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*Article*

# Relation between Water Storage and Photoassimilate Accumulation of *Neosinocalamus affinis* with Phenology

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**Abstract:** Reasonable management could produce the good growth of bamboo plants. There are few studies in bamboo that integrate phenology and ecophysiological traits; in this case, water relations, photosynthetic rates and carbohydrate content in different organs of *Neosinocalamus affinis* were determined. The moisture content was easily affected by the local precipitation and showed a similar trend in leaves and branches, with the highest values in July and August, but did not vary significantly between vegetative phenological stages in culms. The emergence and growth of shoots caused an apparent decrease in the moisture content of 1-year culms. NSC content showed a similar trend in culms and branches in classes of different ages and decreased progressively from March through November and then increased in the following months. Net photosynthetic rate and transpiration pull showed the highest values in July and then decreased constantly, which implied that a great deal of water was consumed for photoassimilate synthesis. The net photosynthetic rates of leaves were significantly affected by the water status of culms in the dry season, but correlated significantly only with the leaf water content in the wet season for the sufficient water supply. The transpiration pulls, water potential and sap flow rates revealed the water status of culms better than the water content of culms. The shoot germination and growth of *N. affinis* were more dependent on the photoassimilate accumulation in the early stage from May to July. There was no real dormancy period for *N. affinis* due to its apparent photoassimilate accumulation and water flow in January. This suggested that proper irrigation was essential during leaf and branch extension during the dry season.

**Keywords:** phenological stage; water status; net photosynthetic rate; non-structural carbohydrates; dormancy; *Neosinocalamus affinis*

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## 1. Introduction

The rapid growth, good specific strength, and ease of processing of bamboo make it an important forest resource [1]. China has approximately 30% of the world's bamboo resources [2,3]. Its bamboo forests cover approximately 4,430,100 ha, and play an important role in the country's forest resources [4]. At present, *Phyllostachys edulis* (Carrière) J. Houz., which accounts for 70% of China's bamboo resources, is the most widely distributed of monopodial bamboo, with leptomorph rhizomes that produce well-spaced culms that provide a multipurpose raw material for the bamboo industry [5,6]. However, the sympodial bamboo with caespitose culms, which accounts for more than 20% of China's bamboo forests, has yet to be effectively utilized [7,8]. *Neosinocalamus affinis* (Rendle) Keng f. sympodial bamboo has a broad distribution in Southwest China, especially in the province of Sichuan. It has a wide distribution area and its output exceeds that of *P. edulis* in Sichuan

Province [9]. *N. affinis* has the characteristics of rapid growth, easy cultivation and reproduction, and high economic output, and its thin culm wall, slender bamboo internode, and long fiber length make it an excellent raw material for paper making and bamboo plaiting articles [10,11]. Therefore, *N. affinis* has good value for development and utilization.

Nonstructural carbohydrate (NSC) is the main product of plant photosynthesis, which not only provides energy for plant growth and development, but also is a key regulator for the plant's physiological response to environmental stress [12–15], such as osmotic conditions and osmotic protection [16–18]. Therefore, it plays an important role in the life processes of plants. The NSC of plants is stored in various vegetative tissues in the form of soluble sugar and starch. Its in-content variation is an important indicator of the plant carbon source and sink capacity [19–21], which essentially reflects the plant vitality and photosynthetic capacity [22,23]. The traditional view is that when the supply exceeds the demand, the NSC reserves will accumulate, and when the supply is insufficient, the NSC reserves will be used for respiration and the reserves will decrease [24]. As one of the fastest-growing plants in the world, bamboo is known for its rapid growth. The growth of bamboo clusters depends on and replenishes the stored NSC throughout the year. The accumulation of high NSC produces more shoots, promotes growth, and is conducive to the overall development of bamboo forests [25]. Therefore, quantitative research on NSC accumulation plays a crucial role in the cultivation and management of bamboo forests.

Water content can even reach around 90% in the leaves of healthy plants [26]. As a medium, raw material, and site of life activities, water is related to photosynthesis and transpiration, the two most important physiological processes in plants [27]. The roots are the main component of plants that absorb water and nutrients from the soil [28]. As a shallow root species, more than 90% of the bamboo root biomass is located in the 0–50 cm soil layer [29,30], which limits its ability to use water in deep soil. Some studies have shown that plants with connecting roots or rhizomes may share resources directly with each other [31], and this is called "physiological integration" [32–34]. Fang and Mei [35] considered that bamboo exchanges water through rhizomes, and the flux at night is very important to support newly sprouted bamboo. A sufficient water supply promotes the rapid growth of bamboo shoots. Leaf gas exchange studies have proven the close relationship that exists between the photosynthesis rate and the water status of the leaves, as reviewed by Xiong and Nadal [36], and they also presented that the photosynthetic performance, in turn, depends on the rate of water loss and the plant's capacitance. The effect of soil water content on photosynthesis has been amply demonstrated in previous studies. Wang et al. [37] showed that soil water was one of the main environmental factors limiting plant growth and photosynthetic capacity. Photosynthetic activity was enhanced under moderate soil moisture, but reduced under both a severe water deficit and excessive water conditions, which may represent the response patterns of plant growth and photosynthetic capacity to the soil water gradient [38]. Water storage in growing tissues and non-growing tissues could buffer against rapid water status fluctuations caused by environmental changes such as air and soil drought [36]. Meanwhile, the precipitation and light duration varied with phenological stages. Therefore, it is important to study the water status of bamboo with phenological periods to obtain an understanding of the physiological status of bamboo and the maintenance of bamboo forests.

Research on bamboo plants is mostly focused on monopodial bamboos, and less on sympodial bamboo. As a type of sympodial bamboo, *N. affinis* is mainly used for building materials, pulp and paper, biomass energy, and highly elastic bamboo belts for the weaving of farm tools in various provinces in Southwest China [39]. Zhan et al. [39] observed the dynamics of NSC in *N. affinis* culms, but did not systematically evaluate the impact of water and other factors on the NSC storage in different phenological stages. The purpose of this study was to discover the response rule of all related physiological indexes to the phenological variations and to provide more detailed information on the effects of the water status on the accumulation of NSC in *N. affinis* with phenology. The results not only enrich the physiological knowledge of the relationship between water storage and photoassimilate accumulation in bamboos, but also provide guidance for the management and conservation of *N. affinis* forests in Southwest China.

## 2. Materials and Methods

### *2.1. Plant Material*

The samples of *N. affinis* used for this experiment were obtained from the bamboo garden of the Southwest Forestry University in Yunnan Province, China. The local climate is described in Table 1. The bamboo age was judged according to the color of the culms and culm sheaths and the shooting time. According to the vegetative phenological stages during the whole year, the samples were successively collected in March, May, July, August, and November, 2021, as well as in January, 2022. Culm samples were divided into three parts from bottom to top, i.e., the 1st internode above ground was defined as the bottom, and the 7 and 14th internodes were defined as the middle and top parts, respectively.

**Table 1.** The climate of Kunming City, Yunnan Province, China.

| | January | March | May | July | August | November |
|---|---|---|---|---|---|---|
| Atmospheric temperature (°C) | 9.3 | 16.5 | 21.6 | 21.3 | 21.2 | 12.4 |
| Precipitation (mm) | 1.8 | 0.5 | 46.5 | 225.2 | 168.2 | 27.2 |
| Daily sunshine duration (h) | 8.1 | 10.2 | 11.4 | 10.3 | 9.6 | 6.6 |
| Relative humidity (%) | 63.8 | 42.8 | 56.7 | 74.4 | 75.6 | 73.3 |

The data were downloaded from the official website of the National Meteorological Science Data Center of China.

Culm sampling was performed by drilling the bamboo block with a diameter of approximately 3 cm in the middle of the internode with an electric drill. The branch and leaf samples were obtained from the middle part of the canopy towards the south side in different age groups using a branch shear. All materials were cut into small pieces, placed into 50 mL centrifuge tubes, and then stored in liquid nitrogen.

