LINTUL3, a simulation model for nitrogen-limited situations: Application to rice

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ABSTRACT

LINTUL3 is a crop model that calculates biomass production based on intercepted photosynthetically active radiation (PAR) and light use efficiency (LUE). It is an adapted version of LINTUL2 (that simulates potential and water-limited crop growth), including nitrogen limitation. Nitrogen stress in the model is defined through the nitrogen nutrition index (NNI): the ratio of actual nitrogen concentration and critical nitrogen concentration in the plant. The effect of nitrogen stress on crop growth is tested in the model either through a reduction in LUE or leaf area (LA) or a combination of these two and further evaluated with independent datasets. However, water limitation is not considered in the present study as the crop is paddy rice. This paper describes the model for the case of rice, test the hypotheses of N stress on crop growth and details of model calibration and testing using independent data sets of nitrogen treatments (with fertilizer rates of 0–400 kg N ha^{-1}) under varying environmental conditions in Asia. Results of calibration and testing are compared graphically, through Root Mean Square Deviation (RMSD), and by Average Absolute Deviation (AAD). Overall average absolute deviation values for calibration and testing of total aboveground biomass show less than 26% mean deviation from the observations though the values for individual experiments show a higher deviation up to 41%. In general, the model responded well to nitrogen stress in all the treatments without fertilizer application as observed, but between fertilized treatments the response was varying.

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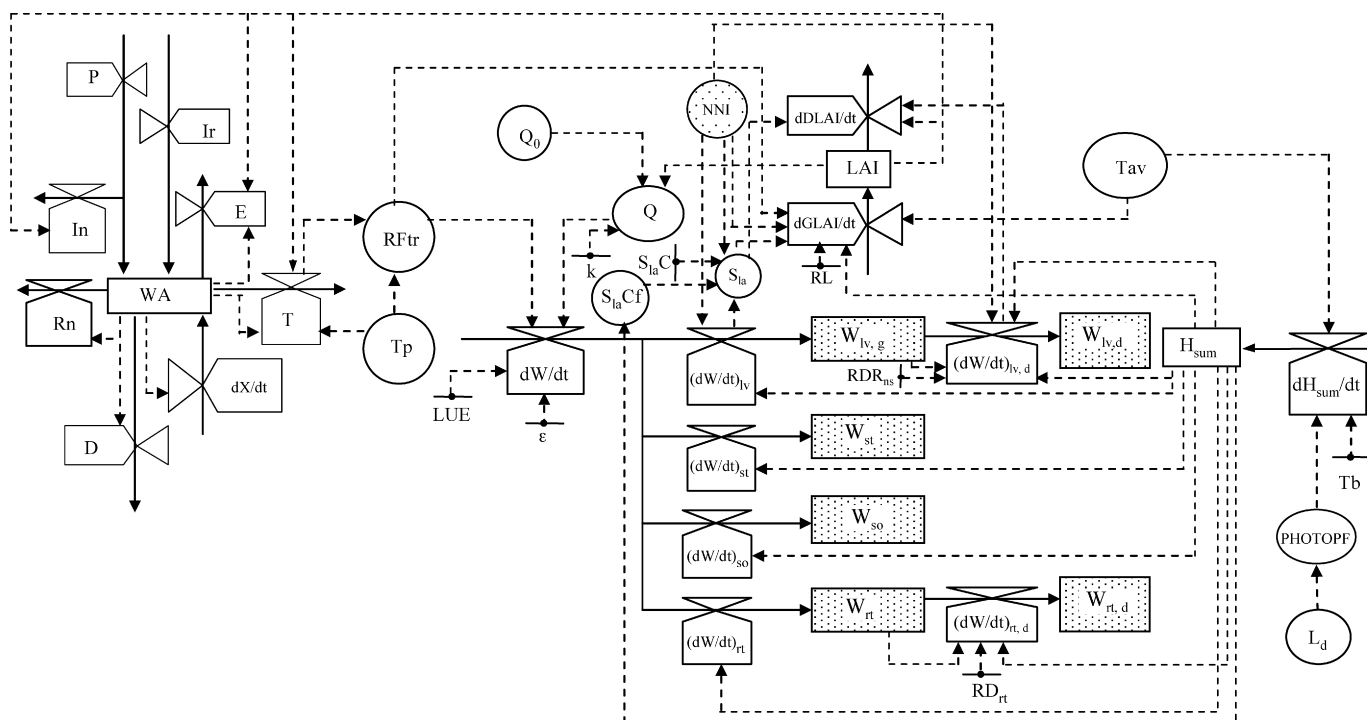
1. Introduction

Photosynthesis, in which atmospheric carbon is fixed into carbohydrates, is the basis of biomass production. Nitrogen (N) availability affects photosynthesis through its impact on leaf area development and photosynthetic capacity (Novoa and Loomis, 1981; Van Keulen et al., 1988), as nitrogen is the major structural component of chlorophyll. Well-tested simulation models, quantitatively describing the processes of the nitrogen balance in the soil, nitrogen uptake by the crop and crop growth, are useful tools to understand and explore changes in crop growth in response to changes in nitrogen management (Van Ittersum et al., 2003). However, a major constraint to use complex process-based simulation models is their large data requirement, because many of these data are difficult to measure in a field situation. Simple crop models, with limited data requirements, can alleviate this constraint (Spitters, 1990). LINTUL (Light Interception and Utilization simulator) is such a simple crop model that simulates dry matter production as a function of light interception using a constant light use efficiency (LUE; Van Oijen, 1992). LINTUL, developed for potential crop growth as LINTUL1 (Spitters, 1990), has later been extended to take into account water-limited conditions (LINTUL2) (Spitters and Schapendonk, 1990). LINTUL has been successfully applied to different crops such as potato (Spitters and Schapendonk, 1990), grassland (LINGRA) (Schapendonk et al., 1998), maize (Farré et al., 2000) and oilseed rape (Habekotté, 1997) in both potential and water-limited situations. LINTUL3, described in this paper, is an adaptation of LINTUL2 and includes a description of the effects of nitrogen limitation on biomass production, for the case of rice.

Under ample nitrogen supply (assuming no limitations for water and other nutrients), N accumulation in the crop is mostly determined by intrinsic crop characteristics (Gastal and Lemaire, 2002). Under nitrogen-deficient conditions, N content in the plant is lower and carbon accumulation is negatively affected. The reduction in biomass production in response to N deficiency is associated with either a reduction in total radiation intercepted by the canopy, or by a decrease in the efficiency with which the intercepted radiation is used to produce dry matter, or a combination of both (Muchow, 1990). Quantification of these effects appears difficult, because of conflicting reports on effects on leaf area index (LAI)

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Fig. 1. Relational diagram of the LINTUL3 model. Abbreviations used in the diagram: P, precipitation; Ir, irrigation; In, intercepted part of precipitation; E, evaporation; Rn, run off; T, transpiration; dX/dt, water exploration; D, drainage; WA, amount of water; RFtr, reduction factor for water stress; Tp, potential transpiration; Q_0, daily global radiation; Q, intercepted PAR; k, light extinction coefficient; LUE, light use efficiency; dW/dt, rate of biomass production; $(dW/dt)_{lv}, (dW/dt)_{st}, (dW/dt)_{so}, (dW/dt)_{rt}$: growth rate of leaves, stems, storage organs and roots, respectively; $(dW/dt)_{lv,d}, (dW/dt)_{rt,d}$: death rate of leaves and roots, respectively; $W_{lv,g}, W_{lv,d}, W_{st}, W_{so}, W_{rt}, W_{rt,d}$: weight of green leaves, dead leaves, stems, storage organs, roots and dead roots, respectively; RD_{rt}, relative death rate of roots; LAI, leaf area index; NNI, nitrogen nutrition index; $dGLAI/dt$, rate of increase in leaf area; $dDLAI/dt$, rate of decrease in leaf area; Tav, daily average temperature; RL, maximum relative growth rate of leaf area index; Tb, base temperature for crop development; dH_{sum}/dt, rate of increase in temperature sum; H_{sum}, temperature sum; PHOTOPF, Photoperiod sensitivity factor; L_d, daylength; S_{la}, specific leaf area; $S_{la}C$, specific leaf area constant; $S_{la}Cf$, specific leaf area correction factor; ε, coefficient for the effect of nitrogen stress on the reduction of LUE; RDR_{ns}, relative death rate of leaf weight due to nitrogen stress. Solid lines and dotted lines are indicating material and information flows, respectively, and shaded state variables and auxiliary function NNI indicate that they are linked to Fig. 3.
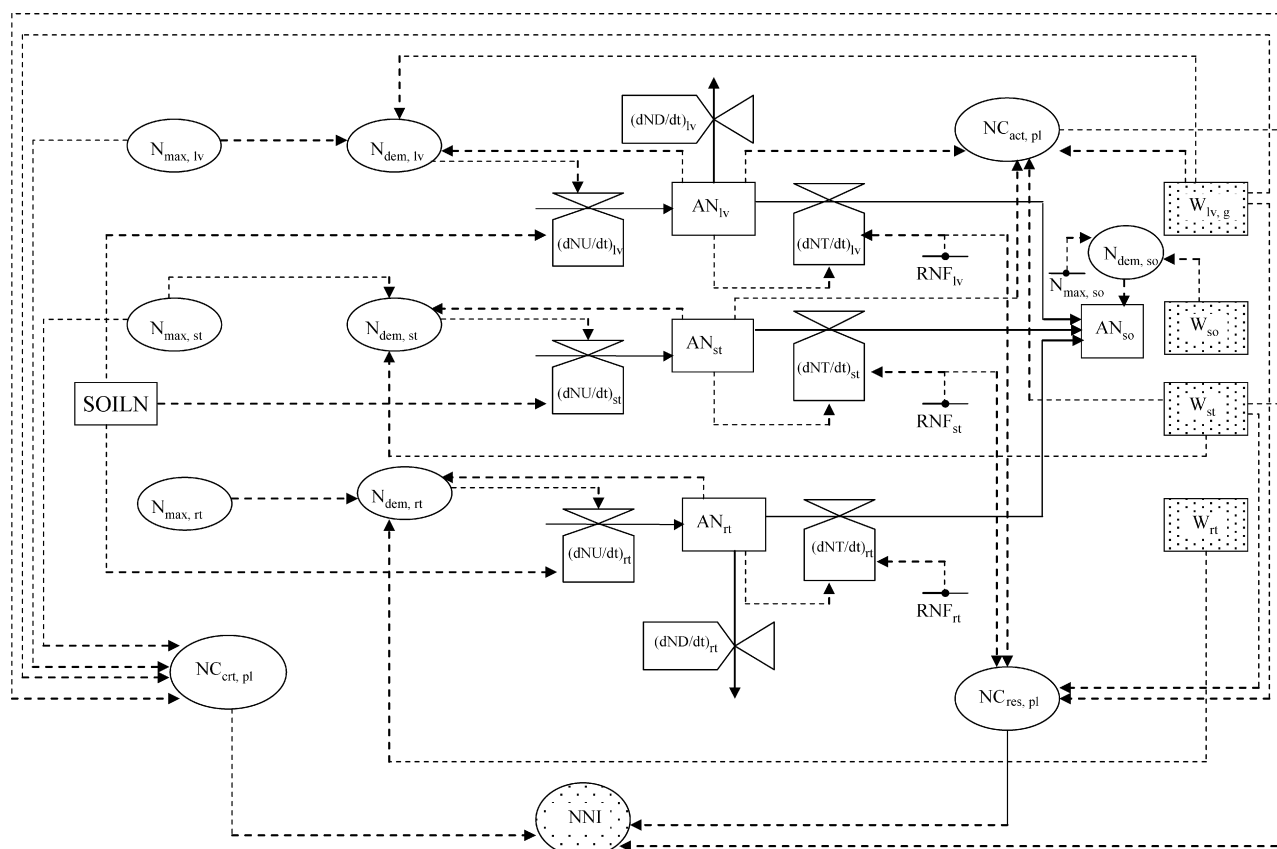
and LUE (Green, 1987; Garcia et al., 1988; Sinclair and Horie, 1989; Jamieson et al., 2000). Two possible crop responses to N shortage can be envisaged (Van Delden, 2001): reduced rate of leaf area expansion while maintaining LUE, or maintaining the expansion of leaf area and intercepted PAR at a reduced LUE. Theoretical studies and studies under controlled conditions (Sinclair and Horie, 1989) in maize, rice and soybean, and field studies in wheat (Green, 1987) have shown a higher LUE in crops with higher leaf nitrogen contents. However, field studies by Garcia et al. (1988) have shown that an increased nitrogen application resulted in an increased light interception in winter wheat due to more rapid leaf expansion. Under field conditions with moderate water and nitrogen stress, LUE will not be affected significantly, whereas under severe stress, such as during a sudden transfer from an optimum nutrient solution to a deficient one, plants may not be able to rapidly modify their morphology, but may reduce LUE (Garcia et al., 1988). To test the above two hypotheses, Vos and Van der Putten (1998) and Vos et al. (2005) studied the crop responses to N shortage for potato and maize on a single leaf basis under similar experimental conditions. Under severely limiting to non-limiting N supply, in maize, the LUE was reduced by 38%, whereas cumulative leaf area by only 30%. In contrast, for potato, the effect was a marginal reduction in LUE with 300–400% reduction in cumulative leaf area due to reduced rate of leaf expansion. They argued that potato and maize showed contrasting strategies to deal with N limitation: potato adapted leaf size and avoided compromising on leaf N concentration and LUE (potato strategy), whereas maize maintained leaf area growth rate at the expense of a decrease in N concentration per unit leaf area and thus a decrease in LUE (maize strategy). However, Hasegawa and Horie (1996) in a similar study at the field level with rice, showed

