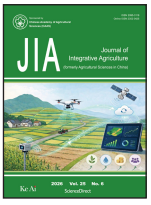
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RESEARCH ARTICLE

Model development and feature parameter extraction to capture variations in rice leaf color changes during the later reproductive period

Yanan Xu[1, 2*], Yi Tao[1*], Chang Ye[1], Deshun Xiao[1], Song Chen[1], Guang Chu[1], Chunmei Xu[1], Jianliang Huang[2#], Danying Wang[1#]

[1] *State Key Laboratory of Rice Biology, China National Rice Research Institute, Hangzhou 310006, China*

[2] *National Key Laboratory of Crop Genetic Improvement/Key Laboratory of Crop Ecophysiology and Farming Systems in the Middle Reaches of the Yangtze River, Ministry of Agriculture and Rural Affairs/College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China*

Highlights

- The leaf color change model and extracted parameters established here can quantitatively depict the leaf color change process during the later reproductive period.
- Significant differences in the leaf color change parameters are observed across leaf positions, rice varieties and nitrogen treatments.
- High-yielding varieties are characterized by a later onset time and a slower rate of leaf color change.

Abstract

The change in leaf color during the later reproductive period of rice is directly related to photoassimilate accumulation and nutrient reuse, and it ultimately affects grain filling and yield. This study aimed to explore an assessment model that depicts the leaf color change process, and extract parameters that can precisely distinguish differences in leaf color changes among different treatments and varieties. A total of 31 rice varieties were selected as the field experiment materials in 2019 and 2023. The SPAD values of the flag, 2nd and 3rd leaves were measured after heading, and they were normalized to the leaf color index (CI). A functional model for the variation of leaf CI with time (t) in the late reproductive stage of rice was established based on $CI=at^2+bt+c$, and seven color change parameters were extracted for the quantitative comparison and assessment of leaf color changes, including three time related parameters for color change (onset time, T_0; midpoint time, T_{50}; and color change duration, T_{100}); one leaf color index (final value of CI, CI_f); and three parameters related to the color change rate (the rate during T_0–T_{50}, R_1; the rate during T_{50}–T_{100}, R_2; and the mean color change rate, R_m). In 2023, Chunyou 927 (CY927) with a dark leaf color and Yongyou 1540 (YY1540) with a normal leaf color were used as materials, and three N fertilizer amounts were applied to explore the effects of N fertilizer on the leaf color change process through the established assessment system. The T_0 of the flag leaf was delayed by 2.6−3.0 d compared to the 2nd and 3rd leaves. The CI_f of the flag leaf was 12.12 and 21.15% higher than those of 2nd and 3rd leaves, respectively. In addition, the R_1, R_2 and R_m of the 3rd leaf were 10.75–19.82%, 17.99–20.09% and 18.23–11.61% higher than the flag and 2nd leaves, respectively. Rice yield was significantly positively correlated with T_0, positively correlated with T_{50} and T_{100}, and negatively correlated with R_1, R_2 and R_m. The average T_0, T_{50}, and T_{100} of rice varieties with yields higher than 8,000 kg ha^{-1} were 6.8, 22.2, and 31.8 d, respectively, with a CI_f of 0.563 and an R_m of 0.015 d^{-1}. N applications delayed T_0 by 4.5–6.2 d, reduced R_m by 30.06–32.33%, and increased CI_f by 35.78–39.69%. The established leaf color change model and extracted parameters quantitatively depicted the leaf color change process during the later reproductive period. They also effectively distinguished the differences in leaf color change among leaf positions, rice varieties and N treatments. This approach is valuable for selecting and cultivating high-yield and nutrient-efficient rice varieties, as well as for

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Yanan Xu, E-mail: xuyanan@caas.cn; Yi Tao, E-mail: ancoinna@163.com; #Correspondence Danying Wang, Tel: +86-571-63370191, E-mail: wangdanying@caas.cn; Jianliang Huang, E-mail: jhuang@mail.hzau.edu.cn
* These authors contributed equally to this study.

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analyzing the underlying mechanisms.

Keywords: rice, leaf color change, grain filling, model, feature parameters

1. Introduction

Leaves are the main site of photosynthesis in green plants, and plant growth status can generally be evaluated according to leaf color (Kitonyo *et al.* 2017; Woo *et al.* 2019; Acevedo-Siaca *et al.* 2021). During the rice grain-filling period, leaf chlorophyll is gradually degraded, and the accompanying leaf color changes from green to yellow. This process is known as leaf color change during grain filling. During this process, large amounts of nutrients in the stems and leaves are activated and then remobilized to the kernels for reutilization, particularly nitrogen (N) which has the highest reutilization efficiency (Soudry *et al.* 2005; Mu *et al.* 2018; Zhang *et al.* 2022). Studies have shown that the activated and reused N during the grain-filling stage account for 73–82% of grain N at maturity (Masoni *et al.* 2007). Leaf color change during the later reproductive stage of rice leads to reductions in leaf photosynthesis and plant dry matter accumulation capacity (Zhou *et al.* 2023). Previous studies, such as those in barley (Mirosavljevic *et al.* 2020), wheat (Gaju *et al.* 2011, 2014), and maize (Zhang *et al.* 2019), have concluded that the "stay green" varieties are more likely to achieve high yields, especially under extreme drought environments (Gregersen *et al.* 2013; Moraga *et al.* 2022). However, the N in senescent leaves is an important source of N nutrients for seeds, and late or no color change in leaves reduces the reutilization of nutrients such as N, Fe, and Zn by more than 30% (Lee and Masclaux-Daubresse 2021), which undermines the achievement of high yields and high efficiency. In rice production, the same variety with a greater leaf color change usually has heavier grains and a higher N harvest index at maturity (in the absence of biological and environmental stresses). Therefore, analyzing the leaf color change process during rice grain filling and clarifying the differences in the onset time, rate and degree of leaf color change among varieties and treatments are crucial for selecting and cultivating high-yield and high-efficiency rice varieties.

