

EFFECT OF DROUGHT STRESS AND SALINITY ON THE DRY MATTER PRODUCTION OF RICE (*Oryza sativa* L.)

Le Thanh Phong
Supervisor: Prof. Dr. Ir. Jan Goudriaan

Crop Science / Crop Production
Department of Theoretical Production Ecology
Wageningen Agricultural University

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Summary

Studies exist on the effect of water deficit and salt stress on rice (*Oryza sativa* L.) production. However, the effects of these constraints together on rice yield has been not researched much. The purpose of this study was to establish different drought stress regimes during vegetative stage of rice and to gain more insight into the damage on rice yield matter at reproductive stage caused by drought and salt stress. Two levels of water, Fresh water and Saline water were used, the latter contained 0.2% of Sodium chloride, and four levels of drought were imposed with 0, 10, 15 and 20 days of drought. Salt stress was imposed at early stage (10 days after sowing) of rice development. The drought stress treatments were started at 40 days after sowing. The CO₂ assimilation of single leaves was measured at three moments: before, during drought stress, and at flowering stage. Dry matter of plant was determined at flowering stage (110 DAS).

Salt stress caused a decrease of green leaf area of plant not only during vegetative stage but also in reproductive stage. A decrease of leaf photosynthesis was recorded at earlier stage but not at later stage. During drought stress periods, both water deficit and salinity acted as limiting factors to assimilation of leaves resulting in a decrease of leaf photosynthesis. At this time water shortage combined with an increase of salt concentration influenced more seriously plant growth, even though drought was not very serious, and drought stress was relieved far ahead of flowering stage, yet salt and drought stress still caused a restriction of growth in all plant parts, such as leaves, stems, roots and panicles. This finally led to less plant dry weight at the reproductive stage. The smallest dry matter yield was recorded in plants in saline water under 15 or 20 days of drought. However, salinity was a much more important factor than drought stress. The dry matter yield of plants in fresh and saline water was tested by the model which based on linearly interpolated value of LAI. The results showed that simulated dry matter yield was close to observed yield.

Introduction

In recent years, the Khao Dawk Mali - 105 rice variety, an aromatic one, has been cultivated in some salinity-affected soil areas in the Mekong Delta (South of Vietnam). This variety is interesting to farmers because of its yield (3-4 tons/ha) and aroma (Soctrang Agricultural Service, 1994. Vietnam). Therefore it is grown for export. In some coastal areas (South of Vietnam) the early sowing season of Khao Dawk Mali - 105 is from the middle of June to July because at this time rain can supply water for early growth stage of rice. Seedlings are transplanted at about 30 to 40 days after sowing. Not long after transplanting, usually a short period of drought appears (in August), which lasts about 1-2 weeks. This usual pattern of weather affects the growth of the rice but its impact on the loss of yield potential is not well known.

Studies exist on the effect of water deficit on rice production and on the effect of salt stress as well. However, the effects of these constraints together on rice yield has been not researched much.

This study was carried out in a glass house mimicing tropical weather conditions. Soil and water management were also adapted to mimic salinity-affected conditions. The purpose of this study is to gain more insight into the damage on rice yield caused by drought and salt stress during the vegetative and reproductive phases.

Chapter 1

Literature review

Drought is defined as the condition in which soil water is insufficient to ensure maximum plant growth (Ghildyal and Tomar, 1982). On a global basis, drought limits plant growth and crop productivity more than any other single environmental factor (Boyer, 1982 as edited by Jones, 1989). Hale and Orcutt (1987) define drought is a meteorological term that means a lack of precipitation over a prolonged period of time.

According to Yoshida (1981), salinity is defined as the presence of excessive concentrations of soluble salts in the soil. Major ionic species of salts are sodium, calcium, magnesium, chloride, and sulphate. Among those, sodium chloride is predominant. Saline soils normally have a pH lower than 8.5 and an electric conductivity of the saturation extract greater than 4 mmho/cm at 25 °C.

The reaction mechanisms of plants under drought and salt stress can be divided conveniently into three categories: phenological, morphological, and physiological.

Dependence of sensitivity on phenological stage

In rice plants there are three phases of growth: the vegetative growth phase, from germination to panicle initiation; the reproductive phase, from panicle initiation to flowering and the ripening phase from flowering to full development of the grain. The vegetative growth phase can be further divided into basic vegetative (bvp) and the photoperiod-sensitive phase (psp). The bvp is the early growth after germination which is unaffected by photoperiod (from 15 to 60 days). It is only

after the bvp has been completed that the plant is able to respond to the photoperiodic stimulus for flowering, this is the psp of the plant (from almost 0 to 12 years) (Chatterjee and Maiti, 1981, 1985).

Khao dawk Mali is a local rice variety of Thailand, in the tropical climate of Vietnam (Mekong Delta in the South of Vietnam) , the bvp of this variety is 24-30 days, the psp is 45-60 days. The plants flower in October (short day length) and are harvested at the end of November. The grain filling duration is 20-25 days and the grain filling rate is 90-110 mg/panicle/day (CLRRI, 1992, 1993).

Maynard et al. (1987) reported that the timing of drought stress conditions in relation to the stage of plant development is also important in terms of internal competition for water. Drought at the tillering stage reduced plant height and leaf length, induced leaf rolling or drying, and prolonged the vegetative stage even after drought stress was removed (Bhattacharjee, 1971 as cited by Murty, 1982).

Water stress is especially critical during reproductive development (Hale and Orcutt, 1987). Moisture stress at booting and flowering reduces plant height and dry matter production, delays panicle exertion, and induces uneven flowering. Photosynthetic efficiency is impaired, resulting in less dry matter accumulation and a low concentration of nonreducing sugar in the stem (Bhattacharjee, 1971 as cited by Murty, 1982). Certain rice varieties exposed to drought at the vegetative stage failed to produce normal panicles even when the stress was relieved far ahead of the flowering stage. In general, varieties with high dry matter production at flowering gave better yields under dryland condition because of a considerable contribution of reserve carbohydrates to grain filling (Murty, 1978 as cited by Murty , 1982).

Crop species show a spectrum of responses to salt, although all have their growth (and yield) reduced by salt. With an EC equal to 7.0, the yield of rice was decreased by 50% (Maas, 1976 as edited by Jones, 1989). The effect of salinity on the growth of rice depends on the stage of development at which salinity occurs (Pearson, 1959 as cited by Chatterjee, 1981, 1985; Bernstein and Hayward, 1958 as cited by Harry Mussell and Richard C. Staples, 1979). Rice is apparently most tolerant to salinity during the germination stage and most sensitive during the seedling stage (Kapp, 1947; Pearson, Bernstein, 1961 as cited by Chatterjee, 1981, 1985). Work at IRRI showed higher sensitivity of rice at the transplanting stage and a greater sensitivity again during the period from panicle initiation to flowering for grain production and from transplanting to panicle initiation for straw production. Maintaining the EC at 7 mhos / cm during the life of the crop caused a notable reduction in grain yields and a sharp reduction in the number of effective tillers and fertile grains. Irrigation with salt water (0.2% NaCl) at the fourth leaf stage of seedling showed two types of leaf injury. The injury was restricted to older leaves in the known tolerant types, while it was observed on the young and actively growing leaves in the susceptible types (Chatterjee and Maiti, 1981, 1985).

Morphological mechanisms

Leaf area

In crop life cycle three phases are also distinguished: an early, exponential phase, a phase of full growth, and a phase of ripening and senescence. During the first, exponential, growth phase, most of space around the plants has not yet been occupied. Each new leaf that is formed, contributes to more light being intercepted so that growth increases even more. There is no mutual shading yet and the

contribution of the new leaf is identical to that of the existing ones. The relative growth rate is then constant. The crop still mostly vegetative in this exponential growth phase. Later on, the leaves will gradually start to overshadow each other, and above an LAI (Leaf Area Index) of $3 \text{ m}^2 \text{ (leaf)} \text{ m}^{-2} \text{ (ground)}$, new leaf area hardly results in any increase in light being intercepted. By now the phase of exponential growth has passed into the phase of linear growth. This does not mean that the LAI no longer increases. When water and nitrogen are optimally supplied, LAI can easily exceed a value of $6 \text{ m}^2 \text{ m}^{-2}$ but such a high value does not contribute further to the production of biomass: growth remains linear. The bulk of dry matter formation occurs during this phase (Goudriaan and Van Laar, 1994). Yoshida (1981) suggests that a LAI of 4-8 is needed for good rice photosynthesis. An increase in leaf area of the mother shoot slightly increased the number of spikelets that emerged (Murty and Ramakrishnayya, 1982). Mild to moderate water stress is sufficient to reduce leaf area in most crop species. Water stress can also affect leaf area by speeding the rate of leaf senescence (Begg and Turner 1976 as cited by Murty, 1982). In determinate crops, the effect of reduction in leaf area is permanent because there is no scope for compensation through an increase in leaf number (Murty and Ramakrishnayya, 1982). The most obvious morphological change with the onset of drought is a reduction in leaf area, either through a reduction in leaf size or by the shedding or death of leaves (Turner, 1976), reducing evapotranspiration as well (Ritchie, 1974). Although leaf senescence has not been as widely studied as leaf expansion, it appears less sensitive to water deficits than leaf expansion (Turner, 1982). Decreased development of leaf area also contributes to a decrease in the photosynthetic productivity of water deficient plants and may be the earliest sign of a water deficit. The loss in leaf area and photosynthetic activity, when taken together, represent a potentially large loss of photosynthate for crops (Kozlowski, 1976). As a result of reduction or even

complete loss of turgor there may be a reduction in cell size accompanied by a reduction of leaf area. Reduction in leaf area as a result of drought stress has secondary effects because of a reduction of the irradiated surface area (Maynard and Orcutt, 1987). In rice, leaf rolling under controlled environment condition decreased the rate of transpiration by up to 50% (O'Toole, 1979 as cited by Turner, 1982).

Shoot and root growth

The root systems of rice cultivars differ. Wetland adapted cultivars have more roots in the surface layers near the center of the plant, dry land adapted cultivars gave deep and more lateral roots. Under drought stress, maximum root length is stimulated strongly than total root volume at all stages of growth. Rice root porosity, number of roots, and root dry weight are low under severe stress. Transpiration of root plants began to decrease when 25% of the total extractable water was left in the root zone (Ritchie, 1973 as cited by Ghildyal, 1982). The amount and rate of water uptake depends on the ability of roots to absorb water from the soil as well as the ability of the soil to supply and transmit water to the roots at a rate sufficient to meet transpiration requirement. Rice root porosity is lower, roots are less dense, and dry weight is lower in unsaturated soil condition than in flooded soil (Pradhan , 1973 as cited by Ghildyal, 1982), mainly because of a high oxygen availability.

In many species under water stress, more growth occurs in root tissue than in leaf tissue, causing an increase in the root-shoot ratio. Water stress that occurs during early growth phases causes a large shift in root-shoot ratio. In contrast, water stress during reproductive phases (late in growing season) has little to no effect on root-

shoot ratio, but flowering and seed set are reduced, or fruit abortion is increased (Nilsen and Orcutt, 1996).

Although plant growth rates are generally reduced when soil water supply is limited, shoot growth is often more inhibited than root growth and in some cases the absolute root biomass of plant in drying soil may increase relative to that of well-watered controls (Sharp and Davies, 1979; Malik, Dhankar and Turner, 1979 as edited by Jones, 1989). It is also commonly observed that the roots of unwatered plants grow deeper into the soil than roots of plants that are watered regularly.

Growth responses of salt-affected plants vary with the constancy of the salinity level. Fluctuations in salinity, typical of habitats with seasonal changes in water potential, are reflected by a concomitant change in the osmotic potential of the shoots and by their metabolism (Raghavendra, 1991). Salinity causes a low soil or root medium water potential, and separating the specific ion effects from the water limitation effects can be difficult (Nilsen and Orcutt, 1996). Initiation of lateral roots is least affected by salinity, whereas extension growth of the laterals seem to be the most sensitive root growth process (Raghavendra, 1991).

Physiological mechanisms

Under moisture stress conditions, solar radiation does not necessarily increase plant growth (its photosynthesis would be restricted by the closure of the stomata); in fact, it might even adversely affect plant growth (Chatterjee and Maiti, 1981, 1985). Drought stress occurs when available water in the soil is reduced and atmospheric conditions cause continued loss of water by transpiration and evaporation. When the transpiration potential is high and the stomates are open,

high rates of transpiration can be expected unless available water is limited. In the later situation, the plant is placed under stress. (Maynard and Orcutt, 1987).

Leaf rolling reduces evapotranspiration but less than proportionally, due to an increase in the sensible heat and vapour pressure deficit within the canopy when the soil surface is dry or because of more rapid evaporation of water when the soil surface is wet (Turner, 1982).

Cell expansion

In general, cell enlargement appears to be more sensitive than cell division (Meyer, 1972 as edited by Kozlowski, 1976). Frequently, a decrease in cell water potential of only 0.1 MPa can cause a decrease in the cell enlargement rate and result in reduced cell size in roots and shoots. Among the various components of water potential, turgor potential (Ψ_t) decreases most rapidly with any change in tissue water potential. Thus, Ψ_t was identified as the best indicator of water stress (Hsiao, 1973 as cited by Nilsen, 1996).

When the water limitation occurred, cell size decreased and turgor pressure remained constant in differentiating cells (Boyer, 1970 as cited by Nilsen, 1996). Mild water limitation may disrupt the structure of microbodies, releasing hydrolyzing enzymes into the cytoplasm. The presence of these lipases and proteases further disrupts the normal structure of all cytosolic membranes. If the tonoplast is degraded, the vacuole fluid can empty into the cytosol (Fellows, 1978 as cited by Nilsen, 1996). Since the vacuole fluid may contain relatively high concentrations of solutes, damage to cytosolic proteins will probably result from a breached tonoplast (Nilsen and Orcutt, 1996).

Hale and Orcutt (1987) mentioned that the first effect of stress may well be a loss of turgor that affects the rate of cell expansion and ultimate cell. Loss of turgor is

probably the process most sensitive to water (drought) stress. The result is a decrease of growth rate, of stem elongation, of leaf expansion, and of stomatal aperture. As water is removed from the cell with the development of water deficits, the solutes inside the plasmalemma are concentrated and the osmotic potential is lowered (Turner, 1982).

Nitrogen metabolism

Most experiments have demonstrated that total nitrogen and protein nitrogen decrease as amino nitrogen increases in shoots of plants under stress (Hsiao, 1973 as cited by Murty, 1982). Water stress might operate directly by mechanisms involving a reduction in chemical potential of water, through a reduction in cell turgor potential, or through an increase in cell solute concentration. Alternatively, water stress could act indirectly, its effect being mediated by hormones that become increasingly available or unavailable during water stress and that then inhibit protein synthesis (Murty and Ramakrishnayya, 1982). Under drought stress, the total nitrogen concentration increased in both leaf and stem. The accumulated protein-N under drought induced continuous tiller production even under stress and vigorous tillers soon after removal of stress in the drought - resistance cultivars (CRRI, 1973 as cited by Murty, 1982). Nitrate reductase activity declines in water stressed leaves. The decrease may be related to a lowered translocation of nitrate in the xylem (Shaner, 1976 as cited by Maynard, 1987).