that the mean difference in LUE between non-fertilized to fertilized treatments over the growing season was only 6% with a maximum of 12% (during the mid-reproductive stage) and the mean difference in LAI was more than 60% with a maximum of 80% (during the initial vegetative phase).

In the current modelling approaches, effects of nitrogen shortage on crop growth have been incorporated through growth reduction factors, similar to water stress (Jamieson et al., 1998),
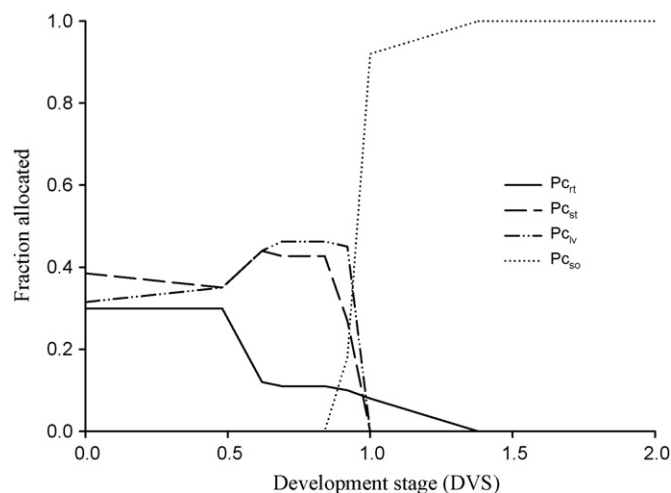
Fig. 2. Biomass partitioning coefficients to roots (Pc_{rt}), stems (Pc_{st}), leaves (Pc_{lv}) and storage organs (Pc_{so}) as a function of development stage under optimal nitrogen supply obtained by calibration.

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Fig. 3. Relational diagram showing nitrogen uptake, translocation and nitrogen content of plant organs in the LINTUL3 model. Abbreviations used in the diagram: SOILN, available N in soil; $N_{max, lv}$, $N_{max, st}$, $N_{max, rt}$, $N_{max, so}$: maximum nitrogen concentration in leaves, stems, roots and storage organs, respectively; $N_{dem, lv}$, $N_{dem, st}$, $N_{dem, rt}$, $N_{dem, so}$: nitrogen demand of leaves, stems, roots and storage organs, respectively; $(dNU/dt)_{lv}$, $(dNU/dt)_{st}$, $(dNU/dt)_{rt}$: rate of nitrogen uptake in leaves, stems and roots, respectively; $(dND/dt)_{lv}$, $(dND/dt)_{rt}$, rate of nitrogen loss by death of leaves and roots, respectively; $(dNT/dt)_{lv}$, $(dNT/dt)_{st}$, $(dNT/dt)_{rt}$: rate of nitrogen translocation from leaves, stems and roots, respectively; RNF_{lv}, RNF_{st}, RNF_{rt}: residual nitrogen concentration in leaves, stems and roots, respectively; AN_{lv}, AN_{st}, AN_{rt}, AN_{so}: amount of nitrogen in leaves, stems, roots and storage organs, respectively; $NC_{act, pl}$, $NC_{crt, pl}$, $NC_{res, pl}$: actual, critical and residual nitrogen concentration, respectively in leaves and stems; $W_{lv, g}$, W_{st}, W_{rt}, W_{so}: weight of green leaves, stems, roots and storage organs, respectively; NNI, nitrogen nutrition index. Solid lines and dotted lines are indicating material and information flows, respectively, and shaded state variables and auxiliary function NNI indicate that they are linked to Fig. 1.

affecting leaf expansion, leaf senescence, and the rate of photosynthesis per unit area of leaves or LUE (for e.g.: CERES (Ritchie and Otter, 1985), SWHEAT (Van Keulen and Seligman, 1987), AFRCWHEAT2 (Porter, 1993), Sirius (Jamieson et al., 1998) and ORYZA (Bouman et al., 2001). However, Jamieson and Semenov (2000) have demonstrated that the effect of N stress could be simplified by confining the effect to only leaf area expansion. These results do not seem conclusive with respect to a definite mechanism of plant behaviour under N stress. In the current study, therefore, we test the above two hypotheses of stress effects on LUE and/or leaf area expansion (LA), which eventually is used in the LINTUL3 model.

2. Model description

The original version of LINTUL (Spitters, 1987) is a potential crop growth model where the yield of storage organs is calculated by multiplying a harvest index (HI) by the total aboveground biomass, that is simulated from intercepted light times LUE. In LINTUL1, the total biomass formed is partitioned into roots, stems, leaves and storage organs (Spitters, 1990; Van Oijen, 1992). Water-limited crop growth (LINTUL2) (Spitters and Schapendonk, 1990; Farré et al., 2000) includes soil water processes such as evapotranspiration, drainage and runoff. The LINTUL3 model describes nitrogen demand and uptake by the crop in detail and the supply of soil nitrogen in a more simplified form. The effect of crop nitrogen deficiency is expressed via a growth reduction factor, called

the nitrogen nutrition index (NNI), which reduces biomass production, specific leaf area and biomass partitioning to leaves and increases leaf senescence. The following section briefly describes the processes comprised in the LINTUL3 model.

2.1. Crop phenology

Crop development, i.e. the order and rate of appearance of vegetative and reproductive organs, is defined in terms of phenological developmental stage (DVS) as a function of heat sum, which is the cumulative daily effective temperature. Daily effective temperature is the average temperature above a crop-specific base temperature (for rice 8 °C). Some rice varieties are photoperiod-sensitive, i.e. flowering depends on the length of the light period during the day in addition to the temperature during the vegetative stage. Earlier versions of LINTUL did not include the effect of daylength on crop development. A new sub-routine has been added in LINTUL3 to calculate the daylength, which affects crop development. Normally, photoperiodic daylength exceeds astronomical daylength (Wormer, 1954; Vergara and Chang, 1985). Photoperiodic daylength (L_d) is calculated in the model as a function of solar elevation (angle of sun above horizon), determined by latitude and day of the year (Goudriaan and Van Laar, 1994). Photoperiod-sensitivity of the rice crop, defined as a function of daylength is included in the model by modifying the daily increment of the heat sum.

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2.2. Light use efficiency and biomass production

Theoretical considerations and extensive experimentation (Monteith, 1977; Gallagher and Biscoe, 1978; Monteith, 1990) have shown that biomass formed per unit intercepted light, LUE (Light Use Efficiency, g dry matter MJ^{-1}), is relatively more stable. Hence, maximum daily growth rate can be defined as the product of intercepted PAR (photosynthetically active radiation, MJ m^{-2} d^{-1}) and LUE. Intercepted PAR depends on incident solar radiation, the fraction that is photosynthetically active (0.5) (Monteith and Unsworth, 1990; Spitters, 1990), and LAI (m^2 leaf m^{-2} soil) according to Lambert–Beer's law:

$$Q = 0.5Q_0[1 - e^{(-k\,LAI)}] \tag{1}$$

where Q is intercepted PAR (MJ m^{-2} d^{-1}), Q_0 is daily global radiation (MJ m^{-2} d^{-1}), and k is the attenuation coefficient for PAR in the canopy.

2.3. Biomass partitioning

Biomass formed at any time during crop growth is partitioned among its organs (Fig. 1), i.e. roots, stems, leaves and storage organs, with partitioning factors defined as a function of development stage (Fig. 2) (Drenth et al., 1994), which thus provides the rates of growth of these organs:

$$\left(\frac{dW}{dt}\right)_i = Pc_i \left(\frac{dW}{dt}\right) \tag{2}$$

where (dW/dt) is the rate of biomass growth (g m^{-2} d^{-1}); (dW/dt)$_i$ and Pc_i are the rate of growth (g m^{-2} d^{-1}) of and the biomass partitioning factor to organ i (g organ-i g^{-1} biomass), respectively.