The degree of color change in leaves at the late reproductive stage depends on the dynamics of changes in chlorophyll (Wang *et al.* 2016a, b; Zakari *et al.* 2020). Among the existing techniques for assessing leaf color, biochemical extraction to detect the contents of chlorophylls *a*/*b* and xanthophylls provides accurate results but is complicated to implement, making it impractical for use in rice production. Manual visual assessment of canopy greenness values (Gaju *et al.* 2011, 2014) is too subjective, and different observers are prone to assign different values. The normalized difference vegetative index (NDVI) can distinguish wheat varieties with different canopy greenness (Latif *et al.* 2020), but it is more suitable for multiple varieties or very large samples (Lopes and Reynolds 2012). The green area of leaves can also reflect the plant senescence process (Zhang *et al.* 2019), but this is rarely used alone because of its inability to describe leaf greenness. Leaf color is now more commonly measured with dual-wavelength chlorophyll meters (Pommel *et al.* 2006; Xie *et al.* 2016). The soil and plant analyzer development (SPAD) value was originally used to infer the N status of leaves (Inada 1963), and later became an indicator for estimating the chlorophyll content of leaves, since it provides rapid and objective leaf color data without destroying the plant (Villegas-Velazquez *et al.* 2022). Based on the leaf color changes at different times during flowering to maturity, Lopes and Reynolds (2012) found that the process of leaf color change in wheat conformed to a linear function, whereas Christopher *et al.* (2014) and Gaju *et al.* (2011, 2014) argued that it could be better fitted with a nonlinear function. In rice, Chang *et al.* (2007) found that the change in SPAD values during the grain-filling period conformed to a quadratic curve. In addition, Xu *et al.* (2009) used the SPAD decay rate ((SPAD value at heading–SPAD value at a certain time)/SPAD value at heading×100, %) to indicate the change in rice leaf color, but no in-depth analysis of the leaf color change process was conducted.

The absence of quantitative evaluation methods and parameters makes it impossible to compare the leaf color change processes in different varieties and treatments, which limits any in-depth discussions on the relationships among leaf color change, nutrient reutilization, and yield formation. Hence, in this study, we used 31 conventional *indica*, *japonica* and *indica–japonica* hybrid rice varieties as materials to compare the SPAD values of rice leaves from heading to maturity. By screening to find the mathematical function that best describes the SPAD change dynamics, we extracted the parameters for leaf color change. These parameters were then applied to quantitatively evaluate the differences in color change dynamics among varieties and leaf positions, as well as the effects of N fertilization on leaf color change dynamics. This approach provides methods for the selection and cultivation of high-yield and high-efficiency rice varieties.

2. Materials and methods

2.1. Site description and experimental design

Two experiments were carried out from June to November in 2019 and 2023 at the experimental farm of the China National Rice Research Institute (CNRRI) (30.3´N, 120.2´E, 11 m a.s.l.), Hangzhou, China. The site is in a subtropical monsoon zone area with an annual rainfall of 1,700 mm, an average annual air temperature of 18°C, and annual sunshine hours of 1,500–1,800 h. The 0–20 cm tillage soil of the paddy field contained organic matter of 42.3 g kg^{-1}, available nitrogen of 156.96 mg kg^{-1}, available phosphorus of 22.49 mg kg^{-1}, available potassium of 139.98 mg kg^{-1}, and a pH of 6.58.

Experiment 1 was a multi-variety leaf color measurement test to construct a mathematical function model of rice leaf color change and extract feature parameters, while

Experiment 2 involved the application and verification of the model and parameters established in Experiment 1. Specifically, it compared the color change dynamics among different leaf positions and N fertilizer dosages based on the feature parameters.

Model establishment In Experiment 1, 31 varieties were selected (Appendix A) as the materials and transplanted on 22 June in 2019 and 11 June in 2023, with 100 hills per variety in each plot and three replicates. The planting density was 20 cm×25 cm, with two seedlings per hill. In total, 150 kg ha^{-1} of N fertilizer, 100 kg ha^{-1} of phosphate fertilizer and 160 kg ha^{-1} of potash fertilizer were applied. Urea (N 46%) was used as the basal fertilizer and tiller fertilizer, each accounting for 60 and 40% respectively; the phosphorus fertilizer was calcium superphosphate (P_2O_5 12%), all of which was used as basal fertilizer; and the potash fertilizer was potassium chloride (K_2O 60%), 50% as basal fertilizer and 50% as tiller fertilizer. Basal fertilizer was applied one day before transplanting and tiller fertilizer was applied 14 days after transplantation. The field was flooded after transplanting, and a flood water depth of 1–4 cm was maintained until 7 days before maturity, except for drainage at the maximum tillering stage to reduce unproductive tillers. Pests and diseases were intensively controlled with chemicals to avoid biomass and yield loss.

