Dynamics of Growth and Nitrogen Capture in Winter Oilseed Rape Hybrid and Line Cultivars under Contrasting N Supply

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Abstract: Cultivation of winter oilseed rape hybrids has been introduced as a promising solution to improve the nitrogen use efficiency (NUE) and to reduce the large N balance surpluses in this crop. To achieve a better understanding of the underlying physiological mechanisms, field experiments were conducted over two years to investigate the dynamics of growth and N capture in an oilseed rape hybrid and its parental lines under both low (0 kg ha⁻¹) and high (180 kg ha⁻¹) N supply. The results showed that the dynamic trajectories of crop growth and N capture could be accurately characterized by logistic equation using growing degree days as the independent variable. At both N rates, the oilseed rape hybrid outperformed the parental lines in seed yield and aboveground biomass accumulation, which was more closely associated with the longer duration (tₚ) of the rapid growth period (RGP), than with the higher maximum growth rate (vₚ). N uptake was the main factor driving genotypic variation in seed yield, with an increasing importance of N utilization efficiency at high N supply. The hybrid had significantly higher N uptake than the parental lines at both low and high N supply, because of larger vₚ for N accumulation during the RGP, which may present a scope for genetically improving NUE in oilseed rape. High N application enhanced crop biomass production and N accumulation, as a result of prolonged tₚ and larger vₚ during the RGP. The initiation of RGP for N accumulation occurred after overwinter period, which could not be accelerated by high N supply, suggesting rational distribution of N fertilizer with reduced basal dose. However, larger amounts in spring would be beneficial for a better synchronization to crop N demand with lower environmental risks.

Keywords: Brassica napus L.; logistic equation; genotypic variation; N use efficiency; hybrid

1. Introduction

Winter oilseed rape (Brassica napus) is a species in the Brassica genus characterized with high nitrogen (N) demand [1,2]. To produce 100 kg seeds, the crop accumulates approximately 6 kg N [3], higher than most other arable crops, such as winter wheat and winter barley [4]. With the use of modern cultivars and increase of N fertilizer input, there has been substantial improvement in oilseed rape production during the last few decades [5,6]. Despite the high N capture by oilseed rape, only 50% or less of the fertilizer N could be harvested in the seeds [7], implying a poor N use efficiency (NUE). For the purposes of decreasing environmental N budget and increasing economic returns, strategies improving NUE have been given prominence in sustainable oilseed rape production in a context of reduced N input [5,8–10].

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Crop NUE is defined as the grain yield (or harvested product) achieved per unit of available N [11]. It is the product of two primary components, namely N uptake and N utilization efficiency (yield per unit N taken up, NUtE) [11,12]. The former measures crop ability in N capture, while the latter reflects the efficiency of N conversion [10]. Although the definition of NUE and its key components has been well established for decades, the estimation of these variables in oilseed rape is complex, since their importance in determining seed yield depend on N availability and how the N absorbed is used within crop during different growth stages, and may vary between different cultivars [2,5,13–15].

A large body of research has been developed in recent years focusing on the improvement in oilseed rape yield (or NUE) through the key determining components or processes [2,5,15–18]. It is generally recognized that varietal difference in seed yield is more closely associated with N uptake at N limiting conditions, while the importance of N utilization efficiency increases with higher N supply [2,19,20]. Furthermore, previous studies have emphasized the importance of N uptake particularly during the generative stage for cultivar performance in seed yield [16,19,21]. Along with prolonged duration of N uptake in the generative developmental phase, the N efficient cultivars were also characterized with a stay-green phenotype, supporting longer duration of photosynthesis [22,23]. However, recent comparisons between oilseed rape hybrids and line cultivars have revealed that the enhanced NUE in oilseed rape hybrids was not attributed to prolonged N uptake or delayed leaf senescence [14]. Instead, clear advantages in N uptake and biomass production during vegetative growth, and therewith more efficient N remobilization from vegetative to reproductive organs were identified as the main contributors [2,5,14].

From another perspective, seed yield of oilseed rape is a function of growth rate, duration of the growing period and harvest index (the ratio of seed to above-ground biomass) [24]. The ideal cultivars might be expected to maintain maximal photosynthetic production throughout the period of high resource availability [4]. N is the most important essential nutrient in the photosynthesis apparatus. It may generally be assumed that higher N capture leads to enhanced photosynthetic activity, and in turn increases the quantity of assimilates allocated to the final sink [5]. In this regard, a better understanding of the growth and N capture trajectories is crucial for the improvement in oilseed rape NUE. Although these processes are dynamic, they are usually investigated experimentally as if they are independent. One reason for this is that on-farm monitoring of these processes requires frequent sampling, which could be time consuming and not practical. In contrast, the simulation of crop growth dynamics is effective and provides the possibility to explicitly explore these key processes [25,26].