### *2.2. Methods*

#### 2.2.1. Moisture Content Determination

The collected samples were dried at 105 °C for 30 min and at 75 °C overnight for moisture content determination. The moisture content was calculated according to the following formula.

$$\text{Moisture content} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Fresh weight}} \times 100\%$$

#### 2.2.2. Determination of Net Photosynthetic Rate (Pn), Transpiration Rate (Tr)

A total of 450 mature leaves in the three age classes (1, 2, and 3 years old), totaling 15 culms, were used for the determination of the Pn and Tr of leaves on three consecutive sunny days by using a Portable Photosynthesis System at different phenological stages (produced by Zhejiang Top Cloud-Agri Technology Co., Ltd. (Hangzhou, China) Model: 3051D). The determinations were conducted every two hours from 8 a.m. to 6 p.m. for three days in each of the vegetative phenological stages.

#### 2.2.3. Determination of Transpiration Pull and Water Potential and Sap Flow

The in situ transpiration pull was determined at the middle parts of culms by a liquid-pressure transducer (Measurement range: −50 to 50 MPa) (Elecall, Elecall Company, Leqing, China), linked with a syringe needle (0.9 × 28 mm) by a 2-m-long PVC pipe (2 mm in diameter) (Figure 1). The syringe needle was inserted into the culm walls, and the pipe was filled with water before measurement. The positive pressure values revealed the dynamic changes in root pressure and the negative values revealed the dynamic changes in transpiration pull. All the indexes were determined at 8:00 AM, 10:00 AM, 12:00 PM, 2:00 PM, 4:00 PM, and 6:00 PM on each day during three consecutive days, in each of the phenological stages.

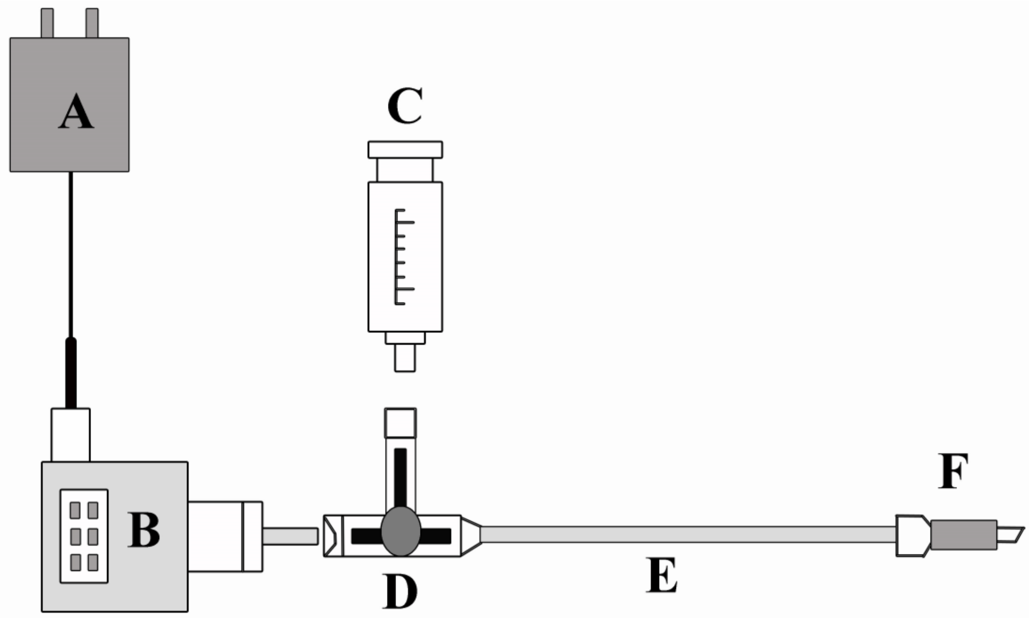


**Figure 1.** The equipment for the determination of in situ tissue water pressure. (**A**) Lithium battery. (**B**) ELE-801S LCD digital display customized pressure sensor (measuring range: −50~50 kPa). (**C**) syringe. (**D**) Three-way valve switch connector. (**E**) PVC pipe (with needle seat and national standard joint). (**F**) Syringe needle.

The in situ water potential and sap flow rates were determined simultaneously at the bottom of culms according to the methods of Dixon et al. [40] and Marshall [41], respectively, by using a PSY1 Stem Psychrometer and a SFM1 Stem Psychrometer (ICT International, Armidale, NSW, Australia), so as to determine the water storage levels in the culms (Figure 2). High transpiration pull in the midculm, associated with a low rate of sap flow and low water potential at the base of the culm, indicated an adequate supply of water stored in the culms to carry out photosynthesis and transpiration reactions.

### 2.2.4. Determination of Soluble Sugars, Starch, and NSC Content

The endogenous soluble sugar and starch content was determined using the phenol–sulfuric acid method according to Glassop et al. [42] and Dubois et al. [43]. Samples (1.0 g) were ground to powder using liquid nitrogen and then extracted with 10 mL of deionized water at 70 °C. The extractions were centrifuged at 12,000 rpm for 20 min, and the supernatants were collected for soluble sugar content determination. The sediments were stored at −20 °C for starch content determination. The sediment was dried, weighed, and boiled with deionized water. The supernatants were used for the determination of starch content. NSC values were defined as the sum of starch and soluble sugar content at each phenological stage in culms of different age groups. All mean values were obtained by measuring three samples, and each sample was measured three times.

### 2.2.5. Statistical Analysis

The mean values derived from the experiments were statistically analyzed and compared by multiple comparisons using the least significant difference method (LSD), to determine the value of significance at $p < 0.05$. The correlation analyses were conducted by using the Pearson correlation coefficient. All the values were analyzed by SPSS 25.0 (SPSS Inc., Chicago, IL, USA).

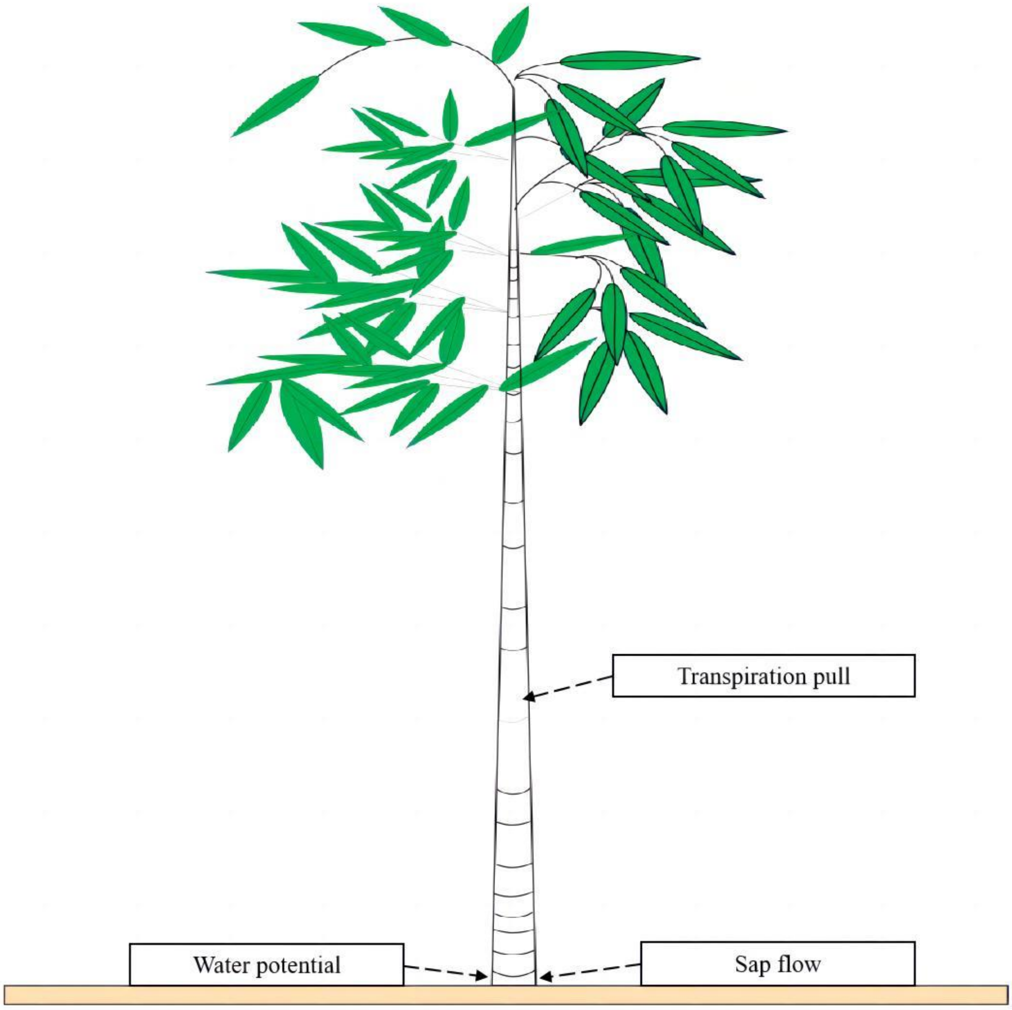


**Figure 2.** Water status was determined as indicated by transpiration pull, water potential, and sap flow, which were determined simultaneously at different parts of the same culms. The difference in the variation trend of their values with phenology revealed the water storage in the culms.