Free proline may accumulate in plants under water stress (Maynard, 1987). Even under mild stress there is a shift from polyribosome content to monoribosomes that are inactive in protein synthesis (Hsiao, 1973 as cited by Maynard, 1987).

The degradation of chlorophyll increases, and the concentration of the chlorophyll decrease during water stress (Nilsen and Orcutt, 1996).

Photosynthesis rate

Among the assimilatory processes, photosynthesis is important for determining growth and yield. The total photosynthate production is the result of multiplicative interaction between the photosynthetic rate and leaf area or the photosynthetic surface. Photosynthesis has two major components, the stomatal and the non-stomatal. Non-stomatal components include activities of the photosynthetic enzymes and light reactions. Water stress affects both the stomatal and non-stomatal components of photosynthesis. Initial photosynthetic reduction may be due to an increase in plant moisture stress arising from a decrease in the conductance of CO_2 through the stomata. Davies and Zhang (1991) (as cited by Nilsen, 1996) also stated that the initial impact of water limitation on photosynthesis is usually stomata closure. Stomata may close because of a root signal probably abscisic acid, or because of low turgor pressure in the guard cells (Rashke, 1975, Collatz, 1991 as cited by Nilsen, 1996). Stomata also close in response to increasing vapour pressure gradient between the leaf and air (VPG), although this may not be associated with a change in water potential (Turner, 1984 as cited by Nilsen, 1996). Stomatal closure induced by water limitation causes a depletion of carbon dioxide in the intercellular spaces (C_i). This is termed stomatal inhibition of photosynthesis. Once C_i has decreased relative to oxygen, photorespiration is stimulated. During the initial phases of water limitation, stomatal closure and non-stomatal inhibition occur concurrently (Nilsen and Orcutt, 1996).

Net photosynthesis is a balance of gross photosynthesis, respiration, and photorespiration if present. Desiccation decreases photosynthesis by decreasing the stomatal conductance to CO_2 diffusion and by changing the balance between CO_2 assimilation and production in the leaf. Water stress reduces net photosynthate

availability by reducing leaf area and increasing stomatal resistance. This is followed by a decrease in the activity of enzymes such as RuBPcase and in the photochemical activity of the chloroplast (Hsaio, 1973 and Boyer, 1976 as cited by C.B Johnson, 1981). Relief of stress would change the revival capacity of the components determining net photosynthate availability. This would be dependent on the degree of stress and the stage at which stress occurs (Murty and Ramakrishnayya, 1982).

As water limitation progresses, photosynthesis decreases before that of respiration; consequently, the ratio between photosynthesis and respiration decreases. The decrease in the ratio of photosynthesis to respiration, and the potential increase in both photorespiration and dark respiration during water stress, have caused many authors to believe that water limitation could cause plant starvation. However, it is more likely that the plant will suffer greater damage to the shoot system from metabolic effects of water limitation other than carbohydrate deprivation (Nilsen and Orcutt, 1996).

The ability of stomata to regulate water loss provides an important mechanism for reducing water loss during drought. Crop plants show a range in sensitivity of stomata to water deficits (Turner, 1982). Stomata also respond to atmospheric humidity (Lang, 1971 as cited by Turner, 1982) or, more correctly, to leaf-to-air vapour pressure deficit. However, the direct response of stomata to humidity must be distinguished from the indirect response through a lowering of the leaf water potential (Turner, 1982). There is an increase in responsiveness of stomata to humidity as leaf water content decreases (Jarvis, 1980 as cited by Turner, 1982).

Since photorespiration in C3 plants does not decrease as rapidly as gross photosynthesis, under severe stress photorespiration rates remain high (Maynard and Orcutt, 1987).

Salinity affects the ionic balance of trees as well as the water-tree relations, depending on water availability, the conducting capability of the plants, and transpiration. Salinity, even at relative low concentrations, reduces the photosynthesis of many plants. The effect of salinity involve the induction of a higher resistance to gas diffusion. Only subsequently can one observe a decrease in the metabolic capability of the leaf cells to fix CO₂. Salt stress increases respiration, routing assimilates from a growth path into an increased use for maintenance (Raghavendra, 1991).

Carbohydrate translocation

Carbohydrate translocation also decreases during water limitation during the day but may increase relative to well-watered plants at night (Bunce, 1982 as cited by Nilsen, 1996). The decrease in sucrose translocation is not due to specific effects on phloem loading processes. In fact, phloem loading is relatively resistant to water limitation (Sung, 1979 as cited by Nilsen, 1996). The cause of reduced photosynthate translocation in the change in source-sink relationships during water stress. Low CO₂ assimilation by leaves and increased respiration in mesophyll cells of leaves decreases the gradient of sucrose between the source leaves and the photosynthate sinks. The reduced gradient from source to sink causes a reduction in carbohydrate flow in the phloem (Nilsen, 1996). A depletion of the water supply in the vegetative phase can lead to little reproductive growth and a severe yield reduction (Barley and Naidu, 1964; Passioura, 1972).

Plants are stressed in two ways in a high salt environment. In addition to the water stress imposed by the increase in osmotic potential of the rooting medium as a result of high solute content, there is the toxic effect of high concentrations of ions. In the saline environment there is a preponderance of non-essential over essential

ion. The plants must absorb the essential ions from a diluted source in the presence of highly concentrated non-essential ions. As a result of site of absorption, there is sometimes a high concentration of salt in the roots and sometimes in the stems of plants, but low concentration of salt in the leaves (Jacoby, 1965 as cited by Hale, 1987). Under salt-stress conditions the osmotic potential of the soil solution is similar to that brought about by drought. Some symptoms of salt stress are those characteristic of water stressed plant. Although salt stressed plant are stunted, they are not wilted, which means that the cells must have water potentials that enable them to compete for water from the xylem. One of the ways the water potential may be lowered is by an increase in solutes (Hale, 1987). When the plant is in low osmotic potential of the soil solution (due to salt stress) the plant is able to reduce the osmotic potential of the cell to avoid dehydration and death. This process is called osmotic adjustment (Yoshida, 1981).

On major effect of salinity, or of water stress, on plants is the promotion of senescence, which is further accelerated by the subsequent production and release of abscisic acid (ABA) and ethylene. ABA affects the transport and use of water and, therefore, also plant growth under stress conditions. The decrease in the availability of cytokinins may also cause growth inhibition of salt-stressed trees (Raghavendra, 1991).

The impact of salinity on Indole Acetic Acid (IAA) level in plants has also been studied in rice. The NaCl caused a statistically significant reduction in IAA concentrations in rice leaves after 5 days. Levels continued to fall up to 15 days after salinization. Gibberellic acid (GA) can overcome high-saline condition in rice leaf to improve growth (Prakash and Prathapasanen ,1990).

The effect of salt stress on phosphorus metabolism varies with plant species and external phosphorus concentration in the rooting medium. Many data point to the fact that salinity damages mechanisms controlling intracellular phosphorus

concentrations (Hale and Orcutt, 1987). Salt stressed plants often look like phosphorus - deficient plants with small dark green leaves, decreased shoot-root ratios, decreased tillering, prolonged dormancy of lateral buds, delayed and reduced flowering, and fewer and smaller fruits (Hewitt, 1963 as cited by Hale, 1987). Leaves of salt stressed plants frequently contain unusually high concentrations of sugars as a result of the effects of the stress on the phloem translocation or on reduced sink size because of reduced growth (Gauch, 1942; Nieman, 1976; Stroganov, 1962 as cited by Hale, 1987).

Chapter 2

Materials and Methods

Plants used in this study were Khao Dawk Mali 105 rice variety which were grown in pots containing approximately 5.25 kg of sandy soil. The experiment was done in a glasshouse of Unifarm, Wageningen Agricultural University from July 7th 1997 to October 24th 1997. Pots were arranged in rows, with the plants spaced at 20 cm in the row and 20 cm across the row, forming a simulated crop of a density of 25 plants m^{-2} . Border pot-plants helped to provide more normal shading. Pots contained plastic bags to keep water inside. A Factorial experiment in a Randomized Complete Block Design with 3 replicates was designed. Two levels of water, Fresh water and Saline water were used, the latter contained 0.2% of Sodium chloride, and four levels of drought were imposed with 0, 10, 15 and 20 days of drought.

Three-leafed seedlings (10 days after sowing) were transplanted into pots at the rate of one seedling per pot. Plants were maintained fertilized at 2 days before transplanting and at 60 days after sowing with levels per ha of 80 kg N, 50 kg P_2O_5 and 60 kg K_2O (Mekong Delta Farming System Research and Development Institute. Cantho. Vietnam), and well-watered before and after drought stress to minimize the increase of salt concentration in pots.

Weather condition in the glass house

Rice was sown in July and harvested in October. Figure 1 shows the monthly climate pattern in the glass house. The mean temperature was 32.8 °C in August, reaching a lower value of 25.7 °C in October. Humidity fluctuated from 59 to 73 %. The mean radiation in glass house was 11.8 MJ $m^{-2} d^{-1}$ in August and decreased to a low value of 4.2 MJ $m^{-2} d^{-1}$ in October.

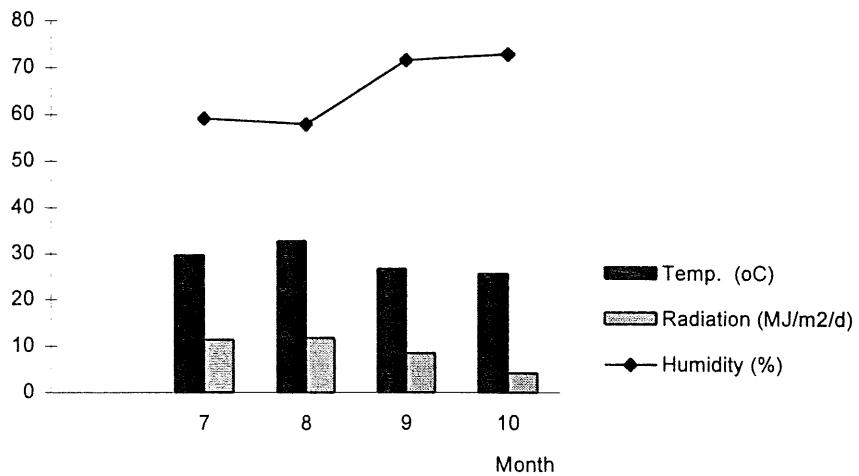


Fig. 1. Monthly climatic condition in the glass house from July 8th to October 24th 1997 (data from Unifarm of Agricultural Wageningen University, the Netherlands)

Soil conditions

The rice pot contained a sandy soil with 31.3 mg P₂O₅, 70 mg K₂O and 137 mg MgO per kg of soil dry weight. Organic matter is 4.7 % and pH-KCl = 5.4 (Company Laboratory Ground Crop Research, 1997. Oosterbeek).

Water status

The drought stress treatments were started at 40 days after sowing. The initial weight of 3 pot-soil-watered per treatment was recorded at beginning of drought which contained a mean weight of 7603.7 g soil and water, in which average amount of water was 2353.7 g water per pot. After 10 days of drought stress each pot in the treatments of 15 and 20 days under drought stress was

rewatered with a amount of 70 ml of water per day (about half of water evaporation / day) to prevent the death of plants under long drought stress.

Measuring CO₂ assimilation of single leaves

The CO₂ assimilation of single leaves was measured at three moments: before, during drought stress, and at flowering stage. The LCA-2 system was used (The Analytical Development Co. Ltd. Pindar Road, Hoddesdon, Herts En I I OAQ. England). The plant material was placed in a cuvette with a measured inflow of air of known water vapour and carbon dioxide content. Gas exchange rates are determined from flow rate and the concentration differences between inlet and exhaust air.

The following sets out the steps to be used in calculation of photosynthesis and transpiration.

a - Calculate the mass flow of air per unit leaf area through the cuvette.

$$W = (V / 1000) * (1 / 22.4) * (273 / (273 + T_a)) * (P / 1.013) * (10000 / a) \\ = ((V * P) / ((273 + T_a) * a)) * 120.311 \text{ mol m}^{-2} \text{ s}^{-1}$$

Where V is the volume flow in ml s⁻¹

P is the atmospheric pressure in bars

a is the projected leaf area in the cuvette in cm²

and T_a is the air temperature.

b - Assuming that dry air enters the cuvette calculate the transpiration rate from the leaf (E).

$$E = (e_o / (P - e_o)) * W \text{ mol m}^{-2} \text{ s}^{-1}$$

where e_o is the vapour pressure in the air emerging from the cuvette

$$e_o = e_s * h_c / 100$$

where e_s is the saturated vapour pressure at cuvette temperature and h_c is the relative humidity in the cuvette (%)

c - Calculate the leaf temperature from the energy balance of the leaf within the cuvette.

The energy absorbed by the leaf (H) is:

$$H = (Q * 698 / 3190) * (0.8 * 0.85 + 0.2 * 0.6) = 0.175 Q$$

where Q is the mol quanta of visible light incident on the cuvette; (698 / 3190) converts this to W m^{-2} ; 0.8 is the fraction of visible light absorbed by leaves and 0.85 is the fraction transmitted through the PLC window); 0.2 is the fraction of infra red absorbed by the leaves and 0.6 is the fraction transmitted through the windows (this assumes a 50:50 split between visible and infra red in the incident beam).

Then:

$$\Delta T = (0.175 Q - \lambda E) / (0.93 * M_a * C_p / r_b + 4 \sigma (T_a + 273)^3)$$

Where λ is the latent heat of vaporisation of water = 45032 J mol^{-1} at 0°C decreasing to 429060 at 50°C

M_a is the molecular weight of air = 28.97 g mol^{-1}

C_p is the specific heat at constant pressure = $1.012 \text{ J g}^{-1} \text{ K}^{-1}$

σ is the Stefan Boltzmann constant = $5.7 * 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$

r_b is the boundary layer resistance over the leaf ($\text{m}^2 \text{ s mol}^{-1}$)

ΔT is the leaf-air temperature difference

d - The stomatal resistance (r_s) may now be calculated

$$r_s = (e_l / e_o - 1) / W - r_b$$

where e_l is the saturated vapour pressure at leaf temperature

The stomata conductance (g_s) is the reciprocal of r_s ($g_s = 1 / r_s$).

e - The photosynthesis rate may now be calculated but first it is necessary to correct the analyser reading for the cross sensitivity to water vapour (The correction is detailed in both the LCA and DL2 manuals.)

$$C_c = C_o - EMAX * f_n C_o * (1 - e^{(-0.07 * e_o * 1000)})$$

where C_c is the corrected concentration and C_o is the measured concentration in vpm and EMAX is typically between 1 to 2 ppm

and $f_n C_o = (1 + 7.87 * 10^{-4} * C_o)$

The diluting effect of water vapour picked up in the leaf cuvette must now be eliminated.

$$C_c = P \cdot C_o / (P - e_o)$$

then the assimilation rate (A) $\text{mol m}^{-2} \text{ s}^{-1}$

$$A = (C_i - C_c) * W$$

where C_i is the concentration (VPM) in the dry air entering the leaf cuvette.

f - Finally the intercellular CO₂ concentration (C_i) may be calculated:

$$C_i = ((g_c - E / 2) * (C_c - A/g_c)) / (g_c + E / 2)$$

where $1 / g_c = 1.6 / g_s + 1.37 / g_b$

Measuring SPAD (Soil-Plant Analyses Development)

The chlorophyll meter (SPAD-502, Soil-Plant Analyses Development (SPAD) Section, Minolta Camera Co., Osaka, Japan) was used to measure the chlorophyll content of leaf at flowering stage. The chlorophyll meter provides a simple, quick, and non-destructive method for estimating leaf chlorophyll content (Watanabe et al., 1980 as cited by Shaobing Peng et al., 1992). The chlorophyll meter calculates the SPAD value based on the intensities of light transmitted in the red band (around 650 nm) where absorption by chlorophyll is high and in the infrared band (around 940 nm) where absorption is low (Minolta, 1989 as cited by Shaobing Peng et al., 1992).