Considerable efforts have been made to describe and predict crop growth process using various crop models, such as SPACSYS [26–28], DNDC [29,30] and DSSAT [31,32]. However, the operation of these models requires various parameters and high level of expertise to appropriate result interpretation. Alternatively, the use of simple nonlinear models, such as the logistic, Gompertz or Weibull equations has been suggested, if only specific or limited model results are needed [25,33–35]. The models have been used effectively in the description of many growth processes including seedling emergence, plant and organ biomass accumulation in various major crops [25,34–36]. These nonlinear functions typically model a sigmoid curve, relating the cumulative quantity to time or thermal unit accumulation. The inflection point and the maximum slope of the curve have a biological meaning in terms of crop rapid growth stage and growth rate [25,33,34]. It has been argued that a selected model should be flexible enough for use in a variety of environments and genotypes [35]. The logistic model has been proven reasonably effective in the characterization of growth dynamics in wheat, maize and cotton [25,34,36], with the characteristic parameters well reflecting crop responses to management practices such as plastic mulching and nitrogen split application. However, it is still unknown if the logistic model could perform well in the simulation of crop dynamics (e.g., aboveground biomass and N capture) in different oilseed rape cultivars under contrasting N supply.

Winter oilseed rape may vary in the developmental progress and N demand due to differences in cultivars and N management strategies, climate and soil conditions [2,3,6]. In European conditions,
autumn-N fertilization was usually omitted or reduced in oilseed rape production, as a result of low yield responses [3]. However, heavy autumn N fertilization was common in farmers’ conventional practice of N application in China. It is necessary to achieve a better understanding of the developmental progress and N demand in this crop at different growth stages.

In the present study, a two-year field experiment was conducted under both low and high N conditions using three oilseed rape cultivars including one hybrid and its parental lines. The dynamic trajectories of aboveground biomass and N capture are simulated, and NUE related parameters were investigated. We have previously found considerable yield heterosis in the oilseed rape hybrid over its parental lines, which was associated with improved capacity of N uptake [37]. In this study, we hypothesize that the logistic model could reasonably characterize the dynamic trajectories of aboveground biomass and N capture in the oilseed rape cultivars under different N supply conditions. The aims of the present study were (1) to evaluate the simulation of the dynamic trajectories of aboveground biomass and N capture in oilseed rape cultivars with the logistic equation, (2) to assess the effects of genotype and N supply on the crop development using characteristic parameters of the logistic equation and (3) to analyze the relationship between trajectories of aboveground biomass and N capture with oilseed rape yield.

2. Materials and Methods

2.1. Field Experiments

The field experiments were conducted over two years, during September 2014-May 2015 and September 2015–May 2016 at Wuxue (30°06'47" N, 115°35'35" E) in Hubei Province, central China. The experimental site was located in the Yangtze River Basin with a subtropical monsoon climate, where the average annual temperature was 16.5–24.2 °C and the annual precipitation was in the range of 700–1900 mm. The details of daily maximum and minimum temperature during the study period are shown in Figure S1. The soil at the experimental site was yellow brown paddy soil that could be classified as Ultisols [38]. Details of presowing soil properties of the top 20 cm are given in Table 1.

| Year      | Site  | pH  | SOM (g kg⁻¹) | Total N (g kg⁻¹) | Nmin (mg kg⁻¹) | Available P (mg kg⁻¹) | Available K (mg kg⁻¹) |
|-----------|-------|-----|--------------|------------------|----------------|-----------------------|-----------------------|
| 2014−2015 | Wuxue | 5.76| 27.45        | 1.62             | 5.24           | 6.22                  | 56.02                 |
| 2015−2016 | Wuxue | 5.99| 34.43        | 2.32             | 6.33           | 7.21                  | 82.47                 |

The experiments were arranged in a split-plot design in both years, with N rate as the main plot and cultivar as the subplot each replicated three times. The plot size was 25 m². Oilseed rape seedlings were transplanted on 3 November 2014 and 3 November 2015 at a density of 112500 plants ha⁻¹. Three cultivars were investigated, viz., HYZ12, R5 and 6098A. Cultivar HYZ12 is the F1 hybrid between R5 and 6098A as male and female lines, respectively. Two different N fertilization rates, 0 and 180 kg N ha⁻¹ were applied, representing low and high N supply according to our previous work that have tested yield responses of these cultivars to series of N rates (0, 60, 120, 180, 240 and 300 kg N ha⁻¹) [37]. The N fertilizer was supplied as urea in three doses, at seedling (60%) and during the over-wintering (20%) and stem elongation period (20%). Apart from N, plants received 90 kg P₂O₅ ha⁻¹, 120 kg K₂O ha⁻¹ and 1.62 kg B ha⁻¹, supplied as calcium superphosphate, potassium chloride and borax at the preplant. Weeds, pests and diseases were well controlled to avoid yield loss.