## 3. Results

### *3.1. Phenological Observation of N. affinis*

*N. affinis* is a typical sympodial bamboo with caespitose culms. The phenological stages of *N. affinis* were observed and recorded consecutively (Table 2 and Figure 3). During the period from January to May, the average atmospheric temperature increased constantly from 9.3 to 21.6 °C (Table 1). Most new culms were generated in July 2021, completed branch and leaf extension by May 2021 (Table 2 and Figure 3A–C), and new shoots generated were mainly at the bases of 1- and 2-year-old culms, and, less frequently, at the bases of 3-year-old culms. The branch and leaf extension was fully completed by July (Table 2 and Figure 3D–F), and the wet season of the local region arrived and the average temperature started decreasing constantly (Table 1). The production of new shoots occurred continually between July (Figure 3G,H) and August (Figure 3I), when they completed their shooting stage. Between December and January, which represented the coldest and driest season of the year, most of the young culms had completed their elongation and entered dormancy (Figure 3J), which occurred during the dry season and the coldest season (Table 1). The culm leaves covering the bottom and mid-region of the culms were shed during this period, and only the ones covering the apexes of the shoots remained. In January, some old leaves of the bamboo cluster began turning yellow and falling off, and their branches and leaves became sparse (Figure 3K). The culms over 1 year old also became yellow during this period (Figure 3L).

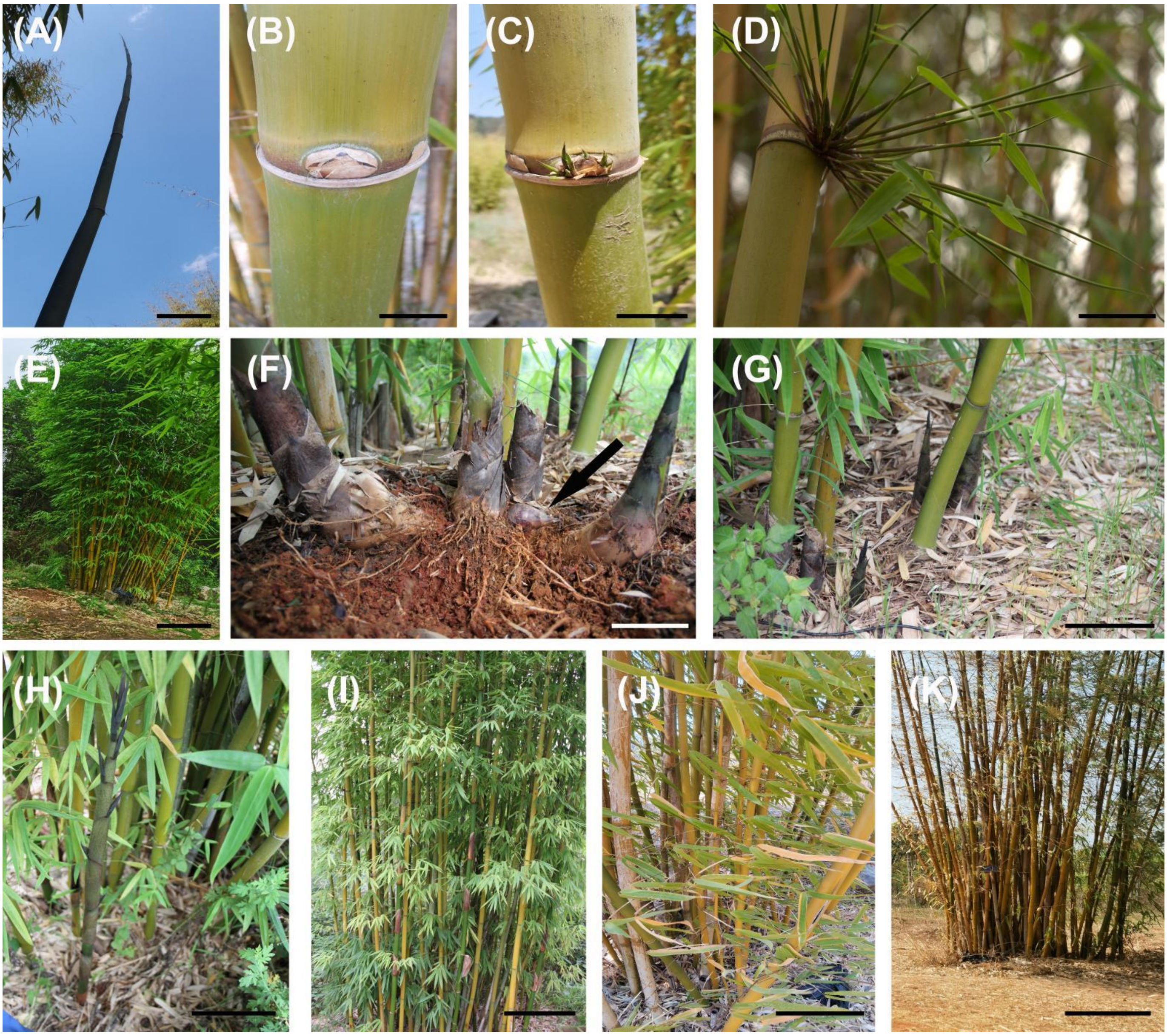


**Figure 3.** Different phenological phenomena of *N. affinis.* (**A**,**B**) The new culms had not yet spread their branches and leaves in March. (**A**) Bar = 25 cm. (**B**) Bar = 2.5 cm. (**C**) Nodal buds of 1-year culms started sprouting in early May. Bar = 5.0 cm. (**D**) New leaves extended with branch extension simultaneously in May. Bar = 2.5 cm. (**E**) The bamboo cluster was luxuriant after branching and leafing in July. Bar = 1.0 m. (**F**) Most shoots started to emerge out of the ground at the bases of 1- and 2-year culms in early August. Bar = 8.0 cm. (**G**) The bamboo cluster was still in shooting in late August. Bar = 20.0 cm. (**H**) Some young shoots that sprouted in late August grew taller and were covered completely with culm sheaths in early November. Bar = 25.0 cm. (**I**) Most shoots completed their height growth in late November, and the culm sheaths began to drop off from the bottom parts of the culms. Bar = 65.0 cm. (**J**) The leaves became withered and yellow in January. Bar = 8.0 cm. (**K**) Most leaves had fallen off and culms turned yellow under the dry conditions in January, and the bamboo clumps also appeared sparse. Bar = 80 cm.