Sampling and statistical analyses

One to two leaves per treatment were used for measurement of CO₂ assimilation at three moments: before, during drought stress and at flowering stage. In each treatment four plants were harvested before drought stress (40 days after sowing) and 5 plants were sampled at flowering stage (110 days after

sowing). The data were recorded as plant height, stem height, number of tillers, number and length of panicles, number of leaves and spikelets, Leaf Area Index and plant dry weight. The chlorophyll content of leaves was also measured at flowering stage on 3 leaves per plant. All data were tested statistically by using T-test to compare mean values (before drought stress) and F-test to compare variances (at flowering stage)

Simulation model

Dry matter yield was simulated by using an FST programme (FORTRAN Simulation Translator) (van Kraalingen, 1990), based on a linear interpolation of observed LAI (Leaf Area Index) and by integration of dry matter over time (Goudriaan, 1994).

Solar radiation in atmosphere was measured in $\text{MJ m}^{-2} \text{ d}^{-1}$. Solar radiation (R) in glass house was determined by using a transmissivity factor of 0.7 for glass house transmissivity (TAU). The light extinction coefficient k was estimated at 0.7. The fraction light interception by plants depends on its LAI and is characterized by inverting Beer's Law (Monsi & Saeki, 1953)

$$\text{FRABS} = 1 - e^{-k \cdot \text{LAI}}$$

Radiation Use Efficiency was estimated at 1 g MJ^{-1} . Initial dry matter was set at 0 g m^{-2} .

The model equations were:

$$\text{LAI} = \text{AFGEN}(\text{LAITB}, \text{TIME})$$

$$\text{FRABS} = 1 - \text{EXP}(-K * \text{LAI})$$

$$\text{BIOM} = \text{INTGRL}(\text{ZERO}, \text{GROWTH})$$

$$\text{GROWTH} = R * \text{TAU} * \text{RUE} * \text{FRABS}$$

Chapter 3

Results

Phenological characters of plants

Rice seeds were sown in fresh water. Seedling emergence was at 3 days after sowing. Tillers developed from the leaf axils at 26 days after sowing (DAS). Plants grown in fresh water reached 50% of tillering at 27 days after sowing, and in saline water at 29 days. In both mediums (fresh and saline water) flower emergence was at 101 days after sowing, reaching 50% of flowering 3 days later.

Morphological characters of plant

The dry weight of all plants in saline water was less than that of plants in fresh water. Leaf area of plants in saline water was smaller resulting in small leaf dry weight compared with that of plants in fresh water (Table 1).

Table 1. Dry weight of plants before drought stress (40 DAS)

	Leaf (g)	Stem (g)	Root (g)	R/S	Plant dry weight (g)	Dry weight (kg/ha)
Fresh water	1.403 *	1.293 *	0.752 *	0.28	3.448 *	861.88 *
Saline water	0.972	0.928	0.525	0.28	2.425	606.25

(*): Significant difference at 0.05

Although stem height of plants was equal in both mediums the stem weight of plants in saline water was less. The root of plants in saline water developed poorly compared with plants in fresh water so it was also less dry weight. However, the root - shoot ratio of plants in both mediums was the same.

The Leaf Area Index (LAI) of plants in saline water was significantly smaller than that of plants in fresh water (Table 2). However, this difference was not very large. The Leaf Area Ratio (LAR) of plants in saline water was significantly larger than that of plants in fresh water. The Leaf Weight Ratio (LWR) of plants in both mediums was equal. Leaf dry weight of plants in fresh water was much larger than that of plants in saline water so the Specific Leaf Weight (SLW, reciprocal of SLA) of these plants was higher than that of plants in saline water and consequently their Specific Leaf Area (SLA) was lower. Plants grown in fresh water had a higher number of tillers than plants in saline water. The height of plants in fresh water was also larger due to longer leaves. However, their stem heights were not different in both mediums.

Table 2. Morphological characters of plant before drought stress (40 DAS)

	LAI (m ² /m ²)	LAR (m ² /g)	LWR (g/g)	SLA (m ² /g)	SLW (g/m ²)	Number of tillers	Plant height (cm)	Stem height (cm)
Fresh water	1.182 *	0.0137	0.407	0.0338	29.667 *	3.95*	111.1*	36.6
Saline water	0.929	0.0154*	0.399	0.0393*	25.953	3.60	106.9	36.4

LAI and dry matter of plant in fresh water and saline water (Fig. 2a, b) were positively related ($R^2 = 0.85$ and 0.6, respectively). In fresh water (Fig. 2c) plants which had a large leaf area had also a high leaf dry weight ($R^2 = 0.9$) compared with that (Fig. 2d) of plants in saline water ($R^2 = 0.8$).

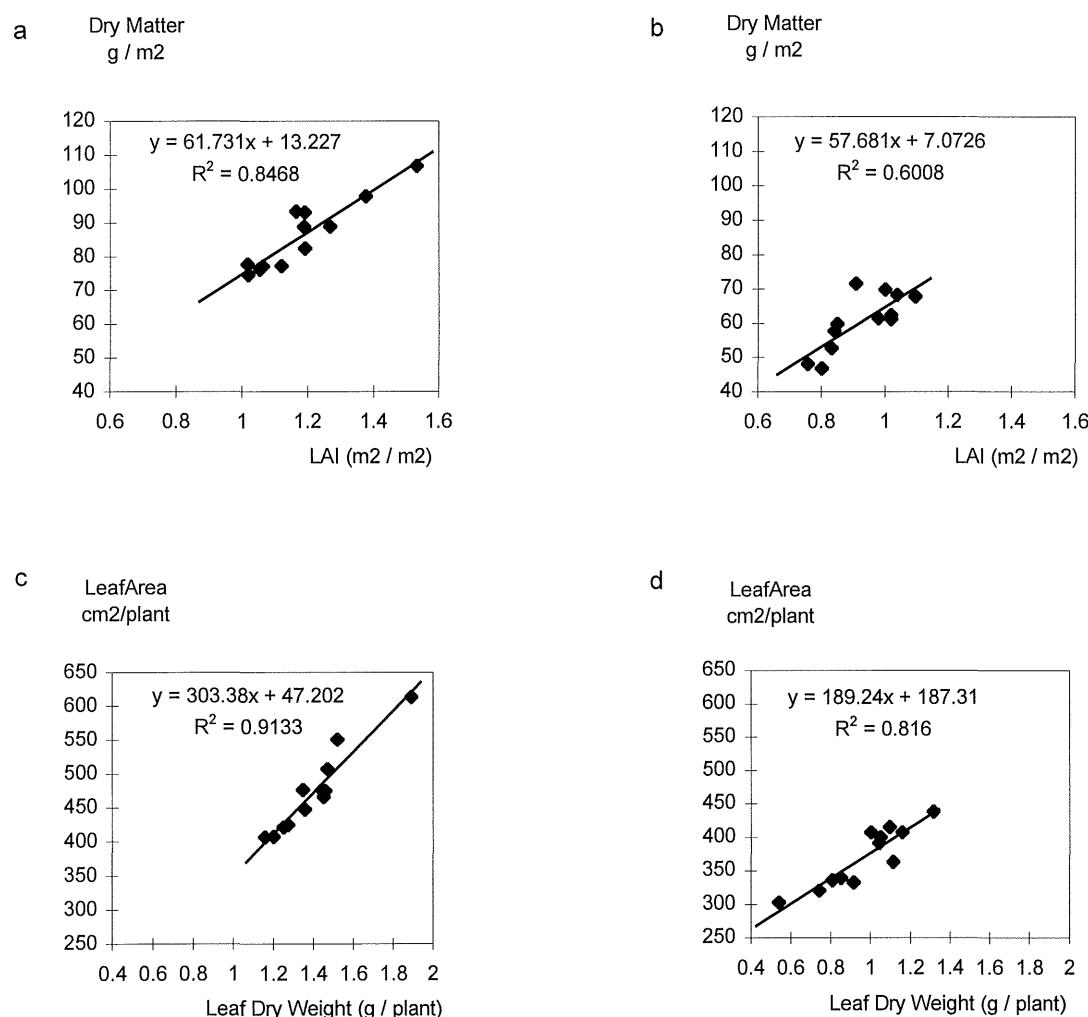


Fig. 2. Relation of LAI and Dry matter (a,b), Leaf area and Leaf dry weight (c,d) of plant in fresh and saline water before drought stress.

Table 3. Dry weight of plant at flowering stage (110 DAS).

	Dry weight of plant (g)	Dry weight (kg / ha)
Fresh water		
No drought	26.975 a	6743.7 a
10 days of drought	25.610 ab	6402.5 ab
15 days of drought	25.018 b	6254.5 b
20 days of drought	25.033 b	6258.2 b
Saline water		
No drought	22.221 cd	5555.3 cd
10 days of drought	23.310 c	5827.5 c
15 days of drought	21.203 de	5300.7 de
20 days of drought	20.018 e	5004.5 e
LSD (0.05)	1.3728	343.4145
CV (%)	3.3	3.3

Note: The same letter means that there is no significant difference

At flowering stage plant dry weight (Table 3) was affected by saline water and drought stress ($P < 0.01$). In fresh water plants without drought stress gave significantly higher dry weight than that of plants under 15 or 20 days of drought stress. In saline water the smaller dry weight was recorded on plants under 15 or 20 days of drought. In this medium the effect of drought was not strong on plants under 0, 10 and 15 days of drought. The reduction of dry weight of plants in fresh water negatively related to time of drought stress ($R^2 = 0.9$). Plants in saline water ($R^2 = 0.46$) also showed the same pattern in reduction of dry matter under drought stress periods (Fig. 3a).

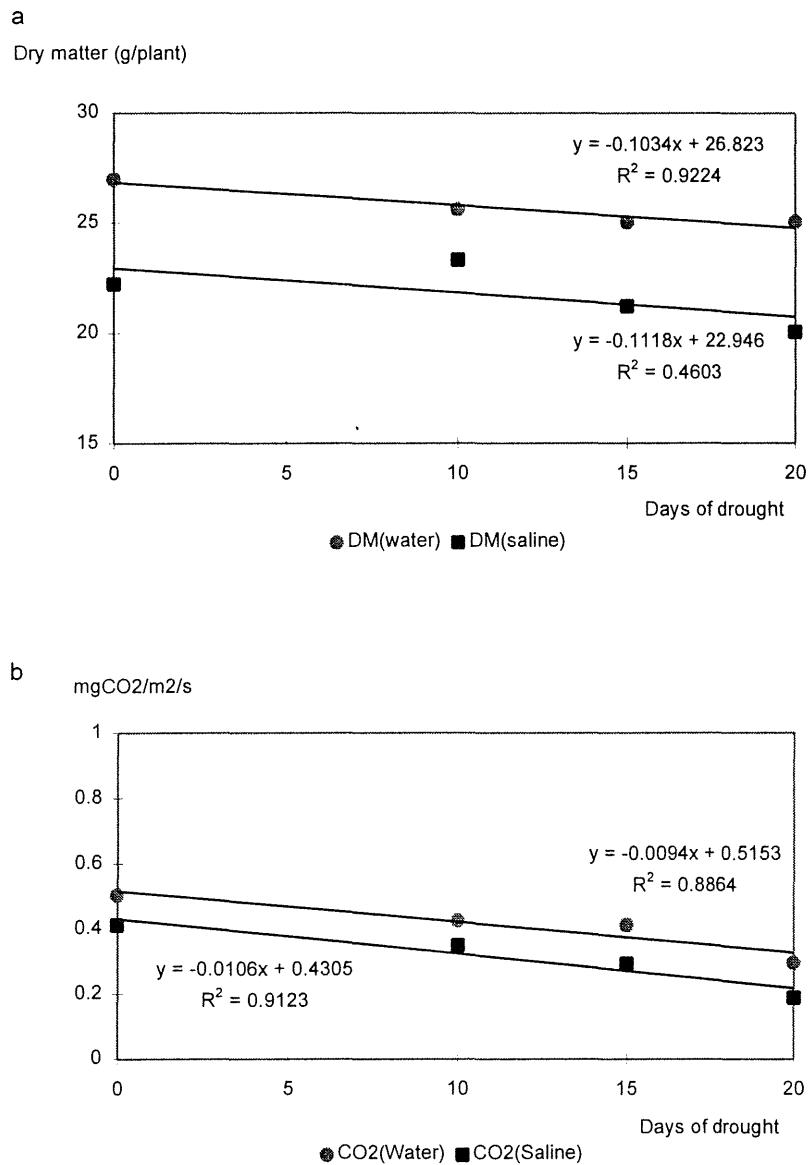


Fig. 3. Reduction in dry matter production (a) and CO₂ assimilation (b) of plants in fresh and saline water under drought stress periods. The symbol is mean value of replicate.

The decrease of CO₂ assimilation of leaves of plants showed the same pattern with dry matter, in fresh water ($R^2 = 0.89$) and saline water ($R^2 = 0.9$) in durations of drought stress (Fig. 3b).

Leaf dry weight (Table 4) of plants at flowering stage was affected by salt stress ($P < 0.01$). Plants under levels of drought in the same medium had similar leaf dry weight. However, plants in fresh water had leaf dry weight larger than that of plants in saline water except for plants under 10 days of drought stress in both mediums.

Saline water and drought stress reduced stem dry weight of plant ($P < 0.01$) at flowering stage, the highest stem dry weight was recorded on plants in fresh water without drought stress. Although stem dry weight of plants in fresh water under 10, 15 and 20 days of drought stress was similar their stem dry weight was higher than that of plants grown in saline water. In saline water plants under 10 days of drought stress had a similar value of stem dry weight as plants without drought stress, in this medium stem dry weight of plants under 15 and 20 days of drought stress was not different which gave smallest stem dry weight.

The effect of salinity and drought on root dry weight of plants was complicated. In fresh water root dry weight of plants under 0, 10, and 20 days was not different except for plants under 15 days of drought that gave smaller root dry weight than control plants. Plants in fresh water without drought stress also showed the largest root dry weight compared with plants in saline water under 0, 15 and 20 days of drought.

Dry weight of panicle was affected by drought stress ($P < 0.01$) and saline water ($P = 0.03$). There was interaction between drought and salinity on dry weight of panicles of plants ($P = 0.03$). In fresh water panicle dry weight of plants without drought stress was higher than that of plants under 10 and 20 days of drought stress, however they showed the same value when compared with plants in saline water under 0 and 15 days of drought stress. Smallest panicle dry weight was recorded on plants in saline water under 20 days of drought. In this medium

panicle dry weight of plants under 0 and 15 days of drought stress was higher than that of plants under 10 days of drought.