Oilseed rape crop development was carefully monitored by intermediate harvests performed at seedling (BBCH15, 12 January 2015 and 16 January 2016), stem extension (BBCH30, 4 March 2105 and 22 February 2016), flowering (BBCH61, 24 March 2015 and 17 March 2016) and pod filling (BBCH 75, 13 April 2015 and 13 April 2016) stages. From each plot four plants were randomly sampled, separated into different organs and oven dried to a constant weight. At maturity (BBCH89), plants in each plot were harvested within a 10 m² area to evaluate seed yield after adjusted to 0% water content.
Subsamples of plant organs including leaves, stems, pod walls and seeds were collected and dried to a constant weight at 65 °C. Total N concentration in the dried and grounded samples was analyzed using a continuous flow analyzer (AA3, SEAL Analytical Inc., Southampton, UK) after digestion with H2SO4-H2O2.

2.2. Model Description and Evaluation

The trajectories of oilseed rape aboveground biomass and N capture were modeled with the logistic equation as follows:

\[ y = \frac{a}{1 + \exp\left(-\frac{(t - t_0)}{b}\right)} \]  

(1)

In which, \( y \) is the cumulative crop aboveground biomass (kg ha\(^{-1}\)) or N capture (kg ha\(^{-1}\)) in this study; \( t \) is the independent thermal unit accumulation (growing degree days, GDD); \( t_0 \) is GDD at which the growth rate is maximized; \( a \) is the uppermost asymptote implying the upper limit of crop growth and \( b \) is the constant to be found.

Considering that the weather conditions and planting dates differed between the two experimental years, GDD rather than the calendar days after planting was used as the independent variable for the logistic equation [25]. GDD was calculated as follows:

\[ GDD = \sum \left( \frac{T_{\text{max}} + T_{\text{min}}}{2} - T_{\text{base}} \right) \]  

(2)

In which, \( T_{\text{max}} \) and \( T_{\text{min}} \) are the daily maximum and minimum temperature (°C), respectively. \( T_{\text{base}} \) is the base temperature with 5 °C for winter oilseed rape [39,40].

The characteristic parameters of the logistic equation were calculated as follows:

\[ t_1 = -b \times \ln(2 + \sqrt{3}) + t_0 \]  

(3)

\[ t_2 = -b \times \ln(2 - \sqrt{3}) + t_0 \]  

(4)

\[ v_m = \frac{a}{4b} \]  

(5)

\[ t_d = t_2 - t_1 \]  

(6)

where \( t_1 \) and \( t_2 \) (°C d) are the initial and end points of the rapid growth period (RGP), respectively; \( v_m \) is the maximum growth rate and \( t_d \) is the duration of the RGP [25].

In order to assess the model performance on simulating the trajectories of oilseed rape aboveground biomass and N capture, a set of statistical indexes was used, including the coefficient of determination \( (R^2) \), the root mean-square error \( (\text{RMSE}) \) and modeling efficiency \( (\text{EF}) \) [41]. The \( R^2 \) measures the relationship between simulated and observed values. The \( \text{RMSE} \) represents the consistence of the simulated with the observed values. \( \text{EF} \) reflects how well the simulation could predict the outcome variable.

2.3. Statistical Analysis

Field data was statistically analyzed with a general linear model. Year, N rate, cultivar effects as well as the cultivar by N rate interactions on seed yield, NUE and characteristic parameters of oilseed rape development were tested with N rate and cultivar as the fixed factor and year as the random factor. The least significance difference test was performed to evaluate the difference among the three cultivars at \( p < 0.05 \) level. Correlation between these parameters was analyzed with the Pearson’s correlation analysis. Stepwise multiple regression was performed to explore the characteristic parameters of oilseed rape growth that could explain variations in aboveground biomass, N uptake
and seed yield. All statistical analyses were performed with SPSS version 20.0 (IBM Corp., Armonk, NY, USA).

3. Results

3.1. Model Evaluation

The results revealed that the simulated values matched reasonably well with the measured values in both crop aboveground biomass (Figure 1a) and N accumulation (Figure 1b). The detailed estimation of logistic model in the simulation of crop aboveground dynamics showed that the $R^2$ ranged from 0.956 to 0.998 with a mean of 0.983 across experimental years, N rates and cultivars. The RMSE values fell in the range of 4.4–13.4% with a mean of 8.84%, and the EF values were in the range of 0.953–0.999 with a mean of 0.981 (Figure 2). Moreover, the comparisons between measured and simulated values in crop N accumulation showed that the $R^2$ values were from 0.911 to 0.999 with a mean of 0.963. The RMSE values ranged from 1.0% to 14.1% with a mean of 8.1%, and the EF values ranged from 0.907 to 0.999 and averaged 0.957 (Figure 3).