Model application and verification In Experiment 2, two *indica–japonica* hybrid varieties with similar growth periods but markedly different leaf colors were used to investigate the effect of N fertilizer amount on leaf color change at the late reproductive stage. Rice variety Chunyou 927 (CY927) had dark green leaves and its SPAD value at flowering was as high as 48, much higher than that of variety Yongyou 1540 (YY1540), which was 41. There were three different N application rates: 0 kg N ha^{-1} (control, LN), 150 kg N ha^{-1} (MN) and 300 kg N ha^{-1} (HN). The experiment was conducted in a randomized complete block design with three replicates, and each plot was 90 m^2. Seedlings were transplanted on 13 June with the same hill spacing as in Experiment 1. N was applied in the form of granular urea in three doses: 40% as basal dressing 1 day before transplanting, 30% as tillering fertilizer 14 days after transplanting, and another 30% as panicle fertilizer at the panicle initiation stage (30 days before flowering). Potassium was applied at a uniform rate of 120 kg K_2O ha^{-1} in two application doses: 50% as a basal dressing and the remaining 50% as a panicle topdressing. Phosphorous was applied as superphosphate (12% P_2O_5) at a uniform rate of 75 kg P_2O_5 ha^{-1} as a basal dressing. To avoid cross-fertilization, each plot was coated with black plastic film and then fertilized and drained separately. Irrigation, pest and disease control methods were the same as in Experiment 1.

2.2. Data collection and statistical analysis

The SPAD values of 10 representative and healthy rice leaves were measured at 3-day intervals from flowering to maturity with a chlorophyll meter (Konica Minolta Co., Japan), and the values were recorded at the middle of each leaf and taken along the leaf blade. In the variety leaf color measurement experiment in 2019, SPAD values were measured only for the flag leaves, while in 2023, SPAD values were measured for the flag, 2nd and 3rd leaves. At maturity, the grain yield was determined from a harvested area of 2.5 m^2 and converted to the corresponding value with 14% moisture content.

Leaf color change dynamics were fitted, and the evaluation parameters were extracted using the least squares method in the scikit-learn library (version 1.0.2) of Python 3.10. The leaf color change parameters were extracted using Microsoft Excel 2021. SAS 9.4 was used for cluster analysis of the leaf color change patterns, and Duncan's tests were used in the analysis of variance for the comparison of leaf color change parameters between the different leaf positions and N treatments (P<0.05).

3. Results

3.1. Leaf color change dynamic model construction and feature parameter extraction

Mathematical function model of rice leaf color changes To describe the dynamics of rice leaf color changes with days from heading to maturity, and eliminate the differences in leaf color among varieties, the degree of leaf color change was normalized to a color index (CI) with the following formula:

$$CI=\frac{\text{SPAD value at } n \text{ days after heading (DAH}n\text{)}}{\text{SPAD value at heading}} \quad (1)$$

The larger the value of CI, the smaller the degree of leaf color change. With CI as the dependent variable and days after heading as the independent variable, according to the methods of Lopes and Reynolds (2012), Chang *et al.* (2007), and Christopher *et al.* (2014), the primary function $CI=at+b$, the quadratic function $CI=at^2+bt+c$, and the logistic function $CI=a/(1+e^{(b(t-c))})$ were used to simulate leaf color change dynamics. The equations for evaluating the parameters of leaf color change dynamics of the 31 rice varieties are shown in Appendix B.

The root mean square error (RMSE), mean absolute error (MAE), and R^2 of the leaf color change dynamics equation obtained using the primary function were in the ranges of 0.026–0.124, 0.02–0.101, and 0.577–0.950, with average values of 0.058, 0.049 and 0.819, respectively. The RMSE, MAE, R^2 of the quadratic function were in the ranges of 0.013–0.103, 0.01–0.09, and 0.709–0.988, with average values of 0.035, 0.028 and 0.934, respectively. In addition, the RMSE, MAE, and R^2 of the logistic function were in the ranges of 0.013–0.516, 0.01–0.379, and 0–0.991, with average values of 0.076, 0.06 and 0.719, respectively. Compared with the primary function, the quadratic function performed better at depicting the leaf color change dynamics with relatively lower RMSE and MAE, as well as higher R^2 for the same variety (expect for V11). For the logistic function, it is worth noting that the RMSE and MAE showed lower values, and the R^2 also showed a higher value than the quadratic function for some varieties. However, the R^2 fitted by the logistic function was 0 for V13, V17, V21, V23, V24, V29, and V30. All of which indicated that the quadratic function could fit the color change dynamics of leaves after heading very well and stably. Since the mean values of RMSE and MAE were lower, and R^2 of the quadratic function

was higher than those of the primary and logistic functions, the mathematical function model of leaf color change in the later reproductive stage of rice was established as a quadratic function (CI=at^2+bt+c) with leaf CI as the dependent variable, and days after heading as the independent variable. Taking the two varieties V9 and V12 with large differences in leaf color change as examples, the dynamic curves of CI obtained using this mathematical function model are shown in Fig. 1.

Parameters of rice leaf color change After establishing the leaf color change model, the first-order derivative of the leaf color change equation (CI=at^2+bt+c) was calculated, resulting in rates of CI change denoted as V (V=2at+b). The parameters depicting the color change process were extracted, including: (i) leaf color change onset time (T_0, d), which was obtained when V=0 and T_0=–b/2a; when T_0>0, it indicated that the onset of leaf color change occurred after heading (Fig. 1-A), and when T_0=0, leaf color change started at the heading stage (Fig. 1-B); (ii) final CI (CI_f, CI at maturation), (iii) midpoint time of leaf color change (T_{50}, d, duration when CI dropped by 50% of the total decline), (iv) duration of the total leaf color change (T_{100}, d, duration from T_0 to maturation), (v) early leaf color change rate (R_1, d^{-1}, mean rate of color change during T_{50}), (vi) later color change rate (R_2, d^{-1}, mean rate of color change from T_{50} to T_{100}), and (vii) mean color change rate (R_m, d^{-1}, mean rate of color change from T_0 to T_{100}) (Table 1; Fig. 1).