Leaf, stem and root weights of the seedlings at the time of transplanting are input parameters for the model. The time course of weights of these organs follows from integration of their net growth rates, i.e. growth rates minus death rates, the latter being defined as a function of physiological age, shading and stress.
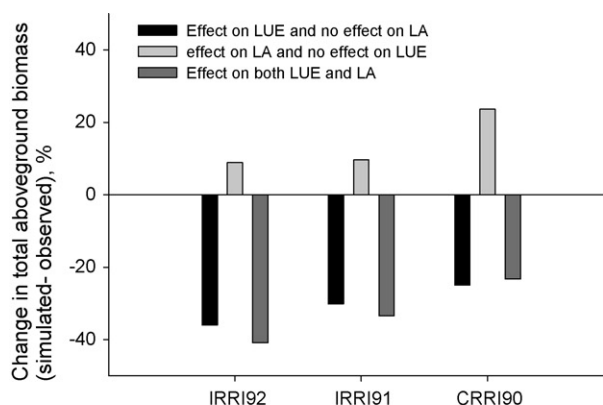
2.4. Leaf area development

The time course of LAI is divided into two stages: an exponential stage during the juvenile phase, where leaf area development is a function of temperature, and a linear stage where it depends on the increase in leaf biomass (Spitters, 1990; Spitters and Schapendonk, 1990). The death of leaves due to senescence that may be enhanced by shading and/or stress leads to a corresponding loss in leaf area. The specific leaf area is used for the conversion of dead leaf biomass to corresponding loss in leaf area. The death of leaves due to senescence occurs only after flowering and the rate depends on crop age (function adopted from ORYZA2000, Bouman et al., 2001). The excessive growth of leaves also result in death of leaves due to mutual shading. The death of leaves due to shading is determined by a maximum death rate and the relative proportion of leaf area above the critical LAI (4.0) (Spitters, 1990; Spitters and Schapendonk, 1990). The net rate of change in leaf area ($dLAI/dt$) is the difference between its growth rate and its death rate:

$$\left(\frac{dLAI}{dt}\right) = \left(\frac{dGLAI}{dt}\right) - \left(\frac{dDLAI}{dt}\right) \tag{3}$$
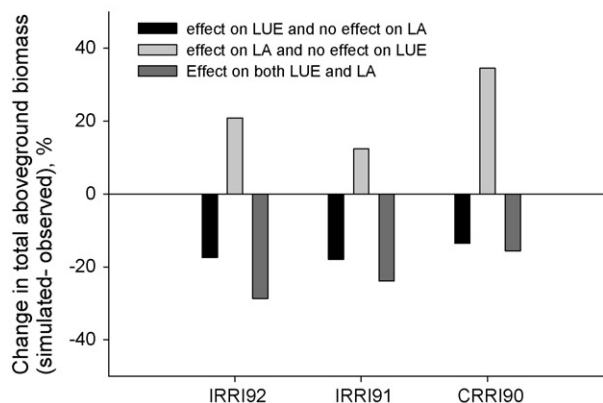
where ($dGLAI/dt$) is the leaf area growth rate and ($dDLAI/dt$) is the leaf area death rate.

2.5. Root growth

The root system is characterized by its vertical extension in the soil profile. At emergence or at transplanting for transplanted rice,
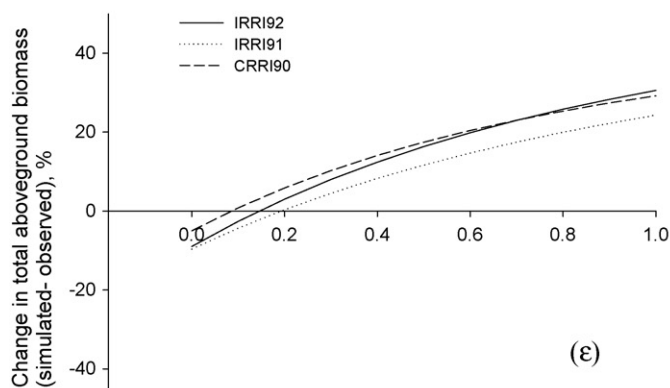
Fig. 4. Effect of N stress (NNI) on crop growth through its effect on LA and LUE.

rooting depth is initialized. Roots elongate at a constant daily rate, until flowering, provided soil water content is above permanent wilting point (PWP), whereas growth ceases when soil is drier than PWP or when a certain preset maximum rooting depth is reached (Spitters and Schapendonk, 1990; Farré et al., 2000). However, in rice in a flooded situation, soil will always be at saturation and, therefore, the maximum rooting depth corresponds to the physiological maximum, which is taken as 0.7 m (Table 3) based on the values reported in the literature (Mishra et al., 1997; Kato et al., 2007).

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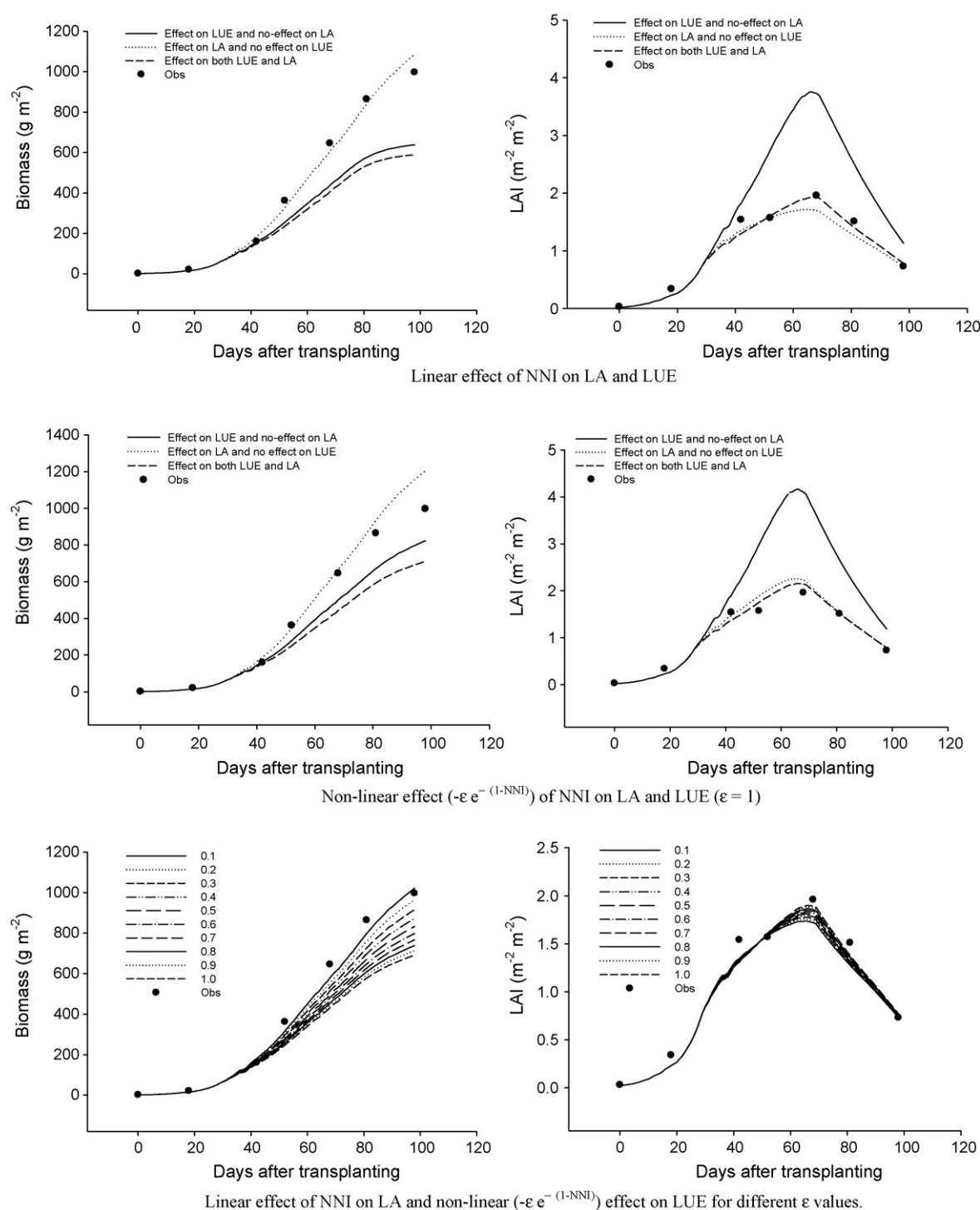
Fig. 5. Effect of N stress (NNI) on crop growth through its effect on LA, LUE or on both LA and LUE for the case of IRRI92-DS under 0 kg N ha^{-1}.

2.6. Soil water balance

The water balance in the model does not deal with a flooded rice system, but the soil is maintained at saturation so that the crop does not experience water stress. The soil water balance is calculated for a single soil layer, whose thickness increases with downward root elongation. The model does not simulate root elongation, but only average root increase in depth. The assumption that the root elongation does not depend on the dryness of the soil until wilting point is originally from LINTUL1 (Spitters, 1990). In the rice situation, we have a saturated soil and the wilting point is not expected occur.

Water and nutrient uptake by the crop is limited to the rooted soil depth. Addition of water to the available store through root extension is calculated from the rate of extension and the (saturated) water content (Spitters and Schapendonk, 1990; Farré et al., 2000).

2.7. Soil–crop nitrogen balance

The mineral nitrogen balance of the soil is the difference between nitrogen added through mineralization and/or fertilizer, and nitrogen removed by crop uptake and losses. The net rate of

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Table 1
Details of datasets used for calibration and testing of LINTUL3.

Data	Variety	Sowing date	Transplanting date (day of year)	N-fertilizer dose (kg ha^{-1})	N-fertilizer splits (kg ha^{-1})	N-application schedule
Calibration						
IRRI91-WS[a]	IR 72	1 July 1990	13 July (194)	0	0	No-N
				80	50, 30	Basal[b], 31 DAT
				110	30, 30, 20, 30	Basal, 25, 60, 83 DAT
IRRI92-DS[a]	IR 72	4 January 1992	16 January (16)	0	0	no-N
				180	120, 60	Basal, 18 DAT
				225	60, 60, 60, 45	Basal, 18 DAT, PI, FL
CRRI90-DS	IR 36	18 December 1989	25 January (25)	0	0	no-N
				50	25, 12.5, 12.5	Basal, 20, 53 DAT
				100	50, 25, 25	Basal, 20, 53 DAT
				150	75, 37.5, 37.5	Basal, 20, 53 DAT
Testing						
IRRI92-WS	IR 72	1 July 1992	14 July (195)	0	0	No-N
				80	80	Basal
				80	40, 40	Basal, MT
				80	27, 27, 27	Basal, MT, PI
IRRI93-DS	IR 72	14 January 1993	25 January (25)	0	0	No-N
				100	14.3, 14.3, 14.3, 14.3, 14.3, 14.3, 14.3	Weekly interval
				400	57.1, 57.1, 57.1, 57.1, 57.1, 57.1, 57.1	Weekly interval
CRRI92-DS	IR 36	8 January 1992	28 January (28)	0	0	No-N
				100	100	PI
				100	100	13 DAT
				200	100, 100	13 DAT, PI

Sources: Drenth et al. (1994), Dash et al. (1994), and Wopereis et al. (1994).

[a] WS: wet season; DS: dry season.

[b] Basal—at transplanting; PI: panicle initiation; FL: flowering; MT: maximum tillering; DAT: days after transplanting.

change of N in soil (dN/dt in g m^{-2} d^{-1}) is:

$$\left(\frac{dN}{dt}\right)_{soil} = N_{min} + (QN_{fer}NRF) - \left(\frac{dNU}{dt}\right) \tag{4}$$

where N_{min} is the nitrogen supply through mineralization and biological N fixation, QN_{fer} is the fertilizer nitrogen application rate, NRF is the fertilizer nitrogen recovery fraction (see Section 2.8) and dNU/dt is the rate of nitrogen uptake by the crop (Fig. 3), which is calculated as the minimum of the N supply from the soil and the N demand from the crop (see section "nitrogen demand").