![Figure 1](image-url)

**Figure 1.** Correlation between the measured and simulated values for (A) aboveground biomass and (B) N accumulation. Data were pooled from three winter oilseed rape cultivars grown under 0 and 180 kg N ha$^{-1}$ supply in the 2014–2015 and 2015–2016 seasons.
Figure 2. Dynamics of the measured and simulated values of aboveground biomass in three oilseed rape cultivars under 0 and 180 kg ha\(^{-1}\) N supply in the 2014–2015 (A, B) and 2015–2016 (C, D) seasons.
Figure 3. Dynamics of the measured and simulated values of nitrogen accumulation in three oilseed rape cultivars under 0 and 180 kg ha$^{-1}$ N supply in the 2014–2015 (A,B) and 2015–2016 (C,D) seasons.

3.2. Characteristics of Oilseed Rape Growth Trajectories

3.2.1. Aboveground Biomass Dynamics

N application significantly enhanced crop aboveground biomass accumulation, as shown in Figure 2. The measured aboveground biomass of oilseed rape was greater under high N than low N treatment at different stages investigated, and the difference increased at the latter part of crop growth. The oilseed rape hybrid had significantly higher aboveground biomass than the parental lines. The cultivar difference was larger with increasing GDD.

N application delayed slightly the initial thermal time ($t_1$; Table 2), but clearly and to a greater extent the terminal thermal time ($t_2$) of the RGP of aboveground biomass, leading to prolonged duration of the RGP ($t_d$). The values of $t_0$ were larger at high than at low N conditions, especially in 2014-2015. Moreover, high N treatment considerably improved the $t_0$ values ($p < 0.01$). Cultivars also differed in the characteristics of aboveground biomass. At both low and high N conditions, the hybrid was generally lower in the $t_1$ values than the parental lines ($p < 0.05$), but they did not differ much in $t_2$ values. Consequently, the $t_d$ values for the hybrid were significantly greater than those for its parental lines ($p < 0.05$). The $t_0$ values were generally the highest in the oilseed rape hybrid ZYZ12, followed by the parental line R5, while line 6098A was the lowest.
Table 2. Biomass dynamic parameters of the oilseed rape cultivars grown at two N rates during the experimental seasons. Values with different letters are significantly different at a probability level of \( p < 0.05 \) within each N rate in the same season. \( t_1 \) and \( t_2 \), the initial and terminal points of the rapid growth period; \( t_d \), the duration of the rapid growth period; \( t_0 \), the point at which the maximum growth rate occurs and \( V_m \), the maximum growth rate. *, \( p < 0.05 \); **, \( p < 0.01 \).

| Year          | N Rate | Cultivar | \( t_1 \)  | \( t_2 \)  | \( t_d \)  | \( t_0 \)  | \( V_m \) |
|---------------|--------|----------|------------|------------|------------|------------|----------|
| 2014–2015     | 0      | ZYZ12    | 1345.1a    | 1742.8b    | 397.7b     | 1543.9a    | 6.3b     |
|               |        | R5       | 1341.6a    | 1701.1a    | 359.5a     | 1521.4a    | 5.2a     |
|               |        | 6098A    | 1389.7b    | 1767.9b    | 378.2ab    | 1578.8b    | 5.1a     |
| 180           |        | ZYZ12    | 1363.0b    | 1792.5a    | 378.2ab    | 1578.8b    | 16.5b    |
|               |        | R5       | 1431.2b    | 1825.1a    | 393.9a     | 1628.1b    | 14.4ab   |
|               |        | 6098A    | 1440.4b    | 1824.1a    | 383.7a     | 1632.3b    | 12.8a    |
| 2015–2016     | 0      | ZYZ12    | 1228.5a    | 1599.2a    | 370.7b     | 1413.9a    | 5.5b     |
|               |        | R5       | 1321.1b    | 1589.9a    | 268.9a     | 1455.5b    | 5.7b     |
|               |        | 6098A    | 1283.5b    | 1588.7a    | 305.1a     | 1436.1b    | 4.9a     |
| 180           |        | ZYZ12    | 1242.5a    | 1625.1a    | 382.6b     | 1433.8a    | 17.3b    |
|               |        | R5       | 1296.9a    | 1623.9a    | 327.0a     | 1460.4a    | 17.2b    |
|               |        | 6098A    | 1292.0b    | 1613.4a    | 321.5a     | 1452.7a    | 15.7a    |

ANOVA

|                | Year | Nitrogen (N) | Cultivar (C) | N × C |
|----------------|------|--------------|--------------|-------|
|                |      | ns           | *            | **    |
|                |      | *            | ns           |       |
|                |      | ns           | ns           |       |

3.2.2. N Capture Dynamics

N application remarkably improved crop N capture at different growth stages (Figure 3). The values of crop N accumulation observed under high N supply were always larger than those under low N supply, and such a difference increased with the crop growth process. The oilseed rape hybrid outperformed its parental lines in N accumulation, and the advantage enlarged at the latter part of crop growth.