**Table 2.** Phenological characteristics of *Neosinocalamus affinis*.

| Sample Timing | Phenological Stage | Phenology of Bamboo Clump |
|---|---|---|
| March 2021 Spring/dry season | Before bud sprout | Few nodal buds sprouted on the new culms generated last year. |
| May 2021 Spring/dry season | Branching and leafing | Most new culms were in the branching and leafing stage, and the shoot buds were also pregnant at the culm base of the new culms and the 2-year culms. |
| July 2021 Summer/rainy season | Before shooting | Shoot bud development continued underground, and a few shoots emerged out of the ground. |
| August 2021 Summer/rainy season | Shooting and height growth | Most shoots emerged out of the ground and completed their height growth in the subsequent three months. |
| November 2021 Autumn/dry season | After culms have achieved maximum height | Height growth of new culms completed. The culm sheath of the middle and bottom parts of the new culms dropped off. The bamboo clump entered the dormancy stage. |
| January 2022 Winter/dry season | Dormancy | New culms ceased growing and the bamboo clumps entered dormancy. |

### *3.2. Phenological Changes in Moisture Content in Different Organs of N. affinis*

The moisture content in different organs of *N. affinis* varied with the phenological stage (Figure 4). There was no significant difference in the moisture content of the leaves of 2- and 3-year-old culms in each phenological period (Figure 4A). The moisture content in the leaves of 2- and 3-year-old culms showed a slight decrease from March to May, and increased later, reaching the maximum levels in July, and then decreased constantly until January. This trend was consistent with the dynamics of local temperature and precipitation, except in May. The local wet season began at the end of May. The moisture content of the leaves was affected by the changes in the local temperature and rainfall. The phenological changes in the moisture content in the leaves of 1-year-old culms were essentially consistent with those of the leaves of 2- and 3-year-old culms. It could also be noticed that the moisture content was higher in the leaves of 1-year-old culms than in those of 2- and 3-year-old culms in May, but was significantly lower in July (Figure 4A). Additionally, the young culms did not generate any branches or leaves in March, and thus there were no recorded data on the moisture content of leaves and branches (Figure 4A,B).

### *3.3. Phenological Changes in In Situ Transpiration Pull, In Situ Water Potential, and Sap Flow Rates in Culms of N. affinis of Different Ages*

The dynamics of in situ transpiration pull in the middle parts of culms of all ages showed a similar trend, which was consistent with the changes in phenology (Figure 5A). From March to July, the transpiration pull values in culms increased consistently over time, with the maximum values in July; they sharply decreased in August and then constantly increased in the following seasons. The transpiration pull of 1-year-old culms was lower during the period from March to May, but higher during the following phenological stages as compared to those of 2- and 3-year-old culms. Especially in July and August, the higher transpiration pull values in 1-year culms implied more water consumed for the photosynthesis and transpiration of their new leaves and supplied more water for new shoot emergence and growth. Similarly, the moisture content in the 1-year-old culms also showed a decrease in August (Figure 4C). The water potential in the *N. affinis* culms of all ages was consistent with the precipitation and relative humidity during the phenological stages. A consistent decline in the water potential of culms of all ages was observed from March to May, which was reverted between July and August, which represented the period in which the highest potential was registered, and it dropped again within the following months (Figure 5B). Although the water potential tended to diminish as the ages of the culms increased, we observed an increase in these values in 3-year-old culms during the month of January.

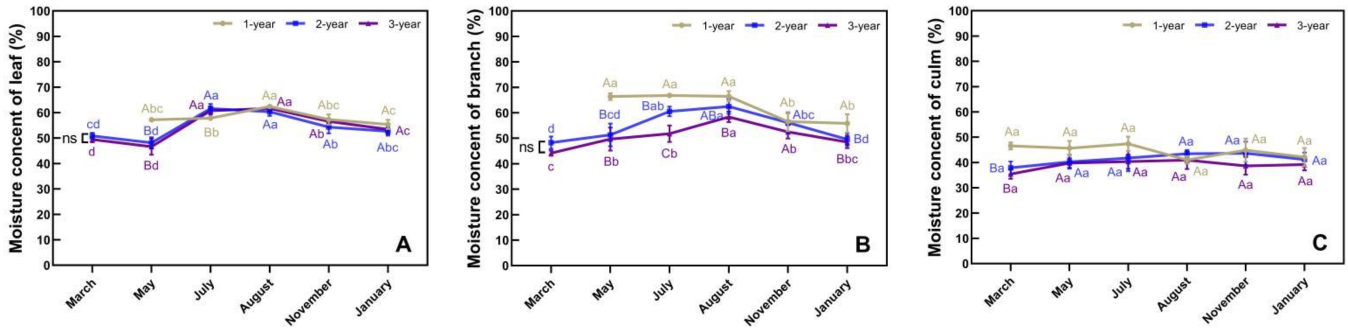


**Figure 4.** The moisture content of *N. affinis* branches also varied significantly with phenology, which was similar to that of the leaves (**A**) We observed a significant increase in the moisture content of leaves and branches of 2- and 3-year-old culms from March through August, followed by a consistent decline, which appeared to be related to the generation of new branches. This was also consistent with the variation trend of the local relative humidity and precipitation in the same period. The moisture content in the new branches of 1-year-old culms showed a decreasing trend with the months, due to the fact that the newly generated branches were tender, with higher moisture content, and decreased with maturation (**B**) We also noticed a decline in the moisture content of the branches in all of the phenological stages taken into account in the present study, suggesting that the moisture content of the branches was not only related to their growth stage, but the age of the culm as well. The moisture content of culms did not change significantly with phenology, but their trend was also similar to that of branches and leaves (**C**) The moisture content of 2- and 3-year-old culms increased constantly and then decreased with the phenological stage, which was essentially similar to the trend of the relative humidity and precipitation during the whole year. However, the moisture content of 1-year culms showed a decrease in August, which was even lower than that of 2- and 3-year-old culms. This might be due to the fact that the new shoots generally sprouted from the bases of 1-year culms, which are likely to consume higher amounts of water during the early growth stages. As with branches, the moisture content in culms also decreased with age in all phenological stages.

Daytime sap flow showed a similar trend to the transpiration pull dynamics in culms of all ages (Figure 5C), which decreased firstly from March to July, and then increased in August and decreased subsequently in 1- and 3-year-old culms. For 2-year-old culms, the increase in transpiration pull occurred in November. Generally, the daytime sap flow in the 1-year-old culms showed the lowest values during the period from March to July, but was higher during the subsequent period as compared to that in the 2- and 3-year-old culms. This might imply that the 2- and 3-year-old culms supplied more water for the bamboo cluster in the first half of the year, but the 1-year-old culms did so in the latter half of the year. Especially in August, the highest sap flow value for 1-year-old culms implied more water supplied for new shoot emergence and height growth as compared to that of 2- and 3-year-old culms. The nighttime sap flow rate was similar to that of the daytime, which also showed lower values in 1-year-old culms (Figure 5D).

By comparing the difference between daytime and nighttime sap flow rates, we observed that the nighttime sap flow rates of *N. affinis* culms at all ages were greater than the daytime ones in the dry season (Figure 5C,D). Meanwhile, in the wet season, the daytime sap flow rates of *N. affinis* culms at all ages were greater than the nighttime ones in both 2- and 3-year-old culms (Figure 6B,C). The daytime and nighttime sap flow were separately driven by the transpiration and root pressure. In the wet season, there was sufficient water supply in the soil for the transpiration of 2- and 3- year-old culms, which coincided with their higher Tr values, which were determined and are shown in Figure 7B. Meanwhile, in the dry season, the deficiency in the water supply in the soil caused a decrease in transpiration, and thus the nighttime sap flow was higher. Therefore, the water transport in culms was more dependent on the nighttime sap flow in the dry season; in other words, it was more determined by the water supply in the soil. The decrease in daytime sap flow could alleviate the transpiration consumption of water in the dry season.

For 1-year-old culms, the sap flow rate was still higher at night than during the day in the wet season (Figure 6A). This meant that the water use pattern of 1-year culms differed from the pattern observed in 2- and 3-year-old culms, and the water supply of the 1-year culms depended more on the nighttime sap flow. This was also related to the fact that more new shoots were generated from the 1-year-old culms.