According to the above methodology, seven parameters characterizing the leaf color changes of 31 test varieties were extracted (Table 2). T_0 ranged from 0 to 11.6 d, with an average of 3.8 d; T_{50} was in the range of 10.2–31.0 d, with an average of 21.5 d; T_{100} ranged from 12.4 to 46.0 d, with the average of 31.4 d; the CI_f range was 0.21–0.75, with an average of 0.54. The values of R_1 ranged from 0.006 to 0.031 d^{-1}, R_2 ranged from 0.012 to 0.094 d^{-1}, R_m ranged from 0.008 to 0.041 d^{-1}, and their respective average values were 0.012, 0.028, and 0.016 d^{-1}, respectively. All parameters were found to be significantly different among the varieties. Notably, the coefficient of variation (CV) was the highest for T_0 as 99.5%, followed by R_m at 44.8%, while CI_f, despite having the lowest CV, still showed a CV value of 22.2%.

3.2. Applications of leaf color change parameters

Varietal clustering analysis based on leaf color change parameters The 31 tested rice varieties were clustered according to their leaf color change parameters, and they were classified into four categories using squared Euclidean distance as the metric (Kövesi *et al.* 1999), and 0.075 as the cutoff distance (Fig. 2; Table 2).

Group I included four conventional *indica* varieties, which started to change color at 0–5.6 d after heading, with an average T_0 of 3.6 d, and T_{100} of 12.4–20.0 d. The average CI_f and R_m were 0.45 and 0.032 d^{-1}, respectively. The varieties in Group I had the characteristics of a larger degree, as well

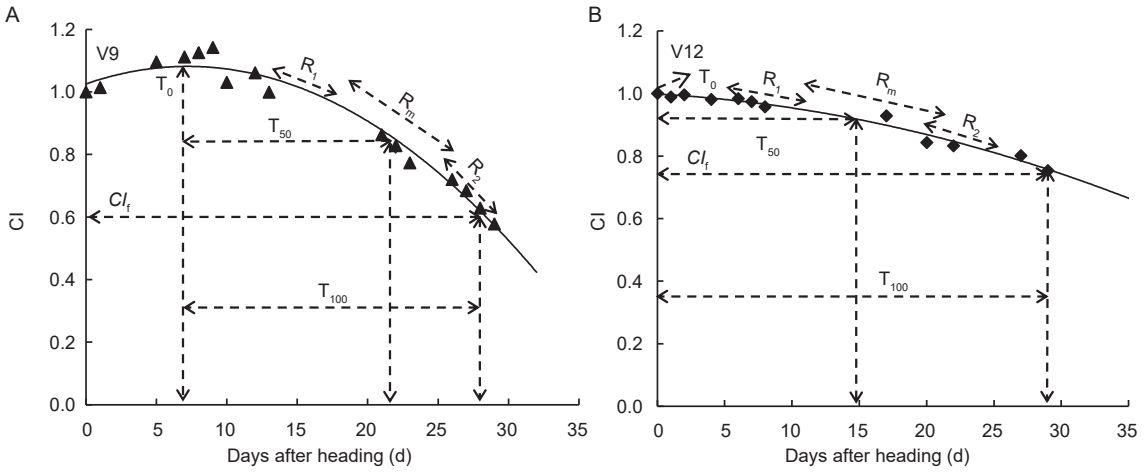


Fig. 1 Leaf color change parameters of rice. A, dynamics of leaf color index changes in V9 (Wuyujing 3) after heading using the quadratic function. B, dynamics of leaf color index changes in V12 (Yunjing 37) after heading using the quadratic function. T_0 (d), leaf color change onset time; T_{50} (d), leaf color change midpoint time; T_{100} (d), leaf color change duration; CI_f, final leaf color index; R_1 (d^{-1}), early leaf color change rate; R_2 (d^{-1}), later leaf color change rate; R_m (d^{-1}), mean leaf color change rate.

Table 1 Descriptions and abbreviations for leaf color change parameters in rice

Abbreviation	Leaf color change parameter	Description
T_0	Leaf color change onset time	Leaf color change onset time after heading (when the instantaneous rate equals zero (Fig. 1-A) or at heading (Fig. 1-B)
T_{50}	Leaf color change midpoint time	Duration from T_0 to the time when it dropped by 50% of the total decline
T_{100}	Leaf color change duration	Duration from T_0 to maturation
CI_f	Final leaf color index	CI at maturation
R_1	Early leaf color change rate	Mean rate of leaf color change during T_{50}
R_2	Later leaf color change rate	Mean rate of leaf color change from T_{50} to T_{100}
R_m	Mean leaf color change rate	Mean rate of leaf color change during T_0 to T_{100}

Table 2 Leaf color change parameters of 31 rice varieties[1)]