Due to the difference of dry weight in leaves, stem and root, the root - shoot ratio of plant was also different among treatments ($P = 0.04$). Root - shoot ratio of plants in fresh water was not different. In saline water this ratio of plants under 10 days of drought stress was higher than that of plants in fresh and salinity under 15 and 20 days of drought, respectively. However, the comparison of root - shoot ratio of plant in both mediums without noticing levels of drought stress resulting in a insignificant difference.

Table 4. Dry weight of plant parts at flowering stage (110 DAS).

	Total leaf (g)	Stem (g)	Root (g)	Panicle (g)	Root Shoot ratio
Fresh water					
No drought	7.321 a	12.509 a	4.913 a	2.232 a	0.22 abc
10 days of drought	7.133 ab	11.725 b	4.737 ab	2.015 bc	0.23 ab
15 days of drought	7.393 a	11.692 b	3.785 bcd	2.148 ab	0.18 bc
20 days of drought	7.476 a	11.264 b	4.443 abc	1.849 c	0.22 abc
Saline water					
No drought	6.017 c	10.069 c	3.884 bc	2.252 a	0.21 abc
10 days of drought	6.592 bc	10.227 c	4.627 ab	1.865 c	0.25 a
15 days of drought	6.131 c	9.280 d	3.577 cd	2.215 a	0.20 abc
20 days of drought	6.332 c	9.331 d	2.868 d	1.487 d	0.17 c
LSD (0.05)	0.6216	0.5482	0.9719	0.1918	0.0554
CV (%)	5.22	2.9	13.53	5.47	14.0

Note: R / S = Root dry weight / (Leaf + Stem and Panicle dry weight)

LAI at flowering stage (Table 5) was affected by salinity ($P < 0.01$), whereas the effects of drought treatments were small or even absent in both fresh and saline water mediums.

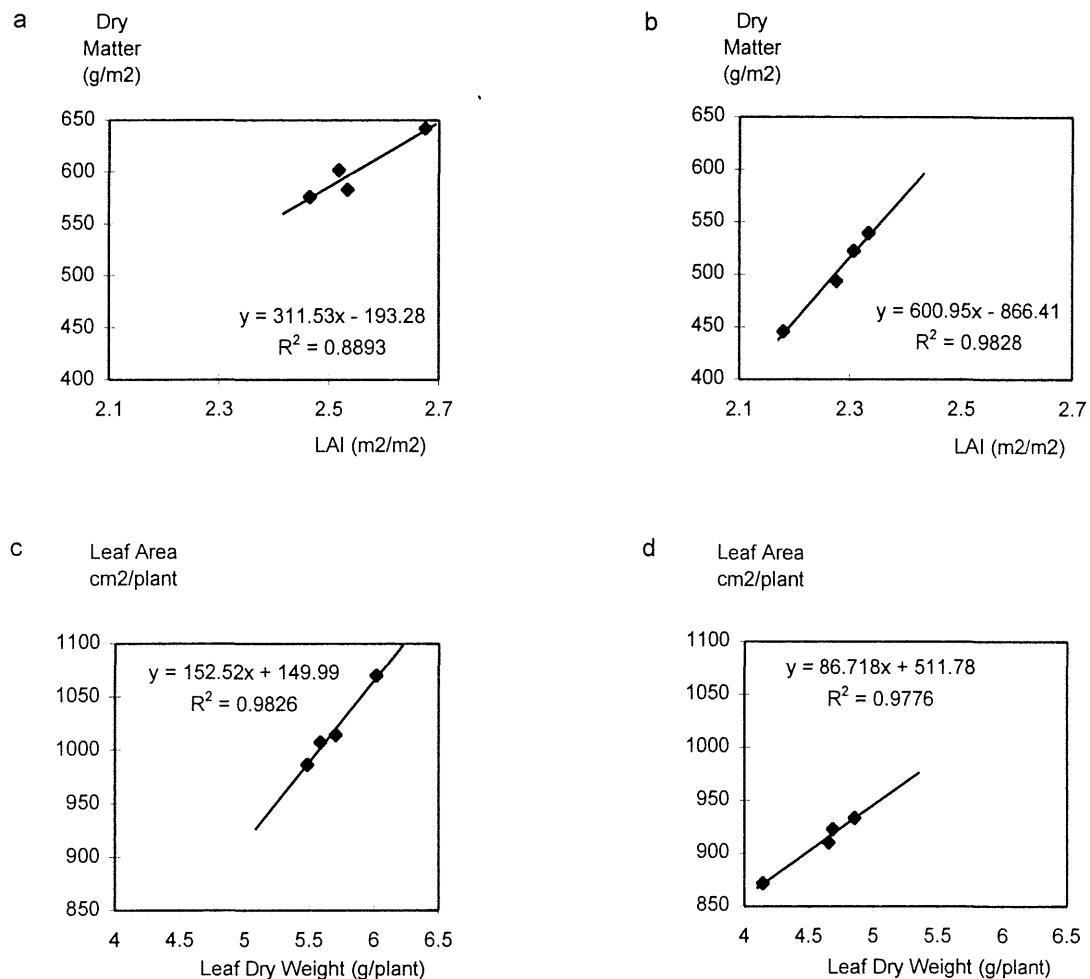


Fig. 4. Relation of LAI and Dry matter (a,b), Leaf area and Leaf dry weight (c,d) of plant in fresh and saline water at flowering stage.

LAI of plants in saline water was not different and it was also same for plants in fresh water under levels of drought stress. However, all plants in fresh water had LAI higher than that of plants in saline water under 20 days of drought. The positive relation of LAI and dry matter (Fig. 4a, b) was recorded on plants in fresh and saline water ($R^2 = 0.89$ and 0.98 , respectively). The relation between leaf area and leaf dry weight (Fig. 4c, d) of plants in fresh and saline water medium at this stage was also quite close ($R^2 = 0.98$ and 0.98 , respectively).

Table 5. Morphological characters of plants at flowering stage (110 DAS)

	LAI (m ² /m ²)	LAR (m ² /g)	LWR (g/g)	SLA (m ² /g)	SLW (g/m ²)	SPAD
Fresh water						
No drought	2.675 a	0.00417 b	0.2347	0.0178 c	56.358 a	38.3
10 days of drought	2.518 abc	0.00418 b	0.2321	0.0181 bc	55.449 ab	38.9
15 days of drought	2.535 abc	0.00435 b	0.2443	0.0178 c	56.192 ab	39.2
20 days of drought	2.466 abcd	0.00428 b	0.2382	0.0180 bc	55.718 ab	38.8
Saline water						
No drought	2.307 cde	0.00441 b	0.2244	0.01966 ab	51.028 bc	38.5
10 days of drought	2.334 bcde	0.00435 b	0.2258	0.01924 abc	52.135 abc	39.1
15 days of drought	2.276 de	0.00462 ab	0.2363	0.01955 abc	51.163 abc	39.1
20 days of drought	2.179 e	0.00489 a	0.2327	0.02105 a	47.586 c	39.5
LSD (0.05)	0.2349	0.0004699		0.001848	5.304	ns
CV (%)	5.57	6.09		5.59	5.69	

Note: SPAD (Soil-Plant Analyses Development)

ns: non significant difference

LAR and SLA of plants (Table 5) were also affected by salt stress ($P = 0.01$ and $P < 0.01$, respectively). The same value of LAR was recorded in all plants in fresh water and plants in saline water under 0, 10 and 15 days of drought. In this medium the highest values of LAR was in plants under 20 days of drought compared with that of plants in both mediums except for plants under 15 days of drought stress.

SLA of plants in fresh water was similar and it was also same case for plants in saline water under levels of drought. The high value of SLA was recorded on plants in saline water without drought compared with all plants in fresh water under levels of drought especially for plants under 0 and 15 days of drought.

Salt stress also played a role in the difference SLW among treatments ($P < 0.01$). The high value of SLW of plants corresponded to small value of their SLA in both mediums. Plants grown in fresh water had the same LWR and plants grown in saline water had also similar LWR.

In saline water plants grown under 20 days of drought stress had the smallest SLW, much smaller than that of all plants in fresh water under levels of drought. The LWR was similar in all plants in both mediums.

The chlorophyll content of leaf was measured at flowering stage by using SPAD (Soil-Plant Analyses Development) resulting in the same value among treatments. At flowering stage the result indicated that saline water caused a difference on value of stem height (Table 6), number of panicle and length of panicle ($P = 0.02$, $P = 0.02$ and $P = 0.01$, respectively).

In the same medium stem height of plants (Table 6) under levels of drought was not different. However, stem height of plants in fresh water under 0 and 15 days of drought was shorter than that of plants in saline water under 10 days of drought stress.

Table 6. Morphological characters of plant at flowering stage (cont.)

	No. of tiller	Plant height (cm)	Stem height (cm)	No. of green leaf	No. of death leaf	Total leaf	No. of panicle	Length of panicle (cm)	No. of spikelet per panicle
Fresh water									
No drought	3.9	172.9	135.4 c	20.9	16.5	37.4	3.9 a	22.5 c	130.7
10 days	3.8	175.8	140.8 abc	19.7	16.1	35.7	3.7 ab	22.8 abc	129.2
15 days	3.8	178.9	138.0 bc	19.8	17.0	36.8	3.7 ab	22.7 abc	140.2
20 days	3.9	172.4	138.4 abc	19.7	17.6	37.3	3.8 ab	22.1 c	124.0
Saline water									
No drought	3.6	175.3	139.5 abc	19.1	14.9	34.0	3.3 b	23.4 abc	126.2
10 days	3.7	177.6	143.9 a	18.9	15.7	34.6	3.4 ab	23.7 ab	134.2
15 days	3.6	178.6	141.4 ab	19.7	16.1	35.8	3.4 ab	23.8 a	121.5
20 days	3.7	172.2	141.5 ab	20.0	17.5	37.5	3.5 ab	22.8 abc	117.3
LSD (0.05)	ns	ns	5.546	ns	ns	ns	0.5702	1.156	ns
CV (%)			2.26				9.1	2.87	

The number of panicle of plants in both mediums under 10, 15 and 20 days of drought was not different but plants in fresh water without drought stress had more panicles than that of plants in saline water at the same level of drought.

The length of panicle of plants in fresh water was similar and it was also same for plants in saline water. However, plants in saline water under 10 and 15 days of drought was significantly higher than that of plants in fresh water under 20 days of drought stress. Drought or saline water did not affect other morphological characters such as plant height, number of tillers, leaves or number of spikelet at flowering stage.

Physiological characters of plants

The CO₂ assimilation rate of single leaves

Table 7. CO₂ assimilation of single leaves before drought stress (40 DAS) and at flowering stage (110 DAS).

	Assimilation (mg CO ₂ /m ² /s)	Transpiration rate (mg H ₂ O/m ² /s)	Stomatal conductance (mm/s)
Before drought			
Fresh water	0.588 *	77.94	21.92
Saline water	0.393	74.68	14.02
Flowering			
Fresh water	0.420	105.58	49.21
Saline water	0.432	107.71	57.77

The assimilation of single leaves was measured before, during drought stress, and at flowering stage. Before drought stress average assimilation rate of leaves on plants in fresh water was significantly higher than that of plants in saline water (P = 0.05). The average stomatal conductance rate of leaves on plants in fresh water was also higher than plants in saline water, however the significant difference was not large (P = 0.1). Transpiration rate of leaves was not correlated to assimilation at this stage.

At flowering stage the photosynthesis process of leaves was not different among treatments (Table 7).

Table 8. Comparison of leaf assimilation rate in stages of without drought (before drought and at flowering stage) and under durations of drought stress.

Duration	Assimilation (mg CO ₂ /m ² /s)	Transpiration rate (mg H ₂ O/m ² /s)	Stomatal conductance (mm/s)
Fresh water			
Before and after drought	0.504 a	91.76 bc	35.57 a
10 days of drought	0.425 b	112.46 ab	26.42 abc
15 days of drought	0.409 b	127.81 a	31.15 ab
20 days of drought	0.297 c	84.67 c	7.14 d
Saline water			
Before and after drought	0.412 b	91.19 bc	35.90 a
10 days of drought	0.353 bc	99.18 bc	14.14 cd
15 days of drought	0.293 c	112.63 ab	21.08 bc
20 days of drought	0.187 d	55.16 d	3.85 d
LSD (0.05)	0.07832	22.14	12.82
CV (%)	11.24	13.05	33.39

The photosynthesis process of leaves in stages of before drought and at flowering (where plants were well watered) compared with that of plants in durations of drought stress (Table 8) the result showed that CO₂ assimilation of leaves was affected by both, drought stress duration and salinity ($P < 0.01$). Salinity and drought also affected on transpiration of leaves ($P = 0.01$ and $P < 0.01$, respectively), and stomatal conductance rate ($P = 0.05$ and $P < 0.01$, respectively).

Before and after drought stress (at flowering stage) where plants in well-watered condition, plants in fresh water had higher value of CO_2 assimilation compared with other plants which were under levels of drought in both mediums. In fresh water the smallest value of CO_2 assimilation was recorded on plants under 20 days of drought and it was similar situation for plants in saline water under the same level of drought. In fresh water transpiration rate of leaves of plants under 20 days of drought was smaller than that of plants under 10 and 15 days of drought. In saline water the smallest value of transpiration rate was on plants under 20 days of drought. Stomatal conductance rate was not different on plants in fresh water before and after drought compared with plants under 10 and 15 days of drought. Plants under 20 days of drought had smallest value of stomatal conductance rate. In saline water plants before and after drought gave higher value of stomatal conductance than that of plants under levels of drought. Smallest value of stomatal conductance was on plants under 20 days of drought

Fig. 5 shows the time course of leaf photosynthesis during drought stress periods (10, 15 and 20 days). Photosynthesis was decreased during dry periods and then increased after water deficit was relieved.

Under drought stress CO_2 assimilation was positively correlated with stomatal conductance of leaf ($R^2 = 0.7$, Fig. 6 b) while before drought stress and flowering stage their relation were looser ($R^2 = 0.5$, $R^2 = 0.5$, Fig. 6 a and c, respectively).

Relation of assimilation, transpiration and stomatal conductance rate.

