	
LSD leaf sheath	44	Na = 1.2853		K = 6.6359		Na = 4.9079		K = 0.7733	
Root	51	2.8695	5.5254	0.1064	0.9926	6.5210	3.2414	0.8949	1.0090
Dead leaves	51	5.3765	6.3964	1.2108	1.0083	27.2114	5.0775	3.1881	1.4533
Leaf position zero	51	1.1652	9.9496	0.0058	1.5601	2.7335	7.3655	0.2780	1.7367
Leaf blade 1	51	1.3933	6.4464	0.0443	0.9030	2.4229	5.1766	0.3988	1.1028
Leaf blade 2	51	1.7392	5.8745	0.1895	0.2714	4.0131	4.7766	0.7069	1.1993
Leaf blade 3	51	1.8591	5.6317	0.3989	0.9775	4.8575	4.1562	0.5072	1.3606
Leaf blade 4	51	1.9276	5.6176	0.3197	1.0315	5.0589	3.3347	1.3587	0.4028
Leaf sheath 1	51	1.9719	13.9196	0.1572	2.4941	5.6600	7.1224	0.6268	2.2567
Leaf sheath 2	51	1.9842	10.5809	0.0701	2.5635	10.3500	6.0816	1.5492	1.1754
Leaf sheath 3	51	2.2258	10.0566	0.0793	2.2462	10.6583	5.687	0.7259	1.3225
Leaf sheath 4	51	6.4459	9.6507	1.5885	0.7140	12.0697	4.944	0.9327	1.1667
LSD leaf blades	51	Na = 0.7373		K = 2.2987		Na = 2.2400		K = 2.9119	
LSD leaf sheath	51	Na = 2.1562		K = 5.7731		Na = 2.7587		K = 4.1726	
Root	61	3.4783	7.7282	0.6604	1.5311	11.1339	3.8188	1.9940	1.5032
Dead leaves	61	2.9347	8.5687	0.4968	1.2804	37.0036	4.3047	2.9259	0.8476
Leaf position zero	61	3.1002	9.9618	1.0108	0.8610	4.3288	6.3834	0.3640	2.1484
Leaf blade 1	61	0.8733	10.8274	0.1161	1.9337	2.9954	6.5165	0.2619	0.6417
Leaf blade 2	61	0.9123	10.6898	0.0544	1.7101	4.6639	6.1277	0.0864	0.5570
Leaf blade 3	61	0.9702	8.2653	0.0743	1.3801	8.2974	5.1604	1.4170	1.2342
Leaf blade 4	61	0.9903	6.8375	0.0835	1.0068	8.4636	3.7713	0.7959	1.0335
Leaf sheath 1	61	1.2604	15.5513	0.1539	1.7584	11.1127	9.6461	0.4272	1.2335
Leaf sheath 2	61	1.4584	14.9006	0.3215	2.1688	14.1982	7.2717	0.9942	0.7868
Leaf sheath 3	61	1.4877	10.6974	0.3477	1.6192	16.1180	6.6735	0.9270	1.2540
Leaf sheath 4	61	2.2575	10.2603	0.1053	1.3564	18.0729	4.6144	2.9134	1.0230
LSD leaf blades	61	Na = 0.2293		K = 4.1720		Na = 2.2217		K = 2.4533	
LSD leaf sheath	61	Na = 0.6859		K = 4.7187		Na = 4.3711		K = 2.9404	

SE (between the replications) and LSD (between leaf blades and leaf sheaths) in IR31785.