Variety	T_0 (d)	T_{50} (d)	T_{100} (d)	CI_f	R_1 (d^{-1})	R_2 (d^{-1})	R_m (d^{-1})
V1	0.0	13.3	20.0	0.21	0.031	0.060	0.041
V2	4.6	10.2	12.4	0.62	0.020	0.094	0.033
V3	0.0	19.4	34.0	0.43	0.015	0.020	0.017
V4	4.3	13.2	18.7	0.48	0.020	0.048	0.028
V5	4.6	17.9	25.4	0.45	0.014	0.035	0.020
V6	5.6	13.0	17.4	0.51	0.018	0.052	0.026
V7	4.2	25.3	31.8	0.33	0.014	0.055	0.022
V8	0.0	16.9	28.0	0.40	0.017	0.026	0.021
V9	10.3	16.1	23.8	0.71	0.011	0.022	0.014
V10	0.0	29.0	43.0	0.66	0.006	0.012	0.008
V11	0.0	31.0	45.0	0.50	0.008	0.018	0.012
V12	0.0	24.0	38.0	0.50	0.011	0.018	0.014
V13	4.7	23.5	32.3	0.49	0.011	0.030	0.016
V14	0.0	22.6	35.0	0.59	0.009	0.016	0.011
V15	0.0	30.1	46.0	0.41	0.011	0.021	0.014
V16	9.4	22.4	31.6	0.62	0.009	0.022	0.013
V17	0.0	26.2	38.0	0.51	0.009	0.021	0.013
V18	9.5	18.0	25.5	0.75	0.009	0.022	0.013
V19	5.6	22.9	32.4	0.56	0.009	0.022	0.013
V20	4.0	24.7	35.0	0.60	0.007	0.018	0.011
V21	0.0	22.9	34.0	0.71	0.007	0.013	0.009
V22	6.4	16.7	23.6	0.75	0.008	0.020	0.012
V23	0.5	22.3	31.5	0.51	0.011	0.027	0.016
V24	0.0	27.1	40.0	0.59	0.007	0.015	0.010
V25	5.0	23.3	33.0	0.57	0.009	0.023	0.013
V26	8.9	20.6	29.1	0.51	0.012	0.030	0.018
V27	11.6	19.3	33.9	0.47	0.014	0.033	0.019
V28	2.8	22.7	32.2	0.70	0.007	0.017	0.010
V29	8.1	24.0	33.9	0.55	0.010	0.023	0.014
V30	0.0	24.0	35.0	0.59	0.009	0.019	0.012
V31	7.4	23.7	33.6	0.55	0.012	0.029	0.017
Mean	3.8	21.5	31.4	0.54	0.012	0.028	0.016
CV (%)	99.5	23.8	24.8	22.2	43.7	60.4	44.8

[1)] T_0, leaf color change onset time; T_{50}, leaf color change midpoint time; T_{100}, leaf color change duration; CI_f, final leaf color index; R_1, early leaf color change rate; R_2, later leaf color change rate; R_m, mean leaf color change rate.

as faster and shorter duration of leaf color change with a low final CI.

Group II also included four conventional *indica* varieties, which started to change color at 0−4.6 d after heading, with an average T_0 of 2.2 d, and T_{100} of 25.4−34.0 d. The average CI_f and R_m were 0.40 and 0.020 d^{-1}, respectively. Like Group I, the varieties in Group II also had the characteristics of a large degree of leaf color change and a low final CI, but the duration of color change was longer, and the rate of color change was significantly slower than those of Group I.

Group III included 12 conventional *japonica* and hybrid varieties, with T_0 of 4.0–11.6 d, average T_0 of 7.6 d, and T_{100} of 23.6–35.0 d. The average CI_f and R_m were 0.59 and 0.014 d^{-1}, respectively. The CI_f of Group III was significantly higher, but R_m was significantly lower than those of Groups I and II. Varieties in Group III exhibited a later color change onset time, a longer duration and smaller degree of leaf color change, and a higher final CI.

Group IV included 11 conventional *japonica* and hybrid varieties, which started to change color at 0–2.8 d after heading, with an average T_0 of 0.3 d, T_{100} of 31.5–46.0 d,

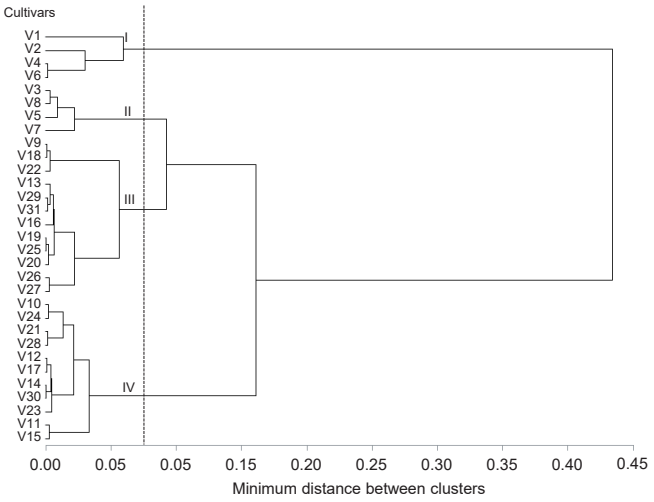


Fig. 2 Cultivar classification based on the leaf color change parameters of rice.

average CI_f of 0.57 and R_m of 0.012 d^{-1}. Compared with Group III, the varieties of Group IV had the same characteristics of slower color change and a higher final CI, but significantly earlier onset and longer duration of color change.

The four rice groups with different leaf color change characteristics also differed significantly in yield. The highest yield was observed in Group III, followed by Groups IV, II and I. The yield of Group III was in the range of 8,042.63–9,616.72 kg ha^{-1}, with an average of 8,891.54 kg ha^{-1}, which was significantly higher than those of Groups I, II and IV by 30.23, 23.70 and 18.65%, respectively. There were no marked differences among Groups I, II and IV (Fig. 3). The most remarkable feature of Group III compared with other groups was that T_0 was significantly delayed by 4–7.3 d, and R_m, R_1, and R_2 were 11.07, 7.24, and 9.14% lower than the mean values of the 31 rice varieties, respectively (Table 2; Fig. 3). These differences indicated that varieties with a later color change onset time and slower color change rate were more likely to have higher yields.