N application generally had little effects on \( t_1 \) values, but significantly delayed the terminal thermal time \( t_2 \) (Table 3). Thus, the durations of the RGP \( t_d \) under high N condition were longer than those under low N. High N application considerably improved the \( V_m \) values. Cultivars differed in the characteristics of N capture. The hybrid was generally higher in \( V_m \) values than the parental lines at both low and high N conditions in the two experimental seasons. In the season 2015–2016, the hybrid had significantly higher \( t_d \) than the parental lines under at both low and high N conditions, but they did not differ in the season 2014–2015.
Table 3. N accumulation dynamic parameters of the oilseed rape cultivars grown at two N rates during the experimental seasons. Values with different letters are significantly different at a probability level of \( p < 0.05 \) within each N rate in the same season. \( t_1 \) and \( t_2 \), the initial and terminal points of the rapid growth period; \( t_d \), the duration of the rapid growth period; \( t_0 \), the point at which the maximum growth rate occurs and \( V_m \), the maximum growth rate. *, \( p < 0.05 \); **, \( p < 0.01 \).

| Year   | N Rate | Cultivar | \( t_1 \)  | \( t_2 \)  | \( t_d \)  | \( t_0 \)  | \( V_m \) |
|--------|--------|----------|------------|------------|------------|------------|---------|
| 2014–2015 | 0      | ZYZ12    | 1101.4a    | 1527.6a    | 426.3a     | 1314.5a    | 0.065b  |
|        |        | R5       | 1138.0b    | 1552.1b    | 414.1a     | 1345.0ab   | 0.050a  |
|        |        | 6098A    | 1156.8b    | 1587.8b    | 431.0a     | 1372.3b    | 0.052a  |
|        | 180    | ZYZ12    | 1087.8a    | 1592.3a    | 504.5a     | 1340.0a    | 0.173b  |
|        |        | R5       | 1171.7b    | 1687.6b    | 515.9a     | 1429.7b    | 0.148a  |
|        |        | 6098A    | 1191.1b    | 1668.9b    | 500.7a     | 1430.0b    | 0.145a  |
| 2015–2016 | 0      | ZYZ12    | 991.9a     | 1478.5ab   | 486.6b     | 1235.2a    | 0.043b  |
|        |        | R5       | 1112.8b    | 1562.8b    | 449.9a     | 1337.8b    | 0.037a  |
|        |        | 6098A    | 1002.1a    | 1448.4a    | 446.3a     | 1225.2a    | 0.034a  |
|        | 180    | ZYZ12    | 993.4a     | 1555.4a    | 562.0b     | 1274.4a    | 0.146b  |
|        |        | R5       | 1110.9b    | 1631.8b    | 520.9a     | 1371.3b    | 0.137ab |
|        |        | 6098A    | 988.2a     | 1500.2a    | 512.0a     | 1244.2a    | 0.126a  |

ANOVA

|          | Year | Nitrogen (N) | Cultivar (C) | N × C |
|----------|------|--------------|--------------|-------|
|          | **   | ns           | *            | **    |
|          | ns   | *            | ns           | **    |
|          | *    | ns           | *            | ns    |
|          | ns   | ns           | ns           | ns    |

3.3. N Uptake and N Utilisation Efficiency

Crop N uptake was significantly improved by high N application (Figure 4a,b). Compared with the low treatment, the mean crop N uptake at high N increased by 2.31 and 3.05 folds in the 2014–2015 and 2015–2016 seasons, respectively. Cultivars differed significantly in crop N uptake. Under low N treatment, the hybrid had significantly higher N uptake than the parental lines in both experimental seasons, while the parental line 6098A was higher in N uptake than R5 only in the 2014–2015 season. Under high N treatment, crop N uptake was the largest in the hybrid, followed by line R5, while line 6098A was the smallest in both seasons. Moreover, cultivars showed larger difference in N uptake at high N than at low N treatment, leading to significant N × cultivar interactions in both seasons.
Figure 4. N uptake (A, B) and utilization efficiency (C, D) of three oilseed rape cultivars grown at two N rates during the two experimental seasons. Bars with different letters are significantly different at a probability level of $p < 0.05$ within each N rate. ANOVA results are also given. **, $p < 0.01$; *, $p < 0.05$; ns, $p > 0.05$.

N utilization efficiency decreased substantially with the increase of N rate (Figure 4c, d, $p < 0.01$). Under low N condition, cultivars did not vary significantly in N utilization efficiency in both seasons. Under high N condition, the hybrid was significantly higher in N utilization efficiency over the parental lines in the season 2015–2016.

3.4. Seed Yield and Yield Components

Compared with low N treatment, high N treatment significantly improved seed yield of all cultivars in both experimental seasons (Table 4). The hybrid had significantly higher seed yield over its parental lines at both N rates in two experimental seasons. There was a trend that the line cultivar 6098A yielded higher than cv R5 at low N, although the difference was not significant ($p > 0.05$). Cv R5 significantly out-yielded cv 6098A at high N supply in both seasons.