2.8. Nitrogen supply from soil

Mineral nitrogen available for crop uptake (SOILN, Fig. 3) originates from three sources: nitrogen present in the soil profile at germination/transplanting, nitrogen from biological fixation and mineralization from soil organic matter during the growing season and nitrogen applied as fertilizer. Under aerobic conditions, indigenous soil nitrogen supply can be quantified reasonably accurately on the basis of soil organic matter content (Sinclair and Amir, 1992). Under anaerobic conditions, however, differences in mineral N supply between fields or seasons could not be explained on the basis of soil organic carbon, total nitrogen or initial inorganic nitrogen (Cassman et al., 1996; Bouman et al., 2001). Hence, indigenous nitrogen supply is introduced as a site-specific exogenous input, rather than simulating nitrogen mineralization. Ten Berge et al. (1997) found indigenous nitrogen supply values for tropical soils in the range of 0.5–0.9 kg ha^{-1} d^{-1}. Fertilizer nitrogen available for plant uptake, taking into account possible losses due to volatilization, denitrification, and leaching, is included in the model as a variable fraction, named nitrogen recovery fraction, NRF. A low N recovery value in flooded rice systems (30–39%, Cassman et al., 1996) is mainly due to volatilization losses. Any form of inorganic nitrogen (NH_4^+ or NO_3^-) when available in free form, if not taken up by the crop, is vulnerable to loss either through volatilization, denitrification or leaching. On a daily basis, the average N recovery value would be more or less stable under flooded conditions. The variable NRF used in the model represents the net recovery fraction of applied fertilizer, which depends on soil type, development stage of the crop, fertilizer type and time and mode of nitrogen application (De Datta, 1986) is determined by calibration. The approach of NRF instead of the mechanistic description was chosen in the model in order to not divert the attention from the main objective of the paper.

2.9. Nitrogen demand, uptake and stress

At sub-optimal nitrogen availability in the soil, nitrogen demand of the crop cannot be satisfied, which leads to sub-optimal crop nitrogen concentration. The crop nitrogen concentration below which a crop experiences nitrogen stress is called the *critical nitrogen concentration*. Nitrogen stress results in reduced rates of biomass production and eventually in reduced yields. A detailed description of crop nitrogen dynamics is given in Fig. 3. The relational diagram shows three reference points of N content in the model, i.e. actual ($NC_{act, pl}$), critical ($NC_{crt, pl}$) and residual ($NC_{res, pl}$) nitrogen content. Actual N content is the accumulated N above residual (which forms part of the cell structure). The critical N content is the one corresponding to half of the maximum. Nitrogen contents of these three reference points include those of leaves and stems (see Fig. 3), whereas roots are not considered since N contents of above-ground (green) parts are more important for photosynthesis, because of their chlorophyll content. However, calculation of N demand and N uptake also includes the belowground part.

2.10. Nitrogen demand

Total crop nitrogen demand equals the sum of the nitrogen demands of its individual organs (excluding storage organs, for which nitrogen demand is met by translocation from the other organs, i.e. roots, stems and leaves) (Fig. 3). Nitrogen demand of the individual organs is calculated as the difference between maximum and actual organ nitrogen contents. The maximum nitrogen content is defined as a function of canopy development stage (Drenth

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Table 2
Weather characteristics of different experimental sites during the growing period of the crop (transplanting to maturity) in the study.

Site/season	Mean daily solar radiation (MJ m^{-2})	Mean daily minimum temperature (°C)	Mean daily maximum temperature (°C)	Mean daily average temperature (°C)	Cumulative precipitation (mm)
IRRI91-WS	14.6	24.2	30.8	27.5	810.0
IRRI92-DS	19.1	22.2	30.8	26.5	92.2
CRRI90-DS	19.4	20.0	32.2	26.1	42.4
IRRI92-WS	16.2	24.1	31.2	27.7	893.8
IRRI93-DS	21.5	22.1	29.9	26.0	20.3
CRRI92-DS	20.1	21.1	33.2	27.2	84.4
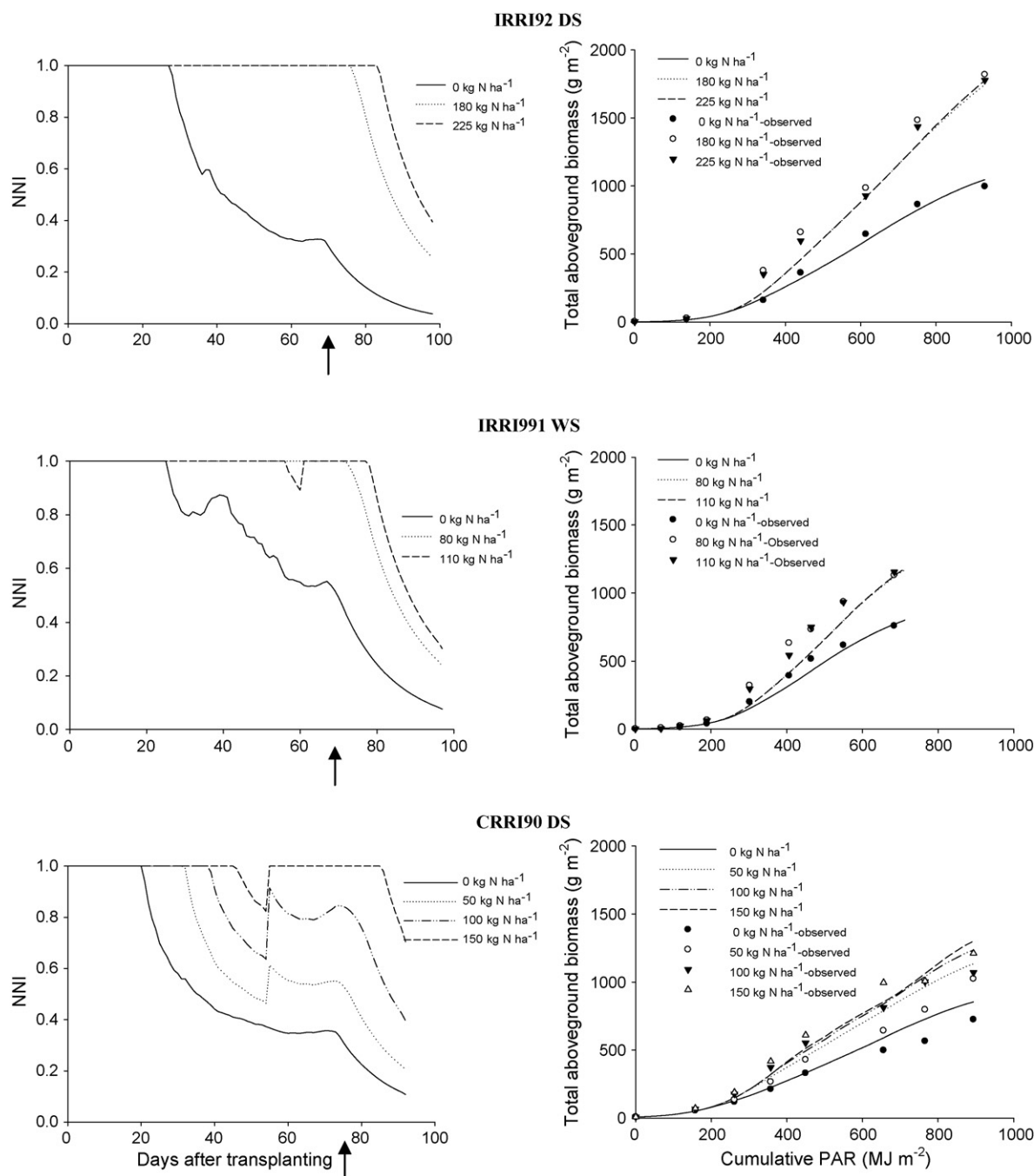
Fig. 6. Nitrogen nutrition index as a function of time and total aboveground biomass as a function of cumulative PAR for different treatments of different experiments used for calibration (lines are simulated; symbols are observations; arrows indicate the time of flowering when N uptake also ceases).

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et al., 1994). Total N demand (TN_{dem}: $g\,m^{-2}\,d^{-1}$) of the crop is:

$$TN_{dem} = \sum_{i=1}^{n} \frac{N_{max,i} - AN_i}{\Delta t} \tag{5}$$

where $N_{max,i}$ is the maximum nitrogen concentration of organ i ($g\,N\,g^{-1}$ biomass, with i referring to leaves, stems and roots), W_i is the weight of organ i (g biomass m^{-2}), and AN_i is the actual nitrogen content of organ i ($g\,N\,m^{-2}$).

2.11. Nitrogen uptake

Nitrogen uptake is determined by crop demand, indigenous soil nitrogen supply and fertilizer application. Nitrogen uptake processes like mass flow and diffusion are not explicitly simulated in the model. Rather, N uptake by the crop is estimated via a simple book keeping approach, similar to that in ORYZA (Bouman et al., 2001). Nitrogen from indigenous sources is assumed to have a higher (nearly 100%) recovery compared to applied fertilizers, as it is the amount of N actually taken up by a crop under zero nitrogen fertilizers. Therefore, in the model, it is assumed that the crop first takes up nitrogen mineralized from indigenous organic matter, and then from fertilizer. Total nitrogen taken up by the crop (dNU/dt) is partitioned (Fig. 3) among the different organs in proportion to their demands:

$$\left(\frac{dNU}{dt}\right)_i = \left(\frac{N_{dem,i}}{TN_{dem}}\right)\left(\frac{dNU}{dt}\right) \tag{6}$$

where $(dNU/dt)_i$, and $N_{dem,i}$ are the rate of nitrogen uptake ($g\,m^{-2}\,d^{-1}$) and nitrogen demand ($g\,m^{-2}\,d^{-1}$) of organ i (i refers to leaves, stems and roots), respectively.

About 75–90% of the total N uptake at harvest takes place before anthesis (Austin et al., 1976; Spiertz and Ellen, 1978; Heitholt et al., 1990) and, in conditions of high soil fertility, post-anthesis N uptake may contribute up to 25% but would exclusively end up in the grain as protein. Therefore, this nitrogen would not play any role in the calculation of nitrogen stress that influences the biomass formation. Therefore, nitrogen uptake is assumed to cease at anthesis, as nitrogen content in the vegetative parts hardly increases after anthesis (Groot, 1987; Sinclair and Amir, 1992). Nitrogen demand of the grains is also assumed to be met exclusively by translocation from leaves, stems, and roots as soon as grain formation starts. Hence, the rate of nitrogen accumulation in the storage organs is determined by their nitrogen demand calculated by the maximum N content and the actual N content and by the total amount of translocatable nitrogen in the other crop organs. Total translocatable nitrogen in the crop equals total nitrogen content of the organs, minus their residual non-transferable nitrogen content, which is the nitrogen incorporated in structural crop components. The net rate of change of nitrogen ($dN/dt)_i$ in each of the organs AN_i, where i refers to leaves, stem and roots, is:

$$\left(\frac{dN}{dt}\right)_i = \left(\frac{dNU}{dt}\right)_i - \left(\frac{dNT}{dt}\right)_i - \left(\frac{dND}{dt}\right)_i \tag{7}$$

where $(dNU/dt)_i$, $(dNT/dt)_i$ and $(dND/dt)_i$ are the contributions of nitrogen uptake to the organ, translocation from the organ and loss of nitrogen due to the death of the organ, respectively. It is assumed that the stem does not die and therefore $(dND/dt)_{stem}$, equals zero and the outflow rate is not included in the relational diagram.

2.12. Nitrogen stress

A crop is assumed to experience N stress at N concentrations below a critical value for unrestricted growth. To quantify crop response to nitrogen shortage, a Nitrogen Nutrition Index (NNI) is

Table 3
Parameters of the LINTUL3 model used for rice.