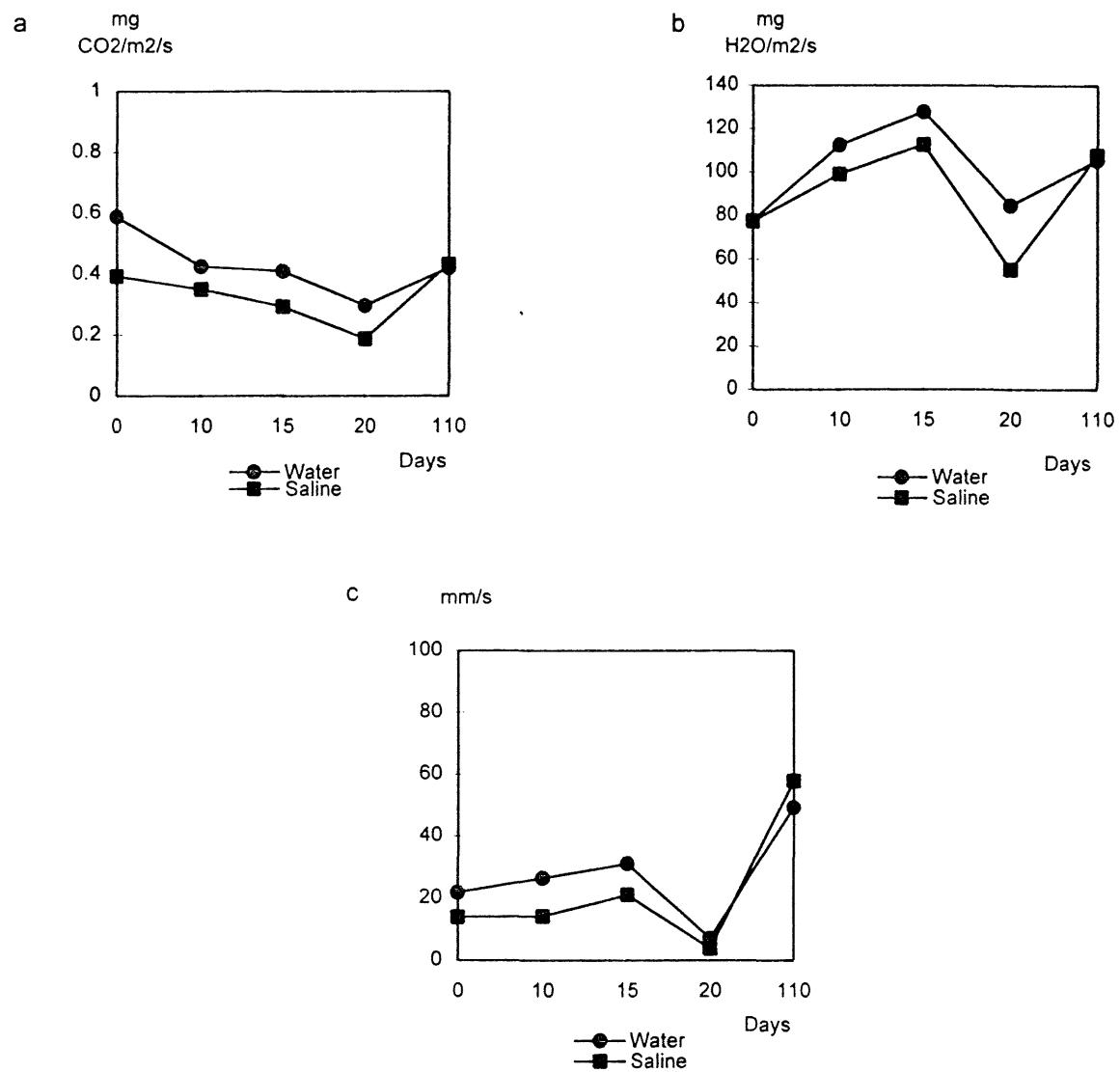


Fig. 5. CO₂ assimilation (a) transpiration (b) and stomatal conductance rate (c) of single leaves before and during drought stress, and at flowering stage.

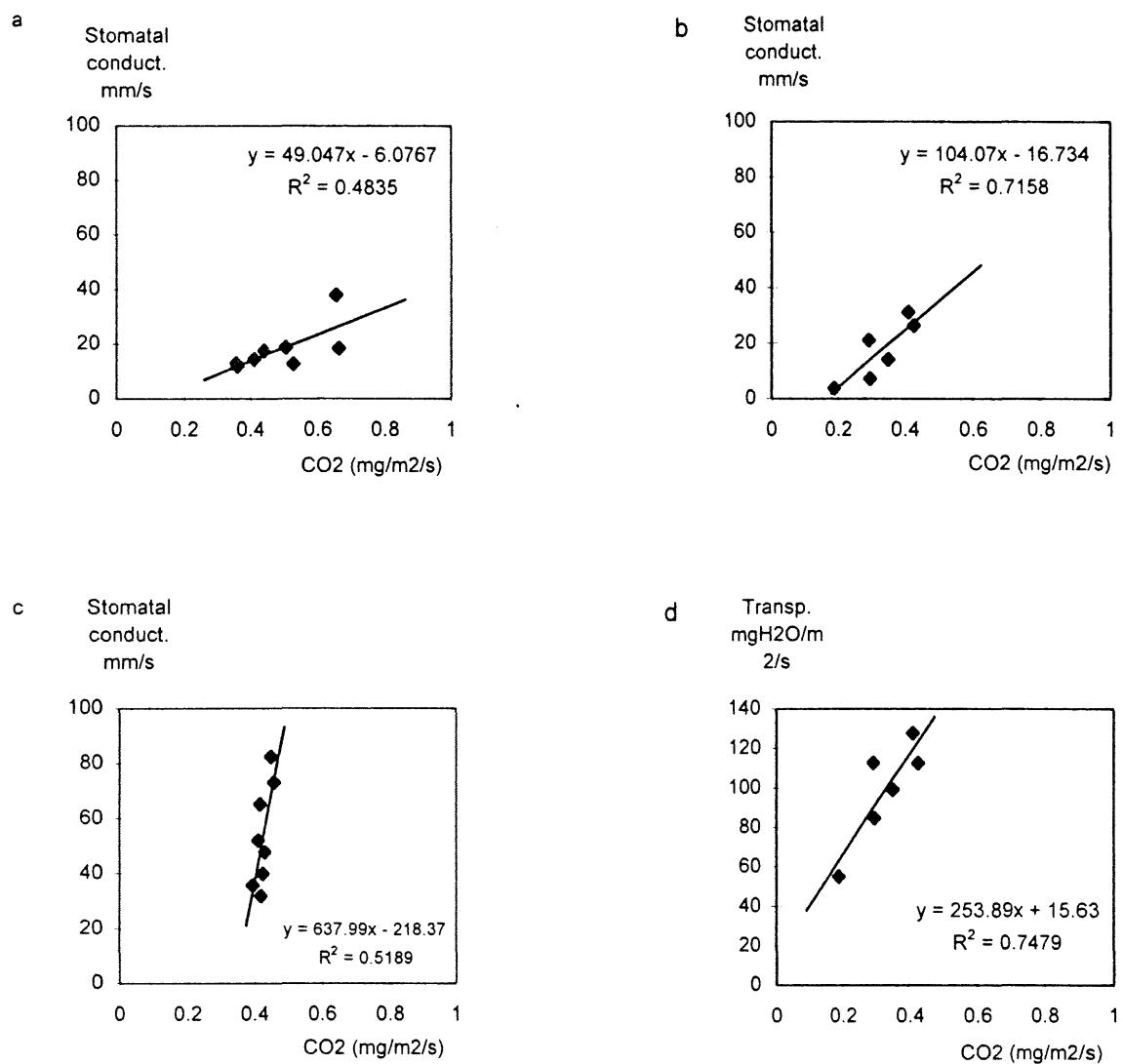


Fig. 6. The relation between assimilation and stomatal conductance rate of single leaves before (a), under levels of drought stress (b), at flowering stage (c), and the relation between assimilation and transpiration rate of leaves under levels of drought stress (d).

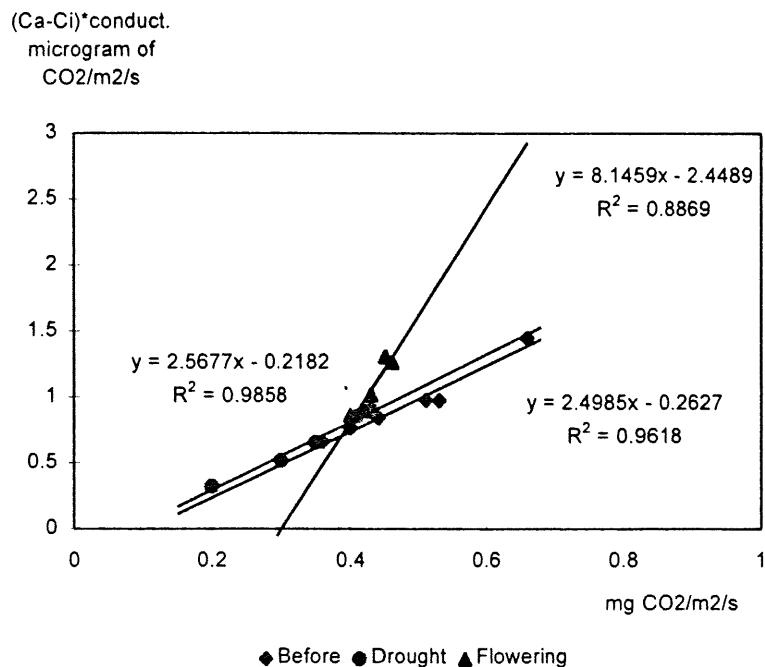


Fig. 7. The assimilation versus $(Ca - Ci) *$ stomatal conductance rate of single leaves before, during drought stress and at flowering stage where Ca is CO_2 in leaf chamber, Ci is CO_2 in stomates.

Transpiration rate of leaves before drought stress and at flowering was not correlated to CO_2 assimilation rate but it was during drought stress periods ($R^2 = 0.75$. Fig. 6 d). The result also showed that CO_2 assimilation before ($y = 2.4985x - 0.2627$, $R^2 = 0.96$), under levels of drought ($y = 2.5677x - 0.2182$, $R^2 = 0.98$) and at flowering ($y = 8.1459x - 2.4489$, $R^2 = 0.89$) was closely correlated to stomatal conductance and concentration of CO_2 ($Ca - Ci$) where Ca is CO_2 from the air goes into leaf chamber, Ci is CO_2 in stomates (Fig. 7). When CO_2 concentration increased in stomates (Fig. 8a) it led to an

increase in assimilation rate of leaf ($R^2 = 0.6$). The increase of stomatal conductance rate positively correlated to reciprocal of vapour pressure deficit (VPD) ($R^2 = 0.9$, Fig. 8 b). At before (Fig. 9a) and during drought stress periods (Fig. 9b), and at flowering stage (Fig. 9c) assimilation rate of leaves was positively correlated with humidity ($R^2 = 0.6$, 0.7 and 0.6, respectively). During drought stress the rate of stomatal conductance and transpiration of leaves were also affected by humidity (Fig. 9d, $R^2 = 0.65$ and 0.7, respectively).

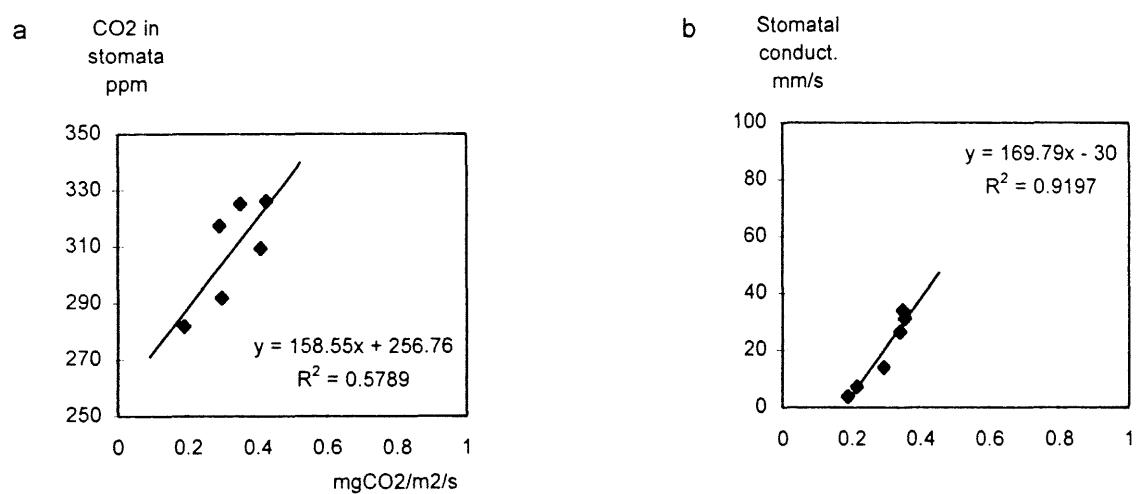


Fig. 8. Assimilation versus CO₂ in stomates (a) and the relation (b) between stomatal conductance and reciprocal of 1+VPD/VPDk (where VPDk = 5 mbars) in drought stress periods.

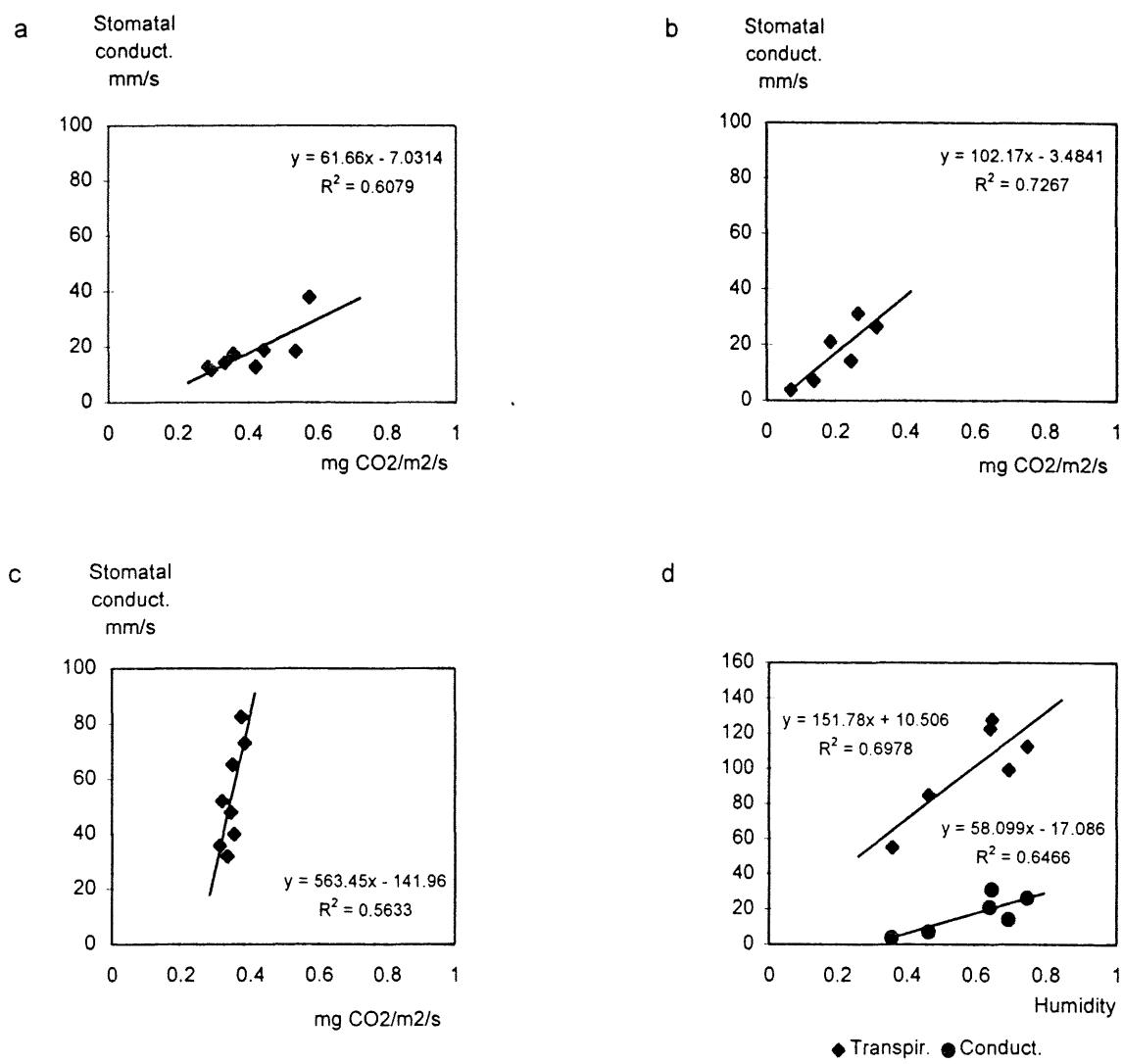


Fig. 9. The effect of humidity on stomatal conductance rate of single leaves (Stomatal conductance versus assimilation rate * humidity) before (a) during drought stress (b), and at flowering (c). Relation of humidity, transpiration and stomatal conductance rate in drought stress periods (d).