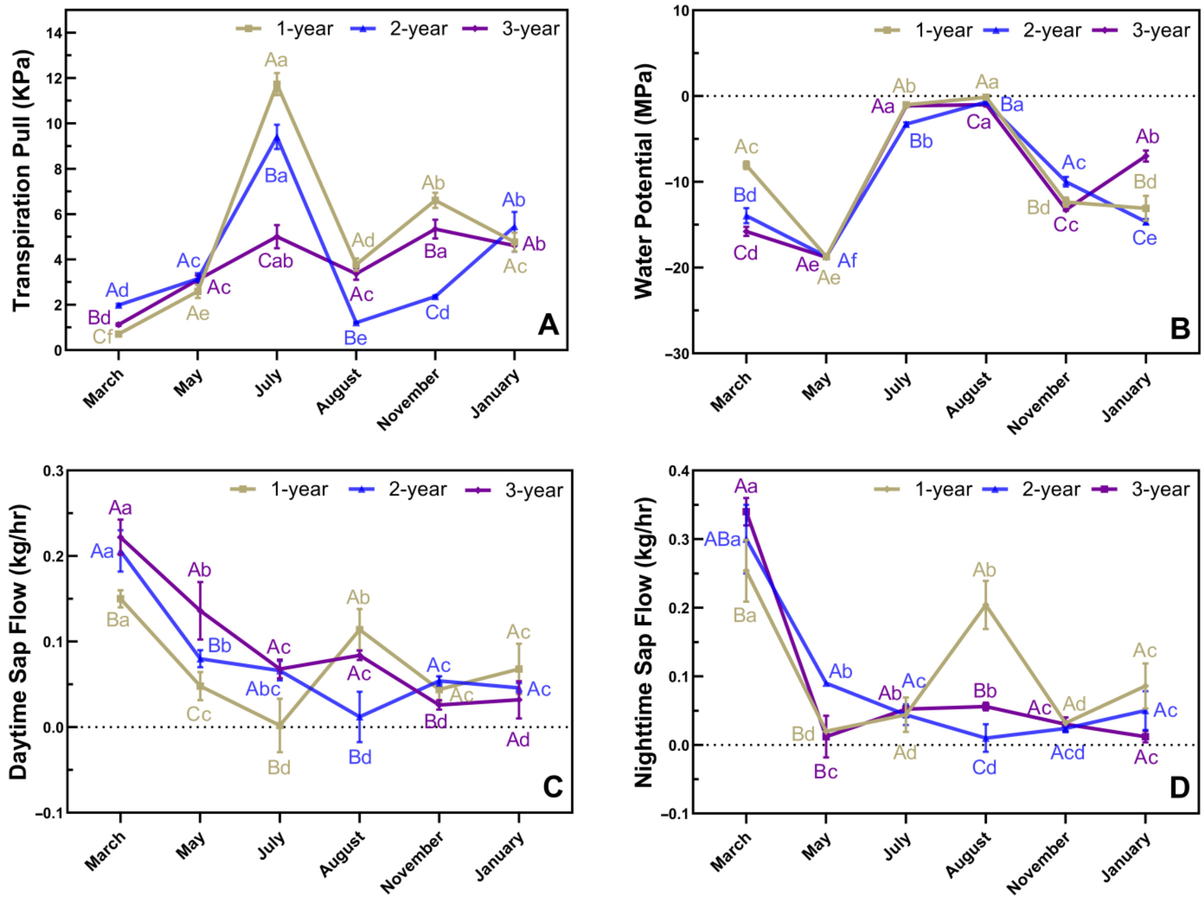


**Figure 5.** Dynamical changes in in situ water potential, transpiration pull, and sap flow rates of *N. affinis* culms of different age classes with phenology. (**A**) Transpiration pull. (**B**) Water potential. (**C**) Daytime sap flow. (**D**) Nighttime sap flow. Different uppercase letters indicate significant differences between years and different lowercase letters indicate significant differences between months at $p < 0.05$ level.

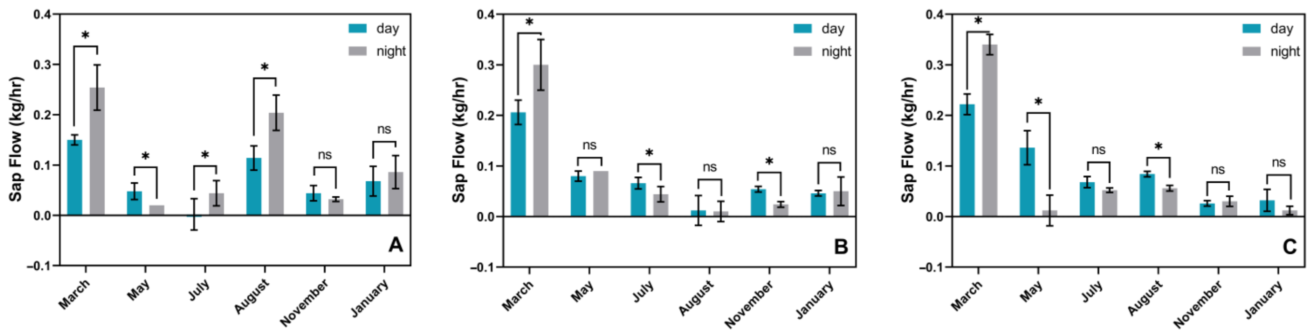


**Figure 6.** Comparisons between daytime and nighttime sap flow in culms of different ages of *N. affinis* with phenology. (**A**) Sap flow rates in 1-year culms. (**B**) Sap flow rates in 2-year culms. (**C**) Sap flow rates in 3-year culms. * indicated significant differences and ns indicated insignificant differences between daytime and nighttime at $p < 0.05$ level.

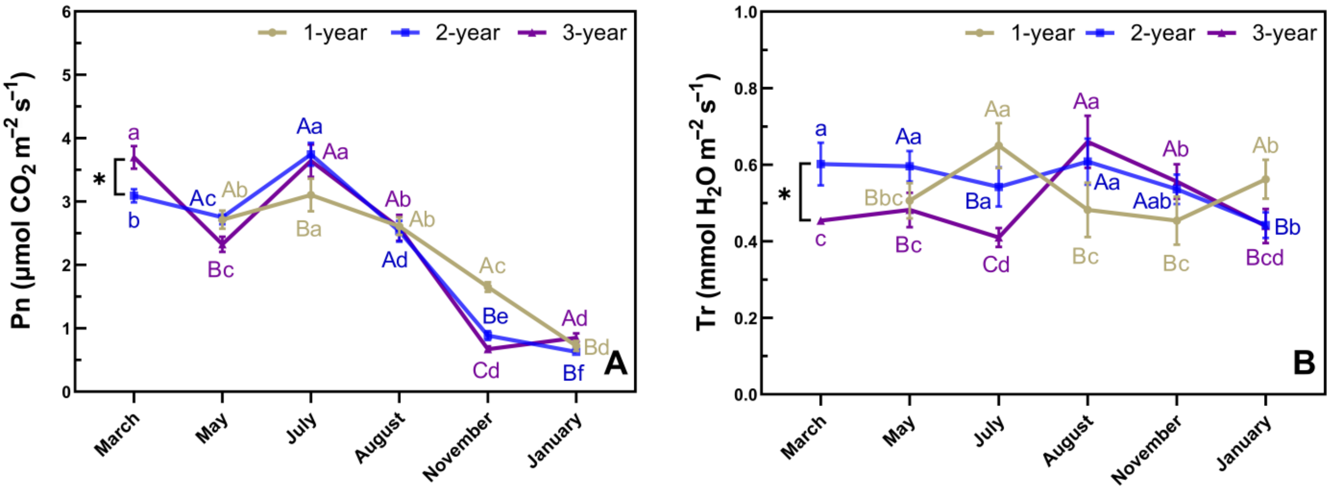


**Figure 7.** Dynamical changes in Pn and Tr of *N. affinis* leaves on the bamboo culms of different age classes with phenology. (**A**) Pn. (**B**) Tr. Different uppercase letters and * indicated significant differences between years and different lowercase letters indicated significant differences between months at $p < 0.05$ level.