Parameter description	Values	Units
Crop-specific parameters		
Light use efficiency, LUE	2.7–3.0	$g\,MJ^{-1}$
Light attenuation coefficient, K	0.6	$m^2\,m^{-2}$
Base temperature for crop development, Tb	8.0	°C
Maximum relative growth rate of leaf area index, RL	0.0085	$(°C\,d)^{-1}$
Specific leaf area constant, $S_{la}C$	0.020	$m^2\,g^{-1}$
Residual N fraction in root, $N_{res,\,rt}$	0.002	$g\,g^{-1}$
Residual N fraction in stem, $N_{res,\,st}$	0.0015	$g\,g^{-1}$
Residual N fraction in leaves, $N_{res,\,lv}$	0.004	$g\,g^{-1}$
Maximum N concentration of stem as fraction of that of leaves, LSNR	0.50	$g\,g^{-1}$
Maximum N concentration of root as fraction of that of leaves, LRNR	0.37	$g\,g^{-1}$
Maximum rooting depth, RD_{max}	0.7	m
Maximum rate of increase in rooting depth, RRD_{max}	0.010	$m\,d^{-1}$
Maximum concentration of nitrogen in storage organs, $N_{max,\,so}$	0.0175	$g\,g^{-1}$
Nitrogen translocation from roots to storage organs as a fraction of total amount of nitrogen translocated from leaves and stem to storage organs, FNTRT	0.15	–
Time coefficient for N translocation, TC_{nt}	10.0	d
Critical N, as a fraction of maximum N concentration, FRNX	0.5	–
Relative death rate of leaf weight due to N stress, RDR_{ns}	0.03	d^{-1}
Coefficient of reduction of LUE under nitrogen stress, ε	0.20	–
Variety-specific parameters		
Heat sum for vegetative crop growth, $H_{sum,\,ant}$	1400–1800	°C d
Heat sum for reproductive crop growth, $H_{sum,\,mat}$	600–900	°C d

defined, ranging from 0 (maximum N shortage) to 1 (no N shortage) (Lemaire et al., 1989; Van Delden, 2001):

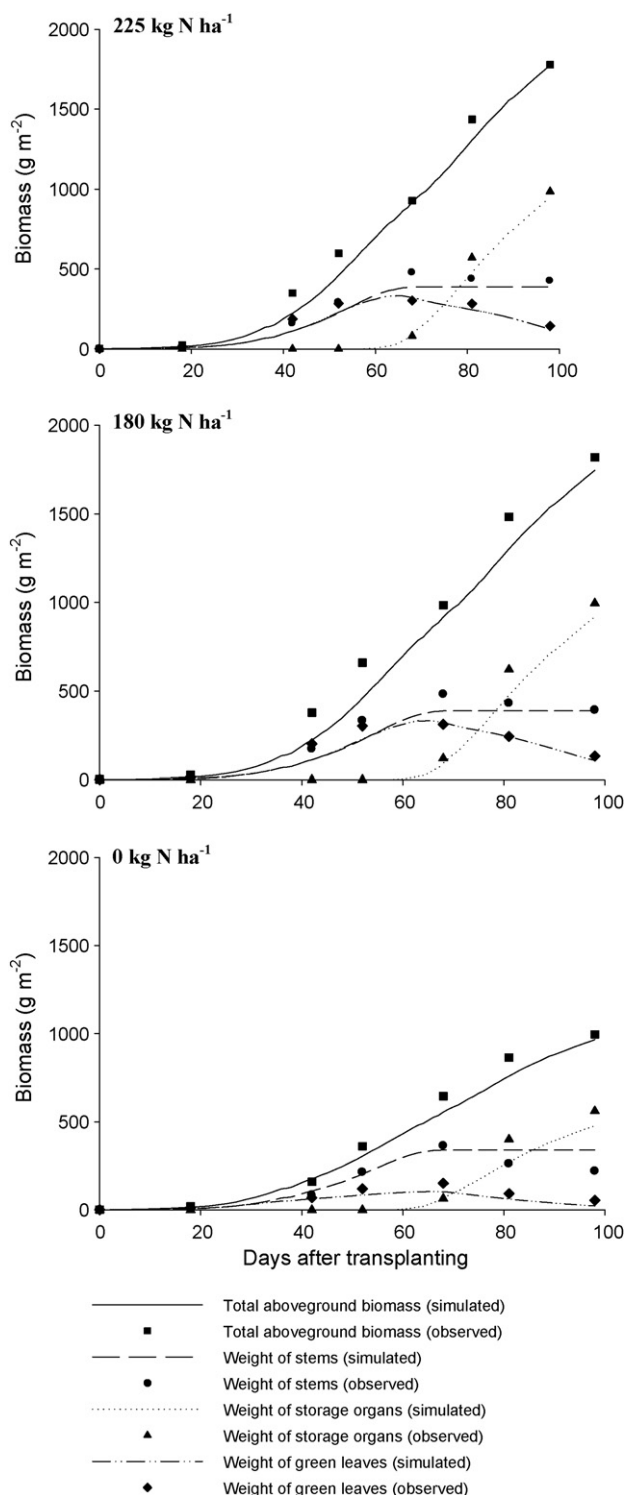$$NNI = \frac{actual\ crop\ [N] - residual\ [N]}{critical\ [N] - residual\ [N]} \tag{8}$$

Critical crop nitrogen concentration, the lower limit of canopy nitrogen concentration in leaves and stems required for unrestricted growth, has been taken as half the maximum nitrogen concentration (Porter, 1993; Jamieson et al., 1998). An experimental basis for such an assumption can be derived from the study of Zhen and Leigh (1990), who reported that nitrate accumulation in plant occurs in significant quantity when the N needs to reach the maximum growth were fulfilled and the mean value of nitrate accumulated beyond the critical N concentration was about 50% for different stages.

2.13. Effects of nitrogen limitation on crop growth

To test the effect of N stress on LA and/or LUE, linear and non-linear functions of NNI were used to be able to modify these variables and to compare the total aboveground biomass with observations. We used the data sets, which are also used for calibration of the model (IRRI92, IRRI91 and CRRI90). We used only the treatments without any fertilizer application for the obvious reason to see the clear effect of N stress. That means, this analysis is based on a limited number (3) of data points. To investigate the hypothesis that N stress had a linear effect on LA, biomass partitioning to leaf and SLA are modified linearly with NNI. Leaf biomass partitioning, SLA and LUE are reduced for the effect of N stress on both LA and LUE. To investigate the hypothesis that N stress had a non-linear effect, these variables were modified as an exponential decay function ($-\varepsilon\,e^{-(1-NNI)}$) of NNI. The exponential decay function is to represent the canopy N profile distribution, which is generally described as a negative exponential function of cumulative LAI (Bindraban, 1999). Canopy N profile changes

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Fig. 7. Calibration results of simulated (lines) and observed (symbols) aboveground biomass, green leaves, stems, and storage organs for IRRI92-DS, for different fertilizer treatments.

from nearly uniform, during early growth stages, to strongly non-uniform.

Fig. 4 shows an underestimation of biomass for a linear modification on both LA and LUE (−23 to −41%) and on LUE alone (−25 to −36%). A linear effect on LA shows an overestimation (9–24%), which is relatively closer to the observed figures (Fig. 5). Similarly, the non-linear effect of NNI only on LUE (−13 to −18%) is found closer to the observed than on both LA and LUE (−15 to −29%).

The non-linear effect only on LA has an overestimation of 12–35% of biomass. This analysis leads us to assume that crops partially follow both of these strategies of LUE and LAI reduction. Therefore, we ran the model for a combination of linear and non-linear effects of NNI on LA and LUE. The coefficient, ε of the exponential function was determined by running the model for a range of ε values (0–1). The best fit was found for a ε value in the range of 0.1–0.2 (Figs. 4 and 5). The results show that a linear effect of NNI on LA and a non-linear effect of NNI on LUE better represent the observed results. Therefore, in our model we used a combination of both strategies to implement N stress on crop performance in addition to the reduced biomass partitioning and accelerated leaf senescence.

(i) Effect of NNI on partitioning factor of biomass to leaves (Pc_{lv}):

$$Pc_{lv,ns} = Pc_{lv}NNI \qquad (9)$$

where Pc_{lv} and $Pc_{lv, ns}$ are the fractions partitioned to leaves at optimal and sub-optimal nitrogen status, respectively.

The amount of biomass growth not partitioned to the leaves due to the N stress is distributed over the remaining plant parts.

(ii) *Effect of NNI on leaf area*: The effect of N stress on leaf area development is implemented in the model during both the juvenile growth phase and the linear growth phase. During the exponential juvenile growth phase, leaf area development is described by

$$\left(\frac{dGLAI}{dt}\right)_{exp} = LAI_t RLT_e NNI \quad \text{for DVS} < 0.2 \text{ and LAI} < 0.75 \quad (10)$$

During the linear growth phase the following equation is used:

$$\left(\frac{dGLAI}{dt}\right)_{lin} = \left(\frac{dW}{dt}\right)_{lv}^{S_{la}} \quad \text{for DVS} \geq 0.2 \text{ or LAI} \geq 0.75 \qquad (11)$$

$$S_{la} = S_{la}CS_{la}CfNNI \quad \text{for DVS} \geq 0.2 \text{ or LAI} \geq 0.7 \qquad (12)$$

where $(dGLAI/dt)_{exp}$ and $(dGLAI/dt)_{lin}$ are leaf area growth rates (m^2 leaf m^{-2} soil d^{-1}) during the sink-limited and the source-limited growth stages, respectively, LAI_t is leaf area index at time t, RL the maximum relative growth rate of LAI (($°C\,d)^{-1}$); T_e daily effective temperature (°C), S_{la} is the specific leaf area ($m^2\,g^{-1}$), $S_{la}C$ is the specific leaf area constant and $S_{la}Cf$ is the correction factor for $S_{la}C$, which is a function of crop age.

(iii) *Effect on biomass growth*: The rate of biomass growth is a function of LUE, daily total radiation (Q_0, MJ $m^{-2}\,d^{-1}$), attenuation coefficient (k, $m^2\,m^{-2}$), LAI and N stress, and is calculated as

$$\left(\frac{dW}{dt}\right) = 0.5Q_0\left(1 - e^{(-kLAI)}\right) LUE\, e^{-\varepsilon(1-NNI)} \qquad (13)$$

where ε is the coefficient of canopy N profile distribution.

(iv) *Effect on leaf death*: If leaf nitrogen concentration per unit leaf area decreases, as nitrogen is translocated from the oldest leaves at the bottom of the canopy to newly formed leaves or to grains, leaves die. Loss of leaf weight (g $m^{-2}\,d^{-1}$) due to nitrogen stress is calculated as

$$\left(\frac{dW}{dt}\right)_{lv,ns} = W_{lv,g}\, RDR_{ns}(1 - NNI) \qquad (14)$$

where $W_{lv,g}$ is the weight of green leaves and RDR_{ns} is the maximum relative death rate of green leaves due to nitrogen stress.