Application of model

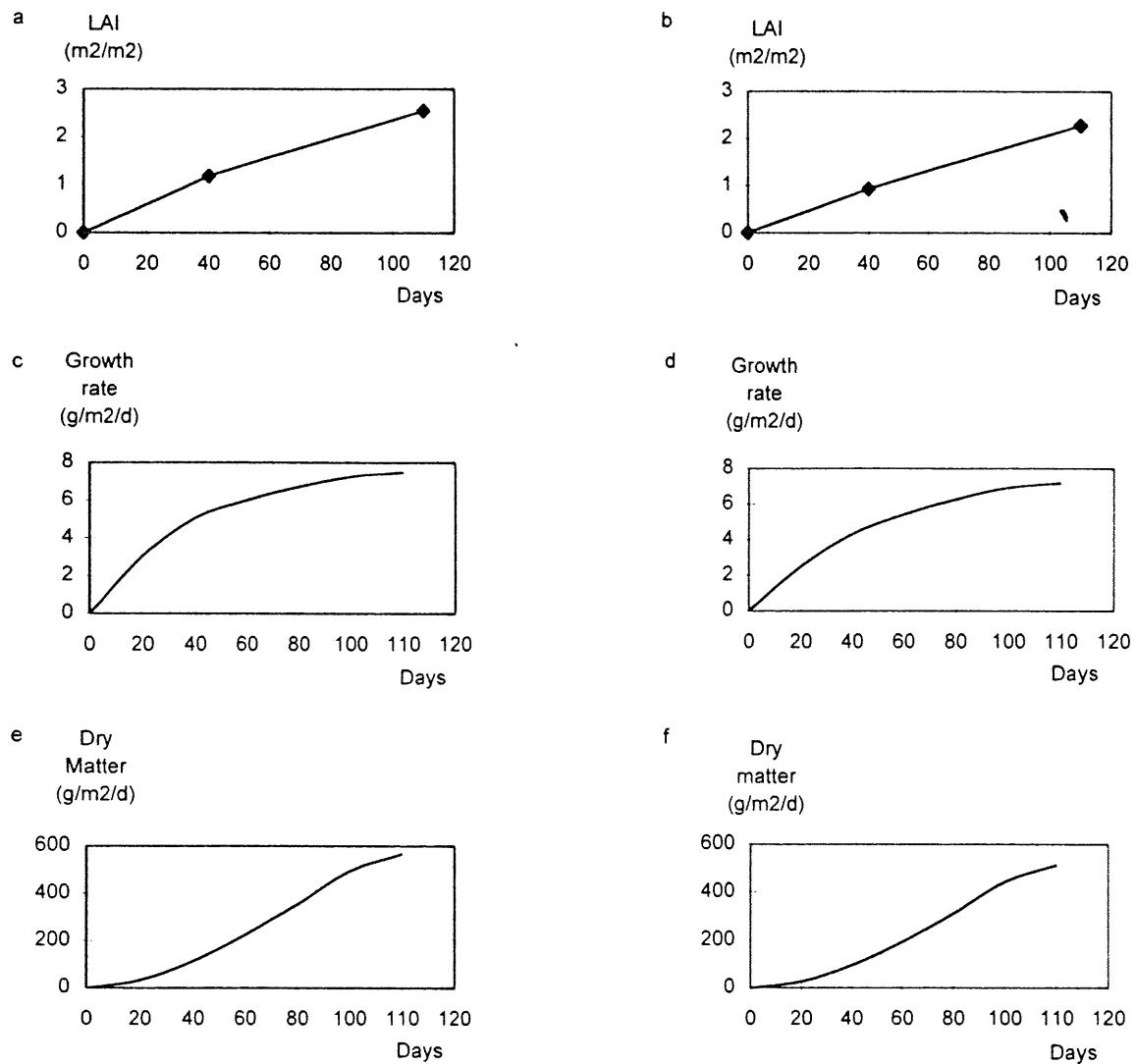


Fig. 10. LAI versus time for plants in fresh water (a) and in saline water (b). Simulation of growth rate of plants in fresh water (c) and in saline water (d). Simulation of dry matter production of plants in fresh water (e) and in saline water (f).

Table 9. Comparison of observed and simulated dry matter yield

	Observed yield (tons/ha)	Simulated yield (tons/ha)
Fresh water		
No drought	6.744	5.722
10 days of drought	6.403	5.774
15 days of drought	6.255	5.675
20 days of drought	6.258	5.522
Mean yield	6.415	5.673
Saline water		
No drought	5.555	5.217
10 days of drought	5.828	5.097
15 days of drought	5.301	5.158
20 days of drought	5.005	5.001
Mean yield	5.422	5.118

The model was based on a linear increase of LAI as a function of time calculated by interpolation. The result showed that average simulated dry matter yield of plants in fresh water was less than observed dry matter yield at 0.742 tons / ha while in case of plants in saline water the difference was smaller at 0.304 tons / ha. The simulated yield of plants in saline water under 20 days of drought stress was almost same as observed yield.

The calibrated value of Radiation Use Efficiency can be estimated from the ratio between observed and simulated yield resulting in 1.13g/MJ for plants in fresh water and 1.06g/MJ for plants in saline water.

Chapter 4

Discussion and conclusions

Phenological and morphological characters

During the growth period the average radiation (outside glass house) gradually dropped from August (16.84 MJ m^{-2}) to October (5.99 MJ m^{-2}). The air temperature was kept quite suitable for rice growth (28.8°C). The plants flowered at about 101 days after sowing compared with a total growth duration in tropical weather (Mekong Delta, South of Vietnam) of about 139 days after sowing at the end of July (Mekong Delta Farming Systems Research and Development Institute, 1995). the days to tillering and flowering of plants was normal for rice in tropical areas. The normal progress in phenological phases of plants reflected a main effect of temperature.

Basically, high temperatures increase the rate of leaf emergence, and provide more tiller buds but under low light condition, some of the tiller buds may not develop into tillers because of lack of carbohydrates necessary for growth (Yoshida, 1981). In addition, under most conditions water temperature (in pot in this case) can be higher than air temperature so leaf elongation and plant height growth may be affected by both air and water temperatures because the growing points of leaves, tillers and panicles are under water. Leaves of plant in both mediums became droopy and stems tended to lodge from early stage of growth until flowering. Moreover, because of the small pots the plants had not enough soil to ensure a normal growth compared with field conditions.

The tillering capacity of plants in both mediums was very poor during growth stages (an average value of about 4 per hill) while in a suitable growth condition tiller potential of plant can reach a value of 40 (Yoshida, 1981). In tropical conditions (Mekong Delta, South of Vietnam) this variety could give a

number of tiller of 11 per hill when they were grown in July (Mekong Delta Farming Systems Research and Development Institute, 1995) or in Northern Thailand it was 12 tillers per hill (Mankeb, 1993). The poor tillering certainly caused less final dry matter production of plant.

Before drought plants in saline water were shorter due to salt stress, because of short leaf length. At flowering stage stem height (culm height) of plants in saline water showed a higher value compared with that of plants in fresh water. However, plant height in both medium was similar. This means that leaf length of plants in saline water was still less than that of plants in fresh water. Although plants in saline water had a tall stem at flowering stage their stem were thin and their number of panicle was less. These effects may be due to the dry matter partitioning in plant parts to maintain balance in growth. It also indicates that effect of drought did not extend to the flowering stage.

The seedlings were grown in saline water from an early stage (10 days after sowing). Although the salt concentration in the water was not very high (about 3.5 mmho/cm) it still affected plant growth, apparently because rice is very sensitive to salt at an early stage after germination. Compared with fresh water, saline water caused a decrease of leaf area of plants. Although plants were under three periods of drought the effect of drought on leaf area did not extend to flowering stage so the difference of LAI at flowering stage was caused by the same factor as before drought stress (salt stress). LAI of plants in both mediums at flowering stage was less than $3 \text{ m}^2 \text{ (leaf) m}^{-2} \text{ (ground)}$ while a LAI of 5-6 is necessary to achieve maximum crop photosynthesis during the reproductive stage (Yoshida, 1981) or a value of $3 \text{ m}^2 \text{ (leaf) m}^{-2} \text{ (ground)}$ is needed for a average crop at linear phase (Goudriaan, 1994). Small LAI of plants in saline water affected light interception so the loss of production may be affected by less photosynthesis under osmotic stress which finally induced a small total dry matter (Fig. 2a,b; Fig. 4a,b). Leaf area ratio (LAR) measures the leafiness of plant. Before drought stress salt caused a decrease of leaf area and

plant weight but more so for dry matter than for leaf area so that LAR and SLA were increased. LAR of plants in both medium at flowering stage was smaller than that of plants before drought stress because of death of leaves at this stage.

The salt tolerance of rice progressively increases during tillering and elongation and decreases at flowering (Yoshida, 1981). Before drought stress when plants were in tillering stage salt stress did not affect the expansion of their foliage resulting in a similar value of LWR among plants in both mediums. The same above result was also recorded at flowering stage.

As before drought SLA of plants in saline water was also reduced by salt stress at flowering stage . SLA lied in a range from 0.03 (before drought stress) to about 0.02 (at flowering stage) compared with normal condition where values of SLA for rice varieties range from 0.02 to 0.045 m^2/g (Yoshida, 1981).

SLW is the reciprocal of SLA and comments made for SLA are equally applicable to SLW. The high value of SLW of plants in fresh water compared with that of plants in saline water at both stages (before drought and flowering stage) may be due to effect of salt on leaf area and decreasing leaf weight (Fig. 2c,d; Fig. 4c,d), by restriction of translocation of nutrients in leaves and a decrease of the accumulation of protein and cell wall material (hemicellulose). Also salt may have affected transpiration rate and influenced the movement of ions from the soil to the plant leaves.

The observations showed that the stems of plants in saline water were thinner than those of plants in fresh water (in both stages of observation). This may be a consequence of less carbohydrate accumulation in stems (and leaf sheaths), resulting in less stem dry weight, even the stem height of plants in salt water was a little bit higher than that of plants in fresh water at flowering stage.

The root length was not recorded. However, root hair development of plants may be influenced by saline water and drought stress.

This may lead to a limitation of water and nutrient uptake. When salinity is increased suddenly (by drought stress), water uptake by the plant may be temporarily impaired due to the low osmotic potential of the soil solution. Because water absorption is proportional to soil water potential, under drought stress the concentration of salt increases simultaneously with water shortage, which causes a more serious decrease of rate of water absorption, resulting in less roots and also in other plant parts. Before drought stress, dry weight of leaf, stem and root among plants in fresh and saline water were similarly affected so that root-shoot ratio of plants in both medium was very similar. Although at flowering stage this ratio of plants in both mediums was not very different drought stress affected root-root ratio of plants after a long water shortage (20 days).

The difference of leaf area contributed to the difference of dry weight of panicles by a limited production of carbohydrates.

Physiological characters

In general the CO_2 assimilation of leaves correlated positively with stomatal conductance rate (Fig. 6a,b,c). Because salt stress caused the stomates to close, salinity caused a decrease in leaf photosynthesis compared with plants in fresh water at least before drought stress. However, at flowering stage leaf photosynthesis was the same in plants in both mediums, corresponding to similar values of chlorophyll content in leaves. This may be related to the sensitiveness or tolerance of plants to salt at different development stages. Rate of net photosynthesis per unit area of leaf declines under saline condition (Flowers, 1985; Yeo et al., 1985a; Rawson, 1986). However, the impact of salt on photosynthetic mechanism of leaf is still not well understood (Cherry, 1989). During drought stress stomatal resistance of leaves increased, causing a decline of assimilation rate. Beside that the osmotic stress by drought and salt contributed to its influence on assimilation rate of leaves (Fig. 5). Under

different levels of drought opening of stomates also varied, an increase of stomatal conductance and internal CO_2 in stomates led to an increase of CO_2 assimilation rate of leaves (Fig. 7, Fig. 8a).

Transpiration occurs mainly through stomates and to a much lesser extent through the cuticle. Thus, the transpiration is controlled primarily by the opening and closing of stomates. A high rate of transpiration implies that stomates are open which makes a high rate of assimilation possible. During drought stress, plants were under an increase of salt concentration, resulting in a decrease of transpiration leading to decrease of CO_2 assimilation per unit leaf area, because there was a positive correlation between CO_2 assimilation and transpiration rate of leaf (Fig. 6d). Moreover, during drought stress periods when vapour pressure deficit increased stomatal conductance was decreased (Fig. 8b). In other words, dry air condition can cause a decrease of CO_2 assimilation compared with that in humid air. This corresponded to a positive correlation of stomatal conductance and humidity (Fig.9).

The LAI was measured at 2 stages, before drought stress (40 days after sowing) and at flowering stage (110 days after sowing). The prediction of model on dry matter of plants in both mediums showed a good fit especially for plants in saline water (Table 9, Fig. 10). This means that most of the difference in dry matter can be explained by the difference in LAI.

The difference of calibrated value of RUE between plants in fresh and saline water was 0.07 g MJ^{-1} . It implies that RUE of plants in saline water was less than that of plants in fresh water due to effect of salt stress which caused a decrease of LAI. If RUE of plants in saline water was 0.9 g MJ^{-1} instead of 1 g MJ^{-1} as the model did, the simulated yield of plants in saline water would become $4.606\text{ tons ha}^{-1}$. In this case the difference between observed and simulated yield of plants in saline water was $0.816\text{ tons ha}^{-1}$ compared with that of plants in fresh water at $0.742\text{ tons ha}^{-1}$. In addition, the difference of

observed yield between plants in fresh and saline water was 0.993 tons ha^{-1} and in case of simulated yield (with $RUE = 0.9 MJ^{-1}$ for plants in saline water) it hold 1.067 tons ha^{-1} . This indicated that RUE was hardly affected by the treatments.

One of the reasons that caused the difference between observed and simulated yield may be death of leaves, because the model calculated plant dry matter based on green leaf area while the observed yield included dead leaves at harvesting time. This means that the contribution of dead leaves to build up plant dry matter was not taken into account during calculation.

The limitation of study is the water potential of leaves was not determined so the relation between photosynthesis process and leaf water potential under combination effect of drought and salt stress that did not know. Moreover, the grain yield was also not harvested so the damage of drought and salt stress caused on final yield of plant is not well understood.

Conclusions

Salt stress was imposed at early stage of rice development so it affected negatively green leaf area during vegetative and reproductive stages. However, a decrease of leaf photosynthesis was recorded at earlier stage but not at later stage. During drought stress periods, both water deficit and salinity acted as limiting factors to assimilation of leaves resulting in a decrease of leaf photosynthesis. At this time water shortage combined with an increase of salt concentration influenced more seriously plant growth, even though drought was not very serious, and drought stress was relieved far ahead of flowering stage, yet salt and drought stress still caused a restriction of growth in all plant parts, such as leaves, stems, roots and panicles. This finally led to less plant dry weight at the reproductive stage and from this a less grain yield can be predicted.