*3.4. Phenological Changes in Pn and Tr*

The Pn values of *N. affinis* leaves of culms of all ages showed the same variation trend with the phenological stage, which decreased firstly from March to May, increased significantly in July, and then decreased constantly in the subsequent stages (Figure 7A). This was consistent with the variation trend of moisture content in the leaf (Figure 4A), which showed a close relationship between the Pn and moisture content in the leaf. For the 1-year-old *N. affinis* culms, there were no branches and leaves in March, and hence there were no data of Pn recorded. Additionally, we also noticed significantly lower Pn rates in 1-year-old culms, compared to those in 2-and 3-year-old culms, during the period from May to August, but they showed significantly higher Pn values after August. This implied that the new leaf flush did not complete its development until August and then began to play an active role in photoassimilate accumulation in the bamboo cluster.

The Tr of leaves of 2- and 3-year-old culms showed a similar trend with the phenological stage, as it decreased from March to July, increased in August, and then declined constantly in the following seasons (Figure 7B). The Tr values of leaves of 2-year-old culms were significantly higher than those of the leaves of 3-year-old culms from March to May, but there was no significant difference in other periods. The Tr in the leaves of 1-year-old culms showed the highest values in July, but those in the leaves of both 2- and 3-year-old culms showed the highest values in August. This result suggested different water use patterns between the newly flushed leaves and those of the 2- and 3-year-old culms. The Tr values were not completely consistent with the dynamical change in Pn, which was mainly because the Tr was more easily affected by the environmental factors as compared to Pn, such as photosynthetically active radiation, environmental temperature, and atmospheric vapor pressure deficit. A similar result was also reported by Fan [44] in the photosynthetic physiological ecology of the main forest-forming species, where photosynthetically active radiation was the most important factor affecting the transpiration rate, followed by the air temperature. Floating clouds significantly affected the transpiration rate due to the sharp decrease in photosynthetic effective radiation, and the air temperature and atmospheric water pressure could also decrease the transpiration rate.

*3.5. Phenological Changes in Photoassimilates in N. affinis*

NSC, as the main energy material of plants, was the sum of soluble sugar and starch, which showed dynamical changes with the phenological stage in one whole year. The NSC content in the leaves, branches, and culms of *N. affinis* was determined during different phenological stages (Figure 8).

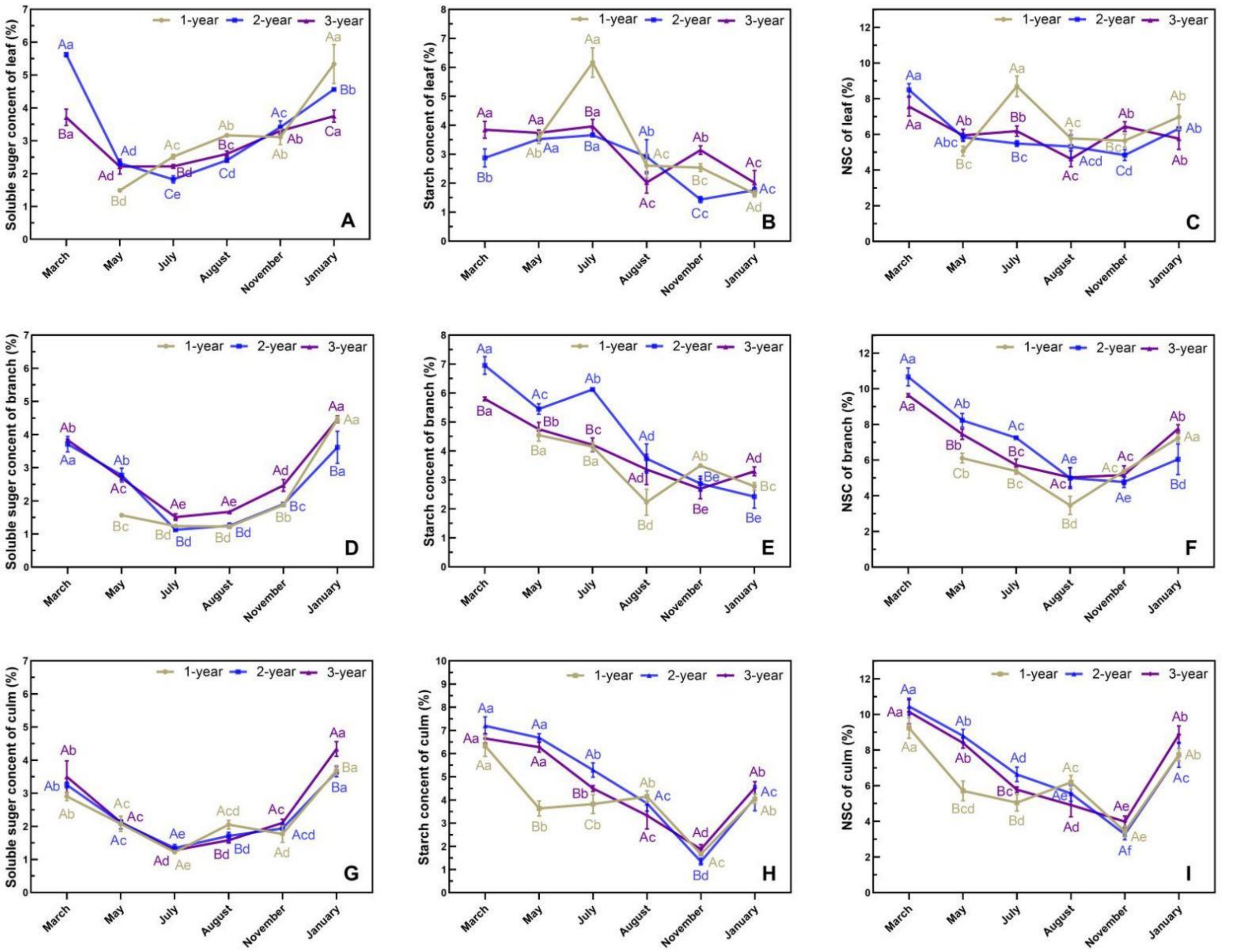


**Figure 8.** Dynamical changes in photoassimilate storage in different organs of *N. affinis* with phenology. (**A**–**C**) Soluble sugar, starch, and NSC content in the leaves of culms of different ages. (**D**–**F**) Soluble sugar, starch, and NSC content in the branches of culms of different ages. (**G**–**I**) Soluble sugar, starch, and NSC content in culms of different ages. Different uppercase letters indicated significant differences between years and different lowercase letters indicated significant differences between months at $p < 0.05$ level.

In order to determine the relationship between the photoassimilate storage patterns during each phenological stage, we proceeded to determine the content of endogenous soluble sugar, starch, and NSC in the leaves (Figure 8A–C). We observed a significant decrease in the content of endogenous sugar in 2- and 3-year-old culms between March and May, followed by a steady increase in the subsequent phenological stages (Figure 8A). Meanwhile, for the 1-year culms, the endogenous soluble sugar content increased constantly after branch and leaf extension in May. The starch content in the leaves of 2- and 3-year-old culms showed a slightly increasing trend from March to July, and then decreased in the subsequent seasons (Figure 8B), while those of the leaves of 1-year-old culms showed a significant increase in July, and then decreased sharply in August and constantly in the following seasons. The NSC content in the leaves of 2- and 3-year-old culms decreased constantly from March to August, and then increased significantly in the winter season

(Figure 8C). A similar trend was observed in the variation in starch content. The NSC content in 1-year-old culms also showed a significant increase in July, followed by a decline until November, and recovery in January. Contrary to the decrease in Pn in the winter season (Figure 7A), the increase in the content of NCS in leaves during the winter period might be interpreted as a low-temperature resistance mechanism (Table 1).

For branches, the endogenous soluble sugar, starch, and NSC content showed a similar trend to those in leaves (Figure 8D–F). The soluble sugar content in the branches of 2- and 3-year-old culms decreased continuously from March to July, and then increased constantly and sharply in January (Figure 8D). The newly generated branches from 1-year-old culms also showed a similar trend as they decreased slightly from May to August and then increased constantly and sharply in the following seasons. In general, the starch content in the branches of all culms showed a decreasing trend with the phenological stage (Figure 8E), except for the branches of 2-year-old culms, which increased significantly in July. This might be due to the significant increase in the Pn of leaves in July (Figure 7A). Similar to that in leaves, the NSC content showed a constant decreasing trend from March to August in the branches of all culms, and then increased sharply until January (Figure 8F). Additionally, the NSC content in the branches of 2-year-old culms showed higher values than those of 1- and 3-year-old culms during the period from March to August, but lower during the following period.