Death of leaves due to nitrogen stress is added to normal senescence due to ageing and represented by $(dW/dt)_{lv,d}$ (Fig. 1), and the corresponding loss of total leaf area is calculated using S_{la}:

$$\left(\frac{dDLAI}{dt}\right) = \left(\frac{dW}{dt}\right)_{lv,d} S_{la} \qquad (15)$$

3. Model evaluation

The model was evaluated against data sets (Table 1) of experiments conducted in Asia that also have been used for evaluation

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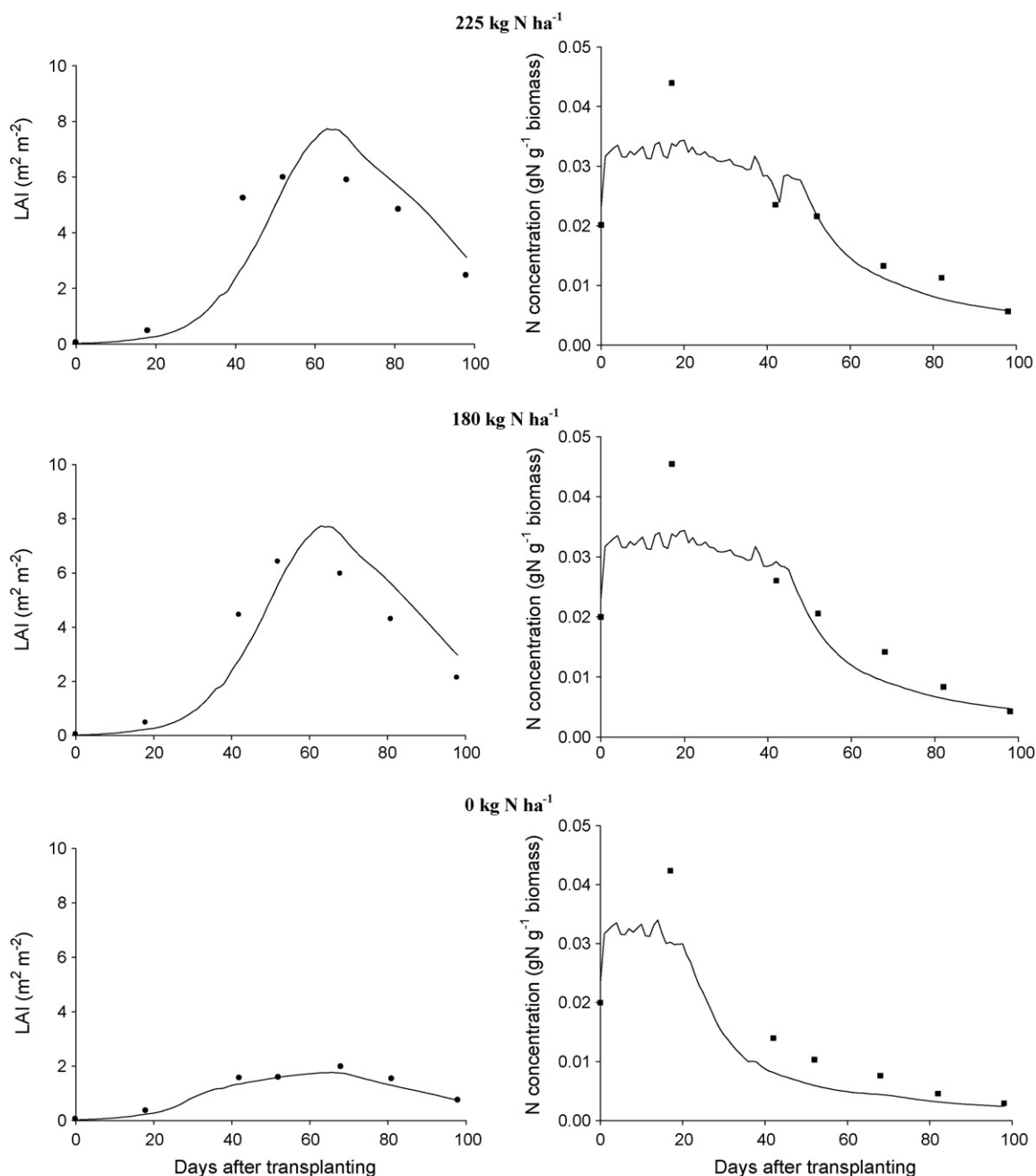
Fig. 8. Calibration results of simulated (lines) and observed (symbols) LAI (left figures) and N concentrations (right figures) in green plant parts (leaves and stems) for IRRI92-DS for different fertilizer treatments.

of the ORYZA group of models (Drenth et al., 1994; Bouman et al., 2007). The mean weather data of different sites during the growing season are given in Table 2. Model results are compared graphically to observed data and Root Mean Square Deviation (RMSD[1]) and Average Absolute Deviation (AAD) were calculated to evaluate model performance during calibration and model testing.[2]

3.1. Calibration

Calibration, the process of adapting model parameters to improve agreement between model results and reality (Van Ittersum et al., 2003), is usually performed in a step-wise manner, starting with the calibration of crop phenology, followed by total biomass production, partitioning and leaf area index. Model parameters (Table 3) were calibrated on the basis of datasets of experiments conducted at the International Rice Research Institute (IRRI), Philippines and at the Central Rice Research Institute (CRRI), India. The calibration was done manually by a trial-and-error method by comparing the model results with the observed results. The model was first calibrated for non-limiting nitrogen situations with the treatments 180 and 225 kg N ha^{-1} of the dataset IRRI92-DS (dry season, DS) and subsequently for the

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[1] $\text{RMSD} = \left[\dfrac{\sum_{i=1}^{n} (Y_i - O_i)^2}{n} \right]^{0.5}$; $\text{AAD} \ (\%) = \left[\sum_{i=1}^{n} \left(\dfrac{\text{Abs}(Y_i - O_i)}{O_i} \right) \right] \dfrac{100}{n}$ where Y_i and O_i are simulated and observed values, respectively.

[2] The term model *testing* instead of *validation* used here is based on the scientific philosophy of Popper that scientific theories can never be proved to be true, but can only be tested to falsify them.

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Table 4
Average absolute deviation (AAD) between observed and simulated values for total biomass, stems, roots, leaves, panicles, LAI, and N concentration for different datasets and fertilizer treatments.

Data	Nitrogen treatment (kg ha⁻¹)	Average absolute deviation (%)							Average
		Total aboveground biomass	Stems	Roots	Leaves	Panicles	LAI	Nitrogen concentration	
IRRI92-DS[a]	0	13	22	–	33	17	12	34	22
	180	22	21	–	23	18	33	20	23
	225	18	19	–	23	11	29	14	19
	Average	18	21		27	15	25	23	21
IRRI91-WS[a]	0	13	25	–	11	8	16	15	15
	80	29	32	–	30	13	32	15	25
	110	37	51	–	32	17	31	9	29
	Average	26	36	–	24	12	26	13	23
CRRI90-DS	0	9	26	55	19	17	–	55	30
	50	14	27	28	48	18	–	41	29
	100	13	32	17	39	29	–	26	26
	150	16	32	19	36	41	–	24	28
	Average	13	29	30	36	26	–	37	28
Testing									
IRRI92-WS	0	6	19	–	22	9	12	67	22
	80	21	28	–	22	21	24	54	28
	80	21	24	–	20	33	45	48	32
	80	17	15	–	19	38	39	49	29
	Average	16	21	–	21	25		55	28
IRRI93-DS	0	32	39	–	24	42	28	–	33
	100	62	38	–	60	103	90	–	71
	400	28	29	–	23	61	23	–	33
	Average	41	35	–	36	69	47		46
CRRI92-DS	0	28	27	49	30	80	–	43	43
	100	40	47	44	47	68	–	30	46
	100	18	24	37	28	78	–	25	35
	200	38	44	36	39	78	–	17	42
	Average	31	35	41	36	76	–	29	41

[a] WS: wet season; DS: dry season.

nitrogen-limited treatments of IRRI91-WS (wet season, WS) and CRRI90-DS.
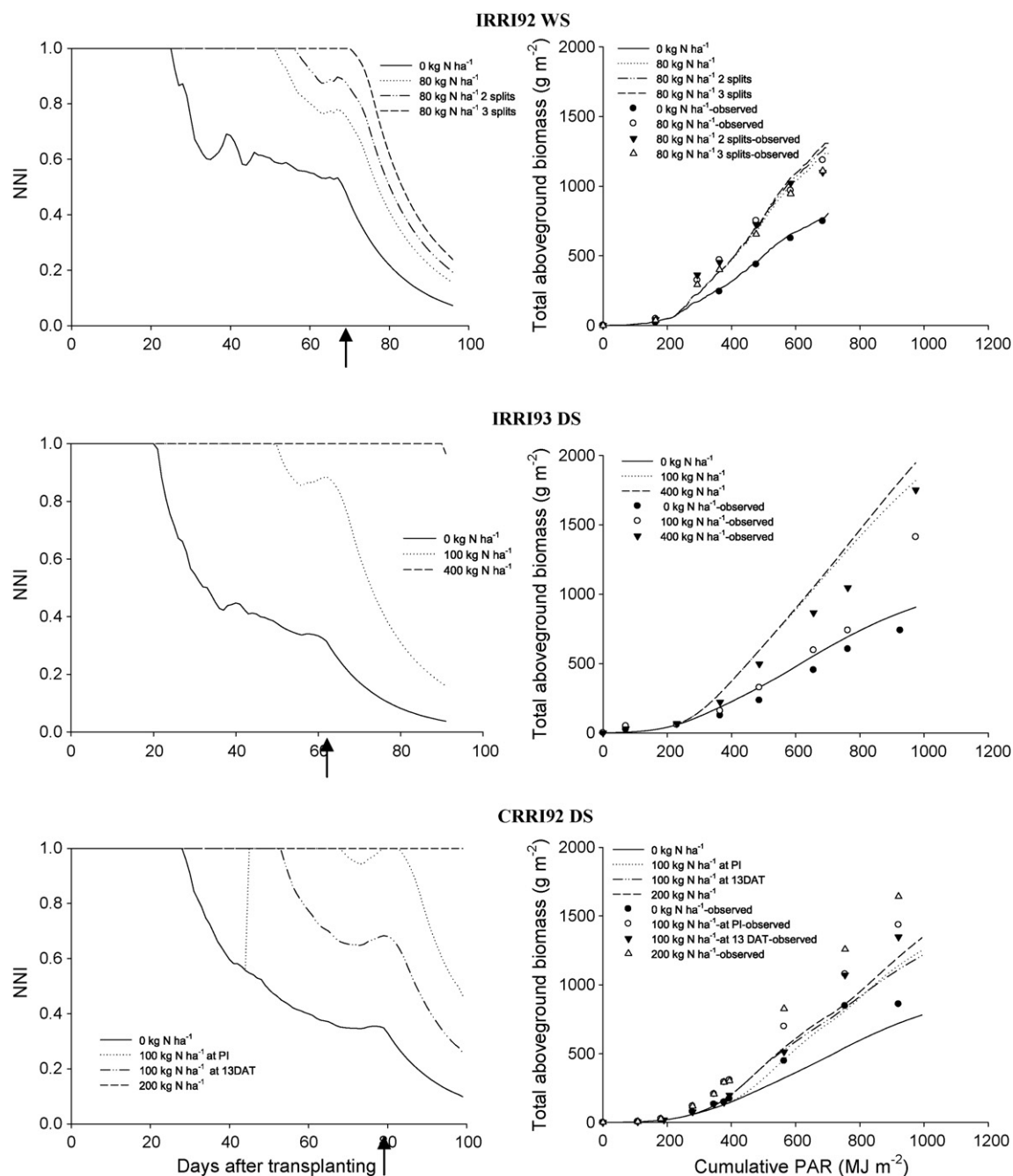
Heat sums for each cultivar were calculated from observed dates of flowering and maturity and from recorded weather data. For each data set, the model was initialized with observed weights of leaves, stems and roots at transplanting. Light use efficiency values were also calibrated, because of variation in radiation and temperature (Table 2) as explained by Choudhury (2001a), resulting in values of 3.0 (g dry matter MJ⁻¹ PAR intercepted) for IR72 at IRRI and 2.7 for IR36 at CRRI. These values refer to total biomass, including roots, and are comparable to reported values of 2.4 (Kiniry et al., 1989; Mitchell et al., 1998; Kiniry et al., 2001) and 2.0 (Choudhury, 2001b), referring to aboveground biomass alone. Assuming a varying root to shoot ratio of 0.5–0.1 over the crop growing period, these experimental values are equivalent to approximately 2.2–3.6 g MJ⁻¹ for total biomass. In the following sections, however, we use aboveground biomass to compare with the observed values, as root biomass values are not available for IRRI datasets.