Comparing the leaf color change process of leaves at different positions In 2023, in addition to extracting the color change parameters of rice flag leaves, the color change dynamics of the 2nd and 3rd leaves of the tested varieties were also analyzed. The mathematical functional equations of the color change and derived parameters are shown in Appendix C. Note that the mean R^2 of the established color change functions for the 2nd and 3rd leaves were 0.939 and 0.944, respectively. This indicated that the established mathematical functional equations were not only applicable to the flag leaf but also to the 2nd and 3rd leaves. As shown in Table 3, the T_0 of the flag leaf was significantly delayed by 2.6–3.0 d compared to the other two leaf positions. However, no significant differences were observed in T_{50} and T_{100} among the three leaf positions. The CI_f differed significantly among the different leaf positions, with flag leaf>2nd leaf>3rd leaf, and the flag leaf was higher than the 2nd and 3rd leaves by 12.12 and 21.15%, respectively. The rate of leaf color

change was the greatest in the 3rd leaf, and R_1, R_2 and R_m were all significantly higher in 3rd leaf than in the flag and 2nd leaves. No remarkable differences in color change rates were seen between the flag and 2nd leaves.

3.3. Analyzing the effects of N treatments on leaf color change during the grain-filling stage

CY927 and YY1540, which have remarkable differences in leaf color, were used to analyze the dynamics of leaf color change under different N fertilizer amounts. The derived color change parameters are shown in Table 4. The results showed that N fertilization significantly delayed T_0, but correspondingly shortened the leaf color change durations of T_{50} and T_{100}, increased CI_f, and reduced the leaf color change rates such as R_1, R_2, and R_m. Compared to LN, the mean T_0 of the flag leaf was delayed by 4.5 d and 6.2 d in MN and HN, respectively. Meanwhile, T_{50} was shortened by 0.5 and 1.3 d, T_{100} was shortened by 1.5 and 1.7 d, and CI_f increased by 39.69 and 35.78%, respectively. Compared to LN, the mean R_1, R_2 and R_m were significantly reduced by 31.85, 21.68 and 32.33% in MN, and by 31.75, 25.88, and 30.06% in HN.

Comparing the color change parameters of different leaf color varieties showed that the N effects on leaf color change parameters showed significant differences between YY1540 with a normal leaf color and CY927 with a dark leaf color. Compared to LN, HN delayed the T_0 of CY927 by 6.3 d, and shortened T_{50} and T_{100} by 2.1 and 1.3 d, respectively, resulting in an increase of 29.42% in CI_f. In addition, HN delayed the T_0 of YY1540 by 6 d, and shortened T_{50} and T_{100} by 0.6 and 2 d, respectively, resulting in an increase of 44.20% in CI_f. The R_m of CY 927 under HN was reduced by 38.91% compared with that of LN, although it was significantly higher than that of YY 1540, which was reduced by 22.62% (Table 4).

4. Discussion

4.1. Leaf color change model development and feature parameter extraction

Chlorophyll degradation during the late reproductive period leads to leaf color changes and triggers a series of changes in carbon (C) and N metabolism (Have *et al.* 2017; Asad *et al.* 2023). These include a reduced C assimilation capacity in yellowing leaves, and the activation of nutrients stored in vegetative organs which are then transported to the spikes to be reutilized. Depicting the leaf color change process at the late reproductive stage provides a simple and highly efficient method to clarify changes in C and N metabolism in the plant, which is beneficial for guiding rice production. To objectively describe the rice leaf color change process during

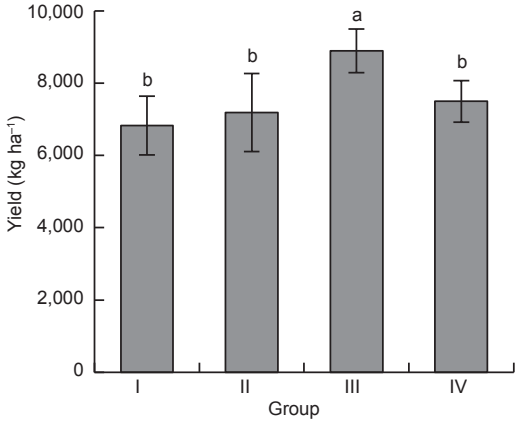


Fig. 3 Yields of different rice groups. Bars indicate SE (n=3). The same lower-case letters among the bars imply no significant difference according to Duncan's multiple range test (P<0.05).

Table 3 Leaf color change parameters at the flag, second and third leaf positions of rice[1)]

Leaf position	T_0 (d)	T_{50} (d)	T_{100} (d)	CI_f	R_1 (d^{-1})	R_2 (d^{-1})	R_m (d^{-1})
Flag	4.7 a	22.6 a	32.7 a	0.59 a	0.009 b	0.022 b	0.013 b
Second	1.7 b	23.8 a	34.7 a	0.53 b	0.010 b	0.022 b	0.014 b
Third	2.1 b	23.8 a	34.3 a	0.49 c	0.011 a	0.027 a	0.016 a

[1)] T_0, leaf color change onset time; T_{50}, leaf color change midpoint time; T_{100}, leaf color change duration; CI_f, final leaf color index; R_1, early leaf color change rate; R_2, later leaf color change rate; R_m, mean leaf color change rate.
Different lowercase letters represent significant differences between the different leaf positions at P<0.05 (LSD).