Organs/DAT		Control Unit = mg^{-1} g DM				Salinity Unit = mg^{-1} g DM			
Replication = 3		Means		SE		Means		SE	
Organs	DAT	Na	K	Na	K	Na	K	Na	K
Root	31	2.9153	11.6888	0.1766	1.9181	7.5936	3.4195	0.9234	0.4785
Dead leaves	31	8.0075	15.8792	0.8651	2.1704	22.8182	6.0091	2.7517	0.8251
Leaf position zero	31	1.7387	16.2186	0.2484	1.4116	4.8539	9.9165	0.1271	1.1998
Leaf blade 1	31	1.2161	13.2774	0.2111	1.4405	4.4659	6.8743	0.3379	0.6242
Leaf blade 2	31	1.3832	9.8693	0.1957	0.3625	4.9814	5.0813	0.2570	0.4932
Leaf blade 3	31	1.7629	9.7238	0.1616	0.1651	5.3656	4.7336	0.7585	0.2900
Leaf blade 4	31	2.7482	9.2972	0.3012	0.6137	5.4273	4.0759	1.0763	0.2618
Leaf sheath 1	31	1.8847	19.6521	0.2690	2.5730	9.2588	10.9907	1.0569	1.3693
Leaf sheath 2	31	1.9286	18.0272	0.4939	2.6615	11.8859	7.5404	1.4979	0.9844
Leaf sheath 3	31	2.8247	16.9884	0.3426	2.9133	12.5026	6.6654	2.0502	0.7294
Leaf sheath 4	31	3.0709	14.4867	0.4824	1.9550	14.7170	5.2795	2.2701	0.9480
LSD leaf blades	31	Na = 0.6024		K = 2.1775		Na = 1.8646		K = 1.1946	
LSD leaf sheath	31	Na = 1.1003		K = 6.8742		Na = 4.8064		K = 2.7866	
Root	44	3.5980	9.2601	0.3998	0.5621	10.0956	2.6652	1.0661	0.2923
Dead leaves	44	5.4010	9.1852	1.0326	0.9311	22.9382	5.6866	4.1638	0.9902
Leaf position zero	44	1.3079	15.0659	0.2520	1.5324	17.1385	5.4254	2.9604	1.0386
Leaf blade 1	44	1.1807	11.3036	0.2501	0.9320	8.4408	4.8888	0.9924	0.5915
Leaf blade 2	4	1.2550	8.3978	0.1134	1.1063	9.0711	4.2041	1.6746	1.0343
Leaf blade 3	44	1.3057	6.7369	0.1348	0.9623	12.9663	2.5494	1.0804	0.3397
Leaf blade 4	44	1.4369	5.5636	0.1914	0.9352	14.9958	2.2913	1.2227	0.4534
Leaf sheath 1	44	2.0202	12.3317	0.0667	1.0468	12.4214	5.6047	0.3170	0.7122
Leaf sheath 2	44	2.2393	9.6511	0.2947	2.2458	13.0575	4.8580	0.7830	0.3389
Leaf sheath 3	44	2.5966	9.3847	0.1100	1.2167	14.3785	3.4611	0.9948	0.3441
Leaf sheath 4	44	3.2390	7.0917	0.7189	1.4812	16.5478	3.4295	1.3453	0.3555
LSD leaf blades	44	Na = 0.4863		K = 2.6593		Na = 3.4234		K = 1.7781	
LSD leaf sheath	44	Na = 1.0614		K = 4.2223		Na = 2.5261		K = 1.2549	
Root	51	3.8180	4.6550	0.3775	0.9512	7.5806	2.7230	0.4749	1.0237
Dead leaves	51	8.5035	4.9204	0.9059	0.3462	31.6140	5.0852	4.1500	1.7180
Leaf position zero	51	1.4035	8.9725	0.1303	1.5977	5.5780	7.3012	0.2915	1.5054
Leaf blade 1	51	1.4889	6.3960	0.3169	0.9798	8.8443	5.8363	0.8928	0.6243
Leaf blade 2	51	1.6665	5.6864	0.0417	0.4639	9.9833	4.9094	0.7376	1.3096
Leaf blade 3	51	1.9285	4.8882	0.1677	1.3674	10.8967	3.9366	0.8093	0.6347
Leaf blade 4	51	2.1065	4.2162	0.1925	0.8929	11.1976	2.7952	2.0047	0.5406
Leaf sheath 1	51	2.2426	9.8104	0.5643	1.1972	13.3667	6.2586	0.8152	1.4987
Leaf sheath 2	51	2.5789	7.9427	0.1318	1.2244	15.1971	5.2114	1.5141	0.4271
Leaf sheath 3	51	3.7872	7.6939	0.3832	2.0374	17.2331	4.3638	1.5902	1.2779
Leaf sheath 4	51	4.6437	7.3916	0.5087	1.1369	19.0063	3.1101	1.2410	0.8487
LSD leaf blades	51	Na = 0.5513		K = 2.6419		Na = 3.3055		K = 2.2552	
LSD leaf sheath	51	Na = 1.1605		K = 3.9007		Na = 3.5725		K = 2.9473	
Root	61	3.5213	6.5076	0.2666	0.6786	16.0570	2.4982	1.6478	1.3252
Dead leaves	61	3.8256	7.2486	0.5550	0.5879	41.9736	4.3303	4.8145	0.2799
Leaf position zero	61	1.2685	9.5035	0.1272	1.5848	10.2341	9.0326	1.3884	1.1027
Leaf blade 1	61	1.1340	8.3285	0.0806	0.8511	14.9633	5.5465	0.9212	1.4659
Leaf blade 2	61	1.2319	7.9469	0.1549	0.7367	22.1027	4.7953	1.3228	0.7309
Leaf blade 3	61	1.4150	5.5387	0.1925	0.5220	27.5313	4.0433	2.6074	1.3267
Leaf blade 4	61	1.4926	5.1374	0.1074	0.8977	31.3401	3.3224	2.1204	0.9704
Leaf sheath 1	61	1.7538	13.2149	0.1100	1.4158	21.9518	5.9436	3.0934	0.9039
Leaf sheath 2	61	2.1391	9.4245	0.1449	0.8346	27.0831	5.4737	2.9686	1.4745
Leaf sheath 3	61	2.8497	8.4250	0.6105	0.8014	34.2552	4.4602	2.3234	0.7773
Leaf sheath 4	61	3.6446	7.9437	0.5612	0.7950	38.2975	3.5018	2.9952	0.6208
LSD leaf blades	61	Na = 0.3790		K = 2.0642		Na = 5.0237		K = 3.1276	
LSD leaf sheath	61	Na = 1.1443		K = 2.6873		Na = 7.7133		K = 2.6891	