Indigenous soil nitrogen supply, which depends on soil characteristics such as texture and organic matter content, and on management, was calibrated on the basis of the zero N-fertilizer treatments, and was set to 0.05 g N m⁻² d⁻¹, for both IRRI and CRRI.

3.2. Results of calibration

Simulated nitrogen nutrition index values for different treatments in the experiments used for calibration show a clear response to nitrogen application (Fig. 6). In the no-fertilizer treatments, the fixed indigenous soil N supply is enough to support crop growth without stress up to 20–30 days after transplanting (before active tillering). The nitrogen demand thereafter, during tillering, can only be met by external sources of nitrogen. Split application of N, as in the 180 and 225 kg ha⁻¹ treatments in IRRI92-DS, cover crop requirements until flowering. Therefore, the model-calculated aboveground biomass for 180 kg N ha⁻¹ is similar to that for 225 kg N ha⁻¹. In the wet season of IRRI91, the biomass formed was lower than that in the DS of IRRI92. The main reason for a low biomass would be the low incident radiation in the wet season (with a cumulative PAR of 712 MJ m⁻² season⁻¹ in contrast to 930 MJ m⁻² season⁻¹ in the dry season of IRRI92). The low incident radiation (23% lower in WS compared to the DS) restricts growth rates and consequently N demand of the crop. Because of a lower growth rate, crop in the WS needs more time (56 DAT) to reach the full canopy (LAI > 4.0) compared DS (47 DAT). This time lag in reaching the peak LAI leads to 'missing' of some light being intercepted, which further decreases the rate of biomass growth. Therefore, high fertilizer application in the wet season may not result in yield increase in proportion to that applied in a dry season. Application of all of the 80 kg N well before flowering in case of 80 kg N ha⁻¹ could meet the nitrogen demand until flowering. However, only 60 kg N applied during the same period in case of 110 kg N ha⁻¹, resulted in a small dip in NNI just before the 3rd application (Fig. 6). Results of CRRI90-DS show the effect of N-dose on NNI and on biomass formation. Simulated NNI values show a clear effect of N dose and splits. For the calibration results, the crop begins to experience N stress 20 DAT in the non-fertilized treatment. However, fertilizer application at 20 DAT in other treatments supports crop growth without N stress for some more days, depending upon the rate of fertilizer application. For example, in the treatment with 150 kg N ha⁻¹, the 'dip' in NNI begins 26 days after the second dose (37.5 kg ha⁻¹) of fertilizer application, whereas in the 50 kg N ha⁻¹ treatment, this

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Fig. 9. Time course of the nitrogen nutrition index (NNI, left figures) and the relation (simulated, lines and observed, symbols) between total aboveground biomass and cumulative PAR (right figures) for different treatments of different experiments used for model testing (arrows indicate the time of flowering when N uptake ceases).
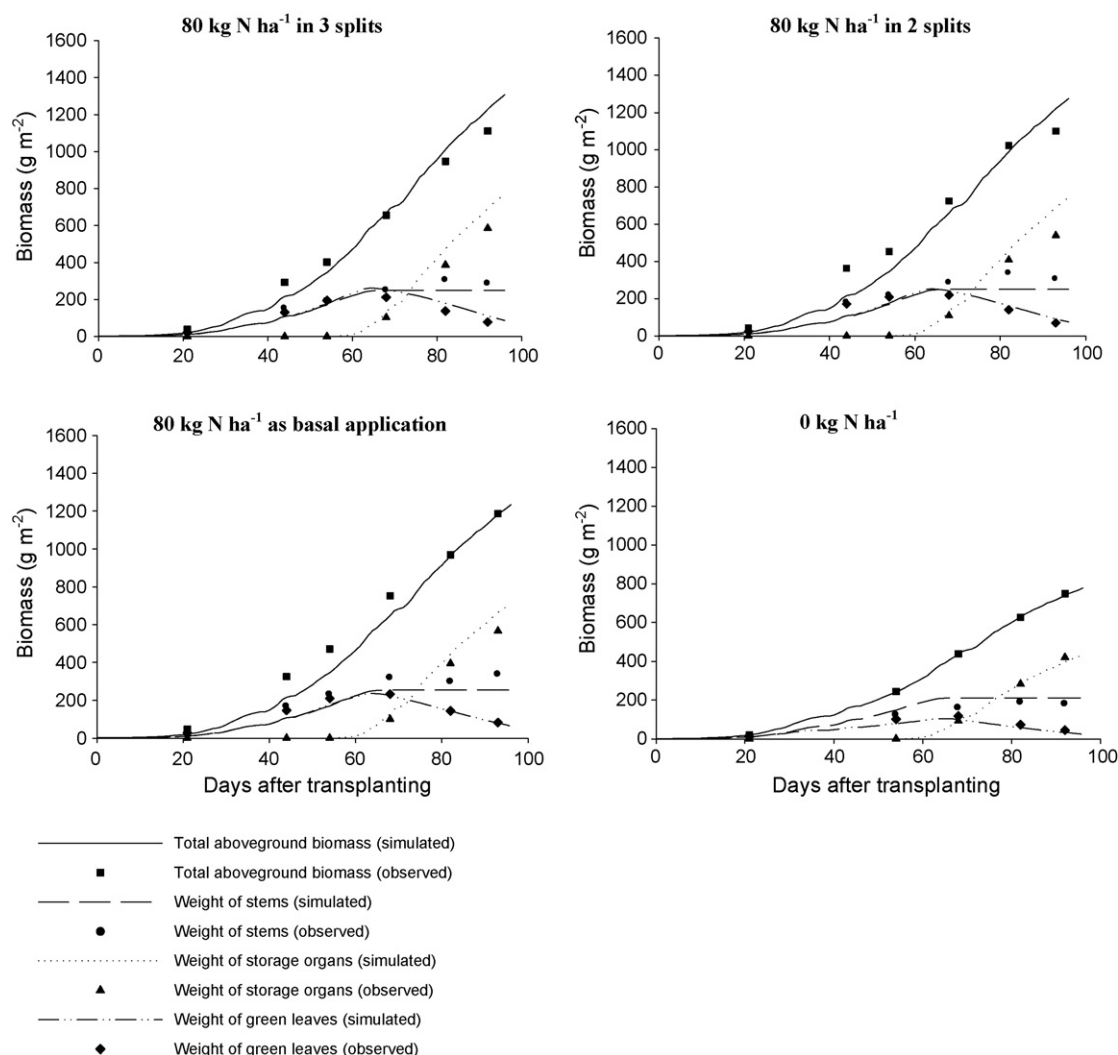
dip starts after 12 days and declines more steeply than at 100 and 150 kg N ha^{-1}. The steep increase in the later part of growth (about 55 DAT) is due to the 3rd split of N application at 53 DAT (Table 1). However, the total aboveground biomass yields were not different for the different fertilizer doses. The high average daily total radiation in CRRI (Table 2) led to a higher biomass production and leaf area index (about 3) in the initial phase, which may have been enough to fully utilize PAR. Therefore, the N stress in the later part of the growing season (30–70 DAT), before anthesis does not strongly affect crop yield.

Calibrated time courses of aboveground biomass, leaf, stem and grain weights for IRRI92-DS show good agreement with observed values, for a range of fertilizer application rates (Fig. 7). However LAI was underestimated in the initial stage and slightly overestimated during the later part especially for fertilized treatments. Though

N concentration followed the observed results under calibration, they failed to reach the peak N concentration on 20 DAT for reasons unknown. Other calibration experiments (not shown) gave similar results. Nitrogen concentrations in the green plant parts (leaves and stems) decrease with crop development for both the observed and calibrated, even under optimal N supply, due to dilution as biomass increases and due to translocation to the storage organs (Fig. 8). In the calibration data set, agreement between observed and simulated results was closest for IRRI92-DS with an AAD of 21% (Table 4). Maximum deviation (29%) of model results compared to the observations was found for CRRI90, especially for the situations without N fertilizer (33%).

Aboveground biomass shows an average deviation of 19%, whereas stem and leaf weights are relatively more scattered compared to the observed for all datasets used in the calibra-

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Fig. 10. Simulated and observed weight of total aboveground biomass, green leaves, stems and storage organs for data set IRRI92-WS in the testing for different fertilizer treatments.

tion (Table 5). In terms of absolute values, the model shows a RMSD of 92 and 88 g m^{-2} for total aboveground biomass and stem weight, respectively. The values for leaves and storage organs are 46 and 59 g m^{-2} and 0.8 (m^2 leaf area m^{-2} soil) and 0.005 (g N g^{-1} biomass) for LAI and N concentration, respectively. Since calibration shows satisfactory agreement with the observations in terms of biomass, LAI and N content under a range of fertilizer treatments, the model was subsequently tested with independent data sets.