Table 4 Effects of nitrogen treatments on leaf color change parameters of rice[1)]

Variety[2)]	N treatment[3)]	T_0 (d)	T_{50} (d)	T_{100} (d)	CI_f	R_1 (d^{-1})	R_2 (d^{-1})	R_m (d^{-1})	Yield (kg ha^{-1})
CY927	LN	7.8 c	27.0 a	37.2 a	0.62 b	0.008 a	0.020 a	0.011 a	6,932.09 b
	MN	12.5 b	25.4 b	35.5 b	0.82 a	0.005 b	0.014 b	0.006 b	10,372.52 a
	HN	14.1 a	24.9 b	35.9 b	0.80 a	0.005 b	0.012 b	0.007 b	10,382.84 a
YY1540	LN	3.9 c	29.4 a	41.1 a	0.47 b	0.010 a	0.021 a	0.013 a	5,675.01 b
	MN	8.3 b	29.9 a	39.7 a	0.70 a	0.007 b	0.019 a	0.010 b	10,174.78 a
	HN	9.9 a	28.8 a	39.1 a	0.67 a	0.007 b	0.018 a	0.010 b	10,709.91 a
Average	LN	5.9	28.2	39.1	0.54	0.009	0.021	0.012	6,303.55
	MN	10.4	27.7	37.6	0.76	0.006	0.016	0.008	10,273.65
	HN	12.0	26.9	37.5	0.74	0.006	0.015	0.008	10,546.37

[1)] T_0, leaf color change onset time; T_{50}, leaf color change midpoint time; T_{100}, leaf color change duration; CI_f, final leaf color index; R_1, early leaf color change rate; R_2, later leaf color change rate; R_m, mean leaf color change rate.
[2)] CY927, Chunyou 927; YY1540, Yongyou 1540.
[3)] LN, MN, and HN, 0, 150, and 300 kg N ha^{-1}, respectively.
Different lowercase letters represent significant differences between different nitrogen treatments at P<0.05 (LSD).

the grain-filling period, the leaf color CI was proposed in this study. This approach eliminates the differences in leaf color between varieties and treatments by calculating the ratio of instantaneous SPAD values to the SPAD at heading, making the dynamics of leaf color changes directly comparable. The results of this study revealed two types of rice leaf color change patterns. In one pattern, the CI increased and then decreased after heading, with the onset of leaf color changes occurring after flowering (Fig. 1-A). The other pattern exhibited a continuous reduction in CI (Fig. 1-B), suggesting that leaf color change onset occurred before or around the heading stage. Previous studies selected NDVI (Christopher *et al.* 2014) and visual assessment scores (Gaju *et al.* 2011, 2014) as plant canopy senescence indicators, and changes in the above indicators during the senescence process were well fitted using a logistic function. In this study, the primary function ($CI=at+b$), the quadratic function ($CI=at^2+bt+c$), and the logistic function ($CI=a/(1+e^{(b(t-c))})$) were used to fit the changes of CI with days after heading. The results showed that the quadratic function not only performed better than the primary function, but it was also better and more stable than the logistic function (Appendix B). In addition, the logistic function is more sensitive to the initial values of the parameters, so the globally optimal solution may be inaccurate due to inappropriate starting values. Therefore, the quadratic function ($CI=at^2+bt+c$) of leaf color change was established, where CI is the leaf color index, t is days after heading, and a, b, and c are coefficients. In a study using NDVI as an indicator of canopy senescence, Christopher *et al.* (2014) extracted the maximum NDVI, mean senescence rate, and four timing indicators (integral, onset, midpoint, and conclusion of senescence) to depict leaf senescence dynamics based on thermal time from anthesis to harvesting. That approach helped to clarify the differences in senescence dynamics in different environments and treatments. In our study, we used DAH as the independent variable to help farmers easily understand the leaf color change onset time, which mainly serves in the actual production of rice. In addition, seven leaf color change parameters were extracted. The three color change time parameters were the onset time of color change (T_0), the duration of 50% color change (T_{50}) and the duration of total color change (T_{100}). The three leaf color change rate parameters were the color change rate for T_0–T_{50} (R_1), the color change rate for T_{50}–T_{100} (R_2), and the average color change rate for the whole process (R_m). One color index parameter was the final value of the leaf color index (CI_f) (Table 1; Fig. 1). In summary, our study provides a new method for quantitatively assessing leaf color change dynamics for different varieties.