Curriculum Vitae

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QUALIFICATIONS

M.Sc.Agr. : Institute of Plant Nutrition, University of Bonn, Germany (2002-2004). Thesis title: **Salinity Effects on Tiller and Leaf Appearance and on Development Rate of Individual Leaf Positions in Irrigated Rice**

B.Sc.Agr. : Tribhuvan University; Institute of Agriculture and Animal Science (IAAS), central campus, Nepal (1991-1994). First division.

I.Sc.Agr. : Tribhuvan University; Institute of Agriculture and Animal Science, central campus, Nepal(1988-1991). First division.

S.L.C. : Adarsha Secondary High School, Nepal (1988). First division.

Experiences

Agriculture Extension officer : Ministry of Agriculture/Nepal (From July 1995 to date).

Instructor for B.Sc.Ag.student : Tribhuvan University; Institute of Agriculture & Animal Science, Central Campus, Nepal (for 2 months).

Research Assistant : Directorate of Research, IAAS (November-May, 1995).
Report writing on
"Profile of Bio-technological works in Nepal from beginning to now"
"Review of Maize Research in Nepal"

Germplasm Collector : Collected local germplasm of wheat, barley, and naked barley from different sports of Dhading(a mid-hill region) district, Nepal under guidance of Professor Dr. Krishna Prasad Sharma and his colleagues (professors) from Japan.

Other activities

Poster presented on "Salinity effects on tiller and leaf number, leaf appearance rate and leaf duration in irrigated rice" Deutscher Tropen Tag **(**DTT**)**, 8-10th October 2003, Goettingen, Germany.

Paper Presented on "Use of embryo tissue culture on orchid for propagation" at IAAS, Central campus, Nepal.

Participated in various trainings and workshops organized by the Department of Agriculture, NGO/INGO, and the Agricultural Research Council etc.