The variation in the photoassimilate levels in culms during the different phenological stages was consistent with the variations observed in leaves and branches (Figure 8G–I). The endogenous soluble sugar content of all aged culms showed a constant decreasing trend from March to July, and then increased until January (Figure 8G). In contrast with the trend observed in leaves and branches, the starch content of 2- and 3-year-old culms decreased significantly from March through November, and then sharply increased in January. Meanwhile, for the 1-year-old culms, the starch content decreased significantly from March to May and increased constantly until August, and then sharply decreased during the period from August to November (Figure 8H). NSC showed a similar trend in culms of all ages (Figure 8G). In 1-year-old culms, the sharp decrease in NSC content during the period from March to May was mainly related to leaf and branch extension, but also to the production of new shoots during the period of August to December. The increase in NSC in all organs in January, especially in culms, implied the accumulation of photoassimilates in winter.

### *3.6. Correlation Analysis*

In order to further uncover the relationships between photoassimilate storage and water status in *N. affinis*, a correlation analysis among all physiological indexes was performed (Figure 9). The correlation analysis revealed that the Pn of leaves showed significant and positive correlations with the transpiration pull values, sap flow rates of daytime and nighttime, and water potential of culms in the dry season (January to May) at the $p \leq 0.05$ level (Figure 9A). This indicated that the water supply from culms significantly affected the photosynthesis of leaves during the dry season, especially the daytime water supply, as indicated by the higher correlation coefficient between the Pn of leaves and the daytime sap flow. In addition, the daytime sap flow of culms was also significantly and positively correlated with the moisture content of leaves and transpiration pull of culms; starch content of branches and culms; and NSC content of leaves, branches, and culms in the dry season. The Pn showed significant and positive correlations with the starch content of leaves, branches, and culms, indicating that the Pn was closely related to the starch accumulation of bamboo in the dry season. These results implied that the water supply of culms played an important role in photosynthesis and photoassimilate storage in the dry season.

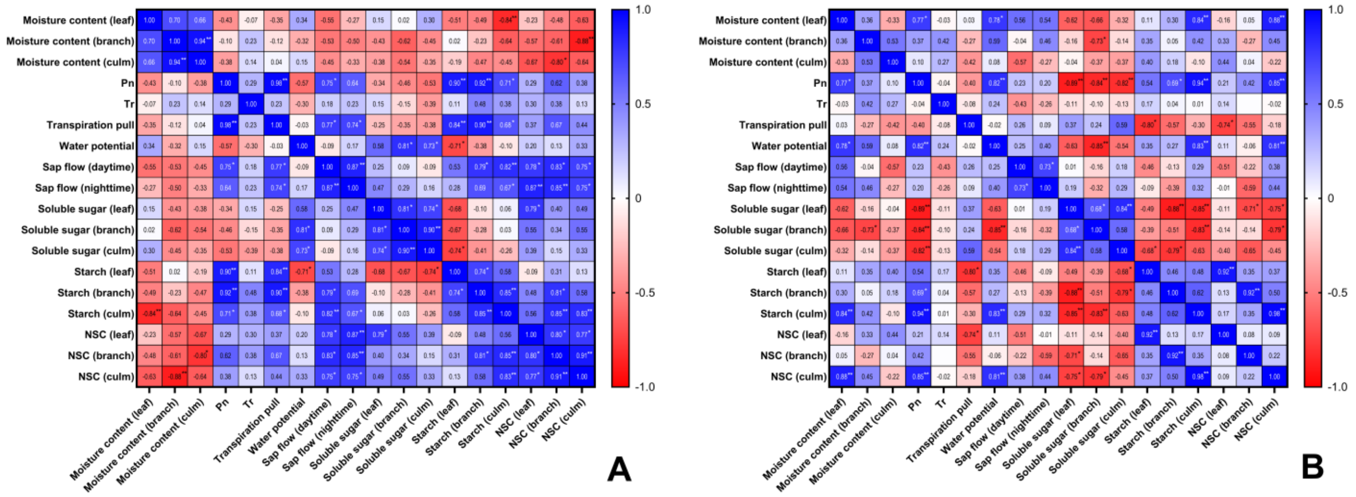


**Figure 9.** Correlation analysis between Pn, Tr, assimilate storage, and water supply in different organs of *N. affinis*. (**A**) Correlation analysis of physiological indexes in the dry season. (**B**) Correlation analysis of physiological indexes in the wet season. * indicated significant correlation at 0.01 level and ** indicated significant correlation at 0.01 level.

In the wet season, the Pn of leaves was only correlated positively with the moisture content of leaves and water potential of culms, and it did not correlate significantly with the moisture content of branches and culms, transpiration pull, and sap flow rates of culms (Figure 9B), which suggested that there was an sufficient water supply for the leaf at this period. The photosynthesis of leaves did not rely on the water storage of culms in the wet season. The Pn was significantly and negatively correlated with the soluble sugar content of leaves, branches, and culms, but significantly and positively correlated with the starch and NSC content of branches and culms, which indicated that the Pn could still significantly affect NSC storage in the wet season, but an excess of soluble sugar content in different organs would inhibit the photosynthesis of leaves.

## 4. Discussion

The growth and development of terrestrial plants are highly dependent on the water and nutrient transport of the whole plant [45]. Due to a lack of secondary growth, rapid water transport in the primary xylem is very important to maintain the water balance in bamboos [46]. As a typical shallow root plant and clonal plant, bamboo is unable to access deep underground water [29,30]. Its rapid growth depends entirely on the absorption and transportation of water and nutrients by the extensive underground rhizome and root network [47–49]. As the main product of plant photosynthesis, the change in the NSC content level is an important indicator of the plant carbon source pool capacity [19–21], which essentially reflects plant vitality and photosynthetic capacity [22,23]. Photosynthesis showed a close relationship with the water status in leaves [36]. Wang et al. [37] showed that soil water was one of the main environmental factors limiting plant growth and photosynthetic capacity. Hence, the relations between the photoassimilates and water status in bamboo with phenological stages need to be analyzed. As a sympodial clump bamboo, *N. affinis* grows its new branches and leaves in May and shoots in August. There are only three months from branching and full leaf extension to shoot emergence for carbohydrate storage. This might be the main reason that the sympodial bamboos extend their branches and leaves simultaneously [39]. Meanwhile, the precipitation and light duration showed considerable variations with the phenological stage. Therefore, the variations in precipitation and in light duration and intensity clearly affect the vegetative phenology of bamboos, which is why it is necessary to further explore the relationship between photoassimilate accumulation dynamics and water relations in bamboos for the management and maintenance of bamboo forests.

### *4.1. Water Status and Photoassimilate Accumulation in N. affinis before and after Branch and Leaf Extension*

During the period from January to May, the local area was entering the dry season, and the sunshine duration and local temperature rose rapidly. However, the air relative humidity and precipitation were decreased from January to March and then increased in May, with the lowest air relative humidity and precipitation in March. Our results indicated that the water content in the leaves of 2- and 3-year-old culms decreased constantly with the sunshine duration and temperature, while those in the branches and culms aged 2 and 3 years old first slightly decreased from January to March and then increased from March to May, and that of the young culms (1 year) decreased slightly at this time. These results revealed that the low precipitation and air relative humidity in March further decreased the water storage in branches and culms. The continuous decrease in water content in leaves also limited the leaf Tr with the increasing temperature during the dry season.