With increasing N supply, plant produced substantially more pods per plant. Like seed yield, also the pod number per plant was generally higher in the hybrid than its parental lines at both low and high N supply. In the 2014–2015 season, cv R5 had a higher pod number per plant than cv 6098A only at high N supply, but they did not differ significantly in the 2015–2016 season.

Seed number per pod was slightly improved by high N supply, but little cultivar difference could be found, except at low N treatment in the 2015–16 season, where cv 6098 was higher than the other cultivars. No significant N effect was detected on the 1000-seed weight. Cv R5 had significantly lower 1000-seed weight than the other two cultivars at both low and high N supply.
Table 4. Yield and yield components of the three oilseed rape cultivars grown at two N rates during the 2014–2015 and 2015–2016 seasons. Values with different letters are significantly different at a probability level of $p < 0.05$ within each N rate in the same season. *, $p < 0.05$; **, $p < 0.01$.

| Year   | N Rate | Cultivar | Yield (kg ha$^{-1}$) | Pod No. (Plant$^{-1}$) | Seed No. (Pod$^{-1}$) | 1000-Seed Weight (g) |
|--------|--------|----------|----------------------|------------------------|-----------------------|-----------------------|
| 2014–2015 | 0      | ZYZ12    | 1179b                | 177b                   | 21.93a                | 3.65b                 |
|         |        | R5       | 849a                 | 120a                   | 22.03a                | 3.14a                 |
|         |        | 6098A    | 978a                 | 125a                   | 23.67a                | 3.84b                 |
|         | 180    | ZYZ12    | 3066c                | 438b                   | 24.37a                | 4.07b                 |
|         |        | R5       | 2760b                | 410b                   | 23.60a                | 3.32a                 |
|         |        | 6098A    | 2367a                | 236a                   | 26.03a                | 3.82b                 |
| 2015–2016 | 0      | ZYZ12    | 912b                 | 154b                   | 19.81a                | 3.49b                 |
|         |        | R5       | 684a                 | 132a                   | 18.79a                | 3.33a                 |
|         |        | 6098A    | 762a                 | 139a                   | 21.49b                | 3.45b                 |
|         | 180    | ZYZ12    | 2420c                | 448b                   | 22.70a                | 3.49b                 |
|         |        | R5       | 1872b                | 354a                   | 22.72a                | 3.30a                 |
|         |        | 6098A    | 1312a                | 311a                   | 22.27a                | 3.48b                 |

ANOVA

| Source of Variation | df | Sum of Squares | Mean Square | F | Significance |
|---------------------|----|----------------|-------------|---|--------------|
| Year                | 1  | ** ns          | **          |   | ** ns        |
| Nitrogen (N)        |   | **            | **          |   | ns           |
| Cultivar (C)        |   | **            | **          |   | ** ns        |
| N × C               |   | **            | **          |   | ns           |

3.5. Inter-Relationships between Growth Parameters and Yield, Biomass and N Uptake

Crop aboveground biomass at low N treatment correlated significantly and positively with $t_v$ and $v_m$ of biomass accumulation, and $v_m$ of N accumulation, but not with $t_v$ of N accumulation (Table 5). Crop aboveground biomass at high N was significantly correlated with $t_v$ of biomass accumulation and $v_m$ of N accumulation. At both N rates, crop N uptake and seed yield correlated significantly and positively with $t_v$ of biomass accumulation and $v_m$ of N accumulation, but not with $v_m$ of biomass accumulation and $t_v$ of N accumulation.

Table 5. Pearson correlation matrix between crop biomass, N uptake and yield in three oilseed rape cultivars with the growth dynamic characteristics at low and high N rate during the 2014–2015 and 2015–2016 seasons. *, $p < 0.05$; **, $p < 0.01$.

| Low N | High N |
|-------|--------|
| Biomass | N Uptake | Yield | Biomass | N Uptake | Yield |
| $t_v$ biomass | 0.897 ** | 0.913 * | 0.905 ** | 0.780 * | 0.811 * | 0.961 ** |
| $v_m$ biomass | 0.662 | 0.546 | 0.556 | 0.448 | 0.356 | 0.114 |
| $t_v$ N accum. | −0.086 | −0.311 | −0.252 | 0.154 | 0.179 | −0.036 |
| $v_m$ N accum. | 0.896 * | 0.961 ** | 0.926 ** | 0.904 * | 0.883 * | 0.921 ** |