4.2. Leaf color change differences among leaf positions, varieties and N treatments

Leaf color changes in the late reproductive stage due to the degradation of photosynthetic pigments (Shin *et al.* 2020) triggered by the expression of senescence-related genes (Antonietta *et al.* 2014; Lei *et al.* 2023). Consequently, the onset and duration of leaf color change, as well as the degree and rate of color change, are all varietal traits. The above leaf color change parameters proposed in this study overcome the drawbacks of previous studies, in which the color change process of varieties could only be described empirically due to the lack of relevant indicators. In this study, we compared the differences in color change dynamics among varieties, leaf positions, and N treatments by using those color change parameters. The leaf color change process analysis in Experiment 1 showed that there were obvious differences in the color change parameters among varieties, and the CVs of T_0, T_{50}, T_{100}, CI_f, R_1, R_2, and R_m reached 99.5, 23.8, 24.8, 22.2, 43.7, 60.4, and 44.8%, respectively. Notably, the T_0 of *indica* varieties was earlier than that of *japonica* rice by 0.7 d, and the T_{100} was 11.1 d shorter than that of *japonica* rice, resulting in the R_m being more than double that of *japonica* rice, which led to a 28.21% reduction in the CI_f compared with that of *japonica* rice (Table 2). Our results are consistent with the genetic findings of Shin *et al.* (2020), who found that the *OsSGR* gene promoter in *indica* rice varieties induces higher and earlier expression of the *OsSGR* gene encoding Mg^{++}-decarboxylase and accelerates leaf senescence compared to *japonica* rice. Experiment 2 in this study quantified the differences in color change between CY927, a rice variety with a dark green leaf color, and YY1540, a rice variety with a normal leaf color. Compared to YY1540, CY927 exhibited a delay of 4.1 days in T_0, a reduction of 27.07% in R_m, and an increase of 21.55% in CI_f (Table 4). A previous study established that the lower functional leaves of rice display an earlier yellowing phenotype, and the chlorophyll reduction rate in flag leaves is lower than in the second and third leaves (Zakari *et al.* 2019). Our results clarified that the T_0 of flag leaves was delayed by 2.6–3.0 d compared with those of the 2nd and 3rd leaves. However, no significant differences in R_m between the flag and 2nd leaves were observed, although both were remarkedly lower than the 3rd leaves. The results of leaf color change under different N applications showed that reduced N applications delayed the T_0 of flag leaves by 4.5–6.2 d, shortened T_{50} and T_{100} by 0.5–1.3 d and 1.5–1.7 d, increased CI_f by 35.79–39.69%, and reduced R_1, R_2 and R_m by 31.75–31.85%, 21.68–25.88%, and 30.06–32.33%, respectively (Table 4). In other words, N deficiency may bring leaf senescence forward and accelerate leaf yellowing, which was associated with low-N induced overexpression of *MdNAC4*, and the activation of transcription of the chlorophyll catabolism genes *MdNYC1* and *MdPAO* (Wen *et al.* 2022). However, the leaf color change during the later stage of rice growth is influenced not only by variety and nitrogen fertilizer application, but also by various stresses, such as high temperature and cold stress, which can cause rapid color changes over a short period. This study primarily focused on leaf color changes under normal growth conditions, and further research is needed to determine whether the leaf color change model and parameters developed here are applicable under stress conditions.

4.3. Relationship between leaf color change traits and yield

The process of leaf color change is closely related to rice grain filling and yield formation. During the late grain-filling stage, leaf photosynthetic pigment degradation leads to a

reduction in photosynthetic assimilates (Gregersen *et al.* 2013; Asad *et al.* 2023), higher greenness of leaves during the grain-filling stage, and the prolongation of the green-holding period, which contributes to higher grain yield by promoting canopy photosynthesis (Tanaka *et al.* 2022). Correlation analysis showed that rice yield was highly significantly positively correlated with T_0 (r^2=0.656, P<0.001), and positively correlated with T_{50} and T_{100}, but negatively correlated with R_1, R_2 and R_m. Varieties with yields exceeding 8,000 kg ha^{-1} in Group III were characterized by a delayed color change onset time, a longer color change duration, a slower color change rate, and a higher final CI compared with the varieties in Groups I, II, and IV, with values for T_0, T_{100}, CI_f, and R_m of 7.6 d, 30.6 d, 0.59, and 0.014 d^{-1}, respectively (Table 2; Fig. 3). Proper N applications increased the yields of CY927 and YY1540 by 49.63−88.72%, through delaying T_0, reducing R_m and increasing CI_f (Table 4). Therefore, applying the leaf color change parameters can help us to deeply understand the differences in dry matter accumulation and yield formation during the grain-filling period, to explore the mechanism of high yield and efficient nutrient utilization in rice production. These feature parameters can help producers judge the appropriate onset time and rate of leaf color change based on SPAD value measurements and then conduct special cultivation measures based on the different color change features of various rice varieties to achieve high yields and high efficiency. However, the correlation of N utilization efficiency and leaf color change has not been examined in the study. Further research is needed on the differences in leaf color changes at different leaf positions across multiple varieties and growing environments, as well as their relationship with yield and nitrogen use efficiency.

5. Conclusion

A mathematical function model for leaf color change in rice after heading was established based on the normalization of leaf SPAD. The model was expressed as (CI=at^2+bt+c), where CI represents the leaf color index, and t is days after heading. Seven leaf color change parameters were extracted for the quantitative comparison and assessment of the leaf color change process, including color change onset time (T_0), midpoint color change time (T_{50}), color change duration (T_{100}), final leaf color index (CI_f), leaf color change rates during T_0–T_{50} (R_1) and T_{50}–T_{100} (R_2), and the mean leaf color change rate (R_m). There were significant differences in the leaf color change parameters among varieties, leaf positions and N treatments. Rice yield is significantly positively correlated with T_0, positively correlated with T_{50} and T_{100}, and negatively correlated with R_1, R_2 and R_m. High yielding varieties were characterized by a delayed onset of color change and a slower rate of color change. In the upper three functional leaves, the T_0 of the flag leaf was delayed by 2.6−3.0 days, although R_m of the flag leaf was similar to that of the 2nd leaf, but significantly lower than that of the 3rd leaf, resulting in the highest CI_f. N fertilizer delayed T_0 and reduced R_m, and the effects of N fertilizer on the process of leaf color change were related to the original leaf color of the variety. The effect of N fertilizer on the reduction of CI_f was greater in the normal green leaf color variety YY1540 than in the dark green leaf color variety CY927, but the effects on T_0 and R_m were greater in CY927 than in YY1540. The established leaf color change model and extracted parameters provide a quantitative description of the process of leaf color transformation. This is highly valuable for selecting and cultivating high-yield and high-efficiency rice varieties and offers a useful analytical method for studying the balance of carbon and nitrogen metabolism in crops.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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