Table 5
Root mean square deviation (RMSD) and average absolute deviation (AAD, %) between observed and simulated values for phenology, biomass components, LAI and nitrogen concentration for the whole dataset used for calibration and testing.
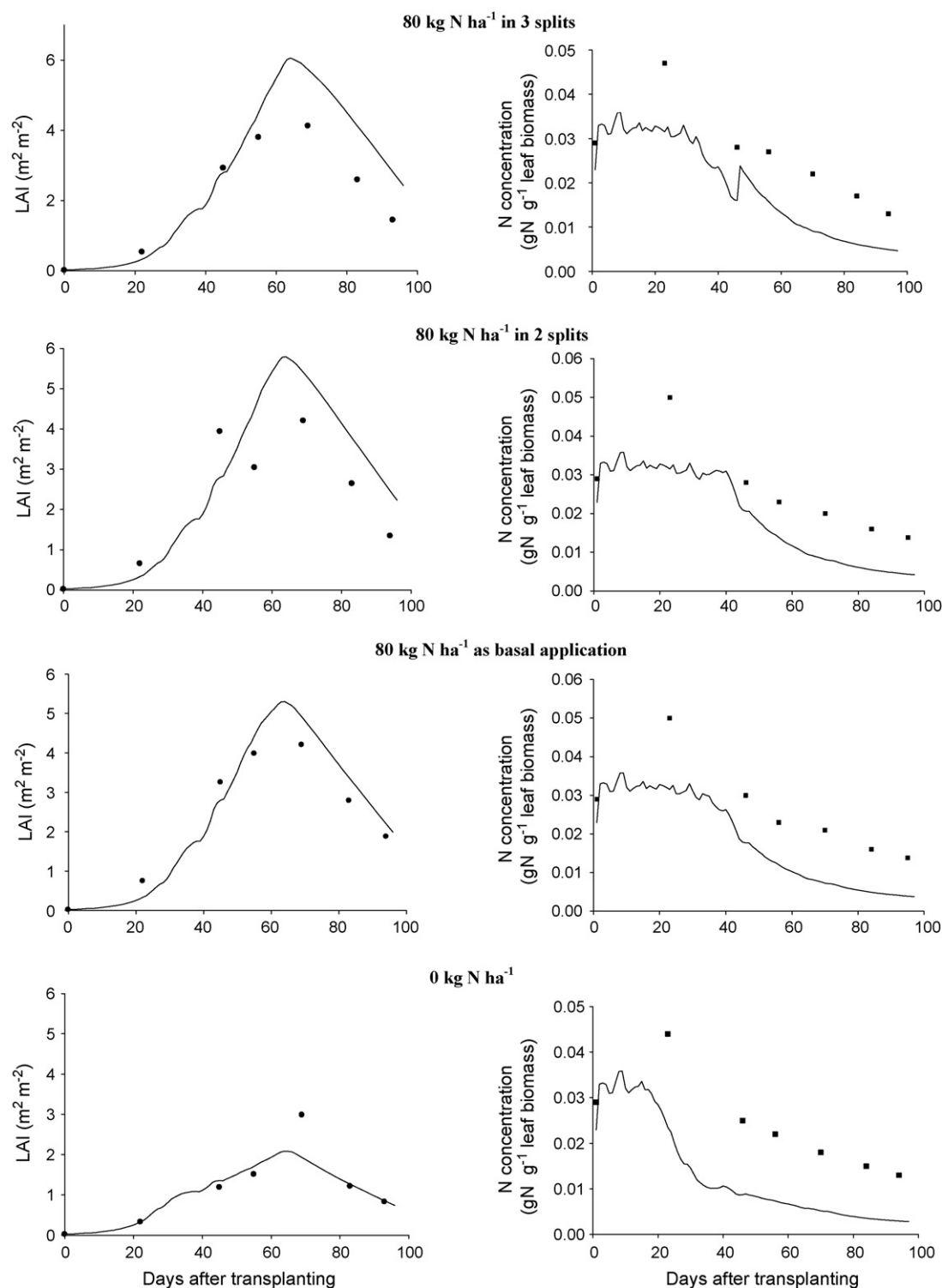
	Calibration		Testing	
	RMSD	AAD	RMSD	AAD
Aboveground biomass (g m^{-2} soil)	92	19	167	26
Weight of stems (g m^{-2} soil)	88	29	76	27
Weight of roots (g m^{-2} soil)	25	30	44	41
Weight of leaves (g m^{-2} soil)	46	29	65	31
Weight of storage organs (g m^{-2} soil)	59	19	90	43
LAI (m^2 leaf m^{-2} soil)	0.8	26	1.2	39
N concentration (g N g^{-1} biomass)	0.005	25	0.009	39

3.3. Model testing

Independent data sets of experiments conducted in the wet season of 1992, and the dry seasons of 1993 at IRRI and of 1992 at CRRI, for fertilizer nitrogen treatments ranging from 0 to 400 kg N ha^{-1} were used in model testing.

3.3.1. Results of model testing

Results of IRRI92-WS show the effect of split applications of a given fertilizer dose (Table 1) on crop growth and yield (Fig. 9). Observed results for a single application of 80 kg ha^{-1} as basal, a 40-40 application as basal and at tillering and a 27-27-27 application as basal, at tillering and at panicle initiation show, contrary to expectations, a marginally higher aboveground biomass as basal compared to the three splits. This may depend on the climatic characteristics of the season. A low incident radiation in the wet season leads to a lower rate of biomass production and subsequent N demand. A higher dose of N application as basal may lead to higher N uptake, which can be stored for later growth (Shangguan et al., 2004). The model results also show hardly any increase in total aboveground biomass with split application compared to a single basal application (Fig. 9). The single basal application of N could meet 100% of the N demand up to 52 DAT and 77% till flowering. Maximum nitrogen concentration in the model, which is

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Fig. 11. Simulated (lines) and observed (symbols) LAI (left figures) and nitrogen concentration in leaves (right figures) for the dataset IRRI92-WS in the testing for different fertilizer treatments.

double the critical N concentration, may have led to luxury N uptake by the crop. For IRRI93-DS, application of 400 kg N ha^{-1} in seven splits resulted in higher biomass yield compared to 100 kg N ha^{-1} in seven splits. However, simulation results for the above two cases do not show any increase in aboveground biomass in proportion to N uptake (Fig. 9). Because, similar to IRRI92-WS, the NNI value under 100 kg N ha^{-1} remains 1 till 50 DAT and declines to only 0.88 by the time of flowering – which is hardly enough to make a differ-

ence in biomass production in comparison to 400 kg N ha^{-1} – the crop does not experience N stress throughout its growing period. Model results for CRRI92-DS show an underestimation of total aboveground biomass (Fig. 9). Aboveground biomass values for N treatments of 100 kg ha^{-1} at 13 DAT and at PI do not show much difference, whereas observed values clearly show a higher biomass for application at PI, which is the most critical stage for nitrogen application in rice. In all the above experiments, the biomass yields

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without any fertilizer application are well simulated except for CRRI92-DS where the model underestimated the total aboveground biomass.

Characteristic simulated time courses of aboveground biomass, stems, leaves and storage organs, LAI and N concentration for IRRI92-WS are given in Figs. 10 and 11. Similar results were obtained for other experiments, but are not given here. Model results of biomass distribution and LAI correspond well with observed results for IRRI92-WS even though N concentration is slightly underestimated in all treatments. In the model testing, deviations for total aboveground biomass, stems, leaves and panicles are higher for IRRI93-DS and CRRI92-DS than for IRRI92-WS (Table 4). Estimated values of RMSD for aboveground biomass, stems, roots, leaves and storage organs are 167, 76, 44, 65 and 90 g m^{-2}, respectively (Table 5). In general, crop variables show a higher deviation in the testing than in the calibration set, as expected.

4. Discussion and conclusions

The LUE based approach calculates the net photosynthesis rate using a single independent variable LUE and PAR intercepted by the canopy. In principle, the value of LUE is determined by crop genetic/varietal characters and the net photosynthetic rate is the product of its interaction with the environment. In LINTUL3, the values of LUE were calibrated for different locations owing to the difference in varieties and due to lack of an established relation between LUE and climatic (temperature and solar radiation) characteristics. Variations in LUE of IRRI and CRRI could be partially explained on the basis of their weather characteristics. A higher mean maximum temperature (32.7 °C) and a lower mean minimum temperature (20.6 °C) in CRRI compared to IRRI (30.7 and 23.2 °C, respectively) may be responsible for low light use efficiency at CRRI (2.7 g MJ^{-1}) compared to IRRI (3.0 g MJ^{-1}). The growth of the rice crop is more affected by a low temperature than by a high temperature (Vergara, 1976; Nishiyama, 1976). In contrast, the mean daily solar radiation (MJ m^{-2} d^{-1}) is higher in CRRI (19.8) compared to IRRI (17.8). The quality of light also influences the radiation use efficiency of the crops: it increases with an increase in the diffuse fraction (Choudhury, 2001b). Establishing dynamic relations between these variables and LUE will help to better understand the effect of these variables on crop growth.

LINTUL3 combines the essential crop growth processes as described in LINTUL1 and LINTUL2 with the major N processes described in ORYZA 2000 (Bouman and Van Laar, 2006). The model does not simulate the flooded conditions typical for the majority of rice systems, but assumes the soil to be continuously saturated. Soil N processes are not described in detail, but represented by exogenously defined values for indigenous nitrogen supply and fertilizer-N recovery that are site- and season-specific. Therefore, soil moisture does not have a direct effect on nitrogen dynamics. The nitrogen part of the model describes total N demand of the crop, N supply from the soil and N stress. Nitrogen supply influences dry matter production and its partitioning within the crop (Van Keulen and Stol, 1991; Lloyd and Taylor, 1994; Reynolds and Chen, 1996; Bannayan et al., 2004). Sensitivity analysis of NNI for the effect of N stress on leaf area and LUE shows that NNI mainly affects leaf area and that its effect on LUE is relatively small (Fig. 4). These results correspond to the reports of Garcia et al. (1988), Porter (1993) and Jamieson et al. (1998), showing that moderate nitrogen stress will not affect LUE significantly, but rather the leaf area. Reducing leaf area growth leads to thicker leaves and thus enables the crop to maintain its nitrogen concentration per unit of leaf area. The effect of N stress on LUE is found to be <20% (Fig. 4), which is comparable to the field study of Hasegawa and Horie (1996) where the mean difference in LUE between non-fertilized and fertilized treatments over the growing season was only 6%. The mechanism resulting in a smaller effect of stress on LUE was explained on the basis of a non-uniform canopy N profile, which is analogous to light attenuation within the canopy (Anten et al., 1995; Goudriaan, 1995).

Model performance in general agreed well with the observations. The model responded similarly to the observations in response to fertilizer application, i.e. with higher biomass production, LAI and N concentration. The response of the aboveground biomass and weight of storage organs to N fertilizer application (Mg biomass/kg N applied) as related to different treatments with and without fertilizers under calibration and validation (Table 6) show (i) that the simulated and observed ratios are close to each other and (ii) that there is a wide range of values from 25 to 142 for above ground biomass and 14 to 73 for storage organs compared to the simulated values of 22 to 158 and 11 to 94 Mg ha^{-1}, respectively. The wide range of values for even the same amount of fertilizer application is due to the different timings of application during the growing season. In all the experiments comprising

Table 6
The response of N fertilizer application on aboveground biomass and storage organs for different treatments under calibration and validation.

Datasets	N fertilizer applied (kg ha^{-1})	Aboveground biomass (kg biomass/kg N)		Storage organs (kg biomass/kg N)	
		Simulated	Observed	Simulated	Observed
Calibration					
IRRI92-DS	180	39	46	22	24
	225	32	35	19	19
IRRi91-WS	80	46	46	28	17
	110	34	36	21	17
CRRI90-WS	50	56	60	29	37
	100	38	35	21	19
	150	30	32	17	21
Testing					
IRRI92-WS	80	147	142	85	71
	80	154	131	91	67
	80	158	133	94	73
IRRI93-DS	100	82	67	52	36
	400	24	25	16	14
CRRI92-DSS	100	37	58	20	23
	100	34	49	16	26
	200	22	39	11	21

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fertilized treatments, the response of biomass to changes in NNI, due to a variation in amount and time of N application, is less well reproduced, even though the model responded well to the treatments without fertilizer application. Simulated total aboveground biomass was more accurate than weights of individual crop components. The model results show that the effect of N stress on dry matter production is well simulated, whereas that on biomass partitioning needs to be further tested under diverse environmental conditions to increase insight in the exact response of this crop characteristic to N stress.

To conclude, a simple model such as LINTUL, adapted with moderately detailed nitrogen process descriptions, does satisfactorily describe the processes for nitrogen-limited growth of rice. The advantage of such a model is that it combines the essential processes of crop growth with simple soil processes to arrive at reasonable estimates of crop yield.

The modelling approach included in LINTUL3 allows the model to be used for other crops with a minimum adaptation of the crop parameters such as maximum, critical and minimum N concentrations. However, the alternative effects of N stress on crop growth, either on LA and/or LUE, depending on the crop species (Vos and Van der Putten, 1998; Vos et al., 2005; Lemaire et al., 2008), has also to be considered. In the present modelling set up of LINTUL3, both these effects can be accommodated depending on the crop response to N stress. Therefore, the model may also be helpful to explore the effect of N stress on crop growth for different crop species.

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