The smallest dry matter yield was recorded in plants in saline water under 15 and 20 days of drought. However, salinity was a much more important factor than drought stress.

The model based on linearly interpolated value of LAI that showed simulated dry matter yield closed to observed yield.

Acknowledgements

I first of all thank the MHO-8 Project and its leaders are Prof. Dr. Tran Thuong Tuan, Prof. Dr. Tran Phuoc Duong and Prof. Dr. Vo Tong Xuan for the scholarship they offered me to pursue my M. Sc study.

I would like to express my deep gratitude to my supervisor Prof. Dr. Ir. J. Goudriaan of Department of Theoretical Production Ecology for his excellent guidance and patience with me.

I would especially like to thank Dr. Tini van Mensvoort of Department of Soil Science and Geology and MHO-8 Project for his help in my study, and his comments, suggestions during the planning stage of my experiment.

Thanks are due to Mr. Taede Stoker and Mr. Anton Vels of Unifarm, Mr. Piet Peters of Department of Soil Science and Geology, Ir. Peter van der Putten of Department of Agronomy and Ir. Aad van Ast of Department of Theoretical Production Ecology who helped me to use the equipment and carrying out the experimental work.

Finally, I sincerely thank my wife and my son for their moral support and patience.

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APPENDIX

Morphological characters of plants before drought stress (40 DAS)

Treatment	Plant height (cm)		Stem height (cm)		No. of tillers	
	Mean	Sd	Mean	Sd	Mean	Sd
REP. I						
SoD1	107.96	1.73436	36.64	1.73868	3.7778	0.440959
SoD2	108.9	1.54758	36.2	1.25499	3.8889	0.600925
SoD3	110.62	3.58845	36.4	2.04328	3.3333	0.5
SoD4	110.74	2.45732	37.7	1.56525	4.2222	0.440959
SD1	105.5	3.72492	36.6	1.63554	3.5556	0.527046
SD2	105.3	2.88531	35.7	1.68077	3.5556	0.527046
SD3	105.26	1.82016	34.44	0.80187	3.4444	0.527046
SD4	105.04	2.06349	35.5	1.5411	3.5556	0.527046
REP. II						
SoD1	113.48	1.49566	37.4	0.65192	4.1111	0.333333
SoD2	113.4	3.11047	36.8	1.98746	4.1111	0.600925
SoD3	108.76	2.66233	35.9	0.41833	4.1111	0.600925
SoD4	112.84	1.9308	37.3	1.68077	3.6667	0.5
SD1	107.8	5.5857	36.7	1.64317	4.2222	0.440959
SD2	106.5	5.3033	36.3	2.07966	3.1111	0.333333
SD3	108.76	2.9177	35.5	0.79057	3.7778	0.666667
SD4	105.5	1.90394	36.94	1.22188	4	0.5
REP. III						
SoD1	113.02	1.09636	36.2	1.09545	4.2222	0.440959
SoD2	110.46	5.46882	35.54	1.1327	3.6667	0.5
SoD3	110.94	1.82839	37	0.5	4.2222	0.666667
SoD4	112.16	4.65328	36.2	1.89077	4.1111	0.781736
SD1	111	3.10242	37.6	1.19373	3.1111	0.600925
SD2	108.44	5.13011	37.24	2.26119	3.4444	0.527046
SD3	108.64	5.32428	37.1	1.63554	3.8889	0.333333
SD4	105.32	2.2786	36.74	0.84439	3.5556	0.527046

SoD1: Fresh water, without drought

SoD2: Fresh water, 10 days of drought

SoD3: Fresh water, 15 days of drought

SoD4: Fresh water, 20 days of drought

SD1: Saline water, without drought

SD2: Saline water, 10 days of drought

SD3: Saline water, 15 days of drought

SD4: Saline water, 20 days of drought

Dry weight of plant before drought stress

	Leaf (g)	Stem (g)	Root (g)	DM of plant (g)	DM/ha (kg)
<i>REP. I</i>					
SoD1	1.2525	1.13	0.665	3.0475	761.875
SoD2	1.275	1.15	0.6625	3.0875	771.875
SoD3	1.2025	1.0775	0.7025	2.9825	745.625
SoD4	1.3575	1.1875	0.5475	3.0925	773.125
SD1	0.855	0.9525	0.585	2.3925	598.125
SD2	0.745	0.6625	0.465	1.8725	468.125
SD3	1.1625	0.8275	0.5025	2.4925	623.125
SD4	1.005	0.87	0.57	2.445	611.25
<i>REP. II</i>					
SoD1	1.46	1.31	0.7825	3.5525	888.125
SoD2	1.4425	1.355	0.925	3.7225	930.625
SoD3	1.4525	1.385	0.8975	3.735	933.75
SoD4	1.3475	1.195	0.755	3.2975	824.375
SD1	1.32	0.8825	0.5075	2.71	677.5
SD2	1.0975	1.0025	0.63	2.73	682.5
SD3	1.0525	1.16	0.5825	2.795	698.75
SD4	1.1175	1.0775	0.67	2.865	716.25
<i>REP. III</i>					
SoD1	1.47	1.3225	0.765	3.5575	889.375
SoD2	1.8925	1.6675	0.7125	4.2725	1068.125
SoD3	1.52	1.4575	0.9375	3.915	978.75
SoD4	1.16	1.275	0.6725	3.1075	776.875
SD1	1.045	0.9425	0.47	2.4575	614.375
SD2	0.81	0.9925	0.505	2.3075	576.875
SD3	0.9175	0.8125	0.3775	2.1075	526.875
SD4	0.5425	0.95	0.4325	1.925	481.25

Treatment	No. of green leaves		No. of dead leaves		No. of total leaves	
	Mean	Sd	Mean	Sd	Mean	Sd
REP. I						
SoD1	19.6	1.51658	16.2	1.09545	35.8	1.92354
SoD2	21	1	15.8	0.44721	36.8	0.83666
SoD3	18.8	2.04939	16.6	0.89443	35.4	2.50998
SoD4	21	0.70711	18.6	1.14018	39.6	1.34164
SD1	19.4	1.34164	15.4	0.54772	34.8	1.30384
SD2	19.8	0.083666	15.2	0.44721	35	1.22474
SD3	19	2	15.4	1.14018	34.4	2.88097
SD4	18.6	1.34164	17	1	35.6	2.07364
REP. II						
SoD1	21.8	1.09545	18.2	0.83666	40	1
SoD2	19.8	1.78885	15.6	0.89443	35.4	1.81659
SoD3	20	1	17.6	1.14018	37.6	1.94936
SoD4	19.6	1.14018	17	1	36.6	2.07364
SD1	20	2.34521	15.8	1.09545	35.8	1.92354
SD2	18.8	0.83666	15.4	0.54772	34.2	0.83666
SD3	18.6	1.51658	15.4	1.51658	34	3
SD4	21.4	1.14018	18	1.22474	39.4	1.67332
REP. III						
SoD1	21.4	0.89443	15	1	36.4	1.14018
SoD2	18.2	0.83666	17	1.41421	35.2	1.64317
SoD3	20.6	0.54772	16.8	1.30384	37.4	1.51658
SoD4	18.4	0.54772	17.2	1.30384	35.6	1.67332
SD1	17.8	0.83666	13.6	0.89443	31.4	1.51658
SD2	18	1.58114	16.6	1.34164	34.6	2.79285
SD3	21.4	0.89443	17.6	1.34164	39	0.70711
SD4	20	1.58114	17.4	0.89443	37.4	1.81659

Dry weight of plant at flowering stage (110 DAS)

	Green leaf (g)	Dead leaf (g)	Total leaf (g)	Stem (g)	Root (g)	Panicle (g)	DM of plant (g)	DM/ha (kg)	DM of plant (g) (*)
<i>REP. I</i>									
SoD1	6.158	0.714	6.872	12.104	4.542	2.154	25.672	6418	24.958
SoD2	5.46	1.624	7.084	11.624	4.794	2.03	25.532	6383	23.908
SoD3	5.336	1.85	7.186	11.592	3.876	1.818	24.472	6118	22.622
SoD4	5.426	2.098	7.524	10.924	4.972	1.61	25.03	6257.5	22.932
SD1	4.554	1.276	5.83	9.446	4.41	2.052	21.738	5434.5	20.462
SD2	4.772	1.77	6.542	9.602	3.882	1.638	21.664	5416	19.894
SD3	4.558	1.47	6.028	8.808	3.036	1.962	19.834	4958.5	18.364
SD4	4.28	1.31	5.59	9.224	2.398	1.368	18.58	4645	17.27
<i>REP. II</i>									
SoD1	5.858	1.642	7.5	13.044	5.068	2.13	27.742	6935.5	26.1
SoD2	6.066	1.458	7.524	11.878	4.544	1.906	25.852	6463	24.394
SoD3	5.72	1.542	7.262	11.186	3.798	2.106	24.352	6088	22.81
SoD4	5.768	1.794	7.562	11.6	3.504	1.94	24.606	6151.5	22.812
SD1	4.974	1.358	6.332	10.308	3.938	2.256	22.834	5708.5	21.476
SD2	4.768	1.564	6.332	10.434	4.48	1.926	23.172	5793	21.608
SD3	4.41	1.274	5.684	9.482	3.786	2.228	21.18	5295	19.906
SD4	4.1	2.576	6.676	9.358	3.392	1.412	20.838	5209.5	18.262
<i>REP. III</i>									
SoD1	6.046	1.544	7.59	12.38	5.128	2.412	27.51	6877.5	25.966
SoD2	5.24	1.55	6.79	11.672	4.874	2.11	25.446	6361.5	23.896
SoD3	6.046	1.686	7.732	12.298	3.68	2.52	26.23	6557.5	24.544
SoD4	5.266	2.076	7.342	11.268	4.854	1.998	25.462	6365.5	23.386
SD1	4.542	1.346	5.888	10.454	3.303	2.448	22.093	5523.3	20.747
SD2	5.038	1.864	6.902	10.644	5.518	2.03	25.094	6273.5	23.23
SD3	5.006	1.674	6.68	9.55	3.908	2.456	22.594	5648.5	20.92
SD4	4.054	2.676	6.73	9.412	2.814	1.68	20.636	5159	17.96

Note (*): Dry weight of plant not including dead leaves

The CO₂ assimilation of single leaf after 10 days of drought stress

<i>Date</i>	<i>Time</i>	<i>Plot</i>	<i>Record</i>	<i>Treat.</i>	<i>Rep.</i>	<i>P max</i> (mg CO ₂ m ² / s)	<i>Transpir.</i> (mg H ₂ O m ² / s)	<i>Stomatal conduc.</i> (mm / s)	<i>Ca</i> (ppm)	<i>Ci</i> (ppm)
40997	1210	1	1	SoD2	I	0.276	93.715	9.32	370.1	341.1
40997	1217	1	2	SoD2	I	0.572	131.274	57.411	345	331.1
40997	1224	2	1	SD2	I	0.333	91.468	8.879	359.2	322.6
40997	1230	2	2	SD2	I	0.304	91.412	9.103	358.5	325.8
40997	1238	13	1	SoD2	II	0.365	117.908	23.249	350	332.8
40997	1245	13	2	SoD2	II	0.403	118.364	23.065	348.7	329.5
40997	1252	15	1	SD2	II	0.311	118.428	22.376	351.4	336.2
40997	1302	15	2	SD2	II	0.42	103.588	16.664	344.3	318
40997	1308	17	1	SD2	III	0.324	92.699	12.201	344.9	318.2
40997	1318	17	2	SD2	III	0.409	97.522	14.949	358	329.9
40997	1328	23	1	SoD2	III	0.39	99.598	16.337	339.9	315.1
40997	1340	23	2	SoD2	III	0.546	113.88	29.112	328.3	306.7
<i>Treat.</i>	<i>Rep.</i>	<i>ABRAD</i>	<i>Leaf temp. (oC)</i>	<i>EO (ppm)</i>	<i>VPD (mbar)</i>	<i>Leaf Area (cm²)</i>				<i>Humidity (%)</i>
SoD2	I	246	28.69	24.208	15.123	5.6	53.8248	45.7511	78.046	61.6
SoD2	I	246	28.96	32.971	6.9794	7.28	53.8248	45.7511	78.046	82.5
SD2	I	246	29.1	24.971	15.305	6.16	53.8248	45.7511	78.046	62
SD2	I	246	28.97	25.036	14.938	6.16	53.8248	45.7511	78.046	62.6
SoD2	II	246	28.8	29.675	9.9075	6.72	53.8248	45.7511	78.046	75
SoD2	II	246	28.88	29.737	10.029	6.72	53.8248	45.7511	78.046	74.8
SD2	II	246	28.99	29.755	10.265	6.72	53.8248	45.7511	78.046	74.4
SD2	II	246	28.98	29.51	10.487	6.72	53.8248	45.7511	78.046	73.8
SD2	III	246	28.82	28.005	11.623	6.72	53.8248	45.7511	78.046	70.7
SD2	III	246	28.63	28.722	10.473	6.72	53.8248	45.7511	78.046	73.3
SoD2	III	246	29.05	30.127	10.032	7.28	53.8248	45.7511	78.046	75
SoD2	III	246	29.09	32.234	8.0182	7.28	53.8248	45.7511	78.046	80

The CO₂ assimilation of single leaf after 20 days of drought stress

<i>Date</i>	<i>Time</i>	<i>Plot</i>	<i>Record</i>	<i>Treat.</i>	<i>Rep.</i>	<i>P max</i> (mg CO ₂ m ² / s)	<i>Transpir.</i> (mg H ₂ O m ² / s)	<i>Stomatal conduc.</i> (mm / s)	<i>Ca</i> (ppm)	<i>Ci</i> (ppm)
140997	1045	7	1	SD4	I	0.172	74.636	5.323	350	319.8
140997	1055	4	1	SoD4	I	0.168	106.22	10.645	348.7	333.2
140997	1104	7	2	SD4	I	0.178	34.04	1.657	350.9	253.2
140997	1112	4	2	SoD4	I	0.291	89.398	7.055	341.2	301.9
140997	1124	12	1	SD4	II	0.257	78.58	5.779	343	301.1
140997	1134	12	2	SD4	II	0.264	91.885	7.849	341.3	309
140997	1147	14	1	SoD4	II	0.362	105.582	11.266	334	302.3
140997	1158	14	2	SoD4	II	0.292	60.855	4.12	337.5	271.7
140997	1214	22	1	SD4	III	0.139	26.862	1.326	348.2	253.4
140997	1220	22	2	SD4	III	0.125	24.941	1.18	349.6	254.2
140997	1230	18	1	SoD4	III	0.326	63.979	3.984	337.3	261.5
140997	1237	18	2	SoD4	III	0.341	81.996	5.783	336.2	280.5
<i>Treat.</i>	<i>Rep.</i>	<i>ABRAD</i>	<i>Leaf temp.</i> (oC)	<i>EO</i> (ppm)	<i>VPD</i> (mbar)	<i>Leaf Area</i> (cm ²)				<i>Humidity</i> (%)
SD4	I	246	26.04	14.3368	19.341	6.16	53.8248	45.7511	78.046	42.6
SoD4	I	246	26.3	18.3959	15.804	6.16	53.8248	45.7511	78.046	53.8
SD4	I	246	26.7	9.44359	25.572	6.72	53.8248	45.7511	78.046	27
SoD4	I	246	26.54	16.2439	18.443	6.16	53.8248	45.7511	78.046	46.8
SD4	II	246	26.26	15.1078	19.011	6.16	53.8248	45.7511	78.046	44.3
SD4	II	246	26.27	16.8749	17.264	6.16	53.8248	45.7511	78.046	49.4
SoD4	II	246	25.96	18.6132	14.906	6.16	53.8248	45.7511	78.046	55.5
SoD4	II	246	26.07	14.2745	19.463	7.28	53.8248	45.7511	78.046	42.3
SD4	III	246	26.05	8.94346	24.755	7.28	53.8248	45.7511	78.046	26.5
SD4	III	246	26.28	8.35531	25.804	6.72	53.8248	45.7511	78.046	24.5
SoD4	III	246	26.48	13.1276	21.437	6.16	53.8248	45.7511	78.046	38
SoD4	III	246	26.48	14.524	20.04	5.6	53.8248	45.7511	78.046	42