The pull of water from the soil to the leaves caused water in the transpiration stream to be under negative pressure, decreasing the water potential below zero [50]. The daytime sap flow was mainly driven by the transpiration pull [51]. The water potential was lowered by transpiration from the leaves, assisted by the cohesive forces between water molecules, causing water to be placed under tension, i.e., under negative pressure [50]. The negative water pressure revealed the transpiration pull in culms; in fact, the more negative the water pressure, the stronger the transpiration pull. The difference between the transpiration pull values of the middle parts of the culms and the sap flow values and water potential in the bottom of the same culms revealed the water storage status of the bamboo culms. Adequate water storage levels in the culms were achieved when the transpiration pull values were high in the mid-region of the culms and the sap flow was low at the base. Once a high sap flow rate and low potential were determined at the bottom, it revealed a deficiency in water storage in the culms, which needed to draw water from the soil via the roots. In the period from March to May, the culms showed increased transpiration pull but significantly decreased water potential, which implied a severe deficiency in water storage in culms. Meanwhile, a sharp decrease in sap flow rates during the daytime and nighttime might reveal the deficiency of water in the soil. Accordingly, the leaf Pn of the mature culms (2 and 3 years old) also decreased significantly from March to May, and the endogenous soluble sugar and starch content decreased sharply in leaves, branches, and culms from March to May. This implied that the water deficiency in culms had caused a decrease in the photosynthesis rate during the dry season.

From late May to July, the local weather entered into the wet season, and the transpiration pull increased sharply but the sap flow rates during the daytime and nighttime at the bottom of culms decreased sharply and the water potential increased sharply, which indicated that the increasing precipitation recharged the water storage in the culms. The sufficient water storage in the culms could meet the increasing water demand caused by the new extended leaves under increasing temperatures and sunshine duration. Additionally, the significant increase in the Pn of leaves and also in the starch and NSC accumulation of leaves and branches in July revealed that the new extended leaves and mature leaves increased the carbohydrate supply in the wet season. However, the starch and NSC content in the culms decreased constantly during this period, which implied that a large amount of carbohydrates was consumed after branch and leaf extension. Our results support the studies conducted by Zhan et al. [39], which revealed a high demand for photoassimilates during the stages of branching, leafing, and shoot bud development, as well as for the subsequent development of new shoots in sympodial bamboo. Correlation analysis also showed a significant and positive correlation between the Pn of leaves and the sap flow rates, and the water potential of culms in the dry season. The daytime sap flow of culms was also significantly and positively correlated with the moisture content of leaves; starch content of branches and culms; and NSC content of leaves, branches, and culms. Xu and Zhou [38] also reported that photosynthetic activity was enhanced under moderate soil moisture, with reductions under both a severe water deficit and excessive water conditions.

Photosynthetic performance was highly dependent on the water status of leaves, which was balanced by the water transport capacity, the water loss rate, as well as the water capacitance of the plant [36]. Hence, the water status of bamboo culms directly limited the leaf water status, and further limited the leaf photosynthesis and photoassimilate accumulation of the bamboo cluster during the dry season. Therefore, it is essential to irrigate the bamboo forest properly during leaf and branch extension in the dry season.

### 4.2. Water Status and Photoassimilate Accumulation in N. affinis during Shoot Emergence

During the period from August to November, the local area was still in the wet season and the bamboo clusters began shoot emergence and completed their height growth. Both leaves and branches showed the highest water content, while the 1-year-old culms showed a slight decrease in August. Meanwhile, the transpiration pull decreased and the water potential increased to the maximum in August and then decreased in November. The sap flow rates in the daytime and nighttime also increased in August as compared to those in July and November, especially for those of 1- and 2-year-old culms, which showed higher values than 3-year-old culms. Hence, it was concluded that the 1- and 2-year-old bamboo needed to supply sufficient water for shoot emergence. This was due to the fact that shoot buds usually sprouted at the bases of the 1- and 2-year culms [36,39,42]. As the mature culms were the main source for shooting in the sympodial bamboo clump, a large amount of water was consumed during the shooting stage [25]. The decrease in transpiration pull and the increase in water potential and sap flow rates in the adult bamboo could be helpful to increase the water storage in bamboo clusters for new shoot emergence and subsequent height growth.

Unlike the sap flow and water potential of culms in August, the Pn values and starch content in all organs of *N. affinis* decreased constantly from July until November, while the endogenous soluble sugar content increased constantly during this period. This result indicated that the increase in soluble sugar content mainly relied on the stored starch degradation. The starch storage of all organs of *N. affinis* was consumed for shoot emergence and height growth. The shoot growth was more dependent on photoassimilate accumulation in the early stage from May to July. The decrease in total NSC in sympodial bamboo was mainly attributed to depletion by shooting, and, hence, Zhan et al. [39] suggested that a suitable fertilizer's application to sympodial bamboo plantations should be scheduled at the end of July.

Additionally, due to sufficient precipitation during this period, the Pn of leaves showed significant and positive correlations only with the water content of leaves and water potential of culms, and not with the moisture content of branches and culms, the transpiration pull, and the sap flow rates of culms. This was because the precipitation supplied sufficient water for the bamboo, and hence the photosynthesis of leaves did not rely entirely on the water storage in culms in the wet season.

### 4.3. Water Status and Photoassimilate Accumulation in N. affinis during the Dormancy Stage

From November to January, the local area entered into the dry season again, and the temperature, sunshine duration, precipitation, and relative humidity all decreased. The moisture content of all organs of *N. affinis* bamboo decreased in all age groups. Zhan et al. [39] also reported a decreasing trend in moisture in three different bamboo types for dormancy and to avoid freeze injury. Furthermore, this was seen in the local dry season as the moisture content decreased. Although the water content, water potential, and sap flow rates were lower in January as compared to those in August, they were still higher than those in November. Meanwhile, the leaf Tr values of 2- and 3-year culms decreased in January but increased significantly in 1-year culms. These results suggest an apparent water flow in bamboo in winter. Generally, a single water content value could not reveal the water status of culms very well, due to its insignificant variation trend in one growth year. However, the transpiration pull, water potential, and sap flow rates could reveal the water status of culms better.

Additionally, the Pn values decreased in January, but the endogenous soluble sugar of all organs and the NSC content in culms increased significantly, implying that photoassimilate transport from leaves to culms, and apparent photoassimilate accumulation in culms, still occurred during this period. Soluble sugars were confirmed to play an important role in enhancing freezing tolerance [52]. The increase in soluble sugars in all organs of *N. affinis* was beneficial to their cold resistance in winter.

To enter dormancy, trees stopped their vegetative growth in the late summer or early autumn, and they spent the early period of the winter in a state of deep sleep, in which they were completely unreceptive to any environmental signals instructing them to exit dormancy [53]. However, the apparent photoassimilate accumulation and water flow of *N. affinis* in January implied that it did not possess a real dormancy period.

## 5. Conclusions

The moisture content showed a similar trend in the leaves and branches, with the highest values in July and August, because of the sufficient precipitation in the wet season. The NSC content showed a similar trend in the culms and branches in all age classes, which decreased constantly from March to November and then increased in the following months. The net photosynthetic rate and transpiration pull showed the highest values in July and then decreased constantly, which implied that a large amount of water was consumed for photoassimilate synthesis. This was also highly consistent with the starch accumulation in leaves in July. The water content did not reveal the water status of culms very well, due to its insignificant variation trend in one growth year. The transpiration pull, water potential, and sap flow rates revealed the water status of culms better as compared to the water content. The water status of bamboo culms directly limited the leaf water status, and further limited the leaf photosynthesis and assimilate accumulation of the bamboo cluster during the dry season. The increasing precipitation recharged the water storage in culms in the wet season. Branch and leaf extension, as well as the shoot emergence and growth, of *N. affinis* were more dependent on photoassimilate accumulation in the early stage from May to July. The net photosynthetic rates of leaves were significantly affected by the water status of culms in the dry season, but correlated significantly with the leaf water content in the wet season for the sufficient water supply. It is essential to irrigate the bamboo forest properly during the leaf and branch extension stage, so as to increase photosynthesis and to accumulate more photoassimilates for subsequent shoot emergence. *N. affinis* did not possess a real dormancy period due to its apparent photoassimilate accumulation and water flow in January.

**Author Contributions:** W.S. and J.L. performed most of the experiments, analyzed the data, and participated in the interpretation. H.Z., L.Y. and C.W. collected and processed the samples, analyzed the data, and participated in the interpretation. S.W. designed the project and provided supervision. W.S. and S.W. participated in the writing of the manuscript. All authors have read and agreed to the published version of the manuscript.

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