Stepwise multiple regression analysis showed that $t_v$ of biomass accumulation was the most important factor influencing crop aboveground biomass, explaining 75.6% and 51.1% of cultivar variance at low and high N, respectively, while 23.3% and 43.7% of the cultivar variance were explained by $v_m$ of biomass accumulation (Table 6). Cultivar variance in seed yield at low N was controlled mainly by $t_v$ of biomass accumulation (77.4%), and less importantly by $v_m$ of biomass accumulation (9.9%), but it was determined mainly by $t_v$ of biomass accumulation (90.5%) at high N supply. Cultivar difference in $v_m$ of N accumulation explained 90.4% and 72.5% of the variance in N uptake at low and high N, while the difference in $t_v$ of N accumulation explained only 7.2% of the variance at high N. From an N uptake perspective, $v_m$ of N accumulation was the main factor determining seed yield, accounting for 82.2% and 81.1% of the variance at low and high N, respectively.
Table 6. Stepwise multiple analysis for the determinants of crop biomass, yield and N uptake yield in three oilseed rape cultivars under low and high N supply during the 2014–2015 and 2015–2016 seasons.

| Dependent Variables | Independent Variables | Standard Coefficient | $R^2_{adj}$ | $p$  |
|---------------------|-----------------------|----------------------|-------------|-----|
| Low N supply        |                       |                      |             |     |
| Biomass             | $t_c$ biomass         | 0.774                | 0.756       | 0.015|
|                     | $v_n$ biomass         | 0.452                | 0.989       | 0.001|
| Yield               | $t_c$ biomass         | 0.814                | 0.774       | 0.013|
|                     | $v_n$ biomass         | 0.335                | 0.873       | 0.021|
| N uptake            | $v_n$ N accum.        | 0.961                | 0.904       | 0.002|
| Yield               | $v_n$ N accum.        | 0.926                | 0.822       | 0.008|
| High N supply       |                       |                      |             |     |
| Biomass             | $t_c$ biomass         | 0.892                | 0.511       | 0.047|
|                     | $v_n$ biomass         | 0.610                | 0.948       | 0.005|
| Yield               | $t_c$ biomass         | 0.961                | 0.905       | 0.002|
| N uptake            | $v_n$ N accum.        | 0.930                | 0.725       | 0.020|
|                     | $t_c$ N accum.        | 0.317                | 0.797       | 0.042|
| Yield               | $v_n$ N accum.        | 0.921                | 0.811       | 0.009|

4. Discussion

4.1. Model Performance

The logistic equation is one of the most frequently used nonlinear functions that have been developed to model important aspects of crop growth, including crop and kernel development, biomass accumulation [33–35]. It performed reasonably well in interpreting the dynamics of biomass and nutrient accumulation in major crops including rice [42,43], cotton [34,36], maize [44] and winter wheat [25]. In the present study, the simulated values of the aboveground biomass and N accumulation in winter oilseed rape cultivars were in good agreement with the measured values with $R^2$ of 0.919–0.999, RMSE of 1.0–14.1% and EF of 0.911–0.999, which could suggest reasonable accuracy in model simulation according to previous studies [27,45]. In another study on winter oilseed rape, however, the logistic was found less accurate than the Gompertz’ curve to fit the progress of plant biomass accumulation [33]. In their study, calendar days after planting rather than thermal time was used as the independent variable, so that the growth increase may skew to the right in the growth curve, because crops underwent a very slow growth before the initiation of stem elongation due to low temperature. In contrast, the thermal time, i.e., GDD was used in the present study, which was biologically sound and able to avoid such problem. Moreover, it was advantageous to use GDD instead of calendar days as the independent variable for the nonlinear equations, as it could reduce the effects of different weather conditions or planting dates, when multiple experimental locations or years were involved in the analysis [25,44]. The results in the presents suggest therefore that the logistic model using GDD as the independent variable could be extended to characterize the dynamics of aboveground biomass and N accumulation in winter oilseed rape cultivars under contrasting N supply.

4.2. Genotypic Variation

Winter oilseed rape hybrids have been well developed and used in China and worldwide as a promising alternative for improving seed yield [5,24,46], as a result of heterosis that may occur at all stages of development [47]. However, the mechanism of improved NUE in oilseed rape hybrids in comparison with the lines remains to be better understood. The hybrid used in this study showed higher accumulation of aboveground biomass than the parental lines at different stages investigated, and the difference became larger with crop development, which was in line with previous studies.
conducted under different soil and climate conditions [47]. Further analysis revealed that the higher seed yield and aboveground biomass accumulation in the hybrid were mainly associated with the longer duration of the rapid growth period, and to a less extent with the higher growth rate. This corroborates previous investigations reporting that a crop type with delayed maturity was the most promising for high seed yield [48], highlighting the importance of growth duration. The line cultivar R5 was genetically characterized with more branches, which facilitated the formation of more pods than cv 6098A. This trait was beneficial for a higher seed yield at high N supply, as increased pod number could compensate for the lower seed number per pod and seed weight. However, it was not the case at low N, because redundant branches may result in pod degradation due to limited assimilates during pod filling.