<i>Date</i>	<i>Time</i>	<i>Plot</i>	<i>Record</i>	<i>Treat.</i>	<i>Rep.</i>	<i>P max</i> (mg CO ₂ m ² / s)	<i>Transpir.</i> (mg H ₂ O m ² / s)	<i>Stomatal conduc.</i> (mm / s)	<i>Ca</i> (ppm)	<i>Ci</i> (ppm)
241097	1413	21	2	SoD1	III	0.393	95.905	17.61	333.5	310.2
241097	1425	22	1	SD4	III	0.447	104.489	36.232	327.1	312.3
241097	1436	22	2	SD4	III	0.476	105.094	35.159	327.8	311.7
241097	1448	23	1	SoD2	III	0.448	107.61	21.232	335.3	312.7
241097	1502	23	2	SoD2	III	0.5	108.412	33.229	325.3	307.6
241097	1512	24	1	SD1	III	0.461	115.635	46.039	329.7	316.9
241097	1525	24	2	SD1	III	0.397	100.547	27.492	331.1	314.9

<i>Treat.</i>	<i>Rep.</i>	<i>ABRAD</i>	<i>Leaf</i>	<i>EO</i>	<i>VPD</i>	<i>Leaf Area</i>			<i>Humidity</i>	
			<i>temp.</i>	(<i>ppm</i>)	(<i>mbar</i>)	(<i>cm2</i>)			(%)	
			(<i>oC</i>)							
SoD3	III	246	26.14	26.333	7.5446	6.72	53.8248	45.7511	78.046	77.7
SoD1	III	246	26.62	26.187	8.6639	6.72	53.8248	45.7511	78.046	75.1
SoD1	III	246	26.71	26.186	8.85	7.84	53.8248	45.7511	78.046	74.7
SD4	III	246	25.98	27.71	5.8493	7.84	53.8248	45.7511	78.046	82.6
SD4	III	246	25.48	26.555	6.0238	7.28	53.8248	45.7511	78.046	81.5
SoD2	III	246	26.6	25.714	9.0958	6.72	53.8248	45.7511	78.046	73.9
SoD2	III	246	26.69	28.349	6.6455	7.84	53.8248	45.7511	78.046	81
SD1	III	246	26.27	28.083	6.0562	7.28	53.8248	45.7511	78.046	82.3
SD1	III	246	26.05	27.029	6.6688	7.84	53.8248	45.7511	78.046	80.2

The monthly climatic condition in the glass house

July 8-31 1997				August 1-31 1997			
Date	Mean temperature (oC)	Radiation outside (J/cm2)	Humidity (%)	Date	Mean temperatur (oC)	Radiation outside (J/cm2)	Humidity (%)
8	29.8	1508	53	1	28.3	1140	66
9	29.3	1159	54	2	30.3	1852	59
10	30.2	1733	51	3	29.4	1296	62
11	33.5	2730	40	4	30	1988	55
12	31.6	1927	58	5	31.1	2362	52
13	31.2	1624	60	6	32.3	2466	50
14	30.3	1842	61	7	32.4	2368	50
15	30.3	2080	57	8	33.1	2362	50
16	29.2	1481	62	9	34.1	2218	51
17	28.4	953	67	10	34	2213	49
18	29	1150	70	11	33.7	2338	45
19	30.4	1829	59	12	33.7	2132	46
20	29.6	1282	66	13	33.2	2084	49
21	29.3	1114	71	14	29.8	1063	61
22	30	1755	65	15	30.9	1732	54
23	31	2430	55	16	31.7	2147	53
24	29.3	1029	65	17	32.9	2012	52
25	28	1119	65	18	32.7	2105	45
26	29.9	2127	56	19	31.6	2161	45
27	28.5	1272	60	20	61.6	1838	52
28	29.6	2034	56	21	62.2	1865	52
29	30.6	2395	51	22	29.2	433	69
30	29.2	1360	57	23	31.1	952	65
31	27.7	1217	59	24	33	1830	58
Mean	29.8291667	1631.25	59.08333	25	31.5	1372	63
				26	29.6	791	66
				27	27.8	1299	74
				28	25.8	534	78
				29	26.2	1190	74
				30	25.7	432	78
				31	28	1627	73
				Mean	32.803226	1683.935	57.93548

TITLE DRY MATTER OF PLANT IN FRESH WATER WITHOUT
 * DROUGHT STRESS (SoD1)
 INITIAL
 INCON ZERO = 0.
 PARAM RUE = 1.0, TAU = 0.7, R = 12.85
 PARAM K = 0.7
 * RUE (Radiation use efficiency) RUE = 1. g/MJ
 * Incident Global Radiation R = 12.85 MJ/m2
 * TAU (Glass house transmissivity) TAU = 0.7
 FUNCTION LAITB = 0.0, 0.0, 40., 1.17, 110.0, 2.675
 PRINT LAI, GROWTH, BIOM
 TIMER STTIME = 0., FINTIM = 110., PRDEL = 5., DELT = 1.
 DYNAMIC
 LAI = AFGEN (LAITB, TIME)
 FRABS = 1.-EXP(-K*LAI)
 BIOM = INTGRL (ZERO, GROWTH)
 GROWTH = R * TAU * RUE * FRABS
 TRANSLATION_GENERAL DRIVER = 'RKDRIV'
 END

*-----
 * Output table number : 0 (=first output table)
 * Output table format : Table output
 * Simulation results
 * DRY MATTER OF PLANT IN FRESH WATER WITHOUT
 * DROUGHT STRESS (SoD1)

TIME	LAI	GROWTH	BIOM
.000000	.00000	.00000	.00000
5.00000	.14625	.87529	2.2256
10.0000	.29250	1.6654	8.6110
15.0000	.43875	2.3786	18.752
20.0000	.58500	3.0225	32.282
25.0000	.73125	3.6037	48.872
30.0000	.87750	4.1283	68.224
35.0000	1.0237	4.6019	90.070
40.0000	1.1700	5.0294	114.17
45.0000	1.2775	5.3168	140.04
50.0000	1.3850	5.5834	167.30
55.0000	1.4925	5.8307	195.84
60.0000	1.6000	6.0601	225.58
65.0000	1.7075	6.2729	256.42
70.0000	1.8150	6.4702	288.28
75.0000	1.9225	6.6532	321.09
80.0000	2.0300	6.8230	354.79
85.0000	2.1375	6.9804	389.30
90.0000	2.2450	7.1264	424.57
95.0000	2.3525	7.2619	460.55
100.000	2.4600	7.3875	497.18
105.000	2.5675	7.5040	534.41
110.000	2.6750	7.6121	572.20

TITLE DRY MATTER OF PLANT IN FRESH WATER UNDER 15 DAYS
* OF DROUGHT STRESS (SOD3)

INITIAL

INCON ZERO = 0.

PARAM RUE = 1.0, TAU = 0.7, R = 12.85

PARAM K = 0.7

* RUE (Radiation use efficiency) RUE = 1.0 g/MJ
* Incident Global Radiation R = 12.85 MJ/m²
* TAU (Glass house transmissivity) TAU = 0.7

FUNCTION LAITB = 0.0, 0.0, 40., 1.187, 110.0, 2.535

PRINT LAI, GROWTH, BIOM

TIMER STTIME = 0., FINTIM = 110., PRDEL = 5., DELT = 1.

DYNAMIC

LAI = AFGEN (LAITB, TIME)
FRABS = 1. - EXP(-K*LAI)
BIOM = INTGRL (ZERO, GROWTH)
GROWTH = R * TAU * RUE * FRABS

TRANSLATION_GENERAL DRIVER = 'RKDRIV'

END

*

* Output table number : 0 (=first output table)
* Output table format : Table output
* Simulation results
* DRY MATTER OF PLANT IN FRESH WATER UNDER 15
* DAYS OF DROUGHT STRESS

TIME	LAI	GROWTH	BIOM
.000000	.00000	.00000	.00000
5.00000	.14838	.88736	2.2568
10.0000	.29675	1.6872	8.7278
15.0000	.44513	2.4081	18.997
20.0000	.59350	3.0579	32.690
25.0000	.74188	3.6436	49.470
30.0000	.89025	4.1715	69.030
35.0000	1.0386	4.6474	91.098
40.0000	1.1870	5.0763	115.43
45.0000	1.2833	5.3317	141.45
50.0000	1.3796	5.5705	168.71
55.0000	1.4759	5.7937	197.13
60.0000	1.5721	6.0023	226.63
65.0000	1.6684	6.1974	257.13
70.0000	1.7647	6.3797	288.58
75.0000	1.8610	6.5502	320.91
80.0000	1.9573	6.7095	354.06
85.0000	2.0536	6.8585	387.99
90.0000	2.1499	6.9978	422.63
95.0000	2.2461	7.1279	457.95
100.000	2.3424	7.2496	493.90
105.000	2.4387	7.3634	530.43
110.000	2.5350	7.4697	567.52

TITLE DRY MATTER OF PLANT IN SALINE WATER WITHOUT
 * DROUGHT STRESS (SD1)
 INITIAL
 INCON ZERO = 0.
 PARAM RUE = 1.0, TAU = 0.7, R = 12.85
 PARAM K = 0.7

* RUE (Radiation use efficiency) RUE = 1. g/MJ
 * Incident Global Radiation R = 12.85 MJ/m2
 * TAU (Glass house transmissivity) TAU = 0.7

FUNCTION LAITB = 0.0, 0.0, 40., 0.975, 110.0, 2.307
 PRINT LAI, GROWTH, BIOM
 TIMER STTIME = 0., FINTIM = 110., PRDEL = 5., DELT = 1.
 DYNAMIC

```

    LAI = AFGEN (LAITB, TIME)
    FRABS = 1.-EXP(-K*LAI)
    BIOM = INTGRL (ZERO, GROWTH)
    GROWTH = R * TAU * RUE * FRABS
  
```

TRANSLATION_GENERAL DRIVER = 'RKDRIV'
 END

*-----
 * Output table number : 0 (=first output table)
 * Output table format : Table output
 * Simulation results
 * DRY MATTER OF PLANT IN SALINE WATER WITHOUT
 * DROUGHT STRESS (SD1)

TIME	LAI	GROWTH	BIOM
.000000	.00000	.00000	.00000
5.00000	.12188	.73556	1.8651
10.0000	.24375	1.4110	7.2554
15.0000	.36563	2.0312	15.883
20.0000	.48750	2.6006	27.482
25.0000	.60938	3.1235	41.811
30.0000	.73125	3.6037	58.646
35.0000	.85313	4.0445	77.783
40.0000	.97500	4.4494	99.032
45.0000	1.0701	4.7422	122.02
50.0000	1.1653	5.0162	146.42
55.0000	1.2604	5.2726	172.15
60.0000	1.3556	5.5124	199.12
65.0000	1.4507	5.7368	227.25
70.0000	1.5459	5.9467	256.47
75.0000	1.6410	6.1431	286.70
80.0000	1.7361	6.3269	317.88
85.0000	1.8313	6.4988	349.94
90.0000	1.9264	6.6596	382.85
95.0000	2.0216	6.8101	416.52
100.000	2.1167	6.9509	450.93
105.000	2.2119	7.0826	486.02
110.000	2.3070	7.2058	521.74

TITLE DRY MATTER OF PLANT IN SALINE WATER UNDER 15 DAYS
* OF DROUGHT STRESS (SD3)

INITIAL

INCON ZERO = 0.

PARAM RUE = 1.0, TAU = 0.7, R = 12.85

PARAM K = 0.7

* RUE (Radiation use efficiency) RUE = 1.0 g/MJ
* Incident Global Radiation R = 12.85 MJ/m²
* TAU (Glass house transmissivity) TAU = 0.7

FUNCTION LAITB = 0.0, 0.0, 40., 0.951, 110.0, 2.276

PRINT LAI, GROWTH, BIOM

TIMER STTIME = 0., FINTIM = 110., PRDEL = 5., DELT = 1.

DYNAMIC

LAI = AFGEN (LAITB, TIME)
FRABS = 1.-EXP(-K*LAI)
BIOM = INTGRL (ZERO, GROWTH)
GROWTH = R * TAU * RUE * FRABS

TRANSLATION_GENERAL DRIVER = 'RKDRIV'

END

*-----
* Output table number : 0 (=first output table)
* Output table format : Table output
* Simulation results
* DRY MATTER OF PLANT IN SALINE WATER UNDER 15
* DAYS OF DROUGHT

TIME	LAI	GROWTH	BIOM
.000000	.00000	.00000	.00000
5.00000	.11887	.71820	1.8204
10.0000	.23775	1.3791	7.0865
15.0000	.35662	1.9871	15.523
20.0000	.47550	2.5467	26.877
25.0000	.59438	3.0615	40.915
30.0000	.71325	3.5353	57.424
35.0000	.83213	3.9712	76.205
40.0000	.95100	4.3723	97.078
45.0000	1.0456	4.6687	119.69
50.0000	1.1403	4.9460	143.73
55.0000	1.2349	5.2056	169.12
60.0000	1.3296	5.4485	195.76
65.0000	1.4242	5.6758	223.58
70.0000	1.5189	5.8886	252.50
75.0000	1.6135	6.0877	282.44
80.0000	1.7081	6.2741	313.35
85.0000	1.8028	6.4485	345.16
90.0000	1.8974	6.6117	377.82
95.0000	1.9921	6.7645	411.26
100.000	2.0867	6.9075	445.45
105.000	2.1814	7.0413	480.32
110.000	2.2760	7.1665	515.84

Experimental Design

REP. I

REP. II

REP. III

SoD2	SD1	SD2
SD2	SD3	SoD4
SD3	SoD3	SD3
SoD4	SD4	SoD3
SD1	SoD2	SoD1
SoD3	SoD4	SD4
SD4	SD2	SoD2
SoD1	SoD1	SD1

Where:

SoD1: Fresh water, without drought

SoD2: Fresh water, 10 days of drought

SoD3: Fresh water, 15 days of drought

SoD4: Fresh water, 20 days of drought

SD1: Saline water, without drought

SD2: Saline water, 10 days of drought

SD3: Saline water, 15 days of drought

SD4: Saline water, 20 days of drought