In accordance with the yield heterosis, the hybrid had significantly higher N uptake than the parental lines at low N supply, but cultivars did not differ in N utilization efficiency, indicating an overwhelming importance of N uptake for genotypic variation in seed yield at N limiting conditions. Similar findings were obtained for wheat [49], and in another study on oilseed rape [20]. The fact that the N utilization efficiency was considerably higher at low than high N supply indicates the potential in the conversion of absorbed N into seed yield might be well exploited in all cultivar when N was strongly limiting. At high N supply, N uptake was also important for seed yield, with an increasing importance of N utilization, supporting former reports that N uptake was an important factor driving genotypic variation in seed yield at all N levels [21]. Earlier studies have attributed genotypic variation in seed yield to N uptake during reproductive growth [16,21], suggesting a prolonged duration of N uptake might be beneficial. In the present study, oilseed rape plants took up most of N until flowering. The N-efficient hybrid even showed an earlier termination of the RGP for N accumulation, indicating the higher yield of the hybrid was clearly not associated with prolonged duration of N uptake. On the contrary, strong and positive correlations were found between seed yield and \( \text{DM} \) for N accumulation at both N rates. These results suggest a higher growth rate for N accumulation during the RGP was the main reason for the yield heterosis, which may present a scope for genetically improving NUE in oilseed rape.

4.3. Perspectives on N Management

Plant biomass production is of primary importance for seed yield in winter oilseed rape [33,50]. The biomass accumulation in oilseed rape generally followed a sigmoidal growth pattern that would change in response to different genotypes and environment conditions [24,50]. In the present study, seed yield was lower in 2015–2016 than in 2014–2015. This might be due to the lower GDD during plant growth in 2015–2016 (2128 °C d in 2015–2016 vs. 2243 °C d in 2014–2015), which limited biomass accumulation and downregulated seed number per pod and 1000-seed weight. High N application promoted biomass production in oilseed rape, as a result of remarkably enhanced maximum growth rate and extended duration of the RGP, which was in accordance with the findings in a previous study [33]. Moreover, our results further revealed that the prolonged duration of RGP of biomass by high N supply was mainly due to the delayed termination rather than earlier initiation of RGP. It seems that the initiation of the RGP depended on GDD but could not be accelerated by high N supply. This was in agreement with a previous finding that the phenological development of winter oilseed rape before flowering was related mainly to the temperature and photoperiod [48]. Similarly, the developmental response of wheat to the environment, as defined in terms of the primordium production rate, was found dependent solely on temperature but independent of N supply [51,52].

As with aboveground biomass, N uptake in oilseed rape was significantly enhanced by high N supply, which could be explained by the longer duration of RGP, and together larger \( \text{DM} \) values for N accumulation during this period. The initiation of RGP for N uptake occurred after the overwinter period (around BBCH 19), slightly earlier than that for biomass accumulation. These results indicate that rational N fertilization with reduced basal dose but larger N amount in spring (i.e., beginning of growth) could match better with crop N demand. Winter oilseed rape appeared to be more vigorous and took up more N than cereals before winter [53]. However, it used autumn N to a lesser extent than spring applied N [54,55]. In the present study, the high N supplied crops received 108 kg N ha\(^{-1}\)
in autumn, but the average N uptake of the cultivars before winter was only 24.6 and 29.4 kg N ha\(^{-1}\) in the 2014–2015 and 2015–2016 seasons, much lower than that reported under European conditions [55]. This might be explained by the fact that oilseed rape seedlings were transplanted in the current study, resulting in considerably lower crop density than direct-sown oilseed rape.

Overdoses of basal N fertilizer in autumn will leave large N reserves in the soil and inevitably increase the risk of N losses to the environment [56]. On the other hand, even if high N supply enhanced crop N uptake before winter, leaves often became frostbitten and lost onto the soil during winter, from which only a little of the N could be used again by the crop after mineralization [53,55,57]. Overall, these results suggest that distribution of N fertilizer with reduced amount in autumn but increased amount applied in spring has great potential to achieve a better synchronization with oilseed rape N demand and to minimize the negative effects on the environment.

5. Conclusions

The logistic equation using GDD as the independent variable could reasonably well characterize the growth and N capture dynamics in winter oilseed rape cultivars under low and high N. The oilseed rape hybrid was superior to its parental lines in seed yield and aboveground biomass accumulation, due mainly to a longer duration of the rapid growth period. N uptake was the main factor driving genotypic variation in seed yield, with an increasing importance of N utilization at high N supply. The improved N uptake in the oilseed rape hybrid was attributed to a larger growth rate for N accumulation during the RGP, presenting a scope for genetical improvement in NUE. The initiation of RGP for N uptake that occurred after the overwinter period, could not be accelerated by high N supply, suggesting rational N fertilization with reduced basal dose but larger spring amounts might be beneficial for a better synchronization with crop N demand.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Figure S1: Daily maximum and minimum temperature during the 2014–15 (A) and 2015–16 (B